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Long-term impact of a stand-replacing fire on ecosystem CO_2 exchange of a ponderosa pine forest

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Abstract

Ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States are a mosaic of stands where undisturbed forests are carbon sinks, and stands recovering from wildfires may be sources of carbon to the atmosphere for decades after the fire. However, the relative magnitude of these sinks and sources has never been directly measured in this region, limiting our understanding of the role of fire in regional and US carbon budgets. We used the eddy covariance technique to measure the CO_2 exchange of two forest sites, one burned by fire in 1996, and an unburned forest. The fire was a high-intensity stand-replacing burn that killed all trees. Ten years after the fire, the burned site was still a source of CO_2 to the atmosphere [109 ± 6 (SEM) $g\,C\,m^{-2}\,yr^{-1}$], whereas the unburned site was a sink ($-164 \pm 23\,g\,C\,m^{-2}\,yr^{-1}$). The fire reduced total carbon storage and shifted ecosystem carbon allocation from the forest floor and living biomass to necromass. Annual ecosystem respiration was lower at the burned site ($480 \pm 5\,g\,C\,m^{-2}\,yr^{-1}$) than at the unburned site ($710 \pm 54\,g\,C\,m^{-2}\,yr^{-1}$), but the difference in gross primary production was even larger ($372 \pm 13\,g\,C\,m^{-2}\,yr^{-1}$ at the burned site and $858 \pm 37\,g\,C\,m^{-2}\,yr^{-1}$at the unburned site). Water availability controlled carbon flux in the warm season at both sites, and the burned site was a source of carbon in all months, even during the summer, when wet and warm conditions favored respiration more than photosynthesis. Our study shows that carbon losses following stand-replacing fires in ponderosa pine forests can persist for decades due to slow recovery of the gross primary production. Because fire exclusion is becoming increasingly difficult in dry western forests, a large US forest carbon sink could shift to a decadal-scale carbon source.

Keywords: carbon, CO_2 flux, conifer, disturbance, eddy covariance, GPP, NEE, *Pinus ponderosa*, respiration

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Introduction

Terrestrial ecosystems strongly influence the global carbon cycle and, combined with oceans, are estimated to absorb about half of the carbon dioxide (CO_2) currently released by human activities (Schimel *et al.*, 2001; Dilling *et al.*, 2003). Simulated global patterns of carbon flux suggest that forests dominated by ponderosa pine (*Pinus ponderosa*), including those represented by our study sites in northern Arizona, are a carbon sink (Potter & Klooster, 1999). Yet regional estimates of carbon sequestration by terrestrial ecosystems are likely overestimated, because most studies avoid recently disturbed sites and do not adequately consider impact of disturbance on carbon fluxes (Pacala *et al.*, 2001; Breshears & Allen, 2002; Hurtt *et al.*, 2002; Schimel & Baker, 2002; Dilling *et al.*, 2003; Litton *et al.*, 2003; Saleska *et al.*, 2003; Law *et al.*, 2004; Misson *et al.*, 2005). Simulations and empirical data suggest that stand-scale CO_2 flux depends strongly on stand age and time since disturbance (Thornton *et al.*, 2002; Amiro *et al.*, 2003; Law *et al.*, 2003; Song & Woodcock, 2003; Pregitzer & Euskirchen, 2004). Elucidation of the magnitude, spatial

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and temporal scales, and biological processes of such influences is essential to improve estimates of carbon balance in forested landscapes.

Stand-replacing wildfires cause a sudden conversion of carbon stored in vegetation and soil to CO_2, which is then released to the atmosphere. Such short-term effects of fire can be reasonably estimated from information on fuel consumption and extent of burning (Auclair & Carter, 1993; Conard & Ivanova, 1997; Harden *et al*., 2000; Page *et al*., 2002; Law *et al*., 2004). Longer term effects of fire on the carbon balance are more uncertain and are influenced by fire effects on local hydrology, surface energy exchange, soil temperature (Amiro *et al*., 1999), rate of vegetation recovery (Amiro *et al*., 2003; Law *et al*., 2003; Litton *et al*., 2003; Kashian *et al*., 2006), soil respiration, and erosion of soil organic carbon (Black & Harden, 1994).

The effects of fire on the carbon balance can last for variable periods, depending on the intensity of the fire and the recovery of the ecosystem. Several studies show that fire reduces net ecosystem production in young, regrowing stands, because decomposition of necromass produced from the disturbance causes heterotrophic respiration to exceed net primary production, changing the ecosystem from a sink to a source of CO_2 (Amiro, 2001; Thornton *et al*., 2002; Wirth *et al*., 2002; Law *et al*., 2004; Randerson *et al*., 2006). In intensively managed pine forests, 2–5 years may elapse after disturbance before regrowing forests shift from a carbon source to a sink (Thornton *et al*., 2002; Misson *et al*., 2005), while the same transition may require 10–30 years for conifers in the Pacific Northwest United States (Cohen *et al*., 1996; Law *et al*., 2001) and many decades for boreal forests (Schulze *et al*., 2000; Fredeen *et al*., 2007). Current understanding of the effects of severe fire or high-intensity harvesting on carbon fluxes in ponderosa pine forests suggests that it may take 50–100 years to replace the carbon lost from these disturbances and a period of 10–20 years to shift the ecosystem from a carbon source to a carbon sink (Law *et al*., 2001). These estimates from more mesic forests (Thornton *et al*., 2002; Amiro *et al*., 2003; Law *et al*., 2003; Litton *et al*., 2003; Kashian *et al*., 2006) may have limited application in southwestern ponderosa pine forests, where the drier climate appears to slow recovery following stand-replacing wildfire (Savage *et al*., 1996; Savage & Mast, 2005).

Over a century of fire suppression and heavy livestock grazing have eliminated the natural low-intensity surface fire regime of ponderosa pine forests in most areas of the southwestern United States (Cooper, 1960; Swetnam & Baisan, 1996; Fulé *et al*., 1997). Ecosystem structure has shifted from open savanna-like forests maintained by frequent (every 3–25 years) surface fires to dense forests of small trees with little understory (Covington *et al*., 1994; Swetnam & Baisan, 1996; Fulé *et al*., 1997). This shift is considered an important component of the recent carbon sink of terrestrial ecosystems (Potter & Klooster, 1999; Houghton *et al*., 2000; Pacala *et al*., 2001; Schimel *et al*., 2001; Hibbard *et al*., 2003), but the sink is not sustainable because increasing carbon storage in woody fuels (Covington *et al*., 1994; Covington *et al*., 2001; Keane *et al*., 2002; Fulé *et al*., 2004; Moore *et al*., 2004) and recent climate warming (Brown *et al*., 2004; Westerling *et al*., 2006) lead to stand-replacing wildfires in arid and semiarid forests that cover large areas of the western United States (GAO, 1998; Breshears & Allen, 2002). Measurements of carbon exchange in burned and fire-suppressed, unburned forests provide data necessary for understanding the carbon balance implications of different forest management strategies in semiarid regions. Attempts to measure or predict spatial variation in carbon sinks for the western United States will have large errors if impacts of severe fire are not considered.

The overall objective of this study was to evaluate the effects of stand-replacing fire on the carbon cycle of ponderosa pine forests in northern Arizona. We measured ecosystem CO_2 and water fluxes for 17 months (2005–2006) in an unburned ponderosa pine forest and a forest that was burned by a high-intensity stand-replacing wildfire that killed all trees in 1996 to (1) compare carbon fluxes, pools, and environmental responses of fluxes, and (2) provide the first data on ecosystem carbon fluxes, using eddy covariance for ponderosa pine forests of the southwestern United States.

Materials and methods

Study sites

Our study compares two ponderosa pine sites: an unmanaged, undisturbed forest and a forest that burned in a stand-replacing wildfire. The sites are located 35 km apart, in the vicinity of Flagstaff, in northern Arizona, United States.

The unburned site is located on the Northern Arizona University Centennial Forest (35°5′20.5″N, 111°45′43.33″W, elevation 2180 m a.s.l.) and represents a typical example of the ponderosa pine forests of this area, with no disturbances (harvests, thinning, or fires) having occurred for many decades. Season maximum leaf area index (LAI, projected area) during the study was 2.3, tree basal area was $30\,m^2\,ha^{-1}$, and average tree age was 87 years (Table 1). The forest is dominated by ponderosa pine and includes a sparse understory (maximum LAI 0.06) of grasses and forbs.

Table 1 Stand and soil characteristics of the unburned and burned sites (±1 SE)

Characteristic	Unit	Unburned	Burned
LAI total	$m^2 m^{-2}$	2.3 (± 0.38)	0/before fire 2.4 (± 0.45)
LAI understory	$m^2 m^{-2}$	0.06 (± 0.02)	0.6 (± 0.17)
Tree density	$N ha^{-1}$	853 (± 189)	0/before fire 343 (± 49)
Basal area	$m^2 ha^{-1}$	30 (± 4.7)	0/before fire 31 (± 6)
Canopy height	m	18	<0.5
Soil type		Complex of Mollic Eutroboralf and Typic Argiboroll	Mollic Eutroboralf
Depth of A horizon	cm	0–5	0–7
Bulk density A horizon	$g cm^{-3}$	1.15	1.01
Sand A horizon	%	37	30
Silt A horizon	%	39	57
Clay A horizon	%	24	13
Depth of B horizon	cm	5–15	7–15
Bulk density B horizon	$g cm^{-3}$	1.15	1.21
Sand B horizon	%	31	20
Silt B horizon	%	34	55
Clay B horizon	%	35	25

The burned site is located on the Coconino National Forest (35°26′43.43″N, 111°46′18.64″W, elevation 2270 m a.s.l.) in a 10 500 ha area burned by a high-intensity stand-replacing wildfire in 1996. The ground surface of the site is covered with sparse grasses, shrubs, and woody debris (WD) produced by the fire. Before the fire, the burned site had stand characteristics similar to the unburned site (Table 1). Since the 1996 fire, no postfire management, such as salvage logging or tree planting, has occurred at the site, and no tree seedlings have established. The vegetation at the site consists of grasses (*Bromus tectorum*, *Elymus repens*), shrubs (*Ceanothus fendleri*), and forbs (*Oxytropis lambertii*, *Verbascum thapsus*, *Linaria dalmatica*, *Circium wheeleri*).

The climate of the area is characterized by cold winters, sunny but dry springs, and irregular and moderate annual precipitation (610 mm, 30-year average, Western Regional Climatic Center, http://www.wrcc.dri.edu/index.html) about equally divided between winter and the July–August monsoon season (Sheppard *et al*., 2002). The two sites had similar incoming radiation and seasonal trends for most of the measured meteorological variables during the study (Table 2, Fig. 1). The main environmental differences between the sites can be explained by the absence of the tree canopy cover at the burned site, where soil and air temperatures were lower in the winter and higher in the summer, soil water content (SWC) was lower, and vapor pressure deficit (VPD) higher compared with that at the unburned site (Table 2, Fig. 1). Precipitation in 2006 was also lower at the burned site than at the unburned site (Table 2, Fig. 1).

Stand characteristics were measured at five 25 m radius circular plots located in the eddy covariance footprint at each site. The plots were located between 150 and 400 m in the prevailing wind direction, in the east–west section from the towers. At the burned site, prefire stand characteristics were determined in 2006 from adjacent, unburned areas. Diameter at breast height (1.4 m above ground) was measured for all trees in the plots and was used to calculate basal area, LAI, and biomass, using allometric equations and specific leaf area developed for ponderosa pine in northern Arizona (Kaye *et al*., 2005; McDowell *et al*., 2006). Allometric equations developed for ponderosa pine in New Mexico (Omdal *et al*., 2001) were used to estimate coarse root biomass at the unburned site. Understory LAI was measured at each site at four, 0.5 m^2 subplots for each of the five plots (total 20 per site). All understory vegetation was clipped from the subplots at the time of peak standing crop (late September 2006), and projected leaf area was measured in the laboratory with an image analyzer (Agvision, Monochrome System, Decagon Devices Inc., Pullman, WA, USA). Fine root biomass (diameter <2 mm) was obtained at the two sites in 2006 at each of the five plots from three soil cores (total 15 per site) of 20.4 cm^2 in area and a depth of 15 cm, where most of the fine root biomass is concentrated (Hart *et al*., 2005). Roots were extracted from the soil with a hydropneumatic elutriation system (Scienceware Bel-Art Products, Pequannock, NJ, USA). The carbon content of the mineral soil was obtained from Grady & Hart's (2006) study of the same fire for samples collected in 2005.

