Agricultural and Forest Meteorology 303 (2021) 108388

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Post-fire co-stimulation of gross primary production and ecosystem respiration in a meadow grassland on the Tibetan Plateau

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ARTICLE INFO

Keywords:
Prescribed fire
Gross primary production
Ecosystem respiration
Net ecosystem exchange
Plant community composition
Microbial biomass
Soil inorganic nitrogen
Soil temperature
Soil volumetric moisture
Meadow grassland
Tibetan Plateau

ABSTRACT

Predicting post-fire ecosystem CO_2 exchange requires an explicit understanding of the sensitivity of gross primary production (GPP), ecosystem respiration (ER) and net ecosystem exchange (NEE) to post-fire conditions. However, the simultaneous effects of fire on GPP, ER and NEE are rarely evaluated. We established a three-year manipulative fire experiment in a meadow grassland on the Tibetan Plateau to investigate the responses of GPP, ER and NEE to prescribed fire. We found that fire on average increased GPP by 13% and ER by 9%, leading to an increase in NEE by 20% across the three years. There was no clear relationship between post-fire changes in soil temperature and ecosystem CO_2 exchange, yet reductions in soil volumetric moisture were positively related to changes in GPP, ER and NEE. These results suggest that post-fire stimulation of GPP, ER and NEE cannot be fully explained by changes in soil temperature and soil moisture. Besides, changes in GPP, ER and NEE were positively related to fire-induced increases in graminoid biomass, legume biomass and soil inorganic nitrogen. Taken together, our results suggest the interwoven control of biotic and abiotic factors on post-fire GPP, ER and NEE, yet also that shifts in plant functional type biomass may outweigh the negative effects of reduced soil moisture on ecosystem CO_2 exchange. These results underscore how simultaneous documentation of GPP, ER and NEE dynamics can advance a mechanistic understanding of CO_2 exchange under fire disturbance.

1. Introduction

As one of the most important ecological disturbances in natural ecosystems, fire has cascading effects on land-atmosphere carbon dioxide (CO_2) exchange (Kelly et al., 2016; Lehmann et al., 2008). It is estimated that fire-caused CO_2 emissions can be up to 4 Pg C per year, which approximately equals to the half of the total CO_2 emissions by fossil-fuel combustion (Bowman et al., 2009; Moritz, 2012). Previous studies have reported that fire could even determine the magnitude of ecosystem carbon (C) balance and therefore regulate global climate change (Page et al., 2002; van der Werf et al., 2004). For example, modeling studies showed that biomass burning accounted for more than 60% of the CO_2 growth rate from 1997 to 2001 (van der Werf et al., 2004). Furthermore, fire regimes are changing in the context of global climate change, in which fire will become more severe and frequent over the coming decades (Bowman et al., 2009; Higuera and Abatzoglou, 2021; Westerling et al., 2006). However, it remains unknown about the patterns and drivers of post-fire ecosystem CO_2 exchange, which limits

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https://doi.org/10.1016/j.agrformet.2021.108388
Received 13 October 2020; Received in revised form 9 January 2021; Accepted 28 February 2021

the understanding and capability to project future global C-climate feedbacks.

Ecosystem CO_2 exchange describes the balance of ecosystem photosynthesis and respiration (Chapin et al., 2006; Chen et al., 2016b). If fire increases photosynthesis more than respiration, the ecosystem will be a net CO_2 sink and *vice versa*. The net CO_2 exchange between terrestrial ecosystem and atmosphere is defined as net ecosystem exchange (NEE), which is divided into two components: gross primary production (GPP) and ecosystem respiration (ER) (Ciais et al., 2005; Luo, 2007). Gross primary production is the total influx of C into ecosystems through the photosynthetic fixation of CO_2, whereas ER is the largest CO_2 emissions from terrestrial ecosystems to the atmosphere (Chapin et al., 2006; Chen et al., 2016b; Falge et al., 2002). While NEE is often directly measured using an eddy covariance flux tower approach, GPP and ER cannot be directly obtained from the flux tower (Beringer et al., 2007; Campioli et al., 2016). In earlier studies, GPP and ER were usually estimated or modeled from eddy covariance data, which inherently has large uncertainties (Dore et al., 2012; Papale et al., 2006). During the last decade, *in situ* NEE and ER have been increasingly being measured using a recently developed static chamber method, despite this method being labor-intensive (Chen et al., 2016b; Niu et al., 2013). However, to our knowledge, GPP, ER and NEE are rarely simultaneously documented after fire disturbance, limiting our understanding of post-fire ecosystem CO_2 exchange.

