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Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire

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Abstract

Carbon uptake by forests is a major sink in the global carbon cycle, helping buffer the rising concentration of CO_2 in the atmosphere, yet the potential for future carbon uptake by forests is uncertain. Climate warming and drought can reduce forest carbon uptake by reducing photosynthesis, increasing respiration, and by increasing the frequency and intensity of wildfires, leading to large releases of stored carbon. Five years of eddy covariance measurements in a ponderosa pine (*Pinus ponderosa*)-dominated ecosystem in northern Arizona showed that an intense wildfire that converted forest into sparse grassland shifted site carbon balance from sink to source for at least 15 years after burning. In contrast, recovery of carbon sink strength after thinning, a management practice used to reduce the likelihood of intense wildfires, was rapid. Comparisons between an undisturbed-control site and an experimentally thinned site showed that thinning reduced carbon sink strength only for the first two posttreatment years. In the third and fourth posttreatment years, annual carbon sink strength of the thinned site was higher than the undisturbed site because thinning reduced aridity and drought limitation to carbon uptake. As a result, annual maximum gross primary production occurred when temperature was 3 °C higher at the thinned site compared with the undisturbed site. The severe fire consistently reduced annual evapotranspiration (range of 12–30%), whereas effects of thinning were smaller and transient, and could not be detected in the fourth year after thinning. Our results show large and persistent effects of intense fire and minor and short-lived effects of thinning on southwestern ponderosa pine ecosystem carbon and water exchanges.

Keywords: carbon, disturbance, eddy covariance, fire, NEE, *Pinus ponderosa*, thinning

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Introduction

Climate warming is strongly predicted to increase drought over large regions of the Earth (Seager *et al.*, 2007; IPCC Synthesis Report, 2007; Overpeck & Udall, 2010). Sequestration of carbon in vegetation, which slows the atmospheric buildup of the greenhouse gas carbon dioxide (CO_2; Pacala & Socolow, 2004; Canadell & Raupach, 2008), is influenced by drought via regulation of the balance between photosynthesis and respiration (Law *et al.*, 2002; Reichstein *et al.*, 2005), particularly in arid regions and mid-latitudes where drought often reduces sequestration (Yi *et al.*, 2010). Climate warming also promotes widespread and intense fires (Westerling *et al.*, 2006; Li *et al.*, 2009), which often endanger human society (Pyne, 2007) and accelerate buildup of CO_2 in the atmosphere directly via combustion (Wiedinmyer & Neff, 2007) and indirectly via deforestation when trees do not regenerate rapidly (Savage & Mast, 2005; Dore *et al.*, 2008; Ryan *et al.*, 2010). Intense fire also affects ecosystem productivity (Bond-Lamberty *et al.*, 2004; Irvine *et al.*, 2007; Amiro *et al.*, 2010; Goulden *et al.*, 2011), water and energy balances (Amiro *et al.*, 2006; Montes-Helu *et al.*, 2009) and shifts ecosystems from a sink to a source of carbon to the atmosphere (Goulden *et al.*, 2011). The time for burned forests to shift back from source to sink of CO_2 can range from a few years to decades depending on climate and vegetation responses (Thornton *et al.*, 2002; Dore *et al.*, 2008; Amiro *et al.*, 2010).

Thinning is a silvicultural practice used to increase tree growth, control composition and structure of forests, and improve forest "health" and economic value. In the southwestern United States, thinning is used frequently to restore dense semi-arid forests to more open conditions similar to presettlement forests (Arno *et al.*,

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1995; Covington *et al.*, 1997; Skov *et al.*, 2004; Boerner *et al.*, 2008) and to lessen wildfire severity through fuels reduction (Agee & Skinner, 2005; Finney, 2005; Hurteau & North, 2009).The current understanding of the impacts of thinning on forest carbon balance is poor, likely system-dependent (Misson *et al.*, 2005; Campbell *et al.*, 2009; Ryan *et al.*, 2010; Hurteau & Brooks, 2011; Hudiburg *et al.*, 2011; Campbell *et al.*, 2012), and is based largely on empirical measurements or model projections of vegetation carbon stocks (e.g., Hurteau & North, 2009; Stephens *et al.*, 2009; Hurteau *et al.*, 2011; Sorensen *et al.*, 2011), rather than on direct measurements of whole-ecosystem carbon exchange.

Here, we report results from a study of the effects of forest thinning and stand-replacing fire on whole-ecosystem carbon exchange using a novel manipulative experiment combined with eddy covariance. Eddy covariance, which measures CO_2 exchange between atmosphere and biosphere over several to a few hundred ha (Baldocchi, 2008), is only beginning to be used to directly measure impacts of disturbance on forest carbon balance largely via comparisons before and after disturbance that often confounds disturbance effects with interannual environmental variation (Misson *et al.*, 2005; Amiro *et al.*, 2010). To separate effects of disturbance from interannual variation, we assessed impacts of forest thinning on ecosystem carbon balance of a semi-arid ponderosa pine (*Pinus ponderosa*) forest with a before-after-control-impact analysis (Stewart-Oaten & Bence, 2001) based on continuous and simultaneous measurements of a treated stand and a control stand for 1 year before and 4 years after thinning. In addition, we assessed the effects of severe fire with a third stand, measured 10–15 years after burning. This report builds on our earlier results for years 2006 and 2007 (Dore *et al.*, 2008; Montes-Helu *et al.*, 2009; Dore *et al.*, 2010) by including measurements made until 2010.

Material and methods

We present 5 years of data collected from 2006 to 2010 using eddy covariance measurements (Aubinet *et al.*, 2000) made simultaneously in three sites (undisturbed, burned, thinned) located less than 35 km apart near Flagstaff, Arizona, USA.

The undisturbed site (UND) was a ponderosa pine stand located in the Northern Arizona University Centennial Forest (35° 5′ 20.5″ N, 111° 45′ 43.33″ W, elevation 2180 m a.s.l.) excluded from silvicultural treatments or fire over the last century. At the beginning of the measurement period in 2006, leaf area index (LAI; projected area) was 2.3 $m^2\ m^{-2}$, basal area was 30 $m^2\ ha^{-1}$, and tree density was 853 trees ha^{-1} (Dore *et al.*, 2010).

The burned site (BUR) was part of a 10 500 ha area in the Coconino National Forest (35° 26′ 43.43″ N, 111° 46′ 18.64″ W, elevation 2270 m a.s.l.) burned by an intense fire in 1996. The fire killed all trees in the stand, which, prior to the fire, had similar tree density and basal area as the UND stand (Dore *et al.*, 2010). More than a decade after the fire, the vegetation of the BUR site consisted of grasses, forbs, and few shrubs, with average ground cover of 40% vegetation, 50% bare soil, and 10% snags and logs (Montes-Helu *et al.*, 2009).

The thinned site (THN) was a ponderosa pine stand also located in the Centennial Forest (35° 8′ 33.48″ N, 111° 43′ 38.37′ ′ W, 2155 m a.s.l.), about 6 km from the UND site. Timber harvests and pulpwood sales during the last century (Finkral & Evans, 2008) resulted in lower LAI (1.5 $m^2\ m^{-2}$), basal area (20 $m^2\ ha^{-1}$), and tree density (472 trees ha^{-1}) than at the UND site before thinning. To reduce tree density and fire risk, and to restore presettlement forest structure, approximately 90 ha of the THN site was thinned in September 2006. The treatment focused on removal of small-diameter trees and reduced tree density 70%, basal area 35%, tree LAI 40%, and stand LAI, including understory, 30%(Finkral & Evans, 2008; Dore *et al.*, 2010).

Climatic and edaphic conditions at the three sites were similar due to their close proximity (Table 1). Winter was cold, spring was dry, and precipitation was concentrated as snow in winter and rain in late summer (Sheppard *et al.*, 2002). Stand characteristics of the sites are summarized in Table 1 and additional information can be found in Dore *et al.* (2008, 2010).

Simultaneous eddy covariance technique measurements were made at the three sites using identical systems, data acquisition, processing, analysis, and quality assessment as described by Dore *et al.* (2008, 2010). Measurements used a 3D sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA) and a closed path CO_2 and water analyzer (Li-7000, Li-Cor, Lincoln, NE, USA), with additional standard air and soil meteorological measurements also recorded at 30 min intervals (Dore *et al.*, 2008). Temperature, water, and CO_2 profile systems (LI-840) were installed at the UND and THN sites.

