

Carbon and water fluxes from ponderosa pine forests disturbed by wildfire and thinning

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Abstract. Disturbances alter ecosystem carbon dynamics, often by reducing carbon uptake and stocks. We compared the impact of two types of disturbances that represent the most likely future conditions of currently dense ponderosa pine forests of the southwestern United States: (1) high-intensity fire and (2) thinning, designed to reduce fire intensity. High-severity fire had a larger impact on ecosystem carbon uptake and storage than thinning. Total ecosystem carbon was 42% lower at the intensely burned site, 10 years after burning, than at the undisturbed site. Eddy covariance measurements over two years showed that the burned site was a net annual source of carbon to the atmosphere whereas the undisturbed site was a sink. Net primary production (NPP), evapotranspiration (ET), and water use efficiency were lower at the burned site than at the undisturbed site. In contrast, thinning decreased total ecosystem carbon by 18%, and changed the site from a carbon sink to a source in the first post-treatment year. Thinning also decreased ET, reduced the limitation of drought on carbon uptake during summer, and did not change water use efficiency. Both disturbances reduced ecosystem carbon uptake by decreasing gross primary production (55% by burning, 30% by thinning) more than total ecosystem respiration (TER; 33–47% by burning, 18% by thinning), and increased the contribution of soil carbon dioxide efflux to TER. The relationship between TER and temperature was not affected by either disturbance. Efforts to accurately estimate regional carbon budgets should consider impacts on carbon dynamics of both large disturbances, such as high-intensity fire, and the partial disturbance of thinning that is often used to prevent intense burning. Our results show that thinned forests of ponderosa pine in the southwestern United States are a desirable alternative to intensively burned forests to maintain carbon stocks and primary production.

Key words: carbon sequestration; disturbance; ecosystem respiration; evapotranspiration; fire; forest management; GPP; NEP; *Pinus ponderosa*; soil respiration; thinning.

INTRODUCTION

Terrestrial ecosystems strongly influence the global carbon cycle and, combined with oceans, absorb about half of the carbon dioxide (CO₂) currently released by human activities (Dilling et al. 2003). This sink influences regional and global climate and is of increasing interest to policy-makers concerned with management of greenhouse gases. Yet, it is widely acknowledged that estimates of the forest carbon sink do not adequately consider impacts of forest management activities, or disturbance by intense fire that often results from the decision to not actively manage (Breshears and Allen 2002, Schimel and Baker 2002). Simulations and limited empirical data suggest that stand-scale CO₂ fluxes depend strongly on forest age and

disturbance (Thornton et al. 2002, Pregitzer and Euskirchen 2004, Misson et al. 2005, Luyssaert et al. 2008). Elucidation of the impacts of forest management actions on carbon exchanges between forests and the atmosphere is needed to understand the magnitude and sustainability of forest carbon sinks and to support emerging efforts to place economic value on carbon sequestration by forests (Birdsey et al. 2006).

Disturbances by fire, insect outbreaks, diseases, wind throw, and harvesting reduce forest capacity for carbon uptake and can increase carbon release to the atmosphere, shifting forested landscapes from carbon sinks to carbon sources (Knohl et al. 2002, Kowalski et al. 2004, Giasson et al. 2006). Forest disturbances primarily affect vegetation, but they also affect soil (Bormann et al. 2008), water and energy fluxes (Montes-Helu et al. 2009), and consequently micro- and meso-climate (Bonan 2008). Return of forest carbon stores and fluxes to pre-disturbance levels can take decades and varies

Manuscript received 28 May 2009; revised 15 July 2009; accepted 21 July 2009. Corresponding Editor: D. R. Zak.

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TABLE 1. Stand, soil, and climate characteristics (mean \pm SD; $n = 5$ plots) of the undisturbed, thinned, and burned sites.

Site characteristic	Undisturbed		Thinned	
	2006	2007	2006	2007
Stand				
LAI trees (m^2/m^2)	2.2 \pm 0.7	2.2 \pm 0.7	1.5 \pm 0.2	0.9 \pm 0.2
LAI understory (m^2/m^2)	0.06 \pm 0.04	0.10 \pm 0.09	0.07 \pm 0.07	0.18 \pm 0.2
Tree density (trees/ha)	853 \pm 424		472 \pm 110	143 \pm 7
Basal area (m^2/ha)	30 \pm 11	30 \pm 9	20 \pm 2	13 \pm 2
Canopy height (m)	18		18	
Soil†				
Soil type	complex of Mollic Eutroboralf and Typic Argiboroll		Typic Eutroboralf	
Depth of A horizon (cm)	5		8	
Bulk density (0–15 cm; Mg/m^3)	0.78		0.98	
Sand A horizon (%)	37		27	
Silt A horizon (%)	39		60	
Clay A horizon (%)	24		13	
Depth of B horizon (cm)	5–15		8–19	
Sand B horizon (%)	31		13	
Silt B horizon (%)	34		47	
Clay B horizon (%)	35		40	
Climate				
Mean air temperature ($^{\circ}C$)	8.8	9.1	9.3	9.3
Maximum air temperature ($^{\circ}C$)	14.4	14.8	14.7	15.0
Minimum air temperature ($^{\circ}C$)	3.4	3.5	4.4	5.2
Annual precipitation (mm)	692	675	601	663
Mean daily PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	431	433	451	454
PPFD diffuse (fraction)	0.34	0.34	0.34	0.34
Mean daily global radiation (W/m^2)	222	223	218	222
Mean VPD (08:00–18:00; kPa)	1.1	1.1	1.2	1.2

Notes: Abbreviations are: LAI, leaf area index; PPFD, photosynthetic photon flux density; VPD, vapor pressure deficit. Uncertainty (SD) is shown for stand structure characteristics only.

† Soil characteristics were not expected to be affected by thinning and were not remeasured.

among forest types and with disturbance intensity (Thornton et al. 2002, Pregitzer and Euskirchen 2004).

Upland landscapes of the southwestern United States are dominated by ponderosa pine (*Pinus ponderosa*) forests that have been subject to fire suppression policy for many decades (Cooper 1960, Van Horne and Fulé 2006). These forests are often dense with small diameter trees prone to burning intensely in natural or human-induced fires (Covington et al. 2001, McHugh and Kolb 2003). Effects of fire on net ecosystem production (NEP) are difficult to generalize because of variation in fire intensity, fire adaptations of biota, and climatic constraints on vegetation recovery. Intense forest fires have been shown to have a greater impact on gross primary production (GPP) than on ecosystem respiration (Irvine et al. 2007, Dore et al. 2008), and in some forests to impact GPP more through plant mortality than through changes in growth rates of surviving trees (Irvine et al. 2007). Vegetation changes induced by intense fire also often alter site water and energy balances and increase soil erosion (Breshears and Allen 2002, Whicker et al. 2008, Montes-Helu et al. 2009).

A well-established way to reduce the risk of high-intensity forest fire in ponderosa pine forest in southwestern United States is to reduce tree density and fuel loads through silvicultural thinning and prescribed fire, often labeled restoration treatments (Covington et al.

1997, Finkral and Evans 2008). Thinning is used to increase wood production, reduce fire risk, control stand structure and composition, and increase forests resistance and resilience to disturbance (Kolb et al. 1998, McDowell et al. 2006, Campbell et al. 2009). Thinning, however, also is a disturbance, even if usually less intense than fire (Thornton et al. 2002), and partial forest disturbances, such as thinning and insect and wind damages, are more common than high-intensity disturbances (Misson et al. 2005, Campbell et al. 2009).

Tree harvesting can alter ecosystem carbon dynamics depending on the type of silvicultural treatment and its intensity (Thornton et al. 2002, Misson et al. 2005, Giasson et al. 2006). Whereas many studies have assessed the effect of thinning or clear cut harvesting on components of ecosystem carbon balance (Black and Harden 1995, Boerner et al. 2008, Finkral and Evans 2008, Sullivan et al. 2008), few have examined whole ecosystem carbon fluxes (Law et al. 2001, Kowalski et al. 2004, Giasson et al. 2006, Humphreys et al. 2006, Campbell et al. 2009). These studies have shown that GPP decreased after harvesting, while ecosystem respiration or soil respiration did not change (Misson et al. 2005, Giasson et al. 2006, Campbell et al. 2009), increased (Concilio et al. 2005), or decreased (Kowalski et al. 2004, Sullivan et al. 2008). Moreover, effects of thinning on NEP cannot be predicted solely

TABLE 1. Extended.

Burned	
2006	2007
before fire, 2.4 ± 1.6 ; after fire, 0.63 ± 0.38	0.55 ± 0.29
before fire, 343 ± 175 ; after fire, 0	
before fire, 31 ± 21 ; after fire, <0.5	
Mollic Eutroboralf	
7	
0.80	
30	
57	
13	
7–15	
20	
55	
25	
8.6	8.8
14.5	14.7
2.0	2.1
517	551
429	443
0.32	0.33
221	226
1.1	1.2

from changes in tree leaf area and GPP as impacts on NEP are also determined by changes in soil CO₂ emissions and the compensatory response of understory vegetation (Campbell et al. 2009).

Thinning is also proposed to enhance hydrological services provided by ponderosa pine watersheds in the southwestern United States (Covington et al. 1997, Simonin et al. 2007). Ponderosa pine forests dominate the headwaters of many watersheds in the western United States and are an important supply of stream flow and ground water (Troendle 1983). Whereas several studies have addressed effects of thinning on ponderosa pine forest water balance components (Baker 1986, Kaye et al. 1999, Simonin et al. 2007), no studies of this forest type have directly measured the impact of thinning on forest-level evapotranspiration (ET), the hydrologic flux that largely controls the amount of precipitation available for soil water storage and drainage to streams and ground water.

Our main focus is to report the first results of a unique study of the impact of thinning and high-intensity fire on NEP and ET in a mature southwestern ponderosa pine stand measured with the eddy covariance technique. Our secondary focus is to compare eddy covariance-based NEP with ecosystem-level carbon flux estimated with biometric methods (NEP = net primary production – heterotrophic respiration) that are increasing in use yet have considerable uncertainty about accuracy (Gough et al. 2008, Campbell et al. 2009).

METHODS

Sites

To analyze the effect of disturbances on carbon and water exchanges of ponderosa pine forests in the southwestern United States, we compared three sites (undisturbed, restoration thinned, wildfire burned), ~35 km apart, in the vicinity of Flagstaff, Arizona during 2006 and 2007. The three sites have similar edaphic and climatic conditions (Table 1). Winter is cold, spring is dry, and precipitation is irregular, concentrated as snow in winter and in the July–August monsoon season (Sheppard et al. 2002).

The undisturbed site was a ponderosa pine stand ($35^{\circ}5'20.5''$ N, $111^{\circ}45'43.33''$ W, elevation 2180 m above sea level) excluded from silvicultural treatments or fire over the last century. The site was located in the Northern Arizona University Centennial Forest, and represented a typical example of the forests of the region, with a continuous canopy cover of ponderosa pine (*Pinus ponderosa*), occasional Gambel oak (*Quercus gambelii*), and a sparse understory. During the 2006–2007 study period, leaf area index (LAI; projected area) was $2.3 \text{ m}^2/\text{m}^2$, basal area was $30 \text{ m}^2/\text{ha}$, and density was 853 trees/ha (Table 1).