The underlying mechanisms associated with the post-fire-induced changes in ecosystem CO_2 exchange are largely unclear. First, increases in soil temperature could promote both photosynthesis and respiration, whereas reductions in soil moisture could suppress them in arid regions (Chen et al., 2016b; Luo, 2007). Many studies have reported the increases in soil temperature but decreases in soil moisture after fire disturbance (Dore et al., 2012; Hu et al., 2020; Ma et al., 2004), yet their combined impacts on ecosystem CO_2 exchange still remains unclear. Second, post-fire photosynthesis and respiration may be modulated by soil nitrogen (N) availability (Fang et al., 2012; Fernández-Martínez et al., 2014). Previous studies reported that fire has positive, negative or neutral impacts on soil N availability (Certini, 2005; Docherty et al., 2012; Grogan et al., 2000), but the extension of such effects to ecosystem CO_2 exchange remains elusive. Third, the impact of fire on ecosystem CO_2 exchange also requires overall consideration of potential shifts in plant functional type biomass (Hart et al., 2005; Ward et al., 2007), because species can differ greatly in their photosynthesis and respiration capabilities or in their CO_2 use efficiencies (Bagchi and Ritchie, 2010; Lavorel and Garnier, 2002). For example, a recent study on the Tibetan Plateau showed that increases in graminoid and legume biomass rather than forb biomass significantly enhanced ecosystem CO_2 sequestration (Chen et al., 2016b). The net effects of fire on ecosystem CO_2 exchange are the results of a range of biotic and abiotic factors, whereas their separate or combined effects are insufficiently understood.

The Tibetan Plateau is considered as “the roof of the world”, with an altitude mostly higher than 3, 000 m above sea level. Due to the high elevation, low temperature, short growing season and large amount of historical organic matter stock (Guo et al., 2018; Hu et al., 2015; Li et al., 2019; Zhang et al., 2014), the Tibetan Plateau is regarded as one of the most ecologically sensitive and susceptible regions to wildfire under a changing climate (Miao et al., 2017; You et al., 2018). Recent studies reported that the frequency and intensity of wildfire has significantly increased over the past centuries on the Tibetan Plateau due to the rapid climate change or the intensified human activities or both (Hao et al., 2020; Sun et al., 2016). Moreover, it is predicted that climate change and human activities will continuously increase the fire intensity and severity on the Tibetan Plateau in the coming decades (Miao et al., 2017; You et al., 2018). Studies from ecologically sensitive regions, such as the Tibetan Plateau, are valuable in advancing the understanding of post-fire ecosystem CO_2 exchange, as responses from ecologically sensitive regions are often unexpected. Considering the cascading but understudied effects of fire on ecosystem functions, such as ecosystem CO_2, more research is urgently required to better inform ecosystem managements as well as regional and global C-climate projections.

The goal of this study was to explore post-fire ecosystem CO_2 exchange processes as well as their underlying mechanisms. Three key questions motivated our work: (1) how will prescribed fire affect soil microclimate, plant functional type biomass, soil inorganic N and soil microbial biomass C and N? (2) how will prescribed fire affect ecosystem CO_2 exchange (GPP, ER and NEE)? and (3) do changes in plant functional type biomass scale up to affect ecosystem CO_2 exchange on the Tibetan Plateau? To answer these questions, a prescribed fire experiment was conducted in a meadow grassland on the Tibetan Plateau. Gross primary production, ER and NEE were simultaneously measured across three consecutive growing seasons. To investigate the possible underlying mechanisms, soil temperature, soil volumetric moisture, soil inorganic N, soil microbial biomass C and N and plant functional type biomass were systematically documented across the three growing seasons.