Table 2 Meteorological parameters for the unburned and burned sites in the year 2006

Parameter		Unit	Unburned	Burned
Soil temperature (10 cm)	Average	°C	8.5	10.4
	Minimum	°C	−2.0	−4.0
	Maximum	°C	22.3	28.8
Air temperature*	Average	°C	8.8	8.5
	Minimum	°C	−12.6	−17.6
	Maximum	°C	29.6	30.1
Precipitation	Total	mm	695.6	516.7
Vapor pressure deficit	Maximum†	kPa	1.3	1.4
	Average	kPa	0.77	0.81
	Sum	Pa	2398	2501
Global radiation	Total	$MJ\,m^{-2}$	6920	6859
Soil water content (10 cm)	Average	Vol.%	18.6	15.8
	Minimum	Vol.%	8.0	6.3

Only periods in which both datasets were complete were included.
*Air temperature is measured above the canopy at both sites (3 m height at the burned site, 22 m at the unburned site).
†Maximum vapor pressure deficit is the average of the maximum daily vapor pressure deficit.

Fine WD (diameter <7.5 cm) was measured at each site, using the Brown method (1974) on four 3.7 m transects from each plot center. Coarse WD (diameter >7.5 cm) was measured on four, 0.04 ha plots per site. Length, top, middle, and base diameters of coarse WD were recorded, and mass was calculated using Newton's formula and a bulk density of $0.4\,g\,cm^{-3}$ (Harmon & Sexton, 1996). WD was calculated as the sum of fine and coarse materials. Forest floor depth was measured on nine evenly spaced points along each transect and converted to mass (Ffolliot *et al*., 1968). Of this mass, 25% was subtracted as mineral soil, and the forest floor carbon pool (Fulé, 1990) was then determined using a carbon concentration of 0.58 g carbon per gram forest floor (Nelson & Sommers, 1982). The carbon concentration of the organic matter of all other pools was assumed to be 0.50 g carbon per gram dry weight. Decomposition of WD was estimated at each site based on changes in specific gravity of WD from a chronosequence (Erickson *et al*., 1985; Harmon & Sexton, 1996). The chronosequence at the burned site consisted of 10-year-old WD produced by the fire ($n = 25$) and fresh WD produced by logging at a nearby site in 2006 ($n = 35$). The chronosequence at the unburned site consisted of 20-year-old WD produced by thinning at a nearby site ($n = 25$ slash piles) and fresh WD produced by logging at another nearby site ($n = 35$).

Eddy measurements

The data we present were collected between September 2005 and December 2006. We used the same equipment at each site: a closed-path analyzer (Li-7000, LI-COR, Lincoln, NE, USA), a 3-D sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA), and a pump (N89, KNF Neuberger, Freiburg, Germany) drawing air with a flow of $10\,L\,min^{-1}$ through Teflon tubing of 4 mm i.d. Tubing was 9 m long at the burned site and 4 m long at the unburned site. Every 2 weeks, the air intake filters (Acro 50, Gelman Sci., Ann Arbor, MI, USA, 1 μm pore diameter) were changed and the analyzers were calibrated maintaining the analyzer cells at the same pressure occurring during sampling. The eddy covariance system was positioned at a height of 23 m, 5 m above the canopy (18 m) at the unburned site and 4 m above the ground at the burned site. Data were recorded at 20 Hz by a datalogger (CR1000, Campbell Scientific, and 2 Gbyte memory cards, SanDisk, USA) and averaged over 30-min intervals. Raw data were postprocessed in the laboratory using the software MASE (designed by G. Manca, JRC Italy, following Aubinet *et al*., 2000). In particular, the 30-min fluxes were quality flagged using the Carboeurope methodology (steady-state test and integral turbulence characteristic test; Foken & Vichura, 1996; http://www.geo.uni-bayreuth.de/mikrometeorologie/QC_Workshop/QA_QC_012.f90). Precipitation, variances in the measured scalars, spikes, and number of rejected data during the 30-min intervals were additional parameters considered in the quality assessment.

At the unburned site, the storage fluxes were computed until July 2006 using the concentration measured by the analyzer at the top of the tower (Hollinger *et al*., 1999; Morgenstern *et al*., 2004), and afterwards using a CO_2, water, and temperature profile. The profile system sampled at 1, 8, and 16 m in addition to the 23 m height sampled by the eddy system analyzer. An infrared gas analyzer (LI-840, LI-COR) measured concentrations of

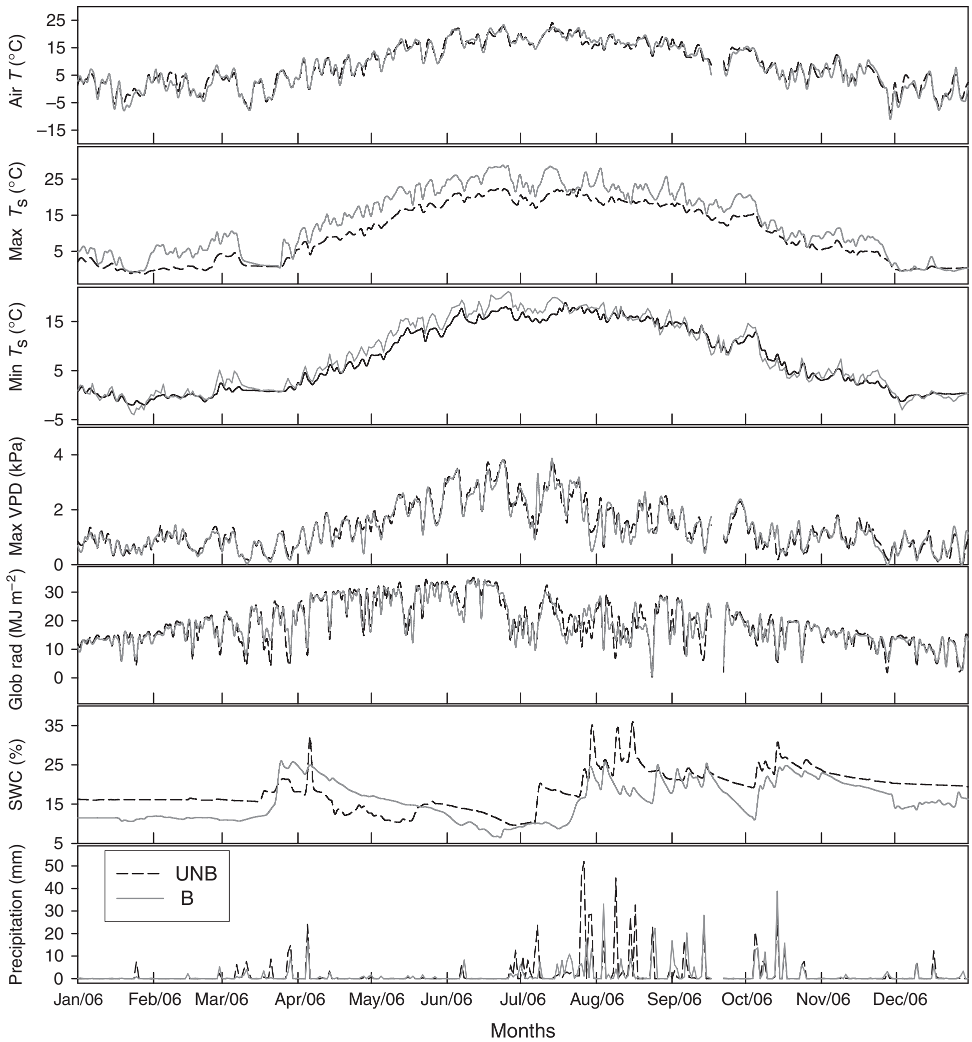

Fig. 1 Daily mean air temperature (Air T), maximum (max T_s) and minimum soil temperature (min T_s), vapor pressure deficit (VPD), global radiation (Glob rad), volumetric soil water content (SWC), and precipitation in the year 2006 for the unburned (UNB) and burned (B) sites.

water and CO_2, switching every 20 s between three lines where the flow was maintained at $1\,L\,min^{-1}$. A 1 L volume buffer, averaging the air collected in the previous minute, allowed the three heights to be measured continuously. At the burned site, no profile was installed because of the low stature of the vegetation, and the storage term was estimated using the top concentration measurements.

Meteorological measurements at the two sites included global and net radiation calculated from the incoming and outgoing short- and long-wave radiation (CNR1, Kipp and Zonen, Delft, the Netherlands), total and diffuse photosynthetic photon flux density (PPFD; with BF3 DeltaT devices, Cambridge, UK), reflected PPFD (LI-190, LI-COR), and precipitation (5.4103.20.041 Thies Clima, Goettingen, Germany). In addition, wind speed and direction, atmospheric pressure, precipitation, air humidity, and air temperature were measured at both sites with the same instrument (WXT510, Vaisala, Helsinki, Finland). Volumetric SWC (ECH2O-EC20 Decagon, Pullman, WA, USA) and soil temperature (107, Campbell Scientific) were measured at mineral soil depths of 2, 10, 20, and 50 cm. The SWC sensors were calibrated for soil A and B horizons of both sites in the laboratory, under controlled conditions (e.g. McMichael & Lascano, 2003). In addition, an equation to correct for the sensor sensitivity to temperature was determined empirically. Soil heat flux was measured at depth of 8 cm (HFP01SC Hukseflux, Delft, the Netherlands) at both sites and additionally at the unburned site with a second sensor (HFT3 REBS Inc., Seattle, WA, USA) because of the high spatial variability at this site. SWC and soil temperature (averaged between 2 and 6 cm mineral soil depths) were measured within 50 cm of the soil heat flux plates to allow for calculation of soil heat storage. All meteorological parameters were measured every 15 s and recorded at 30-min intervals by a datalogger (CR10X + AM16-32 multiplexer, Campbell Scientific). The systems were powered by 12 V solar panels, positioned more than 30 m from the anemometer.

We report carbon source to the atmosphere as a positive flux and carbon sink as a negative flux. Net ecosystem exchange (NEE) included the storage term and is used to refer to instantaneous fluxes, as well as long-term monthly and annual sums. Ecosystem gross primary production (GPP) was considered to be the same as gross ecosystem production (GEP; Law *et al.*, 2002) and was calculated for daytime conditions at a 30-min interval as NEE + total ecosystem respiration (TER). Daytime TER was calculated from the relationship between night-time TER and soil temperature (Law *et al.*, 2002; Richardson *et al.*, 2006). GPP was set to 0 during night-time conditions, even if NEE + TER was negative (thus suggesting night-time carbon uptake; Giasson *et al.*, 2006), and this caused a slight imbalance of carbon fluxes on an annual scale, so that annual NEE was not equal to annual GPP−annual TER (difference of $16\,g\,m^{-2}\,yr^{-1}$ at the unburned site and $1\,g\,m^{-2}\,yr^{-1}$ at the burned site).