The burned site was a 10 500 ha area in the Coconino National Forest ($35^{\circ}26'43.43''$ N, $111^{\circ}46'18.64''$, elevation 2270 m above sea level) burned by an intense wildfire in 1996. Since then, no natural regeneration or operations such as logging or tree planting have occurred. The fire killed all trees, and consumed most of the surface organic soil horizon. Today the vegetation consists of grasses, forbs, and few shrubs, with maximum LAI of $0.6 \text{ m}^2/\text{m}^2$ (late summer) and average vegetation cover of 40% in between bare soil (50% cover) and snags and logs (10% cover; Montes-Helu et al. 2009).

The thinned site ($35^{\circ}8'33.48''$ N, $111^{\circ}43'38.37''$ W, 2155 m above sea level) was a ponderosa pine stand also located in the Centennial Forest, ~6 km from the undisturbed site. Timber harvests and pulpwood sales during the last century (Finkral and Evans 2008) resulted in lower LAI ($1.5 \text{ m}^2/\text{m}^2$), basal area ($20 \text{ m}^2/\text{ha}$), and tree density (472 trees/ha) compared to the undisturbed site (Table 1). Our measurements of tree density and basal area are similar to those reported by Finkral and Evans (2008) from measurement of all 51 240 trees in the 90-ha thinned site prior to treatment ($22 \text{ m}^2/\text{ha}$ basal area, 579 trees/ha tree density, respectively).

Approximately 90 ha of the site were thinned in September 2006. The objective of the thinning was to reduce tree density and fire risk. All trees older than 135 years or with a diameter at breast height (dbh; ~1.4 m height) greater than 41 cm were excluded from thinning. The treatment was conducted with mechanized and hand-felling methods and reduced tree density 70%, basal area 35%, tree LAI 40%, and stand LAI 30%,

because of the post-thinning increase of understory LAI (Table 1).

We measured net ecosystem CO₂ exchange (NEE) using the eddy covariance technique (Aubinet et al. 2000) continuously during 2006 and 2007. Net ecosystem exchange was summed at a yearly interval to produce net ecosystem production (NEP; Chapin et al. 2006). We also estimated NEP with a second independent method using biometric and soil CO₂ flux measurements (Ehman et al. 2002, Howard et al. 2004, Luyssaert et al. 2007):

$$\text{NEP} = -\text{NEE} = \text{NPP} - R_{\text{het}}$$

where net primary production (NPP) is the sum of the productivity of understory, aboveground standing trees, litterfall, and fine and coarse roots and R_{het} is the CO₂ emitted to the atmosphere by heterotrophic organisms in soil and by the decomposition of woody debris (>1 cm diameter). By convention, carbon uptake by the ecosystem is negative in the eddy covariance analysis and positive in the biometric analysis.

Detection of disturbance effects on NEP in our study was challenging because annual carbon balance was close to zero, and thus differences between sites were small in the cold and dry climate of our study area. However, simultaneous measurements at the three sites allowed us to separate the effect of climatic drivers from the effect of disturbances on carbon fluxes. Moreover, using the same instruments, methods, and analyses at the three sites enhanced our ability to detect impacts of disturbances.

Whereas in the case of thinning we used an experimental manipulation design with pre- and post-thinning measurements at the thinned site paired with an undisturbed control site, for the fire we based our analysis on measured differences between burned and undisturbed sites 10 years after the fire, because we lack pretreatment data. Also, as is typical of eddy covariance studies, each level of disturbance was represented by one site. Thus, to quantify effects of fire on carbon pools and fluxes, we used the impact-control site approach. To quantify effects of thinning we used a before-after, control-impact analysis (BACI; Stewart-Oaten and Bence 2001), with the effect size calculated as the difference between thinned (THN) and undisturbed (UND) sites after (post) treatment, adjusted for the pretreatment (pre) difference between sites: $(\text{THN}_{\text{post}} - \text{UND}_{\text{post}}) - (\text{THN}_{\text{pre}} - \text{UND}_{\text{pre}})$. Effects of thinning on shorter temporal scales were estimated using the BACI analysis based on the difference between slopes of linear regression of fluxes at the two sites before and after thinning (Stewart-Oaten and Bence 2001).

Biometric measurements

We measured each biomass component in five, 25 m radius, circular plots located in the eddy covariance footprint. The plots were located between 150 and 400 m in the south section (east to west) from the towers, the

prevailing wind direction. Net primary productivity was determined as the change in biomass for each component between two consecutive years. We calculated tree biomass and LAI with allometric equations developed for ponderosa pine aboveground (Kaye et al. 2005) and coarse root (Omdal and Jacobi 2001) biomass and for oak aboveground (Clary and Tiedemann 1986) and coarse root (Jenkins et al. 2003) biomass.

In fall 2007, we measured dbh and radial increment on all trees in the plots. We determined radial increment for the period 1997–2007 from one core per tree sampled at breast height, and the diameter of years previous to 2007 by subtracting diameter growth of the year from the diameter of the previous year. We measured understory aboveground biomass and projected leaf area at peak biomass (late September) at four 0.5-m² subplots per plot (20 total per site). We collected litterfall twice each year at the forested sites (undisturbed, thinned) using three buckets of 0.159 m² per plot (15 total per site).

We sampled fine root biomass (<2 mm diameter) in May 2006 and June 2007 from three soil cores per plot (15 total per site) of 20.4 cm² in area and 15 cm in depth, where most fine root biomass occurs in the study region (Hart et al. 2006). Roots were extracted from the soil with a hydropneumatic elutriation system (Scienceware Bel-Art Products, Pequannock, New Jersey, USA). We measured soil organic layer mass and carbon content of the mineral soil on six (2005) and four (2007) 30 × 30 cm samples per plot. We measured soil bulk density by sampling four cores (5 cm diameter wide by 15 cm deep) per plot (20 total per site).

We estimated fine root production using the minirhizotron technique. In June 2005, we inserted three acrylic minirhizotron tubes per plot (15 total per site), with an internal diameter of 64 mm and wall thickness of 3 mm, in a trench at a 45° angle to a depth of 30 cm. Data were not used until January 2006 to allow the tubes and soil to equilibrate following the installation disturbance (Hendericks et al. 2006). We collected images every two to four weeks depending on the season with more frequent measurements during the growing season and less frequent during the winter months. Images were collected using a rotating scanner head CI-600 minirhizotron (CID Inc., Vancouver, Washington, USA) at 200 dots per inch (dpi) resolution. The central 292 cm² of each image collected at depths of 0–15 cm and 15–30 cm was digitized and analyzed using RooTracker (Duke University, Durham, North Carolina, USA) at 75 dpi resolution. We converted rhizotron images to root biomass using specific root area (Johnson et al. 2001), which was calculated using roots we harvested from the sites and then scanned in the laboratory. The specific root area was determined separately for the forested (undisturbed, thinned) and burned sites, where tree fine roots were absent. Differences in focal length between the flat bed scanner where the harvested root samples were scanned and the field scanner were accounted for and the ash free dry

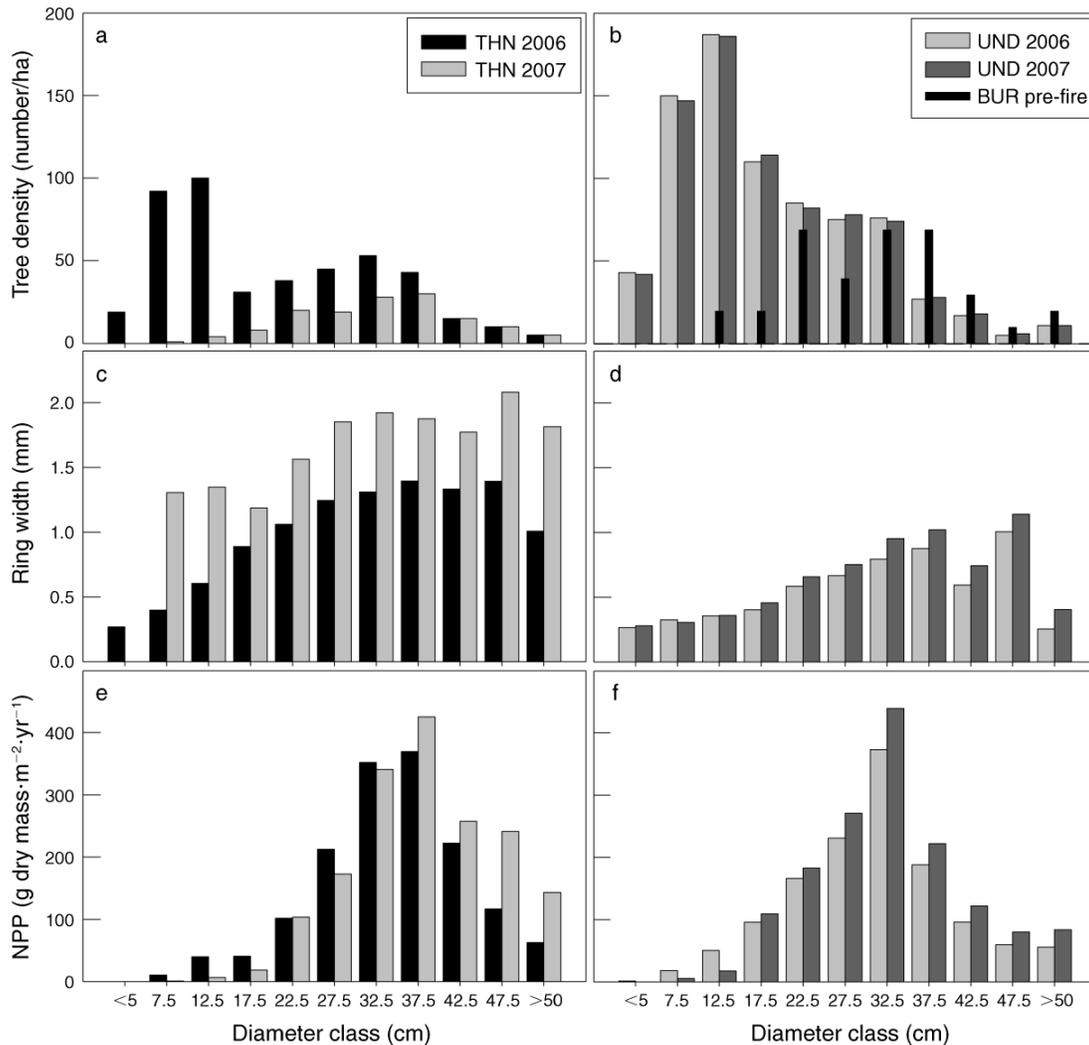


FIG. 1. (a, b) Tree density per diameter class, (c, d) mean ring width per diameter class, and (e, f) tree productivity (excluding fine roots; NPP, net primary productivity) per diameter class at the thinned (THN; a, c, e) and undisturbed (UND; b, d, f) sites in 2006, before thinning, and in 2007, after thinning. In panel (b), the black bars show the prefire number of trees at the burned site (BUR).

mass of the harvested samples determined (Stevens and Jones 2006).

At the undisturbed and burned sites, we measured mass of fine woody debris (between 1 and 7.5 cm diameter) in 2006 using the Brown (1974) method on four 3.7-m transects from each plot center. Coarse woody debris (diameter > 7.5 cm) was measured on four, 0.04-ha plots per site. Details can be found in Dore et al. (2008). At the thinned site, the woody debris before (summer 2006) and after (November 2006) thinning was measured using the Brown method on ten 15-m transects (Finkral and Evans 2008).