2. Materials ad methods

2.1. Study site

The field manipulative fire experiment was established at Haibei Grassland Ecological Monitoring Station (Xihai Town, Qinghai province, 100°51′E, 36°57′N, 3 140 m a.s.l.), a site managed by the China Meteorological Administration. The study site has a typical plateau climate, with relatively high temperature and precipitation during the growing season (April to October) and relatively low temperature and precipitation during the non-growing season (November to April). According to nearby long-term meteorological records (from 1995 to 2013), the mean annual temperature is 1.3 °C and the mean annual precipitation is 409 mm. With a sandy loam structure, the soil is classified as mountain brown in Chinese soil classification system, or cambisols according to the US Food and Agriculture Organization. Soil pH (0-10 cm) was about 7.8 and soil bulk density was about 1.0 g cm^{-3}. We selected a typical meadow grassland on the Tibetan Plateau for our study site. The dominant species consisted of graminoid (*Stipa sareptana var. krylovii, Stipa purpurea, Koeleria cristata* and *Poa crymophila*), legume (*Medicago ruthenica*) and forb (*Kobresia humilis, Artemisia scoparia* and *Aster tataricus*). Detailed information about the study site can be found in Chen *et al.* (2015), Guo *et al.* (2018) and Li *et al.* (2019).

2.2. Prescribed fire experiment

The selected study site had long been managed as traditional free-range winter grazing grassland, with a moderate grazing intensity of 0.5 yak and 2.5 sheep per hectare (Chen et al., 2018). To avoid disturbance caused by grazing, the study site was fenced for three years prior to the establishment of the fire experiment. More information about the fire treatment can be found in Chen et al. (2019). Briefly, we used a randomized block design to simulate fire impacts, with each treatment (ambient and fire) replicated six times to produce 12 experimental blocks. The 12 blocks (30 m × 60 m) were randomly selected from the study site in March 2011, with buffer zones of at least 15 m between adjacent blocks. Six of the 12 selected blocks were randomly selected to simulate the typical fire on the Tibetan Plateau. The fire treatment was performed at the beginning of 2011, before the start of the growing season; there was only one rapid prescribed fire disturbance across the entire experimental period. The prescribed fire consumed almost all aboveground biomass and litter, but with low to moderate fire severity (Chen et al., 2019).

2.3. Soil temperature and soil volumetric moisture

Soil temperature and soil volumetric moisture to 10 cm depth were automatically recorded by HOBO data loggers (16-bit Smart sensors, Onset Computer Company, Pocasset, MA, USA) at five-minute intervals. Soil temperature was measured using a thermocouple probe (12-Bit Temp Smart Sensor, Onset Computer Corporation, Pocasset, MA, USA). Soil volumetric moisture was measured using gypsum cast around two concentric stainless-steel electrodes (EC-5 Soil Moisture Smart Sensor, Wareham, MA, USA). Soil temperature and soil volumetric moisture were continuously measured from all 12 blocks across the three growing seasons.

2.4. *Microbial biomass carbon and nitrogen and soil inorganic nitrogen*

Soil samples were collected at a depth of 10 cm with a soil auger (4 cm in diameter) in mid-August in each growing season from 2011 to 2013. In each block, three soil cores adjacent to the aluminum frames were taken and mixed for a composite soil sample. All soil surface litter was excluded before the soil sampling. The large stones, visible plant and animal debris were removed after soil sampling in the field. Samples were then stored in a portable refrigerated box at 4 °C and immediately shipped to the laboratory for the further analysis within the following two weeks. Soil inorganic nitrogen content was measured from water solutes extracted from the soil samples using a flow injection auto-analyzer (FIAstar 5000 Analyzer, Denmark), which were then transformed into mg kg^{-1} dry soil.

Chloroform fumigation method was adopted to measure microbial biomass C and N. Briefly, about 10 g of fresh soil sample was fumigated with $CHCl_3$ for 24 h and extracted with 0.5 M K_2SO_4 in a shaker for one hour. Meanwhile, another 10 g of fresh soil sample was directly extracted as above without fumigation. Total C and N in both the fumigated and un-fumigated soil samples were measured with a TOC/TN Analyzer (Multi N/C 3100, Analytik Jena, Germany). Microbial biomass C and N were quantified as the differences in total C and N content for soil subsamples with and without fumigation.