Gap-filling

We divided data into three quality classes: good, intermediate, and bad (http://www.geo.uni-bayreuth.de/mikrometeorologie/QC_Workshop/QA_QC_012.f90). The good-quality data were used to determine the relationships of NEE, GPP, and TER with environmental factors. The intermediate-quality data were included in computations of daily, monthly, and annual sums. Bad-quality data were excluded from all analyses and were replaced by modeled data for the daily, monthly, and yearly carbon budget calculations. The datasets of the two sites were treated with the same analytical criteria and procedures.

We estimated uncertainty in the annual carbon budget by assessing the sensitivity of the annual sums to different filtering criteria and different procedures for filling bad-quality and missing data (e.g. McCaughey *et al.*, 2006). Data were gap-filled using look-up tables and nonlinear regressions (Falge *et al.*, 2001). Look-up tables were built using 2 months best quality datasets (up to 4 months for winter TER). For night-time NEE, 2 °C soil temperature classes and SWC classes (from two to three classes depending on the measured range) were used. For daytime NEE, $200\,\mu mol\,m^{-2}\,s^{-1}$ PPFD classes and one additional environmental factor that explained the most variation in NEE were used. This factor was SWC in four to five classes depending on the measured range, or VPD in 0.5 kPa classes, or soil temperature in 2 or 5 °C classes. Nonlinear regressions were fitted on monthly good-quality datasets, using a rectangular hyperbola equation (Ruimy *et al.*, 1995) for daytime NEE, and on a bimonthly basis, using a Q_{10} relationship with soil temperature for night-time NEE (Richardson *et al.*, 2006). Two-month intervals were used to reconcile the lack of best quality data of shorter periods with the need to include the short-time sensitivity of ecosystem respiration to temperature (Reichstein *et al.*, 2005; Richardson *et al.*, 2006). The use of only temperature for this night-time NEE gap-filling approach is based on the assumption that the bimonthly relationship indirectly includes the effect of other parameters, such as SWC, phenology, litter and substrate availability, that are often difficult to measure adequately (Curiel *et al.*, 2004). Next, we used three different data filtering criteria. The first was the replacement of bad-quality data with gap-filled data. The second was the replacement of bad-quality data and the application of u^* filtering, where u^* filtering consists of rejecting night-time TER, when u^* is below a site-specific threshold. The third was the application of only u^* filtering, which is used in most eddy covariance studies (Falge *et al.*, 2001; Aubinet *et al.*, 2002; Hollinger & Richardson, 2005; Humphreys *et al.*, 2006; Morgenstern *et al.*, 2004; Stoy *et al.*, 2006). The combination of different gap-filling and data filtering methods produced seven different procedures: (1) look-up tables applied to bad-quality data, (2) look-up tables applied to bad-quality and u^*-filtered data, (3) nonlinear regression applied to bad-quality data, (4) nonlinear regression applied to bad-quality and u^*-filtered data, (5) nonlinear regression applied to u^*-filtered data, (6) an automatic gap-filling procedure available on the web (Markus Reichstein, Max Planck Institute, Germany; http://gaia.agraria.unitus.it/database/eddyproc/) applied without u^* filtering, and (7) the same automatic gap-filling procedure available on the web, with u^* filtering.

At the burned site, 5% of the data were missing in 2006, 43% of the data were gap-filled because they were missing or bad, and 60% were gap-filled when u^* filtering was also applied. In contrast, the standard u^* filtering application replaced only 25% of the data at the burned site. At the unburned site, 14% of the data were missing in 2006, 32% of the data were gap-filled because they were missing or bad, and 46% were gap-filled when the u^* filtering was also applied. The standard u^* filtering application replaced only 40% of the data at the unburned site. Data losses and data rejection were in the same range as for similar studies (Baldocchi *et al.*,

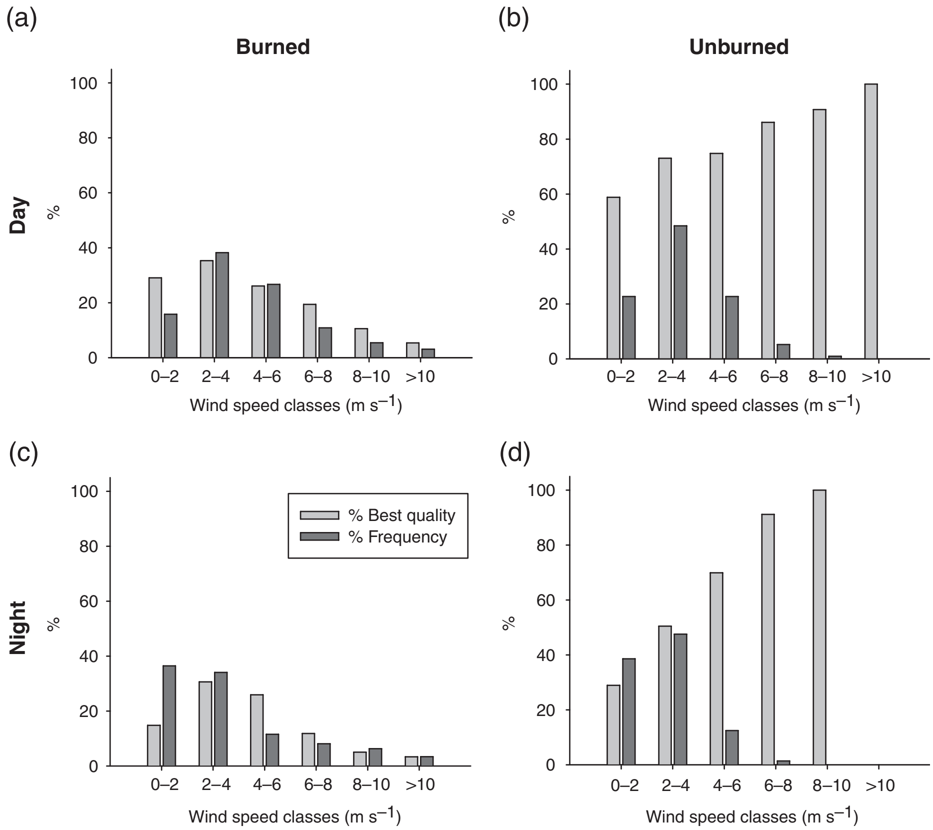

Fig. 2 Wind-speed distribution classes and percentage of good-quality eddy covariance data for the unburned (b, d) and burned sites (a, c), and during daytime (a, b) and night-time periods (c, d).

2001; Falge *et al*., 2001; McCaughey *et al*., 2006). Compared with the unburned site, high wind speed was more frequent during both day and night, and good-quality data, particularly during the day, were always less frequent at the burned site (Fig. 2). An increase in wind speed decreased data quality at the burned site, whereas it increased the data quality at the unburned site (Fig. 2).

The site-specific u^* threshold used in the night-time TER u^* filtering procedure was calculated using only the best quality data following Reichstein *et al*. (2005) and was 0.3 m s^{-1} at the burned site and 0.2 m s^{-1} at the unburned site. The same methodology applied by the automatic on-line gap-filling tool on night-time TER data of all qualities gave a threshold of 0.1 m s^{-1} at both sites and resulted in a lower amount of gap-filled data.

The daily energy balance closure (Aubinet *et al*., 2000; Wilson *et al*., 2002) for 2006, excluding days with snow on the ground, was 0.92 ($r^2 = 0.90$, $P < 0.0001$, $n = 302$) for the burned site and 0.84 ($r^2 = 0.94$, $P < 0.0001$, $n = 262$) for the unburned site (data not shown), and it was in the range of what is often measured by eddy covariance (Wilson *et al*., 2002). The difference in closure between sites can be attributed to site-specific characteristics, considering that identical settings, equipment, and software were used at the two sites. A possible reason for this difference is the high spatial heterogeneity at the unburned site caused by groups of trees alternating with irregularly sized openings, resulting in different footprints for eddy covariance and net radiation measurements.

We analyzed the relationship between NEE and PPFD (30-min data) on a monthly basis by fitting the best quality data with a rectangular hyperbola model, determining night-time TER, apparent quantum yield, and maximum assimilation (Ruimy *et al*., 1995). A Q_{10} function was used for night-time TER. The 30-min residuals (difference between the modeled and the measured values for night-time TER, and for daytime NEE when PPFD $> 800\ \mu mol\ m^{-2}\ s^{-1}$) were regressed against other environmental factors with a second-degree polynomial, and the regression coefficient plotted for each month and factor.

We compared the effect of diffuse light on NEE between the burned and unburned sites. NEE of CO_2 for clear and cloudy conditions (diffuse PPFD $< 30\%$ and $> 60\%$ of total PPFD, respectively) was averaged using 200 $\mu mol\ m^{-2}\ s^{-1}$ PPFD classes. We assumed that night-time NEE data were not affected by the daytime contribution of diffuse PPFD, and thus the night-time average was used for both cloudy and clear sky conditions. Often, on a monthly basis, clear and cloudy conditions did not overlap: cloudy conditions were common only at low PPFD and did not occur at high PPFD, while the opposite trend occurred for clear sky conditions. For each PPFD class, we also calculated average VPD, air temperature, soil temperature, and SWC. For the burned site, the diffuse light analysis was limited by a short growing season, and technical problems with the diffuse PPFD measurements occurred during July–August 2006. Consequently, we analyzed data from October 2006 for both sites and compared August and October 2006 for the unburned site only.

Results and discussion

Carbon fluxes

Because of similar prefire stand and soil characteristic (Table 1) and local climate (Fig. 1, Table 2) between the sites, the differences measured in this study can be attributed to the wildfire. The stand-replacing fire altered both the abiotic (e.g. soil temperature) and the biotic (e.g. biomass, LAI) characteristics of the ecosystem. The fire had a large effect on NEE, even 10 years after the fire (Figs 3, 5 and 6). Compared with the unburned site, NEE was lower at the burned site and CO_2 uptake was limited to a very short period (Fig. 3). In contrast to large parts of the world, including ponderosa pine forests in Oregon (Law *et al*., 2000) and California (Misson *et al*., 2005), where the months of May and June are often characterized by peaks in NEE (Baldocchi *et al*., 2001; Aubinet *et al*., 2002; Morgestern *et al*., 2004; McCaughey *et al*., 2006), NEE was low during June at our sites (Fig. 3) and reached its maximum only during the wet July–August monsoon season (Fig. 3). The NEE peak was in August at the unburned site (monthly light curve maximum assimilation $=-17\,\mu mol\,m^{-2}\,s^{-1}$), and in September, after the full leaf development of the herbaceous annual plants, at the burned site (monthly light curve maximum assimilation $=-7.7\,\mu mol\,m^{-2}\,s^{-1}$). At the unburned site, as in other coniferous (Hollinger *et al*., 1999; Morgenstern *et al*., 2004) and ponderosa pine forests (Anthoni *et al*., 1999; Misson *et al*., 2005), CO_2 uptake occurred in winter, when environmental conditions were favorable (Figs 3 and 5).