We assumed the carbon concentration of the organic matter of all pools to be 0.48 g carbon per g dry mass

(Kaye et al. 2005). Decomposition of woody debris was estimated at each site based on changes in density of woody debris from a chronosequence (Erickson et al. 1985) described in Dore et al. (2008). We estimated uncertainty in yearly biometry-based NEP by applying a Monte Carlo approach randomly varying all components of NEP according to a normal distribution within ± 1 standard deviation of the mean of the components with 100 iterations (Howard et al. 2004).

Stand structure and growth were not identical for the undisturbed and thinned sites before thinning (Fig. 1). The undisturbed site had slightly higher basal area and tree density (Table 1), but less tree radial growth (Fig. 1c). The distribution of trees and productivity over dbh

TABLE 2. Energy balance closure (EN BAL) and uncertainty (UNC) in net ecosystem exchange (NEE) estimates at the undisturbed, thinned, and burned sites in 2006 and 2007.

Site and year	EN BAL		UNC		
	30 minute	Daily sum	Measurement (1a)	Measurement (1b)	Measurement + gap-filling (2)
Undisturbed 2006	0.72 (0.90)	0.85 (0.94)	2.1	5.7	14.3
Undisturbed 2007	0.80 (0.91)	0.99 (0.85)	2.1	6.1	13.8
Burned 2006	0.75 (0.90)	0.93 (0.91)	0.8	2.0	10.7
Burned 2007	0.84 (0.87)	0.94 (0.78)	0.9	2.0	10.7
Thinned 2006	0.70 (0.90)	0.81 (0.93)	2.0	5.9	14.5
Thinned 2007	0.69 (0.90)	0.86 (0.89)	1.7	5.9	13.9

Notes: EN BAL data are the slope ($[W/m^2]/[W/m^2]$) and r^2 of the linear regression between sensible plus latent heat and net radiation minus soil heat flux, calculated using 30-minute data and daily sums. Days with snow on the ground were excluded. Total UNC for NEE ($g \cdot m^{-2} \cdot yr^{-1}$) is the sum of UNC due to (1) measurement error estimated (1a) assuming a 20% random error for each 30-min interval (Morgenstern et al. 2004) or (1b) using equations in Richardson et al. (2006), $0.62 + 0.63(NEE)$ for forest sites or $0.38 + 0.30(NEE)$ for the burned site if $NEE \geq 0$ and $1.42 - 0.19(NEE)$ for forest sites or $0.47 - 0.12(NEE)$ for the burned site if $NEE < 0$; (2) measurement and gap-filling error calculated as a function of missing observations (Richardson and Hollinger 2007); (3) long gaps following Richardson and Hollinger (2007). For each site we used the most complete year (2007) and calculated the standard deviation (SD) of all annual NEE estimates that resulted from first introducing randomly artificial short gaps for a total 30% of the data, and second a combination of increasingly longer gaps (1–25 days) starting progressively later in the year. The relationship between the SD and gap length in days was determined for two-month periods, and the corresponding slope applied to each gap longer than one day that occurred in 2006 and 2007 at each site and (4) technique used for gap-filling, as the SD of the annual sums calculated using seven different combinations of gap-filling methods and data rejection criteria (Dore et al. 2008). To calculate total UNC, we used the highest of 1a and 1b.

classes, however, was similar for both sites; the 5–20 cm dbh classes were most abundant (Fig. 1a, b), and the 25 and 35 cm classes contributed the most to tree NPP (excluding fine roots; Fig. 1e, f). The thinning in September 2006 removed the small diameter classes, but did not affect the largest diameter classes (Fig. 1a). Prefire stand characteristics were estimated in an unburned section of forest adjacent to the burned area in 13, 10 m diameter circular plots (Dore et al. 2008). The prefire burned stand had lower tree density but a higher mean tree dbh (Fig. 1b), similar LAI and basal area (Table 1), and higher aboveground and coarse root biomass (Table 3a) than the undisturbed stand.

Soil CO_2 efflux

We determined soil CO_2 efflux (R_S) as the average of annual sums based on three different techniques applied in 2007 at all sites: closed dynamic chambers, static chambers and soil CO_2 profiles. The first technique was a closed, dynamic system (LI-6400-09; LI-COR, Lincoln, Nebraska, USA). The second technique used 15 cm tall, 30 cm diameter, vented, PVC chambers fitted to 30 cm diameter PVC collars. Gas was sampled (160 mL) from the 15.3 L headspace 0, 15, and 30 minutes after placing the chamber cap on the collar. The third technique used buried solid-state IRGA probes (GMM 222; Vaisala Inc., Helsinki, Finland). We calculated the gradient of CO_2 concentration at different soil depths (2, 10, and 20 cm) and estimated soil diffusivity using the Moldrup model (Moldrup et al. 1999), and then used Fick's first law of diffusion to calculate soil CO_2 efflux at 30-minute intervals. Additional details on the R_S measurements and data processing can be found in Sullivan et al. (2008).

We measured R_S using the dynamic and static chambers at three locations within each of the five plots

per site (total 15 per site). The IRGA probes were positioned in three profiles at one of the five plots per site (nine probes per site). We modeled R_S for each of the three techniques as

$$\ln(R_S) = T_{soil} + swc + swc^2 + (T_{soil} \times swc) + (T_{soil} \times swc^2)$$

where T_{soil} is soil temperature (10 cm deep in the mineral soil) and SWC soil water content (average between 2 and 10 cm in the mineral soil). A previous study conducted at the three sites (B. W. Sullivan, S. Dore, T. E. Kolb, S. C. Hart, and M. C. Montes-Helu, *unpublished manuscript*) showed that this model best fit the empirical data. This study also showed that the empirical and modeled R_S for each technique had similar temporal patterns in R_S , but with different absolute values. Here, model parameters were fitted for the forested sites together, and for the burned site separately, for each of three techniques. Daily R_S values were determined by applying the models to daily soil water content and temperature measured at the eddy towers in 2006 and 2007. At each of the sites, annual totals for each of the three techniques were averaged to obtain annual soil CO_2 efflux.

The heterotrophic component of R_S (R_{het}) was determined using the fraction of heterotrophic (f_{het}) to total soil CO_2 efflux (R_S) plus the contribution from decomposition of woody debris (R_{WD}):

$$R_{het} = (f_{het} \times R_S) + R_{WD}.$$

We estimated f_{het} from an experimental root trenching study performed in 2005 at forested and intensely burned sites near our study sites (Grady 2006). The f_{het} varied with soil temperature and soil water content and ranged in the forests from 0.69 during the warm and wet

TABLE 2. Extended.

UNC		
Long gap (3)	Gap-filling technique (4)	Total
4.4	55	57
0.2	76	77
0.7	14	18
0.1	15	19
7.9	29	34
3.6	66	68

season to 0.80 in the dry summer and winter seasons. At the burned site, f_{het} ranged from 0.59 in the warm and wet season to 0.73 in winter. The R_{WD} was calculated using a site-specific empirically determined annual decomposition constant (k) of 0.031 at the burned site, and 0.014 at the forested sites applied to the woody debris pools (>1 cm diameter; Dore et al. 2008).

Eddy covariance and meteorology

We used the eddy covariance technique to measure exchange of CO_2 , water, and energy between the land and atmosphere (Aubinet et al. 2000) continuously in 2006 and 2007. The instrumentation, meteorological measurements, data processing and analysis were identical at the three sites and were described in Dore et al. (2008).

At the undisturbed site, the fetch of unmanaged forest extended for 1 km from the tower in north and south directions, and 0.5 km from the tower in E and W directions. The prevailing wind direction was from the northeast-east (48% of the time) during the night and S-SW (47% of the time) during the day. During daytime, on average, fluxes originated from an area extending 271 ± 4 m (mean \pm SE) from the tower (70% cumulative footprint; Schmid 1997). At the burned site, the fetch was ~ 2 km to the south and north, and 1 km to the east and west. The prevailing wind direction was from the southeast to southwest (60% of the time), and the daily average footprint was $176 (\pm 3)$ m. At the thinned site the fetch before the thinning was 0.6 km to the north and east, 2 km to the south and west. The thinning included an area extending 0.6 km south and west and 0.4 km north from the tower, and increased the fetch to the east to 2 km from the tower. At the thinned site in 2007 winds came from the southeast-west 45% of the time and the average daytime footprint was 245 ± 4 m. Daytime fluxes were always included in the thinned area. Nighttime fluxes were included in the thinned area 87% of the time.

To assess if post-treatment NEE and latent heat (LE) measurements originated in the thinned area, we averaged 30 min NEE and LE for eight 45° sectors each month. We used the difference between the sector-based values and the average values of all eight sectors calculated for the months January to August 2006 to characterize pre-thinning conditions, and January to

August 2007 to characterize post-thinning conditions. The difference in NEE was similar before and after thinning, with a maximum of $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during daytime and $1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ during nighttime. Similarly, the daytime difference in LE was maximum $50 \text{ W}/\text{m}^2$ both before and after thinning (data not shown). Thus, we concluded that thinning did not increase the heterogeneity of the fetch and most of the measured fluxes were coming from the thinned area.

Gap filling

Past investigations at our sites (Dore et al. 2008) and a general consensus (Morgenstern et al. 2004, Humphreys et al. 2006, Baldocchi 2008) have shown that nighttime data filtering, consisting of rejecting nighttime TER when the friction velocity u^* is below a site-specific threshold, has a stronger effect on the yearly NEE budget than the gap-filling method used. The u^* criteria, however, is not recognized as a necessary analysis step in addition to the quality data assessment we used (Aubinet et al. 2000, Ruppert et al. 2006). Furthermore, literature studies comparing gap-filling methods have shown the lack of a perfect method to gap-fill eddy covariance data (Moffat et al. 2007). Thus, to characterize uncertainty in the yearly sum of NEE at the three sites, we applied different combinations of gap-filling methods and night time data filtering as described in Dore et al. (2008). In short, data were gap-filled using look-up tables and non-linear regressions (Moffat et al. 2007) and three data filtering criteria: the replacement of bad-quality data, the replacement of bad-quality data and the application of u^* filtering, and the application of only u^* filtering. When we applied our strictest data rejection criterion, including both the data quality and the u^* threshold, 40–48% of data were gap filled (though 60% in 2006 at the burned site), similar to other studies (Giasson et al. 2006, Moffat et al. 2007). However, even with this strictest data rejection case, in both years 76%, 80%, and 73% of the gaps for the undisturbed, thinned, and burned sites, respectively, were less than 1 hour. In 2006, gaps longer than 10 days occurred at the burned, thinned, and at the undisturbed sites (maximum 38 days in winter); in 2007 gaps longer than 10 days occurred only at the thinned site (maximum 16 days in winter).