2.5. *Plant biomass*

Because ecosystem CO_2 exchange was repeatedly measured during and across the three growing seasons, a non-destructive method was adopted to estimate plant biomass within each of the 12 aluminum frames within each block each year. Detailed information on the construction of the regression models can be found in Chen et al.(2016b), Chen et al. (2018) and Klein et al. (2004). Specifically, we documented the height and cover of each plant functional type using a 0.25 m^2 square frame with 100 equally distributed small squares near the aluminum frames in the ambient treatment in the middle of August. After the documentation of height and cover, we cut aboveground plants by plant functional types, which were then dried at 65 °C for 72 h for weight. Regression models were then constructed between cover, height and dry biomass for each plant functional type.

To ensure a sufficient sample size for the regression models, we recorded nine plots in each ambient block to produce 54 plots in total. The regression models were then used to estimate plant biomass within the aluminum frames for graminoid ($Y = 13.737 + 1.476\ C + 2.641\ H$, $R^2 = 0.921$, $F = 295$, $p < 0.001$. Y, C and H indicate plant biomass, cover and height, respectively), legume ($Y = -12.472 + 1.493\ C + 4.497\ H$, $R^2 = 0.966$, $F = 727$, $p < 0.001$), forb ($Y = -0.411 + 1.876\ C + 1.302\ H$, $R^2 = 0.589$, $F = 57$, $p < 0.001$) and total aboveground biomass ($Y = -26.236 + 2.242\ C + 7.216\ H$, $R^2 = 0.947$, $F = 455$, $p < 0.001$). Belowground biomass was also measured in each year of the experiment. To this end, a soil auger with 4 cm diameter was used to investigate belowground biomass at a depth of 40 cm, where over 95% of root biomass is located within this ecosystem (Chen et al., 2015). After washing these soil samples to isolate root biomass, roots were oven-dried at 65 °C for 72 h for weight.

2.6. *Measurements of ecosystem CO_2 exchange*

Ecosystem CO_2 exchange components were measured at least twice per month across the growing season (April to October) on clear and sunny days from 9:00 to 11:00 a.m. Measurements were taken from square aluminum frames (0.5 m for each side), which were permanently installed into soil to a depth of 2-3 cm in each ambient and fire block. Aluminum frames provided a flat base for the measurements of ecosystem CO_2 exchange between the CO_2 sampling chamber and soil surface. The chamber method has been widely used to measure grassland ecosystem CO_2 exchange (Niu et al., 2013). Detailed information on the chamber method can be found in our earlier publications (Chen et al., 2016a; Chen et al., 2016b; Chen et al., 2018).

For NEE, a transparent cubic glass chamber (50 cm for each side) attached to an infrared gas analyzer (LI-8100, LI-COR, Inc., Lincoln, NE, USA) was placed and sealed on the aluminum frame, from which CO_2 concentration changes within the chamber were recorded. The transparent chamber allowed over 90% of photosynthetic active radiation inputs. CO_2 concentration within the chamber was consecutively recorded for about two minutes after reaching the steady state condition. Two small electric fans (800~1000 rotations per minute) were installed in the opposite corners within the chamber to continuously stir the air inside the chamber during the measurements. A negative NEE value represents a net C uptake into the ecosystem, while a positive NEE value indicates a net C release to the atmosphere.

Following NEE measurements, the chamber was vented for at least one minute and then covered with an opaque cloth to remove any photosynthetic active radiation. Because light was eliminated, the CO_2 concentration captured was considered as ER. ER was measured using a similar method as the NEE measurement. Previous studies showed that the chamber-induced temperature and CO_2 concentration change were insufficient to affect photosynthesis and respiration during such short measurement periods. GPP was quantified as the difference between ER and NEE. A positive GPP value represents a C uptake into the ecosystem.