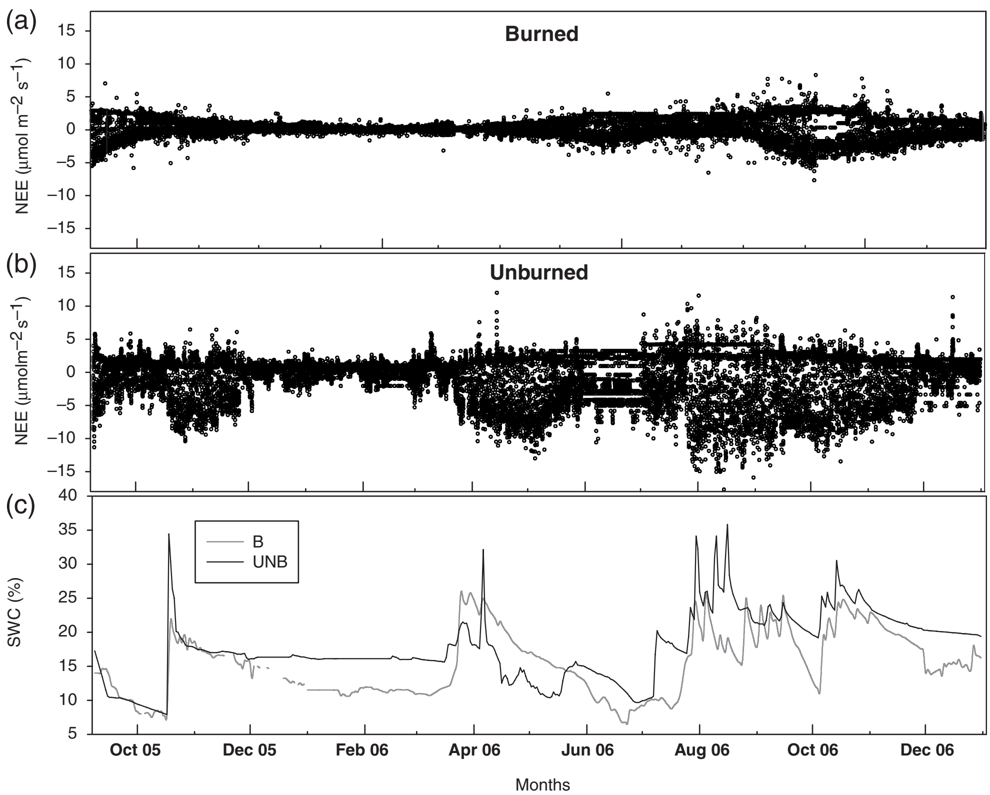

Fig. 3 Thirty-minute, gap-filled net ecosystem exchange of carbon (NEE) from September 2005 to December 2006 for (a) the burned site, (b) the unburned site, and (c) soil water content (SWC) for the burned (B) and unburned sites (UNB).

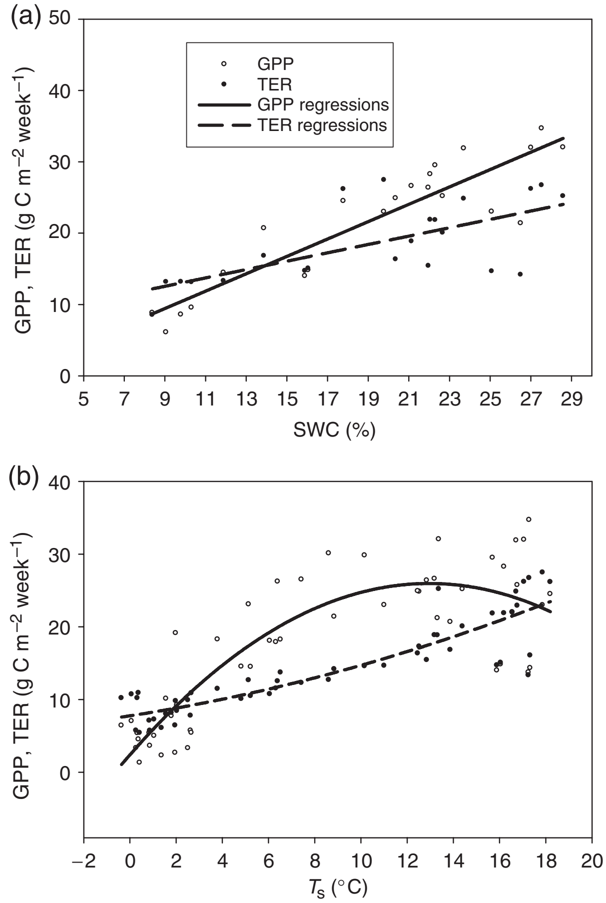

Fig. 4 Relationship of weekly gross ecosystem production (GPP) and total ecosystem respiration (TER) with soil water content (SWC) and soil temperature (T_s), both measured at 10 cm. In the top panel, symbols represent weekly relationship of GPP and TER with SWC for the period 28 May–21 October 2005 and 2006. The fitted regressions have equations GPP = −1.5 + 1.2 × SWC ($r^2 = 0.82$, $P < 0.0001$, $n = 24$); TER = 7.28 + 0.6 × SWC ($r^2 = 0.44$, $P = 0.0007$, $n = 24$). In the bottom panel, symbols represent weekly sums for 2006. The fitted regressions have equations GPP = $2.4 + 3.6 \times T_s - 0.14 \times T_s^2$ ($r^2 = 0.73$, $P < 0.0001$, $n = 52$); TER = $26.59 \times 1.83^{[(T_s-20)/10]}$ ($r^2 = 0.99$, $P < 0.0001$, $n = 52$).

The effect of SWC on CO_2 uptake is illustrated by comparing the dry and warm October 2005 and the wet and cooler October 2006 at the unburned site. Weekly averages of the first 3 weeks of October were used in the comparison. Compared with October 2006, GPP in October 2005 was substantially lower ($23.9\,g\,C\,m^{-2}\,week^{-1}$ vs. $7.4\,g\,C\,m^{-2}\,week^{-1}$), while TER was only moderately lower ($16.9\,g\,C\,m^{-2}\,week^{-1}$ vs. $12.5\,g\,C\,m^{-2}\,week^{-1}$). The changes likely reflect the greater sensitivity of GPP to drought than TER (Fig. 4), as has been reported previously (Misson *et al*., 2005; Granier *et al*., 2007). In addition, only the effect of the increased SWC on TER was counteracted by the effect of the decreased soil temperature, suggesting that TER was more sensitive to temperature than was GPP (Fig. 4). The increase in SWC in late October 2005 was quickly followed by an increase in NEE at the unburned site (Fig. 3). The same SWC increase did not increase NEE at the burned site, because of the already advanced senescence of the herbaceous vegetation.

Wildfire shifted the monthly and annual carbon budgets from a CO_2 sink at the unburned site to a CO_2 source at the burned site (Fig. 5), due primarily to lower GPP at the burned site. In many ecosystems, disturbances, such as fire, are expected to increase TER because of increased above- and belowground necromass and an increase in soil decomposition rate. However, little effects or even reduced TER have been measured in the past in conifers (Amiro, 2001; Kowalski *et al*., 2003; Misson *et al*., 2005; Giasson *et al*., 2006; Irvine *et al*., 2007). Kowalski *et al*. (2004) summarized the effects of disturbance on TER in two different cases depending on species: (1) TER is increased by disturbance in resprouting species, where the belowground

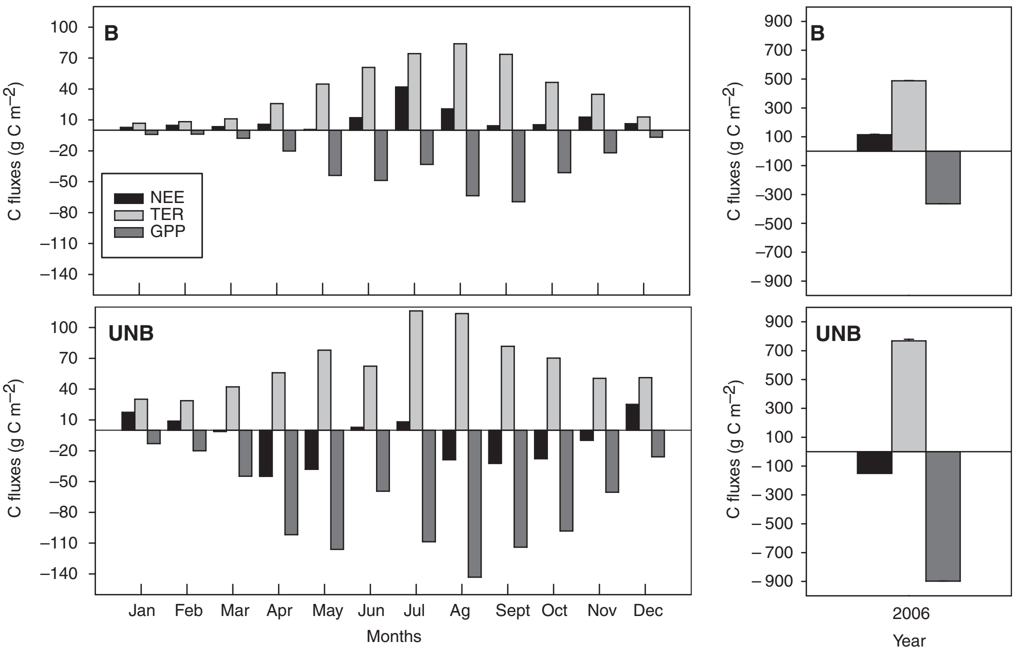

Fig. 5 Monthly net ecosystem carbon exchange (NEE), gross primary production (GPP), and total ecosystem respiration (TER; left panels), and annual NEE, GPP, and TER (right panels) for the burned (B) and unburned sites (UNB) in 2006.

system did not die after the disturbance; (2) TER is decreased by disturbance in nonsprouting species, where the decrease in living biomass, exudates, and photosynthetic assimilates is more important than the increase in decaying necromass. In our study, lower GPP was more important than a change in TER in decreasing NEE at the burned site. The burned site was a source of carbon during every month of 2006 (Fig. 5). Even during the warm and wet conditions in August and September, the most favorable period for carbon uptake at the burned site, TER was stimulated to a greater extent than GPP, resulting in the site being a net source of carbon to the atmosphere.

The different gap-filling methodologies produced different estimates of yearly NEE (Fig. 6), but all estimates showed that the burned site was a net carbon source, whereas the unburned site was a net carbon sink. The use of look-up tables or monthly nonlinear regression for gap-filling had a small effect on the total annual carbon balance at both sites (maximum difference of $9\,g\,C\,m^2\,yr^{-1}$). In contrast, the filtering criteria had larger consequences. For example, a difference of $95\,g\,C\,m^{-2}\,yr^{-1}$ was found if annual NEE at the unburned site was calculated by gap-filling only bad-quality data or by also applying the u^* filtering (Fig. 6). In all cases, adding the quality check of NEE to the traditional u^* filtering increased the amount of gap-filled data, resulting in a difference of $21\,g\,C\,m^{-2}\,yr^{-1}$ in annual NEE at the burned site, and $10\,g\,C\,m^{-2}\,yr^{-1}$ at the unburned site (Fig. 6). Applying the standard on-line gap-filling procedure caused differences in the annual NEE only if the u^* filtering was not considered (Fig. 6).

Annual NEE, calculated as an average ($\pm$ SEM) of the seven methods, was 109 ($\pm$ 6) $g\,C\,m^{-2}$ at the burned site and -164 ($\pm$ 23) $g\,C\,m^{-2}$ at the unburned site; annual TER was 480 ($\pm$ 5) $g\,C\,m^{-2}$ at the burned site and 710 ($\pm$ 54) $g\,C\,m^{-2}$ at the unburned site; annual GPP was -372 ($\pm$ 13) $g\,C\,m^{-2}$ at the burned site and -858 ($\pm$ 37) $g\,C\,m^{-2}$ at the unburned site (Fig. 5). The ratio of annual NEE to GPP was 0.19 for the burned site and 0.30 for the unburned site, compared with 0.27 for a ponderosa pine forest in Oregon (Anthoni *et al.*, 1999). Annual TER/GPP was 1.3 at the burned site and 0.83 at the unburned site, compared with 0.70 reported by Granier *et al.* (2007) for various European forest ecosystems, and very similar to the value reported for conifers (0.85; Law *et al.*, 2002) and to the value found for an unburned ponderosa pine forest in Oregon (0.82; Anthoni *et al.*, 1999).