We applied different combinations of gap-filling and data filtering as described in Dore *et al.* (2008). Quality-filtered, quality- and u*- filtered, and only u*-filtered data were gap-filled using look-up tables and non-linear regressions (Moffat *et al.*, 2007). In our study, the alternative gap-filling approach component contributed the most to total uncertainty (78%–99%) compared with measurement error, gap-filling error, and long gap error (Dore *et al.*, 2010); hence, we used the uncertainty due to the alternative gap-filling procedures to estimate total uncertainty in annual ecosystem fluxes.

We used a negative sign to indicate carbon uptake by the ecosystem, and the term net ecosystem production (NEP) to indicate the annual sum of instantaneous net ecosystem exchange (NEE; Chapin *et al.*, 2006). To partition NEE, gross primary production (GPP) was calculated as daytime NEE +TER (total ecosystem respiration), and TER was measured during the night, and calculated during the day from the night-time relationship of good quality data with soil temperature, and using look-up tables (Falge *et al.*, 2001).We use the term cumulative flux (NEE, GPP, TER) to indicate the sum of the fluxes starting the 1st of January of the same year.

To quantify the effects of intense fire on ecosystem carbon dynamics from 10 to 15 years after the fire, we used a control-

Table 1 Site characteristics (and standard deviation; n = 5 for stand characteristics, and n = 1 for climatic characteristics) of the undisturbed (UND), thinned (THN), and burned (BUR) sites in years 2006 through 2010. The water status is expressed by the ratio of annual latent heat (λe) over equilibrium, non-water-limited latent heat (λe_{eq})

Site Characteristics	Unit	SITE	2006	2007	2008	2009	2010
Soil bulk density	(0–15 cm) Mg m^{-3}	UND	0.78 (0.07)				
		THN	0.98 (0.14)				
		BUR	0.80 (0.15)				
Soil texture	(A horizon)	UND	Clay loam				
		THN	Silty clay loam				
		BUR	Silty clay loam				
Canopy height	m	UND	18 m				
		THN	18 m				
		BUR	< 0.5 m				
LAI trees	m^2 m^{-2}	UND	2.2 (0.3)	2.2 (0.3)	2.1 (0.4)	n. a.	2.3 (0.3)
		THN	1.5 (0.1)	0.9 (0.1)	0.9 (0.1)	n. a.	1 (0.1)
		BUR	Before fire 2.4 (1.6);	After fire: 0			
LAI understory	m^2 m^{-2}	UND	0.06 (0.02)	0.10 (0.04)	0.24 (0.06)	0.06 (0.02)	0.13 (0.05)
		THN	0.07 (0.04)	0.18 (0.09)	0.27 (0.15)	0.09 (0.04)	0.55 (0.43)
		BUR	0.63 (0.15)	0.55 (0.13)	0.93 (0.27)	0.64 (0.28)	1.08 (0.51)
Tree density	N ha^{-1}	UND	853 (424)	143 (7)			
		THN	472 (110)				
		BUR	Before fire: 343 (175); After fire: 0				
Basal area	m^2 ha^{-1}	UND	30 (5)	30 (5)	29 (6)	n. a.	32 (5)
		THN	20 (1)	13 (1)	13 (1)	n. a.	14 (1)
		BUR	Before fire: 31 (21); After fire: 0				
Air temperature	(mean) °C	UND	8.8	9.1	8.6	8.7	8.2
		THN	9.4	10.0	9.4	9.5	9.1
		BUR	8.6	8.8	8.2	8.3	7.9
Precipitation	(sum) mm yr^{-1}	UND	686	653	595	296	581
		THN	605	625	564	366	569
		BUR	517	680	574	408	608
Global radiation	(sum) MJ m^{-2} yr^{-1}	UND	7047	7140	7493	7338	7361
		THN	7015	7036	7463	7204	7253
		BUR	7004	7134	7317	7098	7225
Water status ($\lambda e/\lambda e_{eq}$)	(sum)	UND	156	140	136	107	127
		THN	161	133	143	120	158
		BUR	165	183	148	156	180

impact analysis, using the UND site as the control. To quantify the effects of thinning, we used a before-after-control-impact analysis (BACI; Stewart-Oaten & Bence, 2001), where the after treatment (post) difference between THN and UND sites was adjusted for pretreatment (pre) difference between sites. [i.e. effect = $(THN_{post}-UND_{post})-(THN_{pre}-UND_{pre})$]. The BACI approach was applied also by comparing the slope of the linear regression fitted through simultaneous measurements at the THN and UND sites for prethinning year 2006 to the slopes of the postthinning years 2007–2010.

We used annual cumulative values for the UND and THN sites to assess the effect of thinning and fire on GPP, NEP, TER, and evapotranspiration (ET). In addition, effects of thinning were quantified by comparing daily data obtained simultaneously at the UND and THN sites when environmental conditions (wind, light, air temperature, and ecosystem water availability) were similar. Furthermore, relationships built on only good quality data were used to assess how disturbances affected the control of environmental drivers on ecosystem fluxes.

Soil water content (SWC) data were used to quantify temporal changes in site water availability during the study. For intersite comparisons, because of the difference in the spatial scale between eddy covariance and SWC measurements, we calculated the index $\alpha = \lambda E/\lambda E_{eq}$. This index expresses water availability at the ecosystem scale as the ratio of measured latent heat (λE) to a theoretical, equilibrium, non-water-limited latent heat (λE_{eq}) estimated using the Priestly-Taylor Model (Baldocchi & Xu, 2007). The index α was calculated on a daily basis as $\alpha = (S + \gamma)/S{\cdot}(1 + \beta)$, where S was the slope of the saturation vapor pressure vs. temperature; γ the psychometric constant, and β the daily Bowen ratio. The index α was based on β instead of the net radiation to avoid the inclusion of any energy closure imbalance into the calculation (Krishnan *et al.*, 2006).

We measured carbon stocks in trees and understory plants using methods described in detail in Dore *et al.*

(2010). In short, in five, 0.2-ha plots located within the eddy covariance footprint, tree annual radial increments (for the period 1996–2010) were determined on one core taken (1.4 m height) from two trees randomly selected in each 5-cm diameter class. Local allometric equations were used to calculate tree biomass (aboveground and course-root) and LAI scaled to the plot level based on a census of diameters of all trees in each plot. Tree production was estimated as the difference between stand biomass of two consecutive years. However, leaf turnover and belowground fine root productivity were not included. Peak aboveground understory biomass was used as an estimate of understory aboveground productivity. We measured understory aboveground biomass and LAI via destructive sampling in late September at four 0.5 m^2 subplots per plot (20 total per site).

Results

Effect of disturbances on environment

The UND and BUR sites had similar incoming energy (Table 1), but the BUR site had higher soil temperature, soil heat flux and albedo, and lower net radiation (Table 2). Thinning did not consistently alter any energy balance component (Table 2): soil temperature and net radiation were unchanged over the 4 years after thinning, even though albedo increased slightly. Differences in precipitation between the UND and BUR sites for May through September (period that was snow-free and used in the pre-post thinning comparison because it was also measured in prethinning year at the THN site) ranged from −134 and +109 mm, and between UND and THN sites from −60 and +60 mm (Table 2). Thinning alleviated summer drought, increasing SWC particularly at the 50 cm depth (Fig. 1a,b; $P < 0.001$). Also, thinning increased α ($\lambda E/\lambda E_{eq}$) during June and July (Fig. 1e), indicating that more water was available for evapotranspiration at the THN site than at the UND site during drought. These effects were not explained by precipitation differences between the THN and UND sites during drought (Fig. 1c).

The conversion of forest into grassland by intense fire increased ecosystem water availability. The BUR site had higher annual α than the UND site in all years (Table 1).