Uncertainty and error quantification

To assess data quality at our sites, we first analyzed the energy balance closure (e.g., linear regression between sensible + latent heats and net radiation – soil heat flux; Wilson et al. 2002) at the three sites during 2006 and 2007. The regression slopes ranged between $0.69\text{--}0.84 \text{ (W}/\text{m}^2)/(\text{W}/\text{m}^2)$ for 30-minute values and $0.81\text{--}0.99$ for daily sums (Table 2), and were in the range reported in other studies (Wilson et al. 2002, Baldocchi 2008). For each site and year, the slopes increased (Table 2) when daily sums were used instead of 30 min data, suggesting underestimation of the storage components of the ecosystem energy fluxes. Because the slopes

also increased at the burned site, where the storage has a limited importance because of the low measurement height, the lack of energy balance closure may have resulted from non-eddy covariance components, such as heat storage in biomass and energy fluxes associated with respiration and photosynthesis (Barr et al. 2006). We calculated total uncertainty of the annual NEE as the sum of four sources: measurement error, gap-filling error, long gap error, and gap-filling method applied (details in Table 2). The measurement error (Morgenstern et al. 2004) was $2 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for both forested sites and $1 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ at the burned site. Alternatively our use of the equation in Richardson et al. (2006) for forests and grassland (burned site) increased the error to $6 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the forested sites and $2 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the burned site. The gap-filling error calculated as a function of missing observations (Richardson et al. 2007) was $14 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for forested sites and $11 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for the burned site. The uncertainty due to long gaps varies with absolute flux values, gap length, and season (Richardson et al. 2007). Because we had gaps longer than 10 days during the summer, we calculated the uncertainty due to long gaps following the method in Richardson et al. (2007). The uncertainty due to alternative procedures used to gap-fill data was calculated following Dore et al. (2008). All uncertainties were expressed as standard deviation (Hollinger and Richardson 2005) and summed as root mean square (Richardson et al. 2006). Most errors were constant for 2006 and 2007 (Table 2). Total uncertainty of NEP ranged from 20 to $70 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Table 2), within the range of 30–100 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ reported in Baldocchi (2008), and 30–70 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ reported in Oren et al. (2006). The alternative gap-filling approach component contributed the most to total uncertainty (78–99%). Thus, we used the uncertainty due to the alternative gap-filling procedures to estimate total uncertainty in NEE for periods shorter than one year, and for TER, GPP, and energy fluxes for all time periods.

We are confident in our threshold u^* value of 0.2 m/s because thresholds higher than 0.2 m/s did not have a large effect on annual sums of NEE (3–23 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) or the difference in NEE among sites (4–16 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). However, higher thresholds increased the fraction of gap-filled data adding additional uncertainty (Richardson et al. 2007).

RESULTS

Effect of wildfire

Carbon stocks and exchange measured by biometry and soil CO_2 efflux.—Ten years after the intense fire, the burned site stored ~40% less carbon than the undisturbed site (Table 3a) due to less carbon present in aboveground tree, soil organic matter, and fine root pools. Carbon stocks were lower at the burned site despite the 7- to 10-fold increase in herbaceous vegetation and 5-fold increase in coarse woody debris

compared to the undisturbed site. At the burned site, NPP measured by biometry decreased 40% from 2006 ($296 \pm 46 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ [mean \pm SD]) to 2007 ($178 \pm 36 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) due to both less aboveground (ANPP) and belowground (BNPP) net primary productivity (–32% and –42%, respectively; Table 3b). Net primary production decreased also at the undisturbed site between years (–47%) from $506 \pm 82 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2006 to $268 \pm 15 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2007 because of a reduction in BNPP (–62%), whereas ANPP increased 7%. The NPP at the undisturbed site was greater than NPP at the burned site in both years (70% and 50%, respectively, for 2006 and 2007). At the burned site, the ratio ANPP/BNPP was 0.30 in 2006 and 0.36 in 2007. Biometric-based NEP suggested that the burned site released carbon to the atmosphere both years, with a higher loss in 2007 than in 2006, and that the undisturbed site was a carbon sink in 2006, but a carbon source in 2007 (Table 3b).

Ecosystem carbon fluxes measured by eddy covariance.—The burned site had lower carbon exchange than the undisturbed site as measured by eddy covariance 10 and 11 years after the fire (Fig. 2). The GPP at the burned site was 57% lower than at the undisturbed site in 2006, and 55% lower in 2007. The TER at the burned site was 33% lower than at the undisturbed site in 2006, and 47% lower in 2007 (Table 3b). As a result, the eddy covariance approach estimated a net carbon loss from the burned site in both years: $-109 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2006 and $-45 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2007. The 64 g of additional uptake in 2007 at the burned site was due almost equally to an increase in GPP (+8%) and a decrease in TER (–6%). The eddy covariance approach estimated net carbon uptake at the undisturbed site in both years: $164 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2006 and $58 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 2007 (Table 3b). The difference in annual NEP between sites was higher than the total uncertainty both years (Table 3b, Fig. 3).

The relationship between TER and soil temperature (Fig. 4a) was constant between years and sites; the Q_{10} over the temperature range that occurred at both sites (–0.5° to 20°C) was 1.94 (± 0.08) at the undisturbed site, and 1.84 (± 0.06) at the burned site. At the burned site, however, the basal rate of TER was $2.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, compared to $4.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the undisturbed site.

The absence of evergreen vegetation at the burned site affected the length of the period of net carbon uptake (CUP), defined as the number of days with daily carbon uptake greater than carbon loss (Baldocchi et al. 2001, Churkina et al. 2005). The CUP at the burned site was only 44 days in 2006 and 143 in 2007, and at the undisturbed site the CUP was 216 days in 2006 and 208 days in 2007. The CUP at the burned site started in September in 2006 and in April in 2007 and ended in the middle of October in both years, whereas at the undisturbed site CUP started in March and ended in November.

TABLE 3. (a) Carbon pools and (b) fluxes (mean \pm SD) at the undisturbed, thinned, and burned sites for 2006 and 2007.

Carbon source	Undisturbed		Thinned		Burned	
	2006	2007	2006 Pre-thinning	2007 Post-thinning	2006	2007
a) Carbon pools (g C/m ²)						
Trees aboveground	5533 \pm 1818	5601 \pm 1838	3910 \pm 677	2660 \pm 786	0†	0
Coarse root	827 \pm 276	838 \pm 279	580 \pm 112	418 \pm 138	0	0
Fine root (<2 mm)	153 \pm 56	133 \pm 52	118 \pm 56	76 \pm 37	54 \pm 54	86 \pm 72
Understory	7 \pm 9	7 \pm 9	6 \pm 6	12 \pm 13	69 \pm 34	46 \pm 19
Mineral soil	n.m.	3992 \pm 427	4424 \pm 1819	3326 \pm 798	n.m.	3273 \pm 825
Organic soil	n.m.	1309 \pm 621	873 \pm 401	1116 \pm 652	n.m.	188 \pm 239
Woody debris	498 \pm 268	n.m.	651 \pm 417‡	652 \pm 465	2483 \pm 1549	n.m.
Slash piles				414 \pm 138		
Coarse dead root				162	1105 \pm 312‡	n.m.
Total carbon	12319 \pm 2006	12378 \pm 2024	10562 \pm 2029	8836 \pm 1385	7173 \pm 1799	7182 \pm 1800
b) Carbon fluxes (g C·m ⁻² ·yr ⁻¹)						
Trees aboveground	56 \pm 10	66 \pm 21	64 \pm 6	70 \pm 15	0	0
Litterfall	48 \pm 20	46 \pm 14	32 \pm 3	50 \pm 21	0	0
Coarse root	9 \pm 2	11 \pm 4	11 \pm 1	13 \pm 3	0	0
Fine root	386 \pm 98	138 \pm 26	132 \pm 49	95 \pm 38	227 \pm 59	131 \pm 39
Understory	7 \pm 7	7 \pm 6	6 \pm 3	12 \pm 4	69 \pm 20	47 \pm 12
ANPP	111 \pm 20	119 \pm 23	102 \pm 8	132 \pm 31	69 \pm 20	47 \pm 12
BNPP	395 \pm 118	149 \pm 28	143 \pm 60	108 \pm 49	227 \pm 72	131 \pm 48
NPP	506 \pm 82	268 \pm 15	245 \pm 56	241 \pm 69	296 \pm 46	178 \pm 36
R _S	545 \pm 260	633 \pm 399	477 \pm 176	666 \pm 442	446 \pm 137	470 \pm 114
R _{S,het}	348 \pm 105	430 \pm 230	364 \pm 133	509 \pm 337	299 \pm 94	313 \pm 77
Woody debris§	7	7	6	12	76	76
NEP biometry	145 \pm 139	-169 \pm 244	-140 \pm 140	-327 \pm 543	-90 \pm 110	-209 \pm 83
NEP eddy¶	162 \pm 57	58 \pm 77	118 \pm 53	-51 \pm 68	-109 \pm 20	-45 \pm 19
GPP eddy¶	863 \pm 77	895 \pm 101	909 \pm 103	826 \pm 79	372 \pm 25	401 \pm 6
TER eddy¶	-713 \pm 123	-858 \pm 170	-811 \pm 147	-902 \pm 136	-480 \pm 11	-453 \pm 12

Notes: The pools (and errors) not measured (n.m.) are considered constant between 2006 and 2007. Abbreviations are: R_S, total soil CO₂ efflux; R_{S,het}, the CO₂ emitted to the atmosphere by heterotrophic organisms in soil; ANPP, aboveground net primary productivity (NPP; sum of standing trees, litterfall, and herbaceous production); BNPP, belowground NPP (sum of fine root and coarse root production), and NPP (sum of ANPP and BNPP).

† Before fire: 7793 \pm 1860 g C/m².

‡ Coarse root woody debris does not include decomposition and thus is a high estimate.

§ Sum of fine and coarse woody debris (diameter > 1 cm).

¶ Eddy covariance yearly totals are shown with opposite sign (negative number for carbon losses, positive for carbon uptake) for consistency with the sign for NEP biometry.

Soil CO₂ efflux.—Annual soil CO₂ efflux (R_S) at the burned site was 99 g C·m⁻²·yr⁻¹ lower than at the undisturbed site in 2006, and 163 g C·m⁻²·yr⁻¹ lower in 2007 (Table 3b). The R_S increased from 2006 to 2007 at both sites: 545 \pm 260 to 633 \pm 399 g C·m⁻²·yr⁻¹ at the undisturbed site, and 446 \pm 137 to 470 \pm 114 g C·m⁻²·yr⁻¹ at the burned site. A comparison of modeled daily R_S between sites (Fig. 5a) shows that R_S was correlated between sites in both years ($r = 0.80$ and 0.87 , respectively, 2006 and 2007, $n = 365$ and $P < 0.001$ both years). The R_S was 76% (2006) and 74% (2007) of TER at the undisturbed site, and 92% (2006) and 104% (2007) at the burned site, reflecting the small and temporary contribution of the aboveground vegetation to TER at the burned site.

Evapotranspiration.—Annual evapotranspiration (ET) was lower at the burned site (365 \pm 3 mm in 2006, 441 \pm 15 mm in 2007) than the undisturbed site (481 \pm 3 mm in 2006, 525 \pm 12 mm in 2007) due to lower ET at the burned site in most months (Fig. 6a, b). Temporal variation in ET was similar at the burned and undisturbed sites (Fig. 6a). Ecosystem water use efficien-

cy, expressed as the slope of the relationship between monthly GPP and ET (Baldocchi et al. 2001), was lower at the burned site (1.1 g C·m⁻²·mo⁻¹ per kg H₂O·m⁻²·mo⁻¹) than the undisturbed site (1.65 g C·m⁻²·mo⁻¹ per kg H₂O·m⁻²·mo⁻¹; Fig. 6c).

Effect of thinning

Carbon stocks and exchanges measured by biometry and soil CO₂ efflux.—Thinning decreased total carbon stores by 14%, resulting from a decrease in biomass of aboveground tree (-23%), fine (-20%), and coarse (-20%) roots, combined with an increase in carbon in the soil organic surface horizon (19%), understory biomass (86%), and coarse woody debris (88%; Table 3a).