Ten years after the fire, the burned forest was a moderate carbon source, while the unburned site was a moderate carbon sink. This finding is in agreement with other studies, where disturbances such as fire, wind throw, or harvest caused ecosystems to become carbon sources (Amiro, 2001; Knohl *et al.*, 2002; Thornton *et al.*, 2002; Wirth *et al.*, 2002; Humphreys *et al.*, 2006). Thornton *et al.* (2002) reported that the modeled

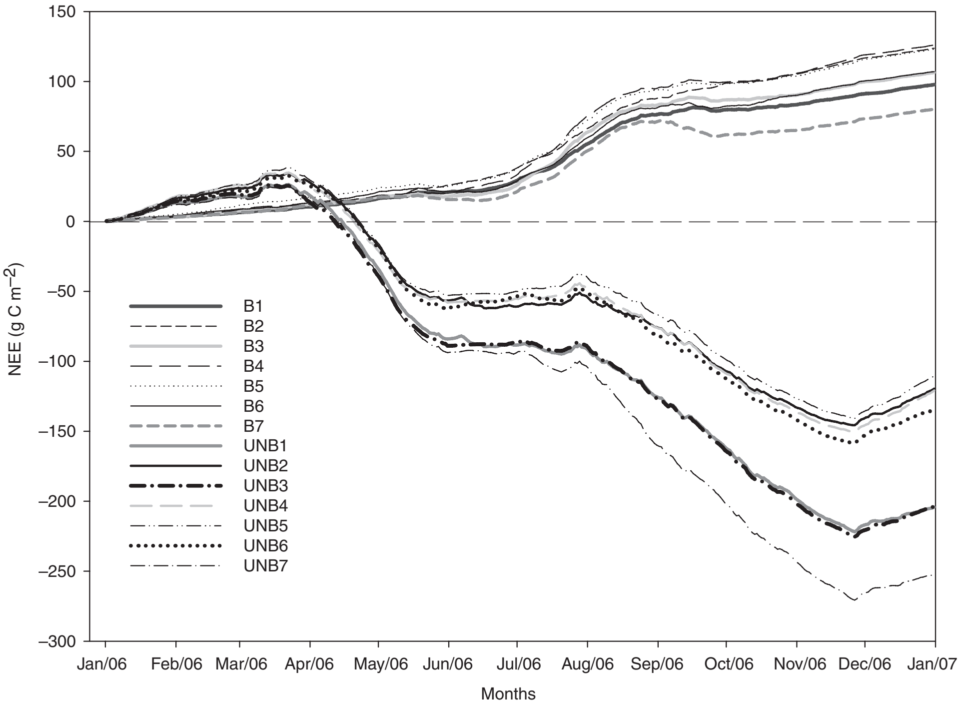

Fig. 6 Cumulative net ecosystem carbon exchange (NEE) at the burned site (B) and the unburned site (UNB) for 2006 calculated using different gap-filling methodologies. B1, UNB1: bad-quality data were gap-filled using look-up tables; B2, UNB2: bad-quality and *u**-filtered data were gap-filled using look-up tables; B3, UNB3: bad-quality data were gap-filled using monthly nonlinear regressions; B4, UNB4: bad-quality and *u**-filtered data were gap-filled using monthly nonlinear regressions; B5, UNB5: only *u**-filtered data were gap-filled using nonlinear regressions; B6, UNB6: on-line gap-filling tool applied with *u** filtering option; B7, UNB7: on-line gap-filling tool applied without *u** filtering.

carbon compensation point, the time taken for an ecosystem to become a net sink for carbon, differed among sites and depended on the type of disturbance, with longer periods for fire and shorter periods for harvests. The carbon compensation point for ponderosa pine forest after stand replacing fire was one of the longest (14–16 years) in the Thornton *et al*. (2002) analysis. The carbon compensation point depends on species, climate, management type and intensity, and frequency of disturbance and is estimated to range from 2 to 30 years (Cohen *et al*., 1996; Schulze *et al*., 1999; Litvak *et al*., 2003; Bond-Lamberty *et al*., 2004; Kowalski *et al*., 2004). Our burned site is still a carbon source of 109 $g\,m^{-2}\,yr^{-1}$ in the 10th year after burning, and no trees have established yet. Likely, the site will not shift to a carbon sink until the vegetation cover re-establishes, which could take many decades (e.g. Savage & Mast, 2005).

Carbon pools

Ten years after the fire, the burned site contained substantially less (53%) total carbon than the unburned site (Table 3). The mineral soil carbon content was similar between sites (Grady & Hart, 2006), but in the burned site, the aboveground biomass carbon was only 2%, the forest floor 12%, and the fine root carbon 31% of the pools found at the unburned site. In contrast, WD at the burned site was five times greater than that at the unburned site and constituted 43% of the total carbon of the burned site (Table 3). But despite the high contribution of this pool to the total ecosystem carbon, the decomposition of the aboveground WD, calculated using a site-specific empirically determined annual decomposition constant (*k*) of 0.031, was only 78 $g\,C\,m^{-2}\,yr^{-1}$, 16% of the yearly TER. At the unburned site, *k* was 0.014 and flux from aboveground WD to the atmosphere was calculated to be 7 $g\,C\,m^{-2}\,yr^{-1}$, 1% of the yearly TER. The *k* values determined in our study are in the same range of other ponderosa pine studies [0.015 in Turner *et al*., in the Rocky Mountains (1995), and 0.027 in Law *et al*. (2001) in Oregon]. The higher *k* at the burned compared with that at the unburned site might be related to colonization of fire-killed trees by bark beetles and wood borers (McHugh *et al*., 2003) that accelerate subsequent decomposition and could explain the slightly higher respiration losses per stored carbon at the burned site: the respiratory loss of carbon per unit of stored carbon was 0.081 $g\,C\,m^{-2}\,yr^{-1}$ at the

Table 3 Ecosystem carbon pools ($g\,C\,m^{-2}$; $\pm$ 1 SE) for the unburned and burned sites

Carbon pool			Unburned	Burned
Biomass	Aboveground		5963 (± 982)	103 (± 9)
	Belowground	Coarse root*	877 (± 147)	0
		Fine root†	127 (± 13)	79.7 (± 18)
Mineral soil carbon			3000 (± 48)	3173 (± 264)
Forest floor			745 (± 133)	87 (± 7)
Woody debris	Aboveground		516 (± 189)	2552 (± 827)
Total carbon			11 228 (± 1512)	5956 (± 1116)

The belowground woody debris was not considered at both sites.
*Coarse root: diameter > 2 mm.
†Fine root: diameter < 2 mm.

burned site, compared with 0.063 $g\,C\,m^{-2}\,yr^{-1}$ at the unburned site.

Environmental control: daytime NEE

We assessed whether SWC and soil temperature at different depths, water vapor deficit (VPD), and air temperature were important controls on daytime NEE by examining residuals (modeled minus measured value) from regression of light-saturated NEE on PPFD. Correlations between residuals and the environmental factors varied over months (Fig. 7a), and the highest value of r^2 was 0.70. In general, the residuals were more weakly correlated with the environmental factors when the relationship between PPFD and NEE was tighter (for example at the unburned site in April 2006, r^2 was 0.86, $P < 0.0001$, $n = 917$) and were more strongly correlated for the unburned site than for the burned site (Fig. 7a). The seasonal trend in the correlations was similar for all SWC and temperature depths, but the relative contribution of the different depths to measured NEE changed each month. In general, the correlation between NEE and SWC was highest from March to August, whereas correlations between NEE and soil temperature increased during winter (Fig. 7a). Most environmental factors were correlated with NEE in May. Air temperature and VPD often were correlated with NEE only at the unburned site. In short, no single environmental factor secondary to PPFD consistently predicted daily NEE, and the two sites did not behave the same. Correlations between NEE and environmental factors other than PPFD were higher in our study than in others, where $r^2 < 0.25$ (Hollinger *et al*., 1994; Aubinet *et al*., 2002; Giasson *et al*., 2006). This difference among sites is likely in part biological and site specific, as the dissimilarity of our two sites shows, and in part methodological, as we restricted the analysis of residuals to the best quality data and the light-saturated part of the day.

At both sites, NEE per unit light availability (quantum yield, Φ) was higher under cloudy conditions than that under clear conditions (Fig. 8, Table 4), consistent with many other studies (Hollinger *et al*., 1994; Goulden *et al*., 1997; Baldocchi *et al*., 2001; Law *et al*., 2002). This effect has been explained as a greater penetration of diffuse light deep into the canopy (Oechel & Lawrence, 1985; Weiss, 2000) or, alternatively, because environmental conditions more favorable for carbon assimilation, such as lower VPD, occur on cloudy days (Gu *et al*., 2002). We expected that at the burned site, where the canopy is very open (LAI 0.6), greater penetration of diffuse radiation in the canopy would be minimal. However, an increase in the apparent quantum yield (Φ) between clear and cloudy conditions occurred at both sites (Table 4). Environmental factors at the unburned site differed between August and October (e.g. air temperature was higher for clear conditions in August but lower in October; Fig. 8), thus confounding the effect of cloudiness and environmental conditions. However, August was mostly warm and wet, and the lower VPD, air temperature, and higher SWC found in cloudy versus clear conditions were more favorable for NEE. In contrast, in October, when lower temperatures limited NEE, cloudy conditions were associated with higher air and soil temperatures, slightly lower SWC, and similar, low VPD (1 kPa compared with 1.6 kPa in August) compared with clear conditions. Thus, we conclude that NEE was stimulated by cloudy conditions because of more favorable environment conditions for photosynthesis and not because of enhancement of photosynthesis by deeper light penetration into the canopy.

Environmental control: night-time NEE

Residuals between night-time TER modeled from temperature and measured night-time TER were weakly correlated with all environmental variables, for both the burned and unburned sites (Fig. 7b). It is possible that a