Interannual variability of ecosystem fluxes

Annual NEP varied over years (Fig. 2 and Table 3). The BUR site was always a source, averaging 58 (±14 SE) g C m^{-2} yr^{-1}. The UND site was a carbon sink in all years, and the THN site was a net source only the first year after thinning (+51 g C m^{-2} yr^{-1} released in 2007). Over the 5-year measurement period (2006–2010), the THN and UND sites had very similar carbon uptake: the UND site averaged −112 (±31 SE) g C m^{-2} yr^{-1}, the THN site averaged −104 (±44 SE) g C m^{-2} yr^{-1}.The coefficient of variation was higher for TER than for GPP at the BUR site (Table 3). At the forest sites, the coefficient of variation was lower for TER than for GPP, especially at the THN site. At the THN site, variation in GPP was the primarily cause of the shift from a loss of 51 g C m^{-2} yr^{-1} the first year after the thinning (2007) to an uptake of −225 g C m^{-2} yr^{-1} 3 years later (2010).

The difference in NEP between the BUR site and the UND site was greater than variation among years (Fig. 2 and Table 3), indicating that fire had a stronger control on fluxes than climate variability. In contrast, at the THN site, interannual variability in NEP was greater

Table 2 Annual comparison of meteorological variables between the undisturbed (UND) and burned (BUR) sites, and the UND and thinned (THN) sites. The table values are the slope of the linear regression (with intercept = 0 to include all variation in the slope coefficient) of simultaneous daily values from January to September 2006–2010; the UND site was kept as independent variable

	BUR vs. UND					THN vs. UND				
	2006	2007	2008	2009	2010	2006	2007	2008	2009	2010
Soil Temperature 10 cm	1.17*	1.14*	1.20*	1.14*	1.13*	0.95	0.98	1.00	1.03	1.03†
Soil Temperature 50 cm	1.14*	1.12*	1.16*	1.12*	1.10*	0.92*	0.94*	0.97†	0.99	0.98†
Global radiation	0.97	0.98	0.97	0.95	0.96	0.99	0.98	0.99	0.97	0.98
Net radiation	0.67*	0.68*	0.64*	0.65*	0.63*	0.98	0.98	1.00	0.99	1.01
Air Temperature	1.00	1.01	1.01	0.99	1.01	1.04	1.06†	1.07	1.06	1.07
VPD day-time	1.05	1.12	0.91	0.88	0.92	1.08*	1.13*†	1.06	1.07	1.07†
Soil heat flux	1.06*	1.48*	1.61	1.72*	1.53	0.93*	1.02*	0.80	1.40	1.21
Δ prec. (May–September)	-134	61	17	109	70	-65	-18	11	60	36
Albedo	1.65*	2.20*	2.55*	1.40*	2.24*	1.00	1.17*†	1.25*	1.04*	1.13*

*indicates statistically significant differences between sites. †indicates after-thinning slopes different from prethinning slopes. The difference in precipitation (Δ prec.) is the difference UND-BUR or UND-THN of the May to September cumulative values.

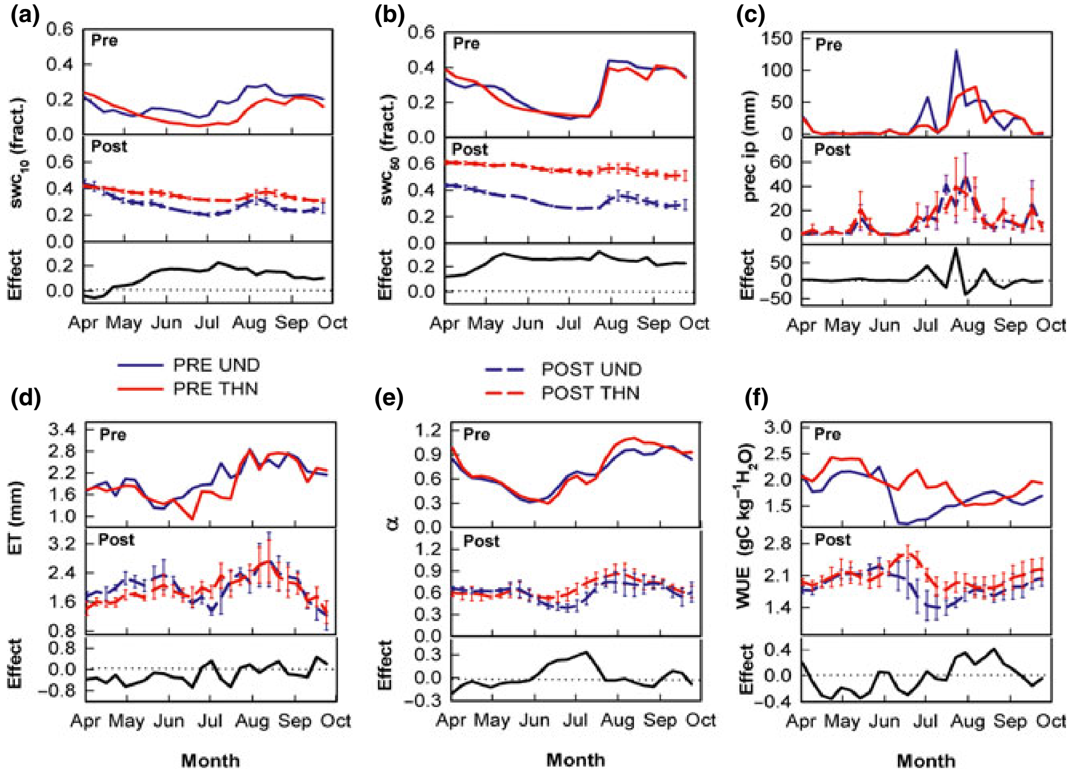

Fig. 1 Water status at the undisturbed (UND) and thinned (THN) sites pre- (2006 in top panels) and post (2007–2010 in middle panels) thinning. Thinning effect (bottom panels) was computed using the BACI approach ($THN_{post} - UND_{post}$) – ($THN_{pre} - UND_{pre}$). Data plotted are weekly averages. a) soil water content 10 cm deep (SWC_{10}; b) soil water content 50 cm deep (SWC_{50}); c) precipitation; d) evapotranspiration (ET); e) $\alpha = \lambda e/\lambda e_{eq}$; f) water use efficiency (WUE), calculated as the weekly ratio of gross primary production over ecosystem evapotranspiration (GPP/ET).

than the difference in NEP with the UND site. At the THN site, the average (2006–2010) difference in NEP between two consecutive years (111 g C m^{-2} yr^{-1}) exceeded the average difference in NEP with the UND sites (73 g C m^{-2} yr^{-1}; Table 3), showing the strong dynamism and fast recovery of ecosystem processes after thinning.

Effect of thinning on ecosystem carbon fluxes

Our two forest study sites in northern Arizona had similar NEE in 2006 prior to thinning (Figs 2 and 3). The thinning immediately reduced tree leaf area index by 40% and live-tree aboveground + coarse root stocks by 36% (~1400 g m^{-2}) via removal of smaller diameter trees (Dore *et al.*, 2010; Sorensen *et al.*, 2011; Table 1). Thinning shifted the site from a carbon sink in 2006 (−118 g C m^{-2} yr^{-1}) to a weak source to the atmosphere (51 g C m^{-2} yr^{-1}) in the first posttreatment year of 2007 (Table 3). Before-after-control-impact analysis via comparisons of changes in slope of daily NEE between the UND and THN sites (Table 4) shows that postdisturbance NEE differences between the THN and UND sites were statistically significant and thus were likely due to the thinning treatment.