The BACI comparison of annual NPP suggested that thinning increased NPP by 234 g C·m⁻²·yr⁻¹ (Table 4), despite the reduction of stand density and LAI. However this NPP increase was determined in the BACI mainly by the large decrease in fine root NPP at the undisturbed site, and not by an increase in NPP at the thinned site between pre- and post-treatment periods

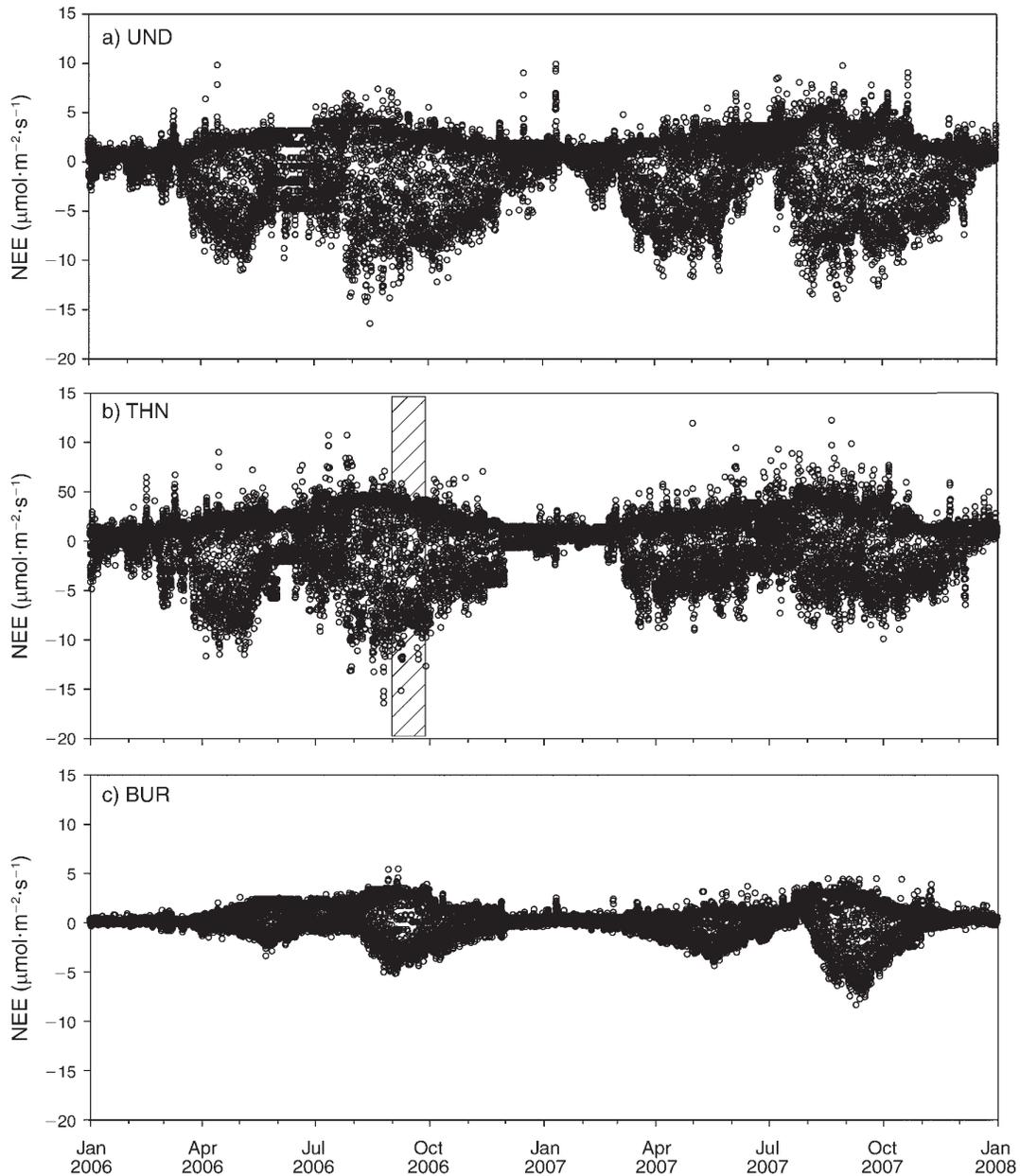


FIG. 2. Thirty-minute net ecosystem carbon exchange (NEE) at the (a) undisturbed (UND), (b) thinned (THN), and (c) burned (BUR) sites in 2006 and 2007. The thinning in September 2006 is shown by the hatched bar.

(Table 3b). The BACI approach suggested that thinning increased ANPP by 19%, due to an increase in litterfall and herbaceous ANPP, and increased BNPP by 36%, due to a 35% increase in fine root NPP (Table 4). Thinning had little effect on tree wood and coarse root NPP (Table 4) because tree removal included mostly small trees and was compensated by an increase in radial growth of trees after thinning (Fig. 1). Fine root NPP at the thinned site was reduced between pre-treatment and

post-treatment periods (Table 3b) and consequently ANPP/BNPP increased from 0.71 to 1.23. The NEP estimated by biometry and soil fluxes suggested that the thinned site was a carbon source in both years, with the magnitude of the source increasing from 2006 to 2007 (Table 3b), and the undisturbed site was a carbon sink in 2006, and a carbon source in 2007 (Table 3b).

Ecosystem carbon fluxes measured by eddy covariance.—Carbon fluxes were similar in the undisturbed

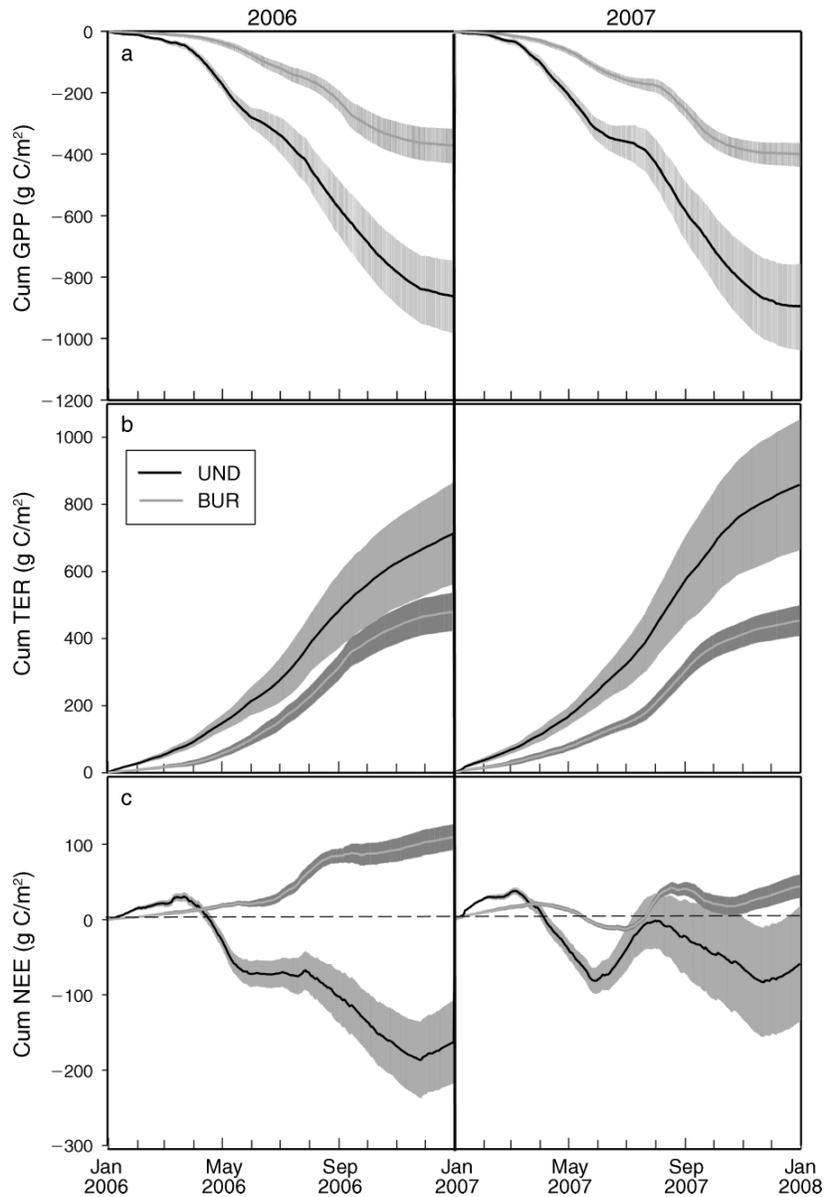


FIG. 3. Comparison of cumulative (Cum) ecosystem carbon fluxes measured by eddy covariance at the undisturbed (UND) and burned (BUR) sites in 2006 and 2007: (a) gross primary production (GPP), (b) total ecosystem respiration (TER), and (c) net ecosystem carbon exchange (NEE). The shaded area represents the SD of five different gap-filling methods, and the solid lines the mean.

and thinned sites in 2006 before thinning (Fig. 2). The comparison of regression slopes of daily simultaneous fluxes between the undisturbed and thinned sites (using the best quality data during the January–August period under similar environmental conditions; Fig. 7) showed that NEE at the thinned site was 91% of NEE at the undisturbed site. The TER and GPP before thinning were even more similar between sites. Thinning had a large effect on carbon fluxes, reducing NEE by 45%,

TER by 26%, and GPP by 29% for the period January–August ($P < 0.001$, $r^2 = 0.83–0.92$; Fig. 7).

The BACI comparison of the impact of thinning on monthly average carbon fluxes for January–August showed that the effect of thinning changed seasonally (Fig. 8a–c). Thinning decreased NEE most months between January and April, because of a decrease in GPP compared to a small effect on TER, which decreased following thinning only in January, May,

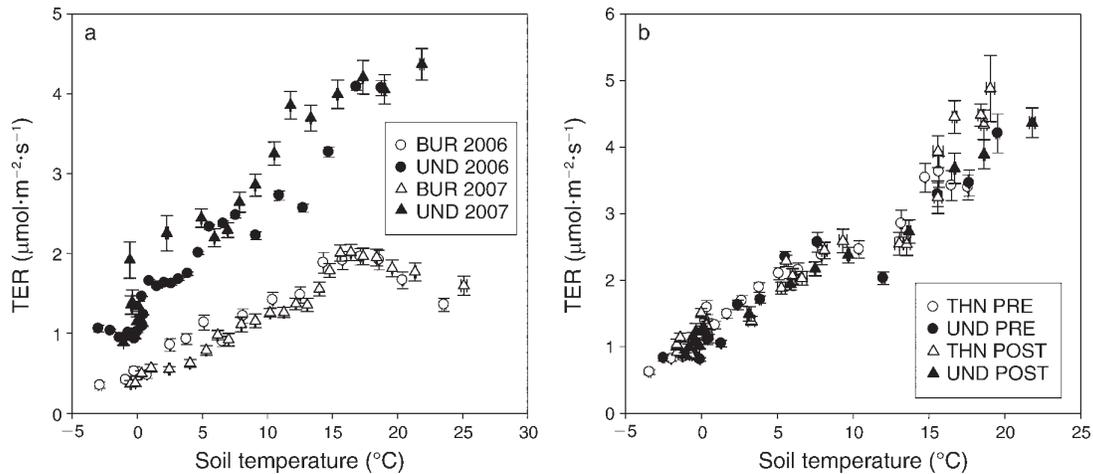


FIG. 4. Relationship between total ecosystem respiration (TER) and soil temperature (2 cm mineral soil depth). Good quality TER data were averaged (\pm SE) in soil temperature classes with $n = 100$ data points per soil temperature class (a) at the burned (BUR) and undisturbed (UND) sites in 2006 and 2007, and (b) before and after thinning (January–August 2006 and 2007) at the undisturbed and thinned (THN) sites. The slopes of the linear regressions are not significantly different at the thinned and undisturbed sites, before and after thinning ($P = 0.95$ on $Y = \log(\text{TER})$).

and August (Fig. 8a–c). In contrast, thinning increased NEE and GPP in June (Fig. 8a, b).