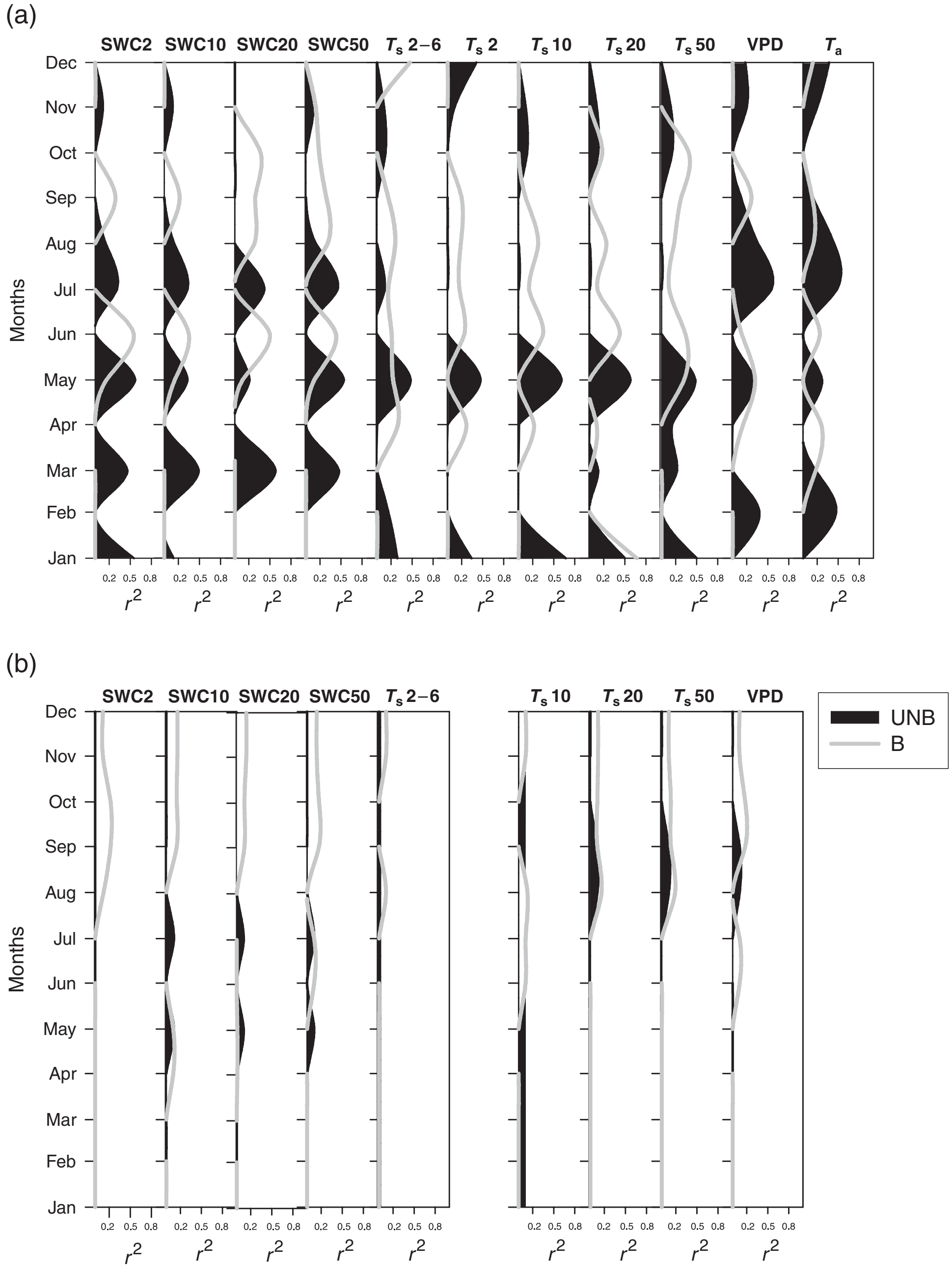

Fig. 7 Correlation coefficients between environmental factors and (a) residuals between measured and modeled daytime net ecosystem exchange of CO_2 (NEE), and (b) residuals between measured NEE and temperature-modeled night-time NEE (2 cm soil temperature at the unburned site, air temperature at the burned site). SWC2, SWC10, SWC20, and SWC50 are the volumetric soil water contents measured at 2, 10, 20, and 50 cm depths, respectively. T_s 2-6 is the average soil temperature between 2 and 6 cm, and T_s 2, T_s 10, T_s 20 and T_s 50 are the soil temperatures measured at 2, 10, 20, and 50 cm, respectively. VPD is the water vapor pressure deficit and T_a the air temperature. Data are shown on monthly intervals and for the unburned (UNB) and burned (B) sites. June is missing at the unburned site.

relationship between TER and environmental factors other than soil temperature was less obvious than for daytime NEE (Fig. 7a) because, unlike for CO_2 uptake, several processes and different CO_2 sources, with possible counterbalancing effects, contribute to TER (Trumbore, 2006; Granier *et al.*, 2007). It is also possible that, compared with the daytime, the lower correlation in the night was caused by the greater difficulty of measuring

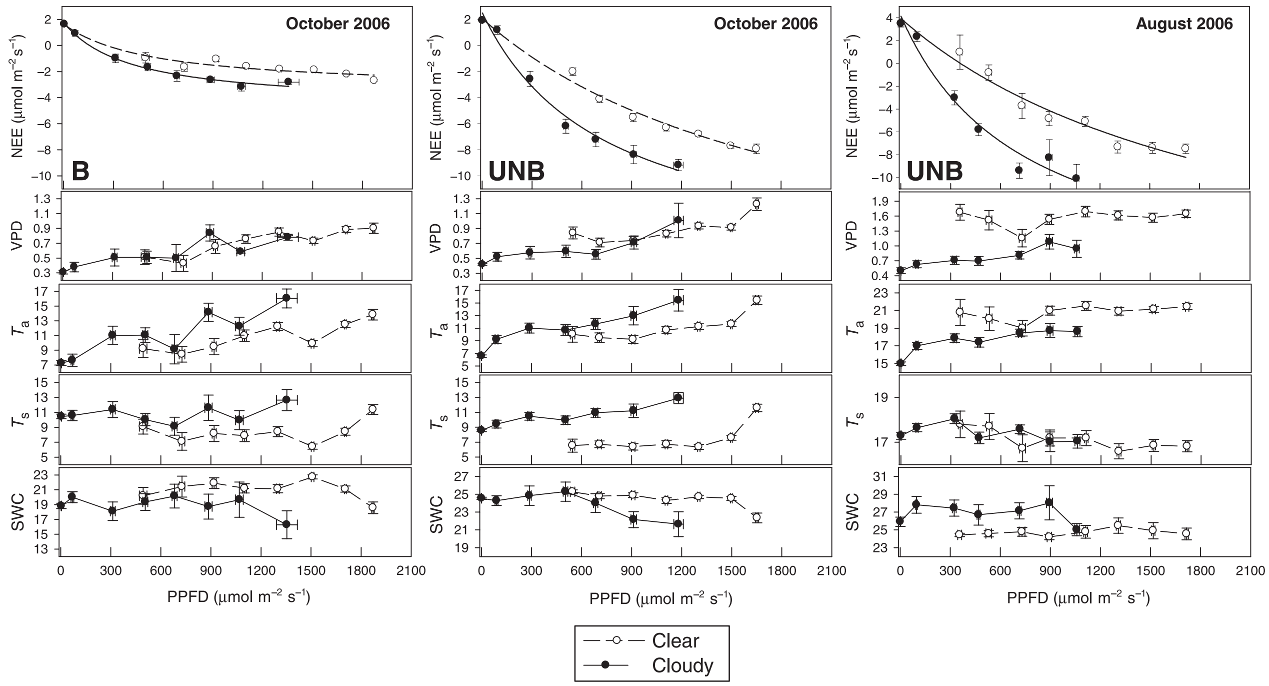

Fig. 8 Light curve for clear [diffuse photosynthetic photon flux density (PPFD) <30%] and cloudy (diffuse PPFD >60%) conditions at the burned (B) and unburned (UNB) sites in October 2006 (left and center panels) and at the UNB site in August 2006 (right panel). Symbols represent bin-averages (±1 standard error) of 200 μmol m^{-2} s^{-1} PPFD classes. For each PPFD class, the average water vapor pressure deficit (VPD in kPa), air temperature (T_a in °C), soil temperature at mineral soil depth of 10 cm (T_s in °C), and volumetric soil water content (SWC in %) are shown. Parameters of the fitted equation are described in Table 4.

Table 4 Parameters of the light response curves for cloudy sky (diffuse light >60%) and clear sky conditions (diffuse light <30%), in October 2006 at the burned site, and August and October 2006 at the unburned site

	Burned (October 2006)		Unburned (October 2006)		Unburned (August 2006)	
Parameter	Clear	Cloudy	Clear	Cloudy	Clear	Cloudy
R_0 (μmol m^{-2} s^{-1})	1.64	1.76	2.05	2.51	3.95	4.18
ϕ	0.01	0.016	0.011	0.026	0.013	0.033
A_{sat} (μmol m^{-2} s^{-1})	5.00	6.37	22.68	19.71	27.19	24.65
r^2	0.94	0.99	0.98	0.98	0.97	0.97

Night respiration (R_0), quantum yield (ϕ), and maximum assimilation (A_{sat}) were determined by fitting averaged NEE within PPFD classes with a rectangular hyperbole (Ruimy 1995). The correlation coefficient (r^2) of the fitted equation is shown.

night-time TER, and thus by the small night-time dataset.

The correlation of soil temperature profiles and night-time TER exhibited different patterns between the two sites (Fig. 7b). At the burned site, 30-min TER was best correlated with the deepest soil temperature (50 cm, $r^2 = 0.23$, $P<0.0001$, $n = 576$) and at the unburned site with the most shallow soil temperature (2 cm, $r^2 = 0.35$, $P<0.0001$, $n = 2804$). The same trend was found by Richardson *et al.* (2006) while comparing a northern hardwood forest and a grassland. The difference could be explained by differences in root distribution between herbaceous and woody species, or by the contribution of the litter layer, which was present only at the unburned site. Clearly, selection of drivers for ecosystem fluxes, such as the soil temperature depth, is difficult to generalize across different ecosystems.

The relationship between soil temperature and night-time TER (1 year of data, temperature measured at a common depth of 10 cm) was similar in shape for the two sites. However, TER was consistently lower at the burned than at the unburned site, even when SWC was

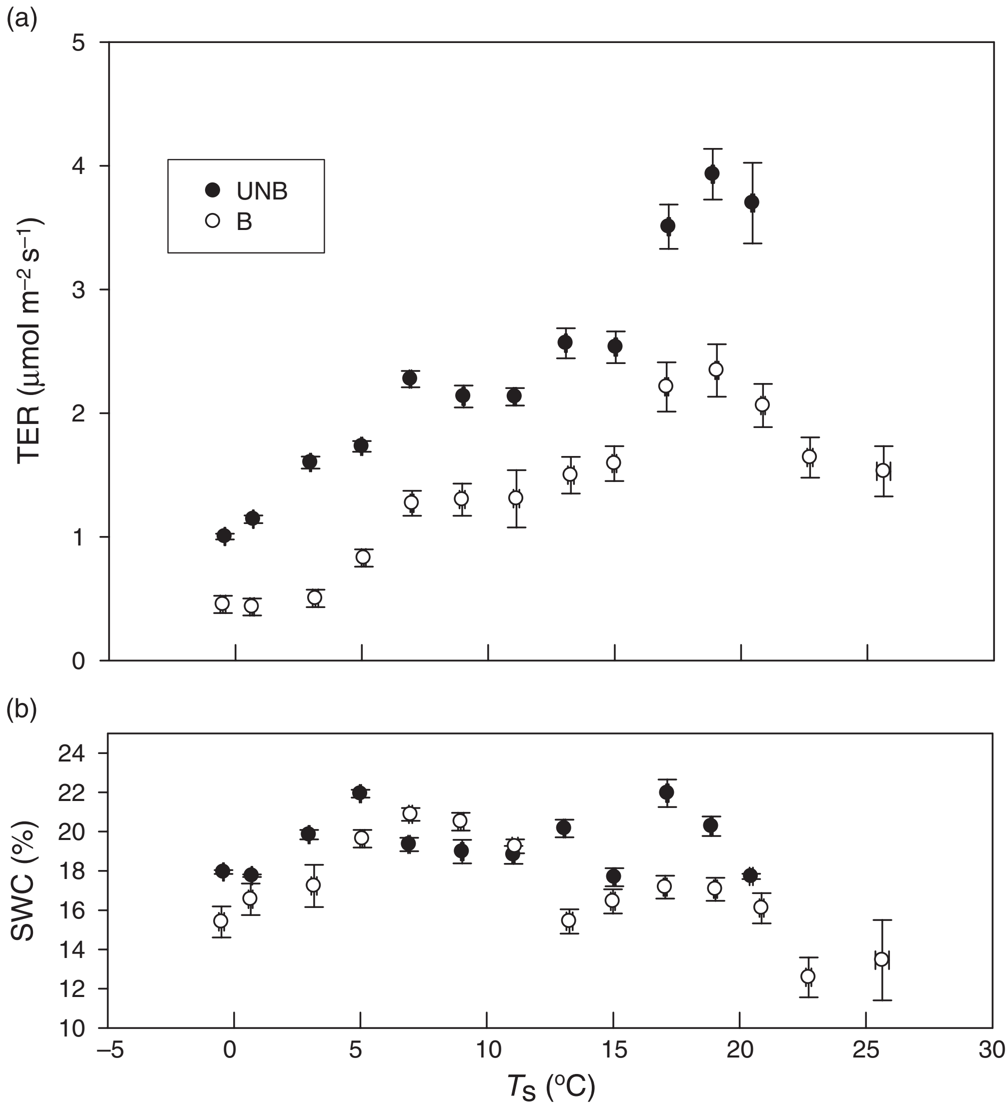

Fig. 9 (a) Average (± standard error) net total ecosystem respiration (TER) for 2 °C soil temperature (T_s) classes (mineral soil depth of 10 cm for both sites) for the unburned (UNB) and burned (B) sites, and (b) average volumetric soil water content (SWC) for each class.