The THN site rapidly recovered C sink strength starting in the second posttreatment year (2008), when its NEP (−114 g C m^{-2} yr^{-1}) was only 20% less than at the UND site (−142 g C m^{-2} yr^{-1}; Fig. 2; Table 3). In the third posttreatment year (2009), cumulative NEE (Fig. 2) became more negative (higher uptake) at the THN site than the UND site in late-summer, during a period of unusually low precipitation and high vapor pressure deficit (data not shown). Cumulative NEE remained higher at the THN site for the remainder of 2009, until it reached by the end of the year −116 g C m^{-2} yr^{-1}sequestrated at the THN site compared with a sum close to zero at the UND site (−19 g C m^{-2} yr^{-1}). In the fourth year posttreatment (2010), cumulative NEE was similar at the two sites during wet and cool periods of winter and early spring, but became higher in magnitude at the THN site during summer (Fig. 2). The NEP in 2010 was again higher at the THN site (−225 g C m^{-2} yr^{-1}) than at the UND site (−170 g C m^{-2} yr^{-1}; Fig. 2; Table 3). If we consider the total carbon exchanged during the four

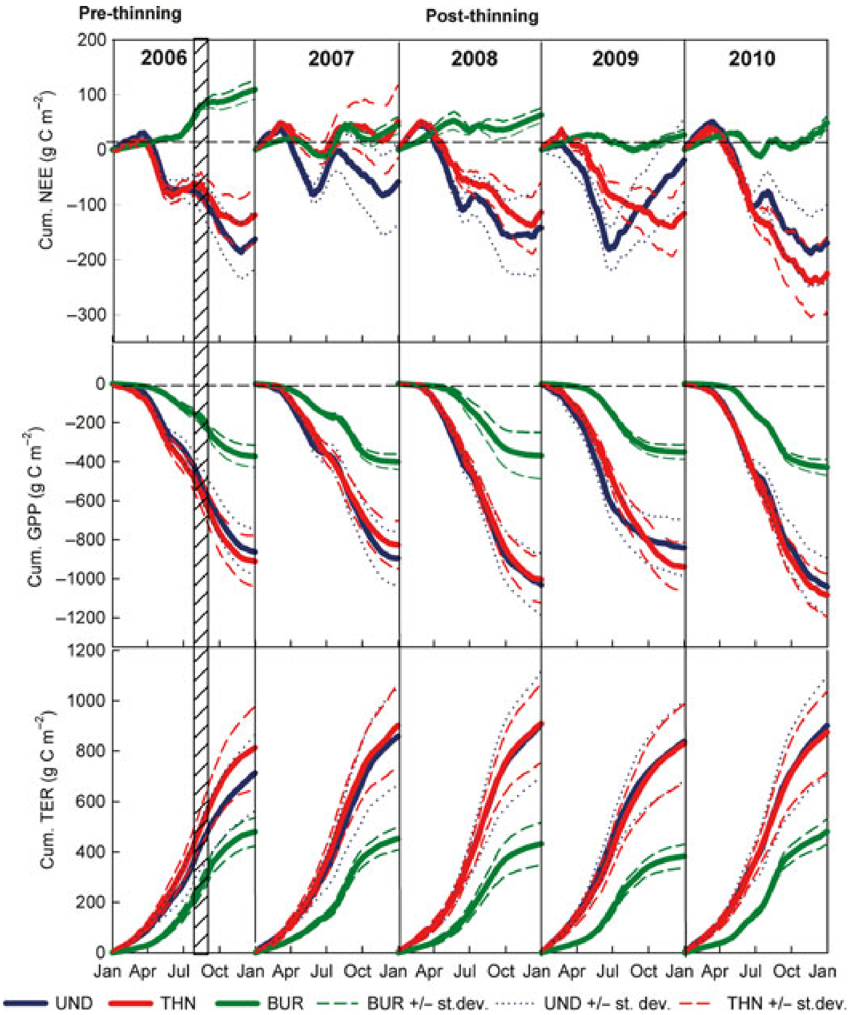

Fig. 2 Cumulative ecosystem carbon fluxes (± standard deviation) and interannual variability for years 2006–2010 of NEE (net ecosystem exchange), TER (total ecosystem respiration) and GPP (gross primary production) at the UND (undisturbed), THN (thinned), and BUR (burned) sites. Positive values indicate an ecosystem carbon loss, and negative values indicate ecosystem carbon uptake. The shaded area shows the thinning.

postthinning years, NEP at the THN site was 15 g C m^{-2} higher (−403 compared to −388 g C m^{-2}), TER 9 g C m^{-2} higher (3516 compared to 3507 g C m^{-2}) and GPP 43 higher (−3852 compared to −3809 g C m^{-2}) than at the UND site.

To quantify the effect of thinning on individual processes, daily ecosystem fluxes measured simultaneously at the THN and UND sites were compared before and after thinning. The decrease in slope in the relationship THN and UND sites between pre- and postthinning years showed that thinning reduced NEE, TER, and GPP ($P < 0.001$, Table 4). The GPP slope decreased sharply (30%) the first year after thinning (2007), with a slight annual increase thereafter. Over the first 4 year after thinning GPP was reduced on average 22%. The TER changed less by thinning (19% in 2007), but was still reduced by 20% in 2010 (Table 4). As a result, daily NEE at the THN was 52% of NEE at the UND site in 2007 and this difference did not change between 2007 and 2009 ($P = 0.56$). In 2010, however, daily NEE at the THN site was 86% of daily NEE at the UND site ($P < 0.001$).

Light response curves of NEE (Fig. 3) show the similarity of the UND and THN sites before thinning, and a reduction in maximum NEE after thinning during wetter months with low-to-moderate VPD (until June 2009, Fig. 3). In 2010, maximum NEE was again similar between UND and THN sites. In contrast, during postthinning months with high VPD, such as June 2007, July through September 2009, and July 2010, maximum NEE was lower at the UND site than at the THN site. In these months, the UND site was drier than the THN site, as indicated by lower α (Fig. 3).

Table 3 Ecosystem carbon and water fluxes for the undisturbed (UND), thinned (THN), and burned (BUR) sites from 2006 to 2010. Net ecosystem exchange (NEP), total ecosystem respiration(TER), gross primary production(GPP), and evapotranspiration (ET)annual values (and uncertainty, see text), period average, range, and coefficient of variation (CV) are shown for each site. Positive values indicate ecosystem carbon lost, negative values ecosystem carbon uptake. For the THN site, only posttreatment years (2007–2010) are summarized. Because annual NEP was calculated by summing each 30 min value, and GPP was set to zero during night-time conditions, NEP ≠ GPP + TER at annual scale. Water use efficiency (WUE) was calculated as growing season, May to October, GPP/ET. Effect size for the fire was calculated as BUR – UND averaged over the 5-year period; effect size for thinning was calculated as $(THN_{post} - UND_{post}) - (THN_{pre} - UND_{pre})$, where *pre* indicates 2006, and *post* the average of the 2007-2010 period

Site	Year		NEP ($g\ C\ m^{-2}\ yr^{-1}$)	TER ($g\ C\ m^{-2}\ yr^{-1}$)	GPP ($g\ C\ m^{-2}\ yr^{-1}$)	ET ($mm\ yr^{-1}$)	ET/PREC ($mm\ mm^{-1}$)	WUE ($g\ C\ kg\ H_2O^{-1}$)
UND	2006		−174 (57)	712 (122)	−868 (81)	491 (7)	0.72	1.7
	2007		−58 (77)	858 (170)	−895 (101)	528 (12)	0.81	1.7
	2008		−142 (71)	909 (164)	−1032 (100)	562 (14)	0.94	1.9
	2009		−19 (76)	839 (130)	−841 (64)	438 (13)	1.10	1.9
	2010		−170 (69)	901 (171)	−1041 (115)	510 (3)	0.88	2.1
2006–2010		Mean	−112	844	−935	506	0.85	1.9
		St dev	70	79	94	46	0.07	0.06
		Range	155	197	200	124	0.4	0.3
		CV	0.62	0.09	0.10	0.09	0.08	0.07
BUR	2006		108 (20)	479 (12)	−373 (24)	363 (4)	0.70	1.1
	2007		45 (19)	453 (12)	−401 (6)	462 (6)	0.68	0.9
	2008		63 (13)	433 (28)	−369 (17)	399 (7)	0.69	0.9
	2009		27 (10)	383 (8)	−350 (5)	379 (10)	0.75	0.9
	2010		49 (12)	428 (3)	−480 (15)	420 (9)	0.69	1.0
2006–2010		Mean	58	446	−384	405	0.68	1.0
		St dev	30	40	31	39	0.04	0.03
		Range	81	97	79	99	0.2	0.2
		CV	0.52	0.09	0.08	0.10	0.09	0.07
		Fire effect	−171 (−170%)	−398 (−47%)	−551 (−59%)	−101 (−20%)	−0.19	−0.9
THN	2006		−118 (53)	811 (148	−909 (103)	468 (11)	0.77	1.9
	2007		51 (66)	902 (136)	−826 (79)	443 (7)	0.71	1.9
	2008		−114 (55)	910 (134)	−1004 (88)	489 (5)	0.87	2.1
	2009		−116 (58)	829 (134)	−939 (83)	407 (6)	0.87	2.4
	2010		−225 (69)	876 (135)	−1083 (71)	517 (8)	0.91	2.1
2007–2010		Mean	−101	+879	−963	464	0.80	2.1
		St dev	114	37	108	49	0.09	0.05
		Range	277	99	256	110	0.4	0.2
		CV	1.13	0.04	0.11	0.10	0.09	0.13
		Thinning effect	60 (36%)	−97 (−14%)	−30 (−4%)	−22 (−4%)	−0.14	0.025

Thinning reduced the sensitivity of GPP to VPD. Whereas the slope of the relationship between GPP and VPD was greater at the THN site than at the UND site in 2006, it was greater at the UND site in all postthinning years (Fig. 4). In low VPD conditions (VPD < than 1.7 kPa; Fig. 4), the lower tree LAI of the THN site (Table 1) caused GPP to be about 20% lower than at the UND site. However, when VPD exceeded 2.5 kPa (Fig. 4), the lower VPD sensitivity at the THN site resulted in GPP being about twofold higher there than at the UND site.