Eddy covariance showed that both the undisturbed and thinned sites were annual carbon sinks in 2006 ($162 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $58 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively). In 2007 after thinning, the undisturbed sites remained a carbon sink ($118 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) whereas the thinned site was a

carbon source ($-51 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, Table 3b). Thinning did not change the relationship between TER and soil temperature, which was the same at the two sites both years, with no evidence of an effect of thinning ($P = 0.95$, Fig. 4b).

Thinning consistently reduced NEE, except for the driest month of June, when NEE at the undisturbed site

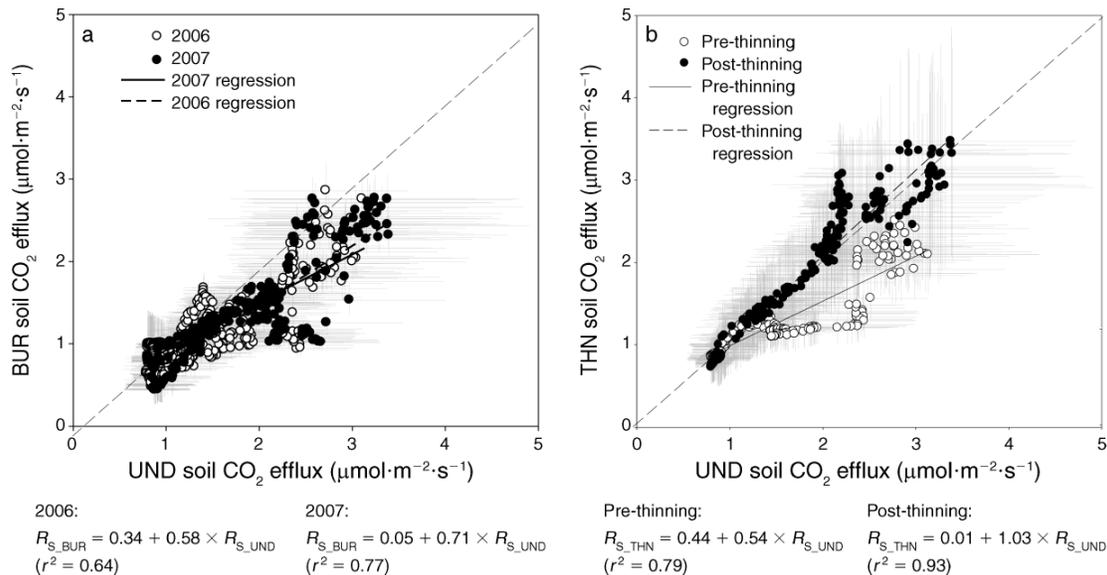


FIG. 5. Comparison between daily modeled values of soil CO_2 efflux (a) at the undisturbed (UND) and burned (BUR) sites, and (b) at the undisturbed and thinned (THN) sites. The linear regression coefficient and r^2 are shown for each year and site ($R_S =$ total soil CO_2 efflux). Gray lines represent \pm SD of each daily flux (symbol), calculated as the average of three different measurement techniques: LiCor 6400, CO_2 concentration profiles, and static chambers. The slopes of the pre- and post-thinned linear regressions at the thinned site in panel (b) are statistically different ($P < 0.001$). The dashed lines show the 1:1 relationships.

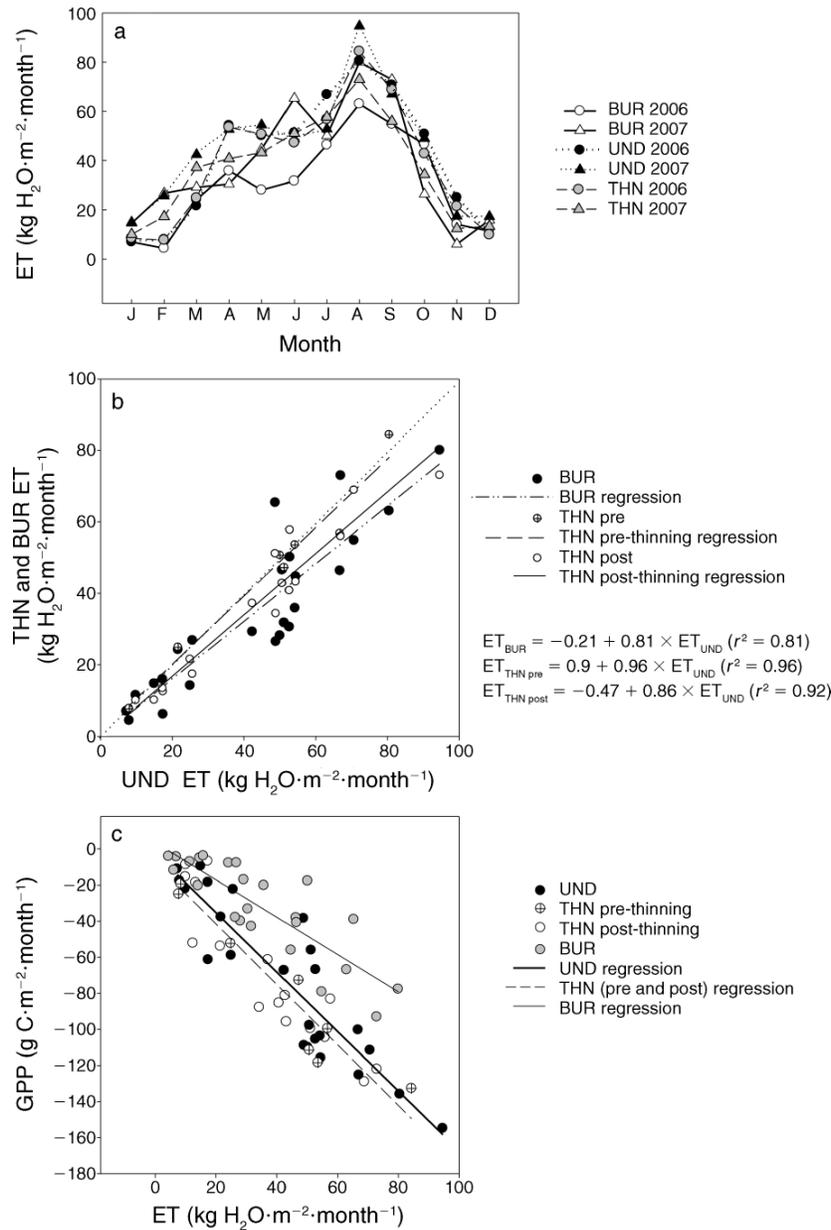


FIG. 6. Water exchanges at the burned (BUR), undisturbed (UND), and thinned (THN) sites in 2006 and 2007. (a) Monthly evapotranspiration (ET) and (b) comparison of monthly ET at the burned and thinned sites compared with ET at the undisturbed site. The thinned site data have been plotted separately for the period before (pre) and after thinning (post). The dotted line represents the 1:1 relationship. (c) Monthly gross primary production (GPP) vs. ET at the three sites, separating pre- and post-thinning months (open and crossed circles, respectively) at the thinned site. Slopes of the linear relationships at the burned and undisturbed sites are different ($P = 0.06$). Slopes at the burned and undisturbed sites and at the thinned site pre and post thinning are not different ($P = 0.97$ and 0.84 , respectively).

was lower than at the thinned site (Fig. 8a). The higher uptake at the thinned site in June was not explained by higher soil water availability at this site, as measured by volumetric water content then transformed to relative water content to better compare the two sites (data not

shown), but by the different limitation of vapor pressure deficit (VPD) on NEE after thinning. Binned light-saturated NEE for VPD classes of 0.07 kPa in the most NEE-limiting VPD range of 1.5–2.7 kPa was calculated for both sites the summer before and after thinning (Fig.

TABLE 4. Mean and standard deviation (SD; $n = 5$ plots) of the effect size of thinning on net primary productivity (NPP) and its components measured by biometry.

Annual flux	Effect		<i>P</i>		
	Mean ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$)	SD	Period	Site	Period \times site
Wood	-27	31.5	0.165	0.154	0.256
Coarse root	-4.2	4.7	0.228	0.080	0.301
Fine root	211.1	66.4	<0.001	<0.001	0.005
Litterfall	20.2	25.3	0.300	0.462	0.185
Herbaceous	9.2	8.8	0.539	0.843	0.145
Aboveground [†]	23.2	31.3	0.068	0.857	0.260
Belowground [‡]	210.9	76.6	<0.001	<0.001	0.005
NPP	234.1	76.6	0.002	<0.001	0.002

Notes: Effect size was calculated as the difference between thinned (THN) and undisturbed (UND) sites after treatment, adjusted for the pre-treatment difference between sites: $(\text{THN}_{\text{post}} - \text{UND}_{\text{post}}) - (\text{THN}_{\text{pre}} - \text{UND}_{\text{pre}})$. Variance for the effect size was estimated as $\sigma_{\text{THNpost}}^2 + \sigma_{\text{THNpre}}^2 - 2\rho\sigma_{\text{THNpost}}\sigma_{\text{THNpre}} + \sigma_{\text{UNDpost}}^2 + \sigma_{\text{UNDpre}}^2 - 2\rho\sigma_{\text{UNDpost}}\sigma_{\text{UNDpre}}$ where σ denotes the standard deviation (and σ^2 the variance) for a given treatment, and ρ indicates the within site correlation between before and after measurements (i.e., accounts for non-independence of time effect within site). The *P* values are from two-way analysis of variance with period (2006 pre-treatment, 2007 post-treatment), site (thinned, undisturbed), and their interaction as factors.

[†] Sum of standing trees, litterfall, and herbaceous production.

[‡] Sum of fine root and coarse root production.

9). Net carbon uptake decreased with VPD at both sites in both years, and the VPD limitation of NEE was similar between sites before thinning (Fig. 9a). After thinning, however, the slope decreased from 4.6 to 2.8 at the thinned site ($P < 0.001$), compared to no significant change in slope at the undisturbed site ($P = 0.68$). This result suggests that thinning reduced the limitation of VPD on NEE during the driest month of June.

Soil CO₂ efflux.—Annual soil CO₂ efflux (R_S) at the thinned site was 12% lower than the undisturbed site the year before thinning (2006), and 5% higher than the undisturbed site the year after thinning (Table 3b). Also the slopes of the relationship of daily R_S between sites, before and after thinning, shows that R_S at the thinned site increased relative to R_S at the undisturbed site after thinning ($P < 0.001$; Fig. 5b). The R_S was almost the same fraction of TER at the undisturbed site in 2006 (76%) and 2007 (74%), whereas it increased at the thinned site from 2006 (59%) to 2007 (74%).