similar between sites (Fig. 9). Moreover, TER at the burned site decreased at the highest temperature and lowest SWC, conditions outside the range of those that occurred at the unburned site (Fig. 9). The absolute difference in TER between the two sites was smallest (0.46 $\mu mol\, m^{-2}\, s^{-1}$) at the lowest soil temperature and largest (2.2 $\mu mol\, m^{-2}\, s^{-1}$) at the highest soil temperature recorded at both sites (Fig. 9). On an annual basis, the burned site lost 480 (± 5 SEM) $g\, C\, m^{-2}\, yr^{-1}$ via TER to the atmosphere, considerably lower than the 710 (± 54 SEM) $g\, C\, m^{-2}\, yr^{-1}$ lost by the unburned site (Fig. 5). A cause of the lower TER at the burned compared with the unburned site is smaller carbon pools at the burned site: while there was no change in the mineral soil carbon and the WD increased, the forest floor, fine root biomass, and the aboveground biomass decreased considerably (Table 3). The lower SWC (at 10 cm) at the burned site (Figs 1 and 3) may also contribute to the lower TER. During all of 2006, in part because of the lower precipitation and in part because of the absence of shade created by the tree canopy, the burned site had lower SWC than the unburned site, even though evapotranspiration (ET) was lower at the burned site than at the unburned site (Fig. 9). Fitting the average night-time TER for each soil temperature class (Fig. 9) with an exponential model based only on soil temperature (Lloyd & Taylor, 1994; Janssens *et al*., 2001; Reichstein *et al*., 2005; Richardson *et al*., 2006) explained 60% of the observed variation at the burned site and 93% at the unburned site. If an equation including SWC was used

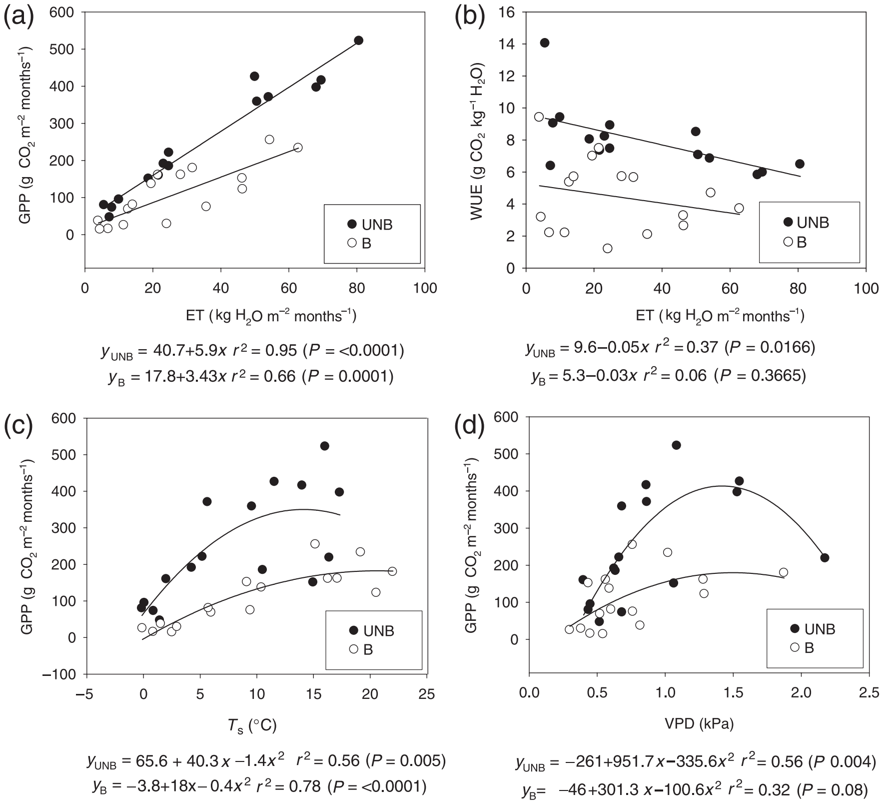

Fig. 10 Monthly gross primary production (GPP) and water use efficiency (WUE) relationships with evapotranspiration (ET) and environmental factors for the unburned (UNB) and burned (B) sites: (a) GPP and ET; (b) WUE and ET; (c) GPP and monthly average soil temperature at mineral soil depth of 10 cm (T_s); and (d) GPP and monthly average daytime vapor pressure deficit (VPD). Plots ($n = 16$) were fitted with linear or second-degree polynomial equations.

(Hanson *et al.*, 1993; Richardson *et al.*, 2006), the explained variation increased to 83% and 97%, respectively, for the burned and unburned sites. The Q_{10} for TER based on soil temperature (10 cm) was 1.75 ($\pm$ 0.10 SEM) at the unburned site and 1.47 ($\pm$ 0.15 SEM) at the burned site, and it increased to 1.92 ($\pm$ 0.16 SEM) at the burned site if the soil temperature was limited to the range also experienced at the unburned site. This result is similar to data reported in other studies of ponderosa pine: a Q_{10} of 1.8 was reported by Law *et al.* (1999) in Oregon and 1.6 by Xu *et al.* (2001) for a young plantation in California. The higher control on TER by SWC at the burned site compared with the unburned site is likely due to higher soil temperature and lower SWC at the burned site. Reduction of TER by dry and warm conditions has often been reported (Janssens *et al.*, 2001; Hart *et al.*, 2006; Granier *et al.*, 2007).

Controls over GPP and water use efficiency

GPP was less strongly linked to ET at the burned site than at the unburned site (Fig. 10a). Lower LAI at the burned site than at the unburned site (Table 2) can explain the difference in the slope between sites. Water use efficiency at the burned site was lower and less tightly related to ET than at the unburned site (Fig. 10b). More of the variation of GPP was explained by soil temperature at the burned site than at the unburned site (Fig. 10c). GPP was more responsive to VPD at the unburned site than at the burned site (Fig. 10d) and followed the same trend observed in other ponderosa pine forests (Anthoni *et al.*, 1999).

Conclusion

The ponderosa pine forest that we studied in northern Arizona, 10 years after a stand-replacing fire, was a moderate carbon source ($109\,g\,C\,m^{-2}\,yr^{-1}$) compared with a moderate carbon sink ($-164\,g\,C\,m^{-2}\,yr^{-1}$) observed in a nearby unburned stand. The most pronounced effect of the fire was to reduce photosynthesis (GPP was circa 60% lower) and next to reduce TER (30% lower). The fire also changed ecosystem carbon pools by reducing carbon in the forest floor and living biomass and increasing carbon in WD. Carbon flux from aboveground WD via decomposition was greater at the burned site than at the unburned site, but both were a small fraction ($<16\%$) of TER. The TER was lower at all soil temperatures at the burned site than at the unburned site, even when SWC was similar, consistent with other reports for conifer forests disturbed by severe fire (Kowalski *et al*., 2004).

The regional climate of the study sites explains part of the slow ecosystem recovery from fire. Cold winters, dry springs, and low and irregular precipitation limit GPP, while the wet, warm summer is often more favorable for carbon losses than for carbon uptake. The burned site was a carbon source to the atmosphere in all months. The severity of the fire, where all trees were killed and most of the forest floor consumed, also had an important role in slowing ecosystem recovery. High-intensity, stand-replacing fires, such as the one we studied, are a consequence of management polices of the past centuries (Covington *et al*., 1994), and, because of climate changes, are expected to become more common in the future (Brown *et al*., 2004; Westerling *et al*., 2006).

Environmental variables secondary to light intensity and temperature, such as SWC, VPD, and soil temperature at different depths, exhibited a control that was seasonally variable and stronger on daytime NEE than night-time TER, and stronger for the unburned than for the burned site. In addition, cloudy conditions were more favorable for carbon uptake than clear sky conditions at both sites, likely because of more favorable environment conditions for photosynthesis on cloudy days.

Stand-replacing fire had a strong and persistent effect on NEE in ponderosa pine forests of northern Arizona. It is unlikely that the burned site will shift from being a carbon source to being a carbon sink in the immediate future due to slow vegetation recovery after fire. Persistent effects of severe fire must be included to accurately quantify the carbon balance of ponderosa pine forests in the southwestern United States, and, in general, in large-scale and long-term biome productivity assessments.

Acknowledgements

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References

Amiro BD (2001) Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. *Global Change Biology*, **7**, 253–268.

Amiro BD, MacPherson JI, Desjardins RL (1999) BOREAS flight measurement of forest-fire effects on carbon dioxide and energy fluxes. *Agricultural and Forest Meteorology*, **96**, 199–208.

Amiro BD, MacPherson JI, Desjardins RL, Chen JM, Liu J (2003) Post-fire carbon dioxide fluxes in the western Canadian boreal forest: evidence from towers, aircraft and remote sensing. *Agricultural and Forest Meteorology*, **115**, 91–107.

Anthoni PM, Law BE, Unsworth MH (1999) Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agricultural and Forest Meteorology*, **95**, 151–168.

Aubinet M, Grelle A, Ibrom A *et al*. (2000) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Advances in Ecological Research*, **30**, 113–175.

Aubinet M, Heinesh B, Longdoz B (2002) Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability. *Global Change Biology*, **8**, 1053–1071.

Auclair AND, Carter TB (1993) Forest wildfires as a recent source of CO_2 at northern latitudes. *Canadian Journal of Forest Research*, **23**, 1528–1536.

Baldocchi D, Falge E, Gu L (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society*, **82**, 2415–2434.

Black TA, Harden JW (1994) Effect of timber harvest on soil carbon storage at Blodgett Experimental Forest, California. *Canadian Journal of Forest Research*, **25**, 1385–1396.

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. *Global Change Biology*, **10**, 473–487.

Breshears DD, Allen CD (2002) The importance of rapid, disturbance-induced losses in carbon management and sequestration. *Global Ecology and Biogeography*, **11**, 1–5.

Brown JK (1974) *Handbook for inventorying downed woody material*. General Technical Report INT-16, USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, Utah, 24 pp.

Brown TJ, Hall BL, Westerling AL (2004) The impact of twenty-first century climate change on wildland fire danger in the western United States: an applications perspective. *Climatic Change*, **62**, 365–388.

Cohen WB, Harmon ME, Wallin DO, Fiorella M (1996) Two decades of carbon flux from forests of the Pacific Northwest. *Bioscience*, **46**, 836–844.

Conard SG, Ivanova GA (1997) Wildfire in Russian foreal forests – potential impacts of fire regime characteristics on emissions and global carbon balance estimates. *Environmental Pollution*, **98**, 305–313.

Cooper CF (1960) Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs*, **30**, 129–164.

Covington WW, Everett RL, Steele R, Irwin LL, Auclair AND (1994) Historical and anticipated changes in forest ecosystems of the inland west of the United States. *Journal of Sustainable Forestry*, **2**, 13–63.

Covington WW, Fulé PZ, Hart SC, Weaver RP (2001) Modeling ecological restoration effects on ponderosa pine forest structure. *Restoration Ecology*, **9**, 421–431.

Curiel YJ, Janssens IA, Carrara A, Ceulemans R (2004) Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology*, **10**, 161–169.

Dilling L, Doney SC, Edmonds J *et al*. (2003) The role of carbon cycle observations and knowledge in carbon management. *Annual Review of Environment and Resources*, **28**, 521–558.

Erickson HE, Edmonds RL, Peterson CE (1985) Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Canadian Journal of Forest Research*, **15**, 914–921.

Falge E, Baldocchi D, Olson R *et al*. (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology*, **107**, 43–69.