Thinning also increased the temperature at which maximum seasonal GPP occurred (Fig. 5). In the pretreatment year of 2006, the air temperature for maximum GPP was about 1 °C lower at the THN site than the UND site, whereas this temperature became 1.4 –2.9 °C greater at the THN site than at the UND site in all posttreatment years. Over the total of the first four posttreatment years, the air temperature for maximum GPP was 3 °C higher (Fig. 5b) at the THN site than at the UND site. Likewise, thinning increased the VPD that corresponded to the temperature for maximum GPP. This VPD was similar (within 0.08 kPa) for the two sites prior to thinning in 2006, and became 0.2–0.5 kPa greater for the THN site than for the UND site in all posttreatment years (Fig. 5b).Very similar results were obtained for the sensitivity of NEE to air temperature, and for the sensitivity of GPP to α (data not shown).

Effect of thinning on biomass and vegetation productivity

Thinning increased radial growth of the remaining trees in the first 4 years after thinning (2007–2010), consistent

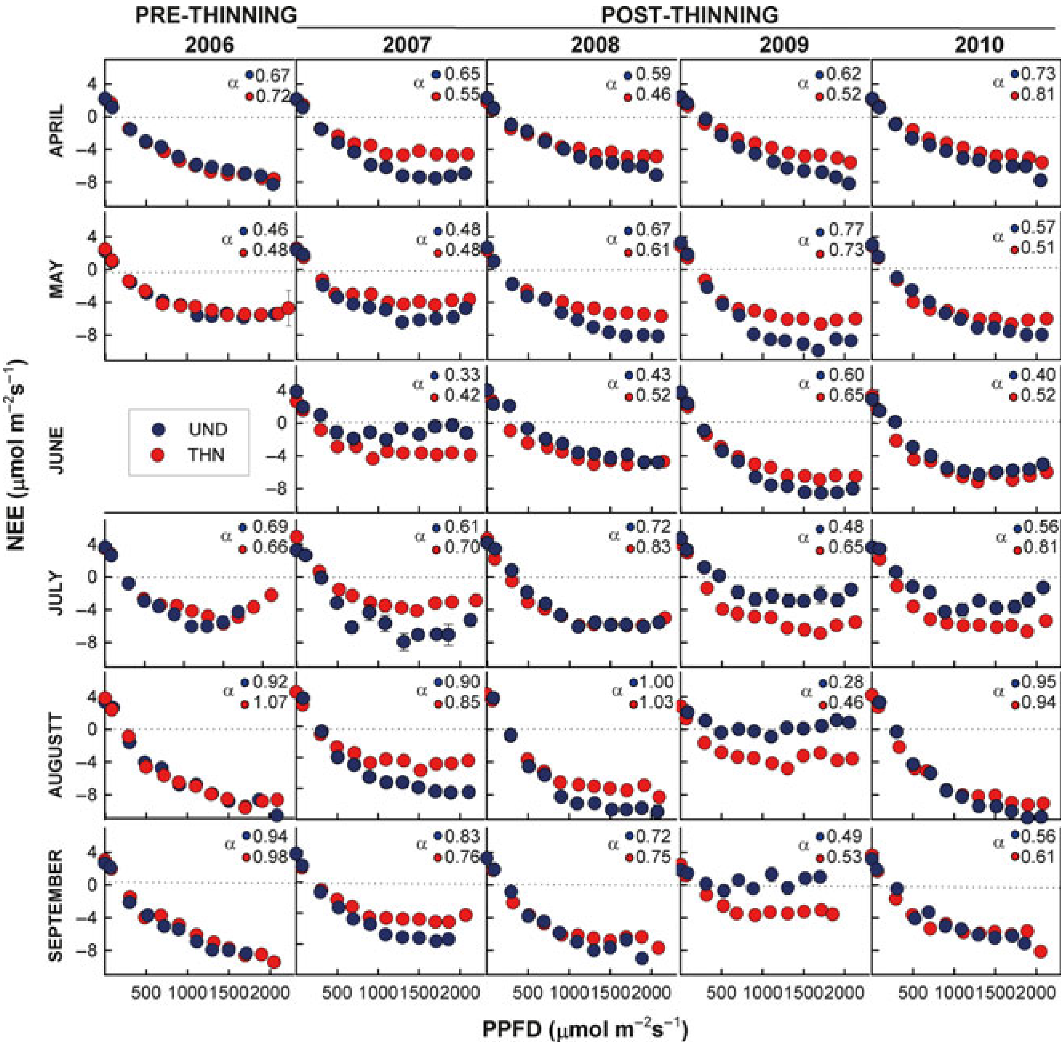

Fig. 3 Monthly relationship between net ecosystem CO_2 exchange (NEE) and photosynthetic photon flux density (PPFD) for April and September 2006–2010 at the undisturbed (UND) and thinned (THN) sites. Only 30-minute, good-quality data measured simultaneously at both sites were used. The α value represents the monthly water status of the sites (see text).

with results obtained the first year after thinning (Dore *et al.*, 2010). At the THN site, average annual radial growth from 2007 to 2010 increased 0.5 mm compared to annual growth from 2003 to 2006. However, tree density was reduced by thinning, and therefore stand level tree productivity (aboveground + coarse roots) decreased by 28 g C m^{-2} yr^{-1} when totaled over the four posttreatment years (Table 5). Because understory aboveground production increased 16 g C m^{-2} yr^{-1}, the net decrease in productivity over the four postthinning years was only 12 g C m^{-2} yr^{-1}(Table 5).

Effect of fire on ecosystem carbon fluxes

Intense, stand-replacing fire had profound impacts on ecosystem fluxes. The BUR site burned in 1996, 10 years before our measurements started. The site was a source of carbon each year between 2006 and 2010, and averaged a loss of 58 g C m^{-2} yr^{-1} (Table 3). On average, TER at the BUR site was 47% lower and GPP 59% lower than at the UND site (Table 3). The sensitivity of TER to soil temperature, 10 –15 years after burning, was unchanged by fire and thinning, but for a given temperature, TER was always lower at the BUR site than at either the UND and THN sites (Fig 6).

Effect of disturbances on ecosystem water fluxes

Annual ET was always lower at the BUR site than at the UND site, and averaged 20% less over the 5-year study (Table 3). The effect of fire on ET was stronger

Table 4 Comparison of simultaneously measured net ecosystem exchange (NEP), total ecosystem respiration(TER), gross primary production (GPP), and evapotranspiration (ET) at the THN and UND sites, before (2006) and after (2007–2010) thinning. Slopes and R^2 of linear regression fitted on the daily values had intercept set to zero to include all variations in the slope coefficient. P values are from the comparison between the slopes of two consecutive years. Data analysis was limited to the January to September period of each year to compare the same time interval before and after thinning. Only days with similar environmental conditions (wind, Ta, PPFD, VPD and α) were used. Each ecosystem flux postthinning slope was significantly different ($P < 0.001$) from the corresponding prethinning slope except for ET 2010 ($P = 0.65$). Each slope was significantly different from one ($P < 0.001$), except for the GPP prethinning ($P = 0.98$)