Evapotranspiration.—Annual evapotranspiration (ET) at the thinned site was similar to the undisturbed site before thinning (467 ± 10 mm and 481 ± 3 mm, respectively) and lower than the undisturbed site after thinning (525 ± 12 mm and 443 ± 3 mm, respectively). The seasonal trend in ET was similar at the undisturbed and thinned sites before and after thinning (Fig. 6a), with similar maximum values during the rainy monsoon season in August. Regression of monthly ET between thinned and undisturbed sites confirmed that ET was similar between sites before thinning (4% difference), and was 10% lower after thinning (Fig. 6b). The BACI comparison using monthly means of ET for January to August showed that thinning reduced ET in all months except July, when thinning increased ET (Fig. 8d). Ecosystem water use efficiency was not different ($P =$

0.97) between the undisturbed (1.68 ± 0.14 g C·m⁻²·mo⁻¹ per kg H₂O·m⁻²·mo⁻¹) and thinned sites (1.65 ± 0.17 g C·m⁻²·mo⁻¹ per kg H₂O·m⁻²·mo⁻¹), and was not affected by thinning ($P = 0.84$; Fig. 6c).

DISCUSSION

We assessed how two different disturbances to ponderosa pine stands in northern Arizona affected stocks and exchanges of carbon and water between biosphere and atmosphere. We included the severe disturbance of an intense wildfire and a partial disturbance of thinning done to reduce fuels and prevent high-intensity fire.

Intense fire was more detrimental to total ecosystem carbon stock and NEP components than thinning. Carbon stocks at the burned site were about 40% of stocks at the undisturbed site 10 years after the fire. All biomass components were much lower at the burned site than the undisturbed site except for woody debris and herbaceous vegetation, a minor component of the total stock. In contrast, thinning reduced total carbon stock by 14% due to reductions of all biomass components, except woody debris, surface organic horizon, and herbaceous vegetation, which all increased after thinning. Thinning had little effect on aboveground woody debris because about 40% of this component was in slash piles that were prescribed burned in 2007. In contrast, 10 years after the fire, the surface organic horizon was absent at the burned site because of combustion during the fire and decomposition and surface erosion the following years.

Thinning increased the growth rate of individual ponderosa pine trees in our study (Fig. 1c) consistent with previous studies in the southwestern United States (Kaye et al. 2005, McDowell et al. 2006). Increased tree growth over several years after thinning, based on

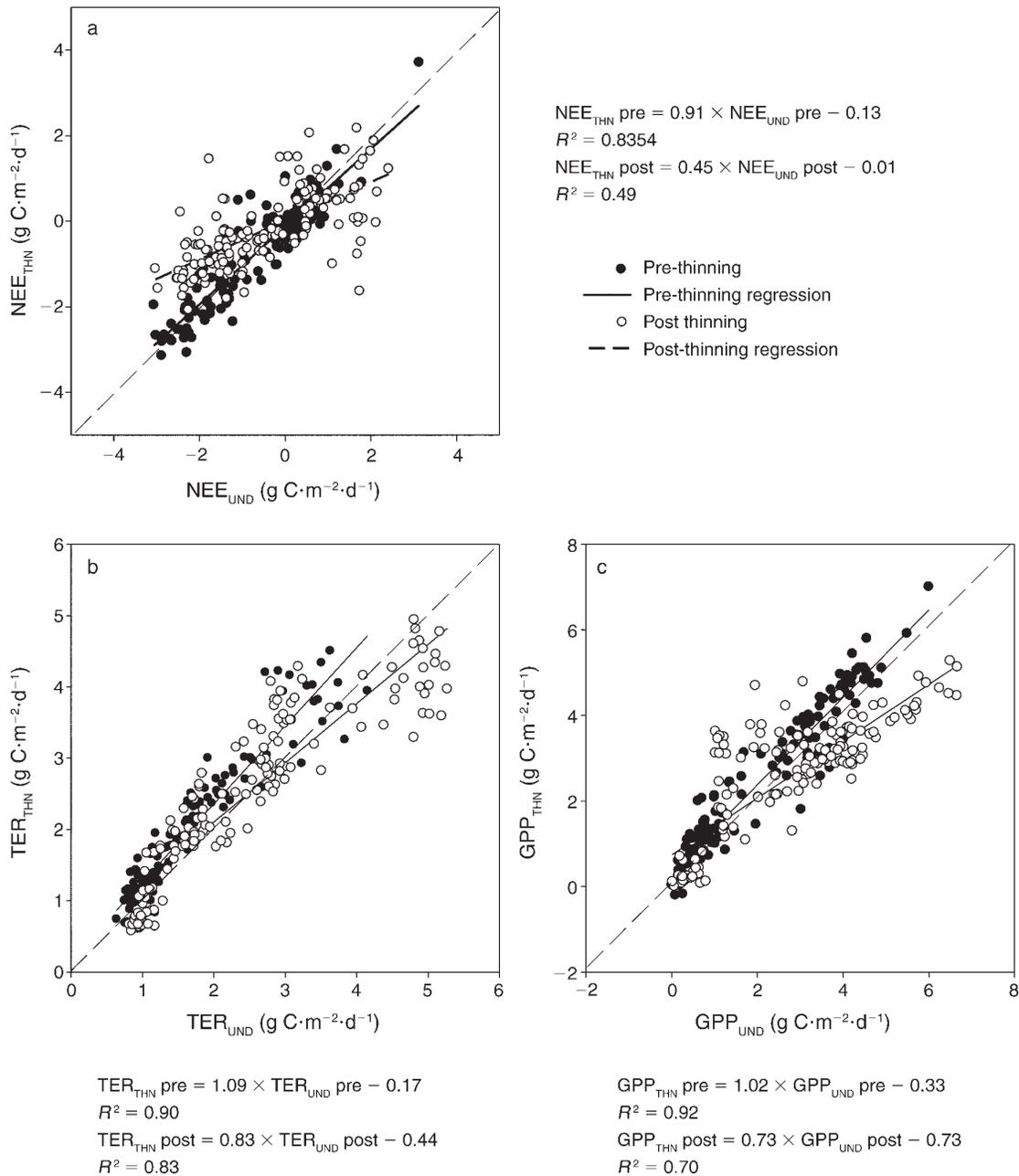


FIG. 7. Comparison of (a) daily net ecosystem exchange (NEE), (b) total ecosystem respiration (TER), and (c) gross primary productivity (GPP) between the undisturbed (UND) and thinned (THN) sites for the pre-thinning period (January–August 2006) and post-thinning period (January–August 2007). We selected only days when the number of gap-filled 30-minute data was <20 and weather was not different (daily difference between the sites for VPD < 0.2 kPa; air temperature < 1.75°C; global radiation sum < 2000 W/m²; and diffuse PAR fraction < 0.075). The dashed line denotes the 1:1 relationship in each panel. Slopes of linear regressions of NEE, TER, and GPP before and after thinning are significantly different ($P < 0.001$).

previously reported growth responses to a single thinning in the region of our study sites (Zausen et al. 2005, Kolb et al. 2007), will promote recovery of carbon stocks initially removed by harvesting. Quantification of

the magnitude and rate of this recovery will require future measurements.

The NEP measured by eddy covariance was not consistent with NEP measured by biometry and soil CO₂

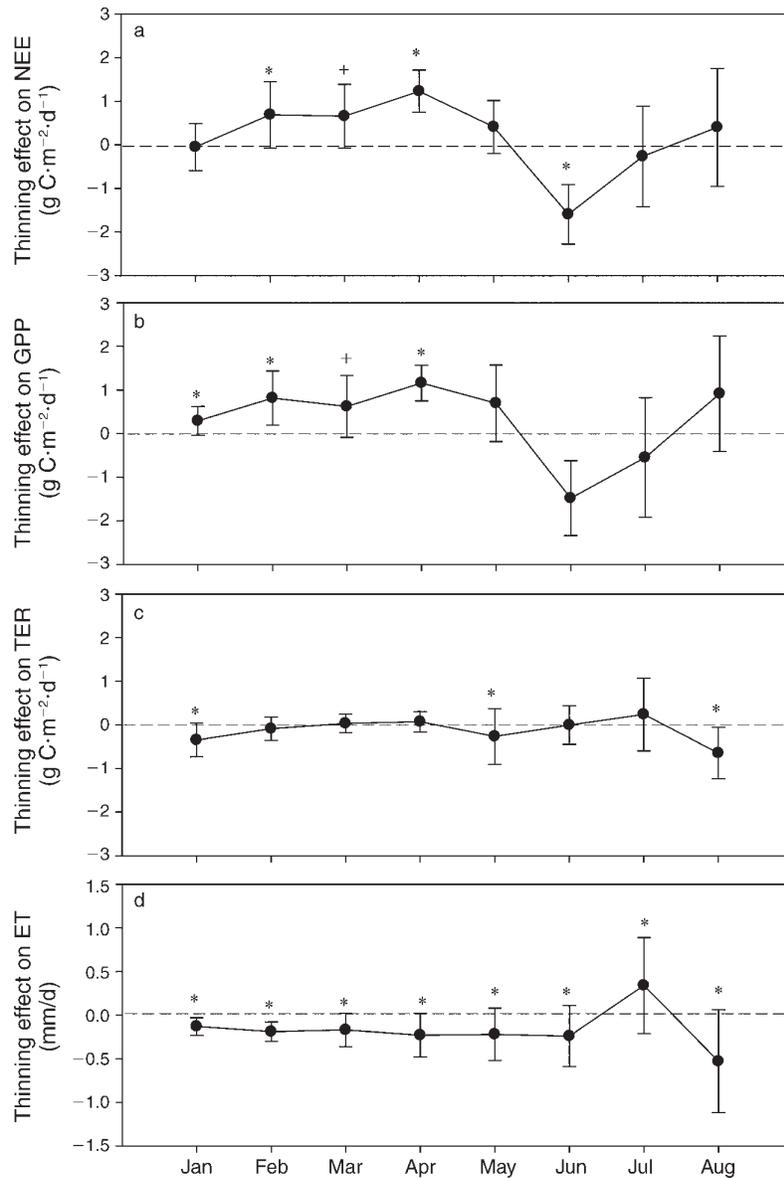


FIG. 8. Effect of the thinning (\pm SD) over time on daily (a) net ecosystem carbon exchange (NEE), (b) gross primary productivity (GPP), (c) total ecosystem respiration (TER), and (d) evapotranspiration (ET) averaged over each month from January to August 2007. Asterisks (*) indicate significant effects of thinning ($P < 0.05$) on effect size for monthly data sets; plus signs (+) indicate marginally significant effects ($P < 0.10$). Effect size was calculated as the difference between thinned (THN) and undisturbed (UND) sites after treatment, adjusted for the pre-treatment difference: $(\text{THN}_{\text{post}} - \text{UND}_{\text{post}}) - (\text{THN}_{\text{pre}} - \text{UND}_{\text{pre}})$. By the sign convention we used, positive effects denote a decrease in carbon flux following thinning for GPP and NEE; positive effects indicate an increase in flux for TER and ET.

efflux. The NEP estimates from eddy covariance showed that the undisturbed site was a small annual carbon sink, which was shifted to a source by high-intensity fire and by thinning in the first year after treatment. The NEP estimates from biometry and soil CO₂ efflux suggested that all stands were a carbon source except for the undisturbed site in 2007. The highest uncertainties were

in our biometry-based NEP estimates and particularly in fine root NPP, soil CO₂ efflux, and its heterotrophic component (f_{het}). Because the f_{het} we used was higher than reported by other studies (Hanson et al. 2000, Curtis et al. 2002, Howard et al. 2004), including other studies of ponderosa pine forests (Irvine et al. 2007, Campbell et al. 2009), we calculated NEP also using a