Ffolliot PF, Clary WP, Davis JR (1968) Some characteristics of the forest floor under ponderosa pine in Arizona. USDA Forest Service Research note RM-127.

Foken T, Wichura B (1996) Tools for quality assessment of surface-based flux measurements. *Agricultural and Forest Meteorology*, **78**, 83–105.

Fredeen AL, Waughtal JD, Pypker TG (2007) When do replanted sub-boreal clearcuts become net sinks for CO_2? *Forest Ecology and Management*, **239**, 210–216.

Fulé PZ (1990) *Predicting forest floor fuel loading under ponderosa pine at Grand Canyon National Park, Arizona*. Master thesis, Northern Arizona University, Flagstaff, AZ.

Fulé PZ, Covington WW, Moore MM (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications*, **7**, 895–908.

Fulé PZ, Crouse JE, Cocke AE, Moore MM, Covington WW (2004) Changes in canopy fuels and potential fire behavior 1880–2040: Grand Canyon National Park. *Ecological Modelling*, **175**, 231–248.

GAO (US General Accounting Office) (1998) Western national forests: catastrophic wildfires threaten resources and communities. US GAO/T-RCED-98-273.

Giasson M, Coursolle C, Margolis HA (2006) Ecosystem-level CO_2 fluxes from a boreal cutover in eastern Canada before and after scarification. *Agricultural and Forest Meteorology*, **140**, 23–40.

Goulden ML, Daube BC, Fan S, Sutton DJ, Bazzaz A, Munger JW, Wofsy SC (1997) Physiological responses of a black spruce forest to weather. *Journal of Geophysical Research*, **102**, 987–28,996.

Grady KC, Hart SC (2006) Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. *Forest Ecology and Management*, **234**, 123–135.

Granier A, Reichstein M, Bréda N *et al*. (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, **143**, 123–145.

Gu L, Baldocchi D, Verma SB, Black TA, Vesala T, Falge EM, Dowty PR (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research*, **107**, 4050.

Hanson PJ, Wullschleger SD, Bohlman SA, Todd DE (1993) Seasonal and topographic patterns of forest floor CO_2 efflux from upland oak forest. *Tree Physiology*, **13**, 1–15.

Harden JW, Trumbore SEW, Stocks BJ, Hirsh A, Gower ST, O'Neill KP, Kasischke ES (2000) The role of fire in the boreal carbon budget. *Global Change Biology*, **6** (Suppl. 1), 174–184.

Harmon ME, Sexton J (1996) *Guideline for Measurements of Woody Detritus in Forest Ecosystems* Publication no. 20. U.S. LTER Network Office, University of Washington, Seattle, WA.

Hart SC, Classen AT, Wright RJ (2005) Long-term interval burning alters fine root and mycorrhizal dynamics in a ponderosa pine forest. *Journal of Applied Ecology*, **42**, 752–761.

Hart SC, Selmants PC, Boyle SI, Overby ST (2006) Carbon and nitrogen cycling in southwestern ponderosa pine forests. *Forest Science*, **52**, 683–693.

Hibbard KA, Schimel DS, Archer S, Ojima DS, Parton W (2003) Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications*, **132**, 911–926.

Hollinger DY, Goltz SM, Davidson EA, Lee JT, Tu K, Valentine HT (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biology*, **5**, 891–902.

Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology*, **75**, 134.

Hollinger DY, Richardson AD (2005) Uncertainty in eddy covariance measurements and its application to physiological models. *Tree Physiology*, **25**, 873–885.

Houghton RA, Hackler JL, Lawrence KT (2000) Changes in terrestrial carbon storage in the United States. 2: the role of fire and fire management. *Global Ecology and Biogeography*, **9**, 145–170.

Humphreys ER, Black TA, Morgenstern K, Cai T, Drewitt GB, Nesic Z, Trofymow JA (2006) Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agricultural and Forest Meteorology*, **140**, 6–22.

Hurtt GC, Pacala SW, Moorcroft PR, Caspersen J, Shevliakova E, Houghton RA, Moore III B (2002) Projecting the future of the U.S. carbon sink. *Proceedings of the National Academy of Sciences*, **99**, 1389–1394.

Irvine J, Law BE, Hibbard KA (2007) Post-fire carbon pools and fluxes in semi-arid ponderosa pine in central Oregon. *Global Change Biology*, **13**, 1–13. doi: 10.1111/j.1365-2486.2007.01368.x.

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**, 269–278.

Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG (2006) Carbon storage on landscapes with stand-replacing fires. *Bioscience*, **56**, 598–606.

Kaye JP, Hart SC, Fulé PZ, Covington WW, Moore MM, Kaye MW (2005) Initial carbon, nitrogen, and phosphorus fluxes following ponderosa pine restoration treatments. *Ecological Applications*, **15**, 1581–1593.

Keane RE, Ryan KC, Veblen TT, Allen CD, Logan J, Hawkes B (2002) *Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review.* General Technical Report GTR-91, USDA Forest Service, Rocky Mountain Research Station.

Knohl A, Kolle O, Minayeva TY, Milyukova IM, Vygodskaya NN, Foken T, Schulze E (2002) Carbon dioxide exchange of a Russian boreal forest after disturbance by wind throw. *Global Change Biology*, **8**, 231–246.

Kowalski AS, Loustau D, Berbigier P *et al*. (2004) Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. *Global Change Biology*, **10**, 1707–1723.

Kowalski AS, Sartore M, Burlett R, Berbigier P, Loustau D (2003) The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. *Global Change Biology*, **9**, 1051–1065.

Law BE, Falge E, Gu L *et al*. (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, **113**, 97–120.

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 (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental 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 effects on carbon stocks and fluxes across Western Oregon USA. *Global Change Biology*, **10**, 1429–1444.

Law BE, Waring RH, Anthoni PM, Aber JD (2000) Measurements of gross and net ecosystem productivity and water vapour exchange of a *Pinus ponderosa* ecosystem, and an evaluation of two generalized models. *Global Change Biology*, **6**, 155–168.

Litton CM, Ryan MG, Knight DH, Stahl PD (2003) Soil-surface carbon dioxide efflux and microbial biomass in relation to tree density 13 years after a stand replacing fire in a lodgepole pine ecosystem. *Global Change Biology*, **9**, 680–696.

Litvak M, Miller S, Wofsy SC, Goulden M (2003) Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest. *Journal of Geophysical Research*, **108**, 8225.

Lloyd J, Taylor J (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

McCaughey JH, Pejam MR, Arain MA, Cameron DA (2006) Carbon dioxide and energy fluxes from a boreal mixed wood forest ecosystem in Ontario, Canada. *Agricultural and Forest Meteorology*, **140**, 79–96.

McDowell MG, Adams HD, Bailey JD, Hess M, Kolb TE (2006) Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*, **16**, 1164–1182.

McHugh C, Kolb TE, Wilson JL (2003) Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environmental Entomology*, **32**, 510–522.

McMichael B, Lascano RJ (2003) Laboratory evaluation of a commercial dielectric soil water sensor. *Vadose Zone Journal*, **2**, 650–654.

Misson L, Tang J, Xu M, McKay M, Goldstein A (2005) Influences of recovery from clear-cut, climate variability, and thinning on the carbon balance of a young ponderosa pine plantation. *Agricultural and Forest Meteorology*, **130**, 207–222.

Moore MM, Huffman DW, Fulé PZ, Covington WW, Crouse JW (2004) Comparison of historical and contemporary forest structure and composition on permanent plots in southwestern ponderosa pine forests. *Forest Science*, **50**, 162–176.

Morgenstern K, Black TA, Humphreys ER *et al*. (2004) Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agricultural and Forest Meteorology*, **123**, 201–219.

Nelson DW, Sommers LE (1982) Total carbon, organic carbon, and organic matter. In: *Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties. Agronomy Monograph* 9 (ed. Page AL *et al*.), pp. 539–579. ASA, Madison, WI.

Oechel WC, Lawrence WT (1985) Taiga. In: *Physiological Ecology of North American Plant Communities* (eds Chabot BF, Mooney HA), pp. 66–94. Chapman & Hall, New York, London.

Omdal DW, Jacobi WR, Shaw CG (2001) Estimating large-root biomass from breast-height diameters for ponderosa pine in northern New Mexico. *Western Journal of Applied Forestry*, **16**, 18–21.

Pacala SW, Hurtt GC, Baker D *et al*. (2001) Consistent land- and atmosphere-based U.S. carbon sink estimates. *Science*, **292**, 2316–2320.

Page SE, Siegert F, Rieley JO, Boehm JO, Jaya A, Limin S (2002) The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature*, **420**, 61–66.

Potter CS, Klooster SA (1999) Detecting a terrestrial biosphere sink for carbon dioxide: interannual ecosystem modeling for the mid-1980s. *Climatic Change*, **42**, 489–503.

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology*, **10**, 2052–2077.

Randerson JT, Liu H, Flanner MG *et al*. (2006) The impact of boreal forest fire on climate warming (reports). *Science*, **314**, 1130.

Reichstein M, Falge E, Baldocchi D *et al*. (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.

Richardson AD, Braswell BH, Hollinger DY *et al*. (2006) Comparing simple respiration models for eddy flux and dynamic chamber data. *Agricultural and Forest Meteorology*, **141**, 219–234.

Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO_2 fluxes over plant canopy and solar radiation: a review. *Advances in Ecological Research*, **26**, 1–64.

Saleska SR, Miller SD, Matross DM *et al*. (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science*, **302**, 1554–1557.

Savage M, Brown PM, Feddema J (1996) The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, **3**, 310–318.

Savage M, Mast JN (2005) How resilient are southwestern ponderosa pine forests after crown fires? *Canadian Journal of Forest Research*, **35**, 967–977.

Schimel D, Baker D (2002) The wildfire factor. *Nature*, **420**, 29.

Schimel DS, House JI, Hibbard KA *et al*. (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–176.

Schulze E-D, Lloyd J, Kelliher FM *et al*. (1999) Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink – a synthesis. *Global Change Biology*, **5**, 703–722.

Schulze E-D, Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science*, **289**, 2058–2059.

Sheppard PR, Comrie AC, Packin GD, Angersbach K, Hughes MK (2002) The climate of the US Southwest. *Climate Research*, **21**, 219–238.

Song C, Woodcock CE (2003) A regional forest ecosystem carbon budget model: impacts of forest age structure and land use history. *Ecological Modelling*, **164**, 33–47.

Stoy PC, Katul GG, Siqueira MBS *et al*. (2006) Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern US. *Global Change Biology*, **12**, 2115–2135.

Swetnam TW, Baisan CH (1996) Historical fire regime patterns in the southwestern United States since AD 1700. In: *Fire Effects in Southwestern Forests. USDA Forest Service General Technical Report RM-246* (ed. Allen CD), pp. 11–32.

Thornton PE, Law BE, Gholz HL *et al*. (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agricultural and Forest Meteorology*, **113**, 185–222.

Trumbore S (2006) Carbon respired by terrestrial ecosystems – recent progress and challenges. *Global Change Biology*, **12**, 141–153.

Turner DP, Koerper GJ, Harmon ME, Lee JJ (1995) A carbon budget for forests of the conterminous United States. *Ecological Applications*, **5**, 421–436.

Weiss SB (2000) Vertical and temporal distribution of insulation in gaps in an old-growth coniferous forest. *Canadian Journal of Forest Research*, **30**, 1953–1964.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increases western U.S. forest wildfire activity. *Science*, **313**, 940–943.

Wilson K, Goldstein A, Falge E *et al*. (2002) Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology*, **113**, 223–243.

Wirth C, Schulze E-D, Lühker B *et al*. (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil*, **242**, 41–63.

Xu M, DeBiase TA, Qi Y, Goldstein A, Liu Z (2001) Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. *Tree Physiology*, **21**, 309–318.