Ecosystem flux		Year	Slope	R^2	Comparison with slope of previous year (P value)
NEE	Prethinning	2006	0.97	0.85	
	Postthinning	2007	0.52	0.66	<0.001
		2008	0.51	0.61	0.56
		2009	0.51	0.30	0.18
		2010	0.86	0.77	<0.001
TER	Prethinning	2006	1.15	0.90	
	Postthinning	2007	0.96	0.78	<0.001
		2008	1.00	0.89	<0.001
		2009	0.93	0.86	<0.001
		2010	0.95	0.82	0.51
GPP	Prethinning	2006	1.11^{+}	0.90	
	Postthinning	2007	0.82	0.90	<0.001
		2008	0.89	0.74	0.36
		2009	0.88	0.32	<0.001
		2010	0.96	0.85	<0.001
ET	Prethinning	2006	0.98	0.90	
	Postthinning	2007	0.85	0.75	<0.001
		2008	0.85	0.85	0.75
		2009	0.84	0.61	0.20
		2010	0.91	0.90	<0.001

and more persistent than the effect of thinning, which could not be detected 4 years after thinning (Table 4). This decrease in ET after fire was confirmed when annual ET was standardized by total annual precipitation (Table 3) to take account of precipitation differences between sites. On average, the fraction of annual precipitation lost as ET was 0.85 at the UND site, 0.80 at the THN site, and 0.68 at the BUR site. Annual ecosystem water use efficiency (WUE = GPP/ET) calculated using growing season data from April to October (Beer *et al.*, 2009) was lower at the BUR site than at the UND ($P < 0.001$) and THN ($P < 0.001$) sites, at both annual (Table 3) and monthly time scales (Fig 7).

Annual ET over all four posttreatment years was 45 mm/yr lower at the THN site than at the UND site (Table 3) and the net effect of thinning on annual ET was a 4% decrease. Annual ET was lower at the THN than at the UND site from 2007 to 2009. In 2010, ET at the THN and UND site was similar (7 mm higher at the THN than at the UND site). At the daily scale, the slope of the relationship of ET between the THN and UND sites decreased in the posttreatment years 2007–2009. By the fourth posttreatment year (2010), ET at the THN site had recovered to values similar to the pretreatment levels (Table 4).

On an annual scale, WUE was only slightly higher at the THN site than at the UND site, and was not greatly affected by thinning (Table 3, $P = 0.09$). On a monthly scale, WUE was generally higher at the THN site than at the UND site, especially when WUE was low (Fig. 7).

Thinning reduced ecosystem aridity during the dry season. Comparisons of α (Fig. 1e) and SWC (Fig. 1a,b) showed that the THN site was drier than the UND site during the pretreatment period of June 2006, but was wetter during the same period in the years after thinning. Lower aridity of the THN site compared with the UND site during the dry season was explained by lower ET in late spring (Fig. 1d), but not by precipitation differences (Fig. 1c). During the dry season, WUE at the THN site was higher than at the UND site every year after thinning; however, the effect of thinning on WUE was minor, because WUE was also higher before treatment (Fig. 1f).

Discussion

Recovery from thinning of the ecosystem carbon uptake of a northern Arizona ponderosa pine forest was rapid. Thinning did not reduce the carbon uptake over the first four postthinning years: the average 4-year uptake (2007–2010) was similar for the UND (-97 g C m^{-2} yr^{-1}) and THN (-101 g C m^{-2} yr^{-1}) sites and, after adjusting for the lower NEP at the THN site before thinning, was on average 60 g C m^{-2} yr^{-1} higher at the THN site (Table 3). The reduction in stand leaf area due to thinning decreased carbon uptake at the THN site compared with the UND site, as exemplified in the lower daily NEE (Table 3), instantaneous responses of NEE to light (Fig. 3), and cumulative NEE until the dry period in June (Fig. 1). However, in dry periods the THN site experienced lower limitations to GPP than did the UND site (Fig. 6), reaching a higher temperature for maximum GPP (Fig. 7). As a result, the THN site had higher NEP than the UND site in the third and fourth years after thinning. In the third year after thinning, drought ($\alpha < 0.4$) at the UND site lasted from the 23rd of June through November. Cumulative NEE at the beginning of the drought was 98 g C m^{-2} lower at

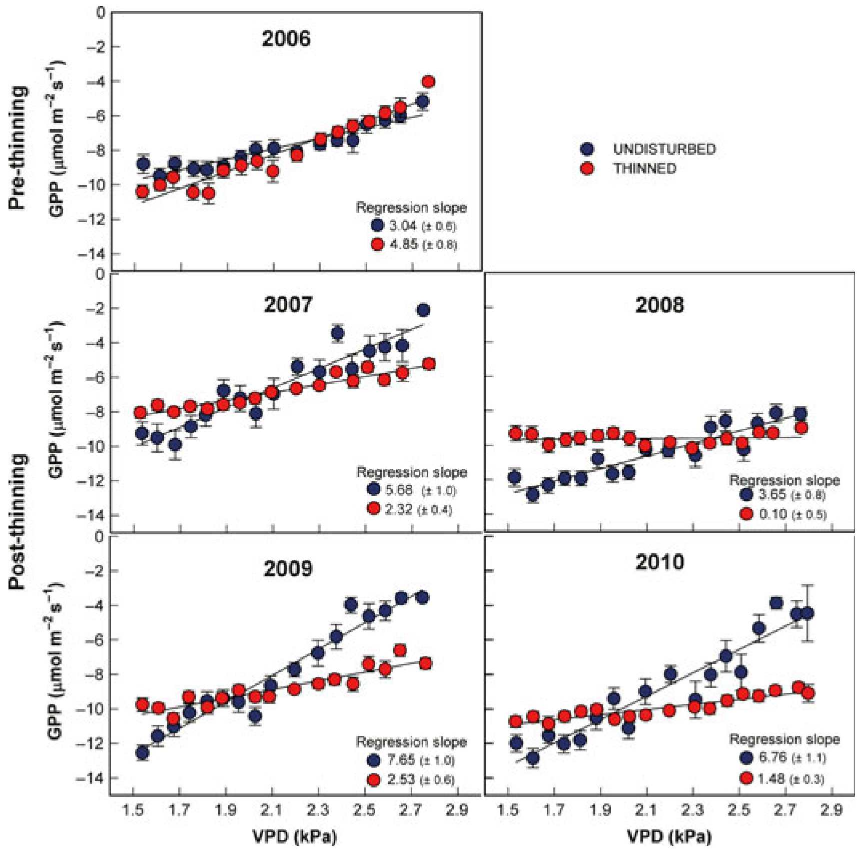

Fig. 4 Relationship between gross primary production (GPP) and vapor pressure deficit (VPD) for the unthinned and thinned sites, pre- and postthinning. The symbols are the mean (± standard error) of 0.07 kPa VPD classes for 30-min. Good-quality data from May to October. The slope (± 95% confidence interval) of the linear regression line for each site and year is shown.

the THN site than at the UND site. However, between the beginning and the end of the drought, the THN site added 49 g C m^{-2}, whereas the UND site lost 114 g C m^{-2}. Thus, in the third year after thinning, the higher carbon uptake at the THN site was mostly due to the severe limitation of carbon uptake at the UND site during the particularly prolonged summer drought. In the fourth year, a wet year, drought at the UND site ($\alpha < 0.4$) lasted from June 1st to July 23rd. The THN site and the UND site had same cumulative NEE (2 g C m^{-2} NEE difference) at the beginning of the drought, but from June 1st to July 23rd, the THN site fixed 50 g C m^{-2} more than the UND site, and 56 g C m^{-2} more by the end of 2010. Thus, higher carbon uptake at the THN site was in part due to the lower NEE limitation during drought, and in part due to the restored photosynthetic capacity of the stand (Table 3; Figs 2 and 3). Limitation on GPP and NEE during drought determined annual NEP more than the absolute photosynthetic capacity of the stands.

The postthinning reduced limitation of NEE during drought of our study on ponderosa pine is consistent with results from Moreaux *et al.*'s study (2011) on maritime pine (*Pinuspinaster*). Similar to our results, a fast (1 year) recovery of NEE after thinning was reported for a boreal pine forest (Vesala *et al.*, 2005) and a young ponderosa pine plantation in California (Misson *et al.*, 2005).

Effect of thinning on a daily scale and similar climatic conditions differed from effects on annual scale. For example, thinning decreased NEP on a daily scale, but increased it on an annual scale, and decreased GPP 22% on a daily scale, but only 4% on an annual scale. Differences reflected the interaction of single processes with climate and the water cycle, balancing and reducing short-term differences during the course of the year.