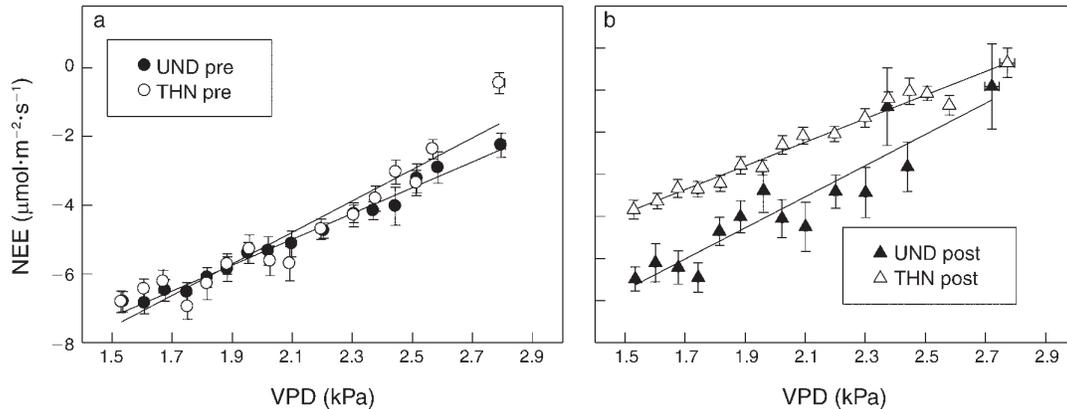


FIG. 9. Relationship between vapor pressure deficit (VPD) and light-saturated net ecosystem exchange (NEE) at the undisturbed (UND) and thinned (THN) sites before (pre, April–August 2006) and after (post, April–August 2007) thinning. Light-saturated NEE (photosynthetic photon flux density [PPFD] > 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was averaged in 0.07 kPa VPD classes over the range 1.5–2.7 kPa (only VPD classes with ≥ 10 light-saturated NEE were considered). The slope of the linear regressions for UND and THN sites was changed by thinning (3.7 and 4.6 before thinning, 3.7 and 2.8 after thinning, respectively; $P < 0.001$).

f_{het} of 0.50 estimated from a literature review of forests (Hanson et al. 2000). The different f_{het} added 73–255 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ of additional carbon uptake and resulted in NEP estimates closer to the eddy covariance estimates, with a maximum difference of 125 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ compared with 280 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ if the local estimate of f_{het} was used. The recalculated NEP, however, did not switch any site or year from being a source to a sink of carbon, or vice versa.

The comparison between NEP based on eddy covariance and on biometry was closer when BNPP was excluded. For example, the ratio ANPP (biometry) and GPP (eddy) was similar between years for each forest site: 0.13 (both years) at the undisturbed site, 0.11 (2006) and 0.16 (2007) at the thinned site. Furthermore, uncertainty in annual NEP obtained using the biometric approach was higher (maximum uncertainty of 543 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ compared to 77 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for eddy covariance; Table 3b). The high temporal resolution of measured fluxes using eddy covariance allowed BACI comparisons and regression of simultaneously measured fluxes that were not possible with the yearly biometric-based NEP estimates. Regardless of uncertainty in annual ecosystem carbon and water estimates, effects of disturbances on ecosystem fluxes were even more pronounced on shorter time scales (Figs. 6–9) and when relationships between carbon fluxes and driving variables were analyzed (Figs. 4 and 9).

Our finding that annual NEP estimates based on the eddy covariance did not match well with NEP based on biometry and soil efflux measurements is consistent with previous studies in other vegetation types. For example, Ehman et al. (2002) measured higher annual NEP with biometry than with eddy covariance. Kominami et al. (2008) and Curtis et al. (2002) reported contradictory results between eddy- and biometry-based NEP. Gough et al. (2008) reported greater uncertainty for annual

NEP estimated with biometry compared with eddy covariance, and a good agreement only when the comparison was made over five years. For ponderosa pine forests in Oregon, Campbell et al. (2009) reported that the same sites varied between annual carbon sources and sinks, depending on the assumptions used in the biometric approach. All such studies describe belowground carbon dynamics as the major source of uncertainty in biometric-based estimates of NEP, as we do in the present study.

Although estimates of BNPP and heterotrophic respiration can be highly uncertain, biometry is still useful to quantify and understand individual components and processes of net ecosystem carbon fluxes. For example, biometry is invaluable for quantifying contributions of different species or vegetation components, or to separate R_S and TER. It is often the only method available because of financial or logistical constraints, or conditions that violate assumptions necessary to apply the eddy covariance technique, and to assess inter site variability.

Disturbance by both intense fire and thinning had a larger impact on GPP than TER. The ratio TER/GPP was 0.83–0.89 at the undisturbed site, 0.89 at the thinned site before thinning and 1.09 after thinning, and 1.13–1.29 at the burned site; these ratios for the forested sites are consistent with 0.87 reported for temperate semiarid evergreen forests (Luyssaert et al. 2007), and 0.85 reported for coniferous forests (Law et al. 2002). Lower GPP following fire or thinning in our study is explained by reduced LAI consistent with previous reports (Kowalski et al. 2004, Giasson et al. 2006), and for the burned site, a shorter annual duration of net carbon uptake (CUP was 172 to 65 days shorter at the burned site than the undisturbed site) because of the absence of evergreen species. The larger negative effect

of both disturbances on GPP than TER caused both disturbed sites to be carbon sources to the atmosphere.

Reduced TER by forest disturbance in our study is consistent with some other studies on pine forests (Kowalski et al. 2004), but is in contrast to other studies where disturbances have increased or had no effect on TER (Misson et al. 2005, Giasson et al. 2006, Campbell et al. 2009). These contrasting results highlight that impacts of forest disturbance on TER vary among climates, vegetations, and disturbance intensities and types.

Thinning ameliorated constraints on NEE by high VPD. The NEE was lower at the thinned site after thinning compared to the undisturbed site (Figs. 2 and 8). The opposite pattern occurred in the driest summer month, June, when NEE was higher at the thinned site than the undisturbed site. Relationships between NEE and VPD (Fig. 9) showed that NEE at the thinned site became less responsive to VPD after thinning relative to the undisturbed site. Thus, we conclude that improved tree water status after thinning (e.g., Feeney et al. 1998, Kolb et al. 1998, Simonin et al. 2006) reduced stomatal sensitivity to high VPD.

Disturbances increased the importance of soil CO_2 efflux to TER. The ratio R_S/TER at both the undisturbed site (0.74–0.76) and thinned site (0.59 before thinning and 0.74 after thinning) is similar to the value of 0.77 reported by Law et al. (2001) for ponderosa pine forests in Oregon, and consistent with a compilation of values for different forests (0.76–0.88; Pallardy 2008). The R_S/TER ratio at the burned site was higher than the undisturbed and thinned sites, and close to one (0.93–1.04, depending on year). The R_S/TER ratio near one at the burned site shows that little TER was from plant respiration. This result is consistent with the low LAI and short growing season by the herbaceous plants that dominated the burned site a decade after the burning killed the trees. Comparisons of annual R_S , as well as changes in the slope of the relationship between R_S of the thinned site and undisturbed site before and after thinning, show that thinning increased R_S and thus R_S/TER . An earlier chamber-based study conducted during the summer at the thinned site concluded that thinning decreased R_S in July, but had little effect in June and August (Sullivan et al. 2008), and this decrease was associated with a reduction in live fine roots. In the present study we improved our understanding of the impacts of thinning by predicting annual R_S from a model based on soil water content and temperature, parameterized with independent data from three measurement techniques (dynamic chamber, static chamber, CO_2 profile; B. W. Sullivan, S. Dore, T. E. Kolb, S. C. Hart, and M. C. Montes-Helu, *unpublished manuscript*).

Disturbances did not alter the relationship between TER and soil temperature, whereas after the intense fire basal respiration decreased. The TER was strongly and positively related to soil temperature (Tsoil) at all sites

and years, consistent with previous reports (Lloyd and Taylor 1994). Both disturbances did not affect the relationship between Tsoil and TER. However, TER of the burned site was lower at a given Tsoil than TER of the undisturbed site. Lower TER at a given Tsoil at the burned than the undisturbed site can be explained by lower GPP (Litton et al. 2007), lower fine root biomass and BNPP, less organic matter for decomposition, and drier surface soil at the burned than at the undisturbed site.

Annual ET of the burned site was about 19% lower than ET of the undisturbed site in the decade after burning, whereas annual ET of the thinned site was about 13% lower in the first year after thinning. The fire-induced vegetation change from forest to grassland showed reduced ET because less leaf area led to a higher albedo and lower net radiation, and thus less energy was available to evaporate water (Montes-Helu et al. 2009). The reduction in ET in the first year after thinning can be attributed to lower LAI, but not changes in albedo and net radiation (data not shown). The 13% reduction in ET by thinning was not monotonic with the 40% reduction in LAI likely because of increased stomatal conductance and transpiration of residual trees (Skov et al. 2004, Simonin et al. 2006).

Ecosystem water use efficiency was lower at the burned site than the undisturbed site, whereas thinning had no effect (Fig. 6c). No effect of thinning on water use efficiency was also reported for a young ponderosa pine plantation in California (Misson et al. 2005). Lower water use efficiency at burned sites compared to forests has been previously reported (Webb et al. 1978, Ponton et al. 2006), and can be explained by the need to maximize photosynthesis in vegetation with short seasonal activity (Baldocchi et al. 2001, Ponton et al. 2006), and by the low productivity (Webb et al. 1978) and LAI (Hu et al. 2008) of sparse herbaceous vegetation, and the consequent small role of plants in controlling water losses by the ecosystem.

In conclusion, our results suggest that high-intensity fire in southwestern ponderosa pine forests has stronger impacts on carbon balance than thinning. Whereas thinning reduces risk of high-intensity fires (Finkral and Evans 2008, Hurteau et al. 2008) and the large decrease in carbon stock (~40%) and sink strength associated with the fire-induced conversion from forest to grass vegetation, it also causes moderate reductions in carbon stock (~14%) and reduces carbon sink strength because GPP is reduced more than TER. Other impacts of thinning on carbon balance depend on the fate of wood products. In our study, thinning and wood utilization released an additional $311 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ to the atmosphere if the wood was used only as fuel, but sequestered $335 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ if the wood was used for a mixture of pallets and construction products (Finkral and Evans 2008). Our finding that the effect of thinning on carbon sink strength was negative in wet months, but positive in the driest summer month suggests an increase in carbon

sequestration capacity of thinned forests relative to unthinned dense forests with the expansion of drought during future climate warming. In contrast to carbon fluxes, the disturbances of fire and thinning caused small changes in ET (reductions of 10–19%) limiting opportunities to increase aquifer recharge and stream flows by vegetation management in southwestern ponderosa pine forests. Efforts to accurately estimate regional carbon budgets should consider impacts on carbon stocks and fluxes of both large disturbances such as high-intensity fire, and the partial disturbance of thinning. Furthermore, our results show that thinned stands are a desirable alternative to intensively burned stands in the effort to maintain carbon stores in ponderosa pine forests of the southwestern United States.

ACKNOWLEDGMENTS

This research was supported by grants from the North American Carbon Program/USDA CREES NRI (2004-35111-15057), the U.S. National Science Foundation MRI Program, Science Foundation Arizona (CAA 0-203-08), the Arizona Water Institute, and the Mission Research Program, School of Forestry, Northern Arizona University (McIntire-Stennis/Arizona Bureau of Forestry). We thank G. Manca (JRC, Italy) for help with the eddy covariance software, and the Northern Arizona University Centennial Forest and the Coconino National Forest for allowing our research on their lands.

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