Our study provided additional evidence that biometry and eddy covariance results can diverge. For example, our tree and understory productivity data suggested a small loss of carbon to the atmosphere over the first 4 years after thinning. However, based on the eddy covariance data, thinning increased carbon accumulation by 60 g C m^{-2} yr^{-1} over the same period.

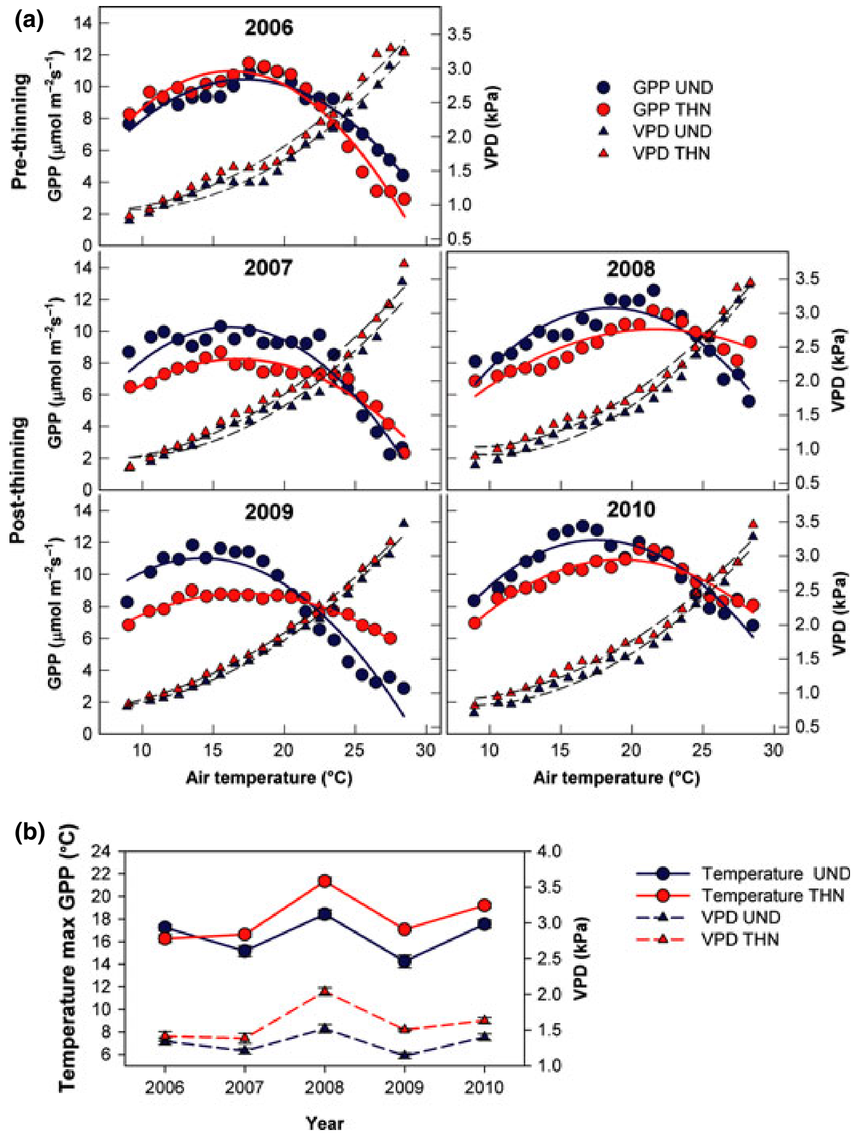

Fig. 5 Assessment of air temperature corresponding to maximum gross primary production (GPP). a) Relationship between light saturated GPP (positive uptake = −GPP) and air temperature used to calculate the temperature (circles) corresponding to maximum GPP at the undisturbed (UND) and thinned (THN) sites for 2006 through 2010. Good-quality 30-min GPP data, when photosynthetic photon flux density was >1500 μmol m^{-2} s^{-1},were averaged over one degree C air temperature classes. VPD (triangles) values of GPP included in each temperature class were averaged. The air temperature corresponding to the maximum of the GPP curve was calculated as $-b_1/2 \times b_2$ where b_1 and b_2 are the coefficient of the quadratic equation GPP = a + $b_1 \cdot T$ + $b_2 \cdot T^2$ (Zar, 1999). b) Air temperature (circles) for maximum GPP and corresponding VPD (triangles) for the undisturbed and thinned sites pre- and postthinning. The vertical bars show ±95% confidence intervals.

Discrepancies between biometric and eddy-covariance estimates of forest carbon balance have being previously reported at our study sites (Dore *et al*., 2010) and elsewhere (Campbell *et al*., 2009; Luyssaert *et al*., 2009) and in our case can be partly explained by the absence of important components, such us the fine root and leaf productivity in the biometry-based NEP. Interestingly, the large decrease in NEP estimated by eddy covariance at the UND site in 2009 was also evident as low understory productivity, but was not observable as a reduction of tree productivity, which in 2009 was 113 g C m^{-2} yr^{-1} and not different from the previous year (Table 5). Possible explanations for this difference are an intense tree growth during the particularly wet spring of 2009, before the prolonged drought affected other components of ecosystem carbon balance, or some regulation of tree growth by carbon stored in previous years. The positive tree productivity in the dry

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Table 5 Tree and understory productivity measured by biometry and size of the effect of thinning on tree, understory, and their sum. Effect was calculated using the BACI approach, as (THN_{post} − UND_{post}) − (THN_{pre} − UND_{pre}). Where *pre* is the average over years 2005 and 2006, and *post* is the average over years 2007 through 2010. Leaf turnover and fine root productivity are components of net primary productivity not included in our measurements

	Biomass productivity (g C m^{-2} yr^{-1})												
	2005		2006		2007		2008		2009		2010		Effect
	UND	THN	UND	THN	UND	THN	UND	THN	UND	THN	UND	THN	BACI
Trees	96	160	65	75	77	82	116	99	113	102	122	180	−28
Understory	12	6	12	6	7	13	13	34	5	9	11	28	16
Trees + Understory	109	167	77	81	84	95	129	133	118	111	133	208	−12

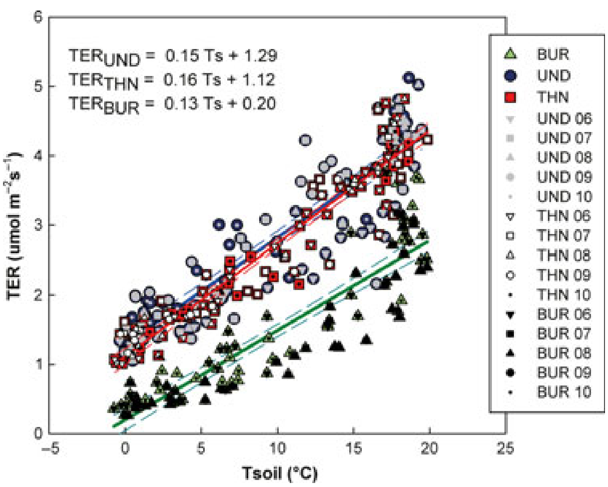

Fig. 6 Relationship between total ecosystem respiration (TER) and soil temperature (10 cm depth) at the undisturbed (UND), thinned (THN), and burned (BUR) sites. Linear relationship was computed on monthly data between 2006 and 2010. Different symbols represent different years and sites. Temperature was limited to the range measured at all sites. Equations with slopes and intercepts for the undisturbed (UND), thinned (THN) and burned (BUR) site are shown.

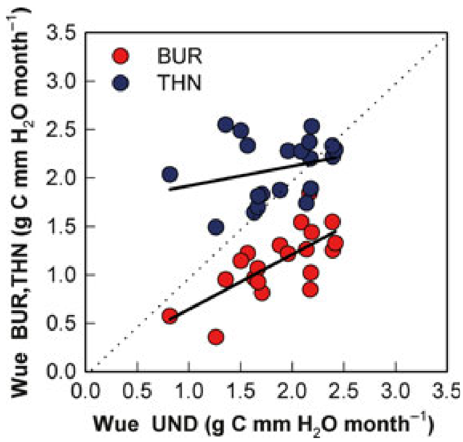

Fig. 7 Ecosystem water use efficiency (WUE = GPP/ET, where GPP is gross primary production and ET evapotranspiration) compared for simultaneous monthly measurements of the burned (BUR) and undisturbed (UND) sites, and thinned (THN) and UND sites during the postthinning years 2007–2010. Months are limited to snow-free period (May–October). Dotted line represents the 1 : 1 line.

year 2009, while ecosystem productivity estimated from eddy covariance was close to zero, demonstrates how inference of annual net ecosystem carbon exchange from measurements of only tree-diameter increments can be misleading.

The severe fire had a large and persistent effect on ecosystem carbon stocks and fluxes. Past results at the BUR site showed that, 10 years after the fire, ecosystem-level carbon was approximately 40% of the carbon stored by the UND site, mostly because of a decrease in trees biomass and organic soil (Dore *et al.*, 2008). Our measurements were made a decade after burning, during which time additional carbon was lost from the site via decomposition and erosion, and little was stored as new vegetation because of the lack of tree regeneration. If we consider coniferous forests can lose up to 20% of total ecosystem carbon during combustion (Krishnan *et al.*, 2006; Campbell *et al.*, 2012), our study supports the results of those who documented after-fire carbon losses higher than direct losses during fire (Kashian *et al.*, 2006; and Wirth *et al.*, 2002).

No measurable pulse of respiration occurred at the BUR site 10–15 years after the fire, despite high above- and belowground necromass. Instead, soil CO_2 efflux (Sullivan *et al.*, 2011) and TER were reduced after fire, probably because of a slow decomposition and a reduction in belowground autotrophic respiration. Our results were consistent with results from 2006 and with reports for other ponderosa pine and conifer forests after disturbances (Law *et al.*, 2003; Irvine *et al.*, 2007; Amiro *et al.*, 2010; Goulden *et al.*, 2011). Although TER was reduced by fire, GPP was reduced more than TER (Fig 2 and Table 3).

The additional 4 years of data reported here demonstrate that the shift from carbon sink to source after the severe fire was persistent and was not simply a result of climatic variability. During a 5-year period, 10–15 years after a fire which converted the forest into a sparse grassland, the BUR site was consistently a net annual carbon source. The time necessary for this ponderosa pine ecosystem to recover from severe fire and to shift back from carbon source to sink is longer than most ecosystems, and probably will exceed the maximum recovery time of 20 years reported by Amiro *et al.* (2010) for disturbances in North American forests. The recovery time was about 10 years after fire for boreal forests (Amiro *et al.*, 2010) and 4–6 years in subtropical ecosystems (Thornton *et al.*, 2002). Our results from a thinned and an intensely burned ponderosa pine stands are consistent with reports that recovery time is generally shorter for managed than natural disturbances (Thornton *et al.*, 2002; Knohl *et al.*, 2002), is shorter for moderate compared with severe disturbances (Amiro *et al.*, 2010), and is longer for conifers compared with deciduous, sprouting species (Kowalski *et al.*, 2004).

While stand-replacing fires can have a null effect on forest carbon storage over long (centuries) timescales (Kashian *et al.*, 2006; Campbell *et al.*, 2012), carbon dynamics in our study were strongly affected on a decadal timescale, resulting in an intense carbon release to the atmosphere. Final effects of fire on ecosystem carbon storage are determined by how well photosynthesis by new vegetation can compensate for carbon lost during and after burning. Lack of full recovery to predisturbance conditions results in a net loss of stored carbon (Kashian *et al.*, 2006). Causes of a failing recovery can be changes in forest structure, soil carbon, species composition. A shift in vegetation can occur especially when the species that dominate the site before burning are conifers that do not sprout vegetatively, or species far from their optimum areas, or when soil erosion, invasive species, insects, drought stress are direct or indirect consequences of fires. If species are conifer that lack cone serotiny, tree regeneration depends on seed input from nearby forests and on favorable environmental conditions in the first decade following the disturbance (Kashian *et al.*, 2006). How often ecosystems return to exactly the same conditions present before the stand-replacing fire is poorly quantified and certainly is species-, region-, climate-, and case-specific. However, a postfire shift in vegetation type because of tree regeneration failure is not a result limited to our study. For example, Roccaforte *et al.* (2012) studied ponderosa pine regeneration dynamics after severe fires. Overstory and regeneration were completely lacking in 50% and 57% of the sites, respectively, probably shifting forests to shrublands or grasslands for extended periods. Savage & Mast (2005) found ponderosa pine forests responded to high severity fires by either high regeneration that returned the forest to a fire-prone "hyperdense" condition, or by long-term conversion into a non-forested grassland or shrubland. Strom and Fulé (2007) documented dominance by sprouting shrubs after intense burning of ponderosa pine forests. In different regions, Coop *et al.* (2010) reported that tree regeneration of subalpine vegetation declined with altitude and distance from unburned edges. Barrett *et al.* (2012) documented afterfire vegetation shifts in arctic tundra that persisted at least 17 years. Repeated intense fires were found to be one of the main causes of deforestation in the subarctic zone (Sirois & Payette, 1991).

The intense disturbance of stand-replacing fire had a stronger and more persistent effect on evapotranspiration than the moderate disturbance of thinning. The 20% lower ET at the BUR than at the UND site can be explained by less leaf area and a higher albedo, both of which reduced net radiation in the BUR site. ET was lower at the BUR site than at the UND site each year during the period 10–15 years after the fire, including 2009, when precipitation was higher at the BUR than at the UND site (Tables 1 and 4). In contrast, thinning reduced daily ET by only 12% over the posttreatment years, and no effect could be detected 4 years after thinning (Tables 3 and 4). Thinning reduced ET of a maritime pine plantation analyzed by Moreaux *et al.* (2011) by 15%, a result very similar to what we measured for ponderosa pine. Overall, our results show that fuel reduction thinning in Arizona ponderosa pine forests has little impact on ET, and thus little impact on water available for aquifer recharge.

Lower ET after fire contrasted with other studies that found an increase in ET after fire because of the loss of the regulation that vegetation exercises on water exchanges and the increased evaporation from higher radiation reaching the ground (Amiro *et al.*, 2006; Santos *et al.*, 2003). Unlike these previous studies, our study was conducted in a semiarid region with a low LAI and with a decadal shift in vegetation cover from forest to sparse grassland. The low or no vegetation cover determined a high ratio of evaporation over transpiration, and thus a low control of vegetation over water exchanges even prior to any disturbance. It also explains our water use efficiency values generally <2 g C kg^{-1}as for recently disturbed sites in the study of Mkhabela *et al.* (2009). Ponton *et al.* (2006). Law *et al.* (2002) also report lower WUE value in grasslands than in forest sites.

Our findings about rapid recovery of carbon sequestration after thinning and a lack of recovery for at least 15 years after severe fire in Arizona ponderosa pine

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forests provide new insights into the effects of forest management on carbon storage. First, our results challenge the notion that fuel reduction treatments cause long-term reductions in carbon sequestration of semi-arid forests (Mitchell *et al.*, 2009; Sorensen *et al.*, 2011; Hurteau & Brooks, 2011; Hudiburg *et al.*, 2011; Campbell *et al.*, 2012). We documented rapid recovery of ecosystem carbon sink strength after forest thinning despite low tree leaf area index. We estimate that the thinned site will recover the ~1400 g m^{-2} of above- and belowground carbon stock lost directly from the site via tree removal (Dore *et al.*, 2010; Sorensen *et al.*, 2011) in about 12 years, assuming that the average annual NEP of −171 g m^{-2} at the thinned site in the third and fourth posttreatment years is sustained. For full carbon accounting, we estimate about 19 years for recovery of all thinning-related carbon releases (total of 2477 g m^{-2}) reported for the THN site, when considering the CO_2 emitted by burning logging slash, use of fossil fuels for logging equipment, and decay of short-lived wood products made from removed logs to the previously mentioned change in tree stocks (Sorensen *et al.*, 2011). Second, our finding that forest thinning shifts temperature for maximum GPP by 3 °C and ameliorates impacts of high VPD on GPP has implications about impacts of forest management on carbon storage in a future warmer climate. Thinning of semi-arid, fire-prone forests, by reducing soil moisture stress, strengthen GPP during periods with high temperature and VPD. In addition to lower likelihood of severe fires and consequent vegetation shifts, thinned ponderosa pine forests of the southwestern U.S. have greater carbon sink strength than unthinned forests during drought, which is predicted to increase with climate warming.

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