2.7. *Data analysis*

All observational data were first tested for normality using the Kolmogorov–Smirnov method, while all original data in this study could satisfy the normal distribution. Growing season averages of GPP, ER and NEE were computed from the monthly averages, which were firstly averaged in each month. Because all variables were repeatedly documented within a growing season or across the three growing seasons, a two-way repeated analysis of variance (ANOVA) was adopted to explore the effects of fire treatment, measuring time and their interactive effects on the studied variables. The two-way ANOVA was conducted in R using linear mixed-effects models in "*nlme*" package (Pinheiro et al., 2013). In the linear mixed-effects models, we set fire treatment, measuring time and their interactive effects as fixed effects and block as a random effect. Residuals and residual variances of the two-way ANOVA analysis were examined to ensure the normality and homogeneity.

The relationships between changes in ecosystem CO_2 exchange (GPP, ER and NEE) and changes in plant functional type biomass, soil temperature, soil volumetric moisture and soil inorganic N were also separately assessed using linear mixed-effects models in "*nlme*" package (Pinheiro et al., 2013). The R^2 value for the linear mixed models was computed by using the "*r.squaredGLMM*" function in the "*MuMIn*" package at $p < 0.05$. All data used in this study are available from the figshare (Wang et al., 2021) or from the online supplementary file.

3. Results

3.1. *Fire effects on biotic and abiotic factors*

Fire significantly increased growing season soil temperature by 0.9 °C in 2011, 1.0 °C in 2012 and 0.4 °C in 2013, with an average increase of 0.8 °C (by 6%) across the three growing seasons (Table 1). By contrast, fire significantly decreased growing season soil volumetric moisture by 3.7% in 2011, 3.2% in 2012 and by 2.5 % in 2013, with an average decrease of 3.1% across the three growing seasons (Table 1). Significant year effects were observed for both soil temperature and soil volumetric moisture, while the significant interactive effects of fire and year were only observed for soil volumetric moisture (Table S1).

Fire significantly increased aboveground biomass by 12, 22 and 19% in 2011, 2012 and 2013, respectively (Fig. 1). Regarding plant functional type biomass, fire significantly increased graminoid biomass by 11, 19 and 16% and legume biomass by 20, 31 and 30% in 2011, 2012 and 2013, respectively. Fire significantly increased forb biomass by 19% in 2012. Averaged across the three growing seasons, fire significantly increased aboveground biomass, graminoid biomass and legume biomass by 18, 16 and 27%, respectively. Similarly, fire significantly increased belowground biomass by 35% in 2011, by 51% in 2012 and by 36% in 2013, with an average increase of 41% across the three growing seasons. Two-way ANOVA analysis showed significant year effects and significant interactive effects of fire and year on aboveground biomass, graminoid biomass and legume biomass, whereas those effects were not observed either for forb biomass or for belowground biomass (Table S1).

When separately analyzed in each growing season, fire significantly decreased microbial biomass C by 12 and 15% in 2011 and 2012, respectively (Fig. 2), whereas microbial biomass N was not affect in any of the three growing seasons. Consequently, fire significantly decreased microbial biomass C:N by 9% in 2012 (Fig. 2). In addition, fire significantly increased soil inorganic N by 12% in 2011, by 15% in 2012 and by 12% in 2013, with an average increase of 13% across the three growing seasons (Fig. 2). Significant year effects were observed for microbial biomass C, microbial biomass N, microbial biomass C:N and soil inorganic N, whereas there was no interactive effects of fire and year on these variables (Table S1).

Table 1
Precipitation, air temperature, soil temperature and soil volumetric moisture during the three growing seasons.

Year	Soil temperature (°C)		Soil volumetric moisture (%)		Precipitation (mm)	Air temperature (°C)
	Ambient	Fire	Ambient	Fire		
2011	10.9 ± 0.1	11.8 ± 0.1*	13.8 ± 0.3	10.1 ± 0.3*	447	1.5
2012	11.6 ± 0.1	12.6 ± 0.1*	14.4 ± 0.3	11.2 ± 0.3*	471	1.4
2013	12.6 ± 0.1	13.0 ± 0.2*	11.8 ± 0.2	9.3 ± 0.2*	455	2.0
Mean	11.7 ± 0.1	12.5 ± 0.1*	13.3 ± 0.2	10.2 ± 0.2*	458	1.6

Data presented are means ± standard errors for six replicates. Asterisks indicate significant difference at $p < 0.05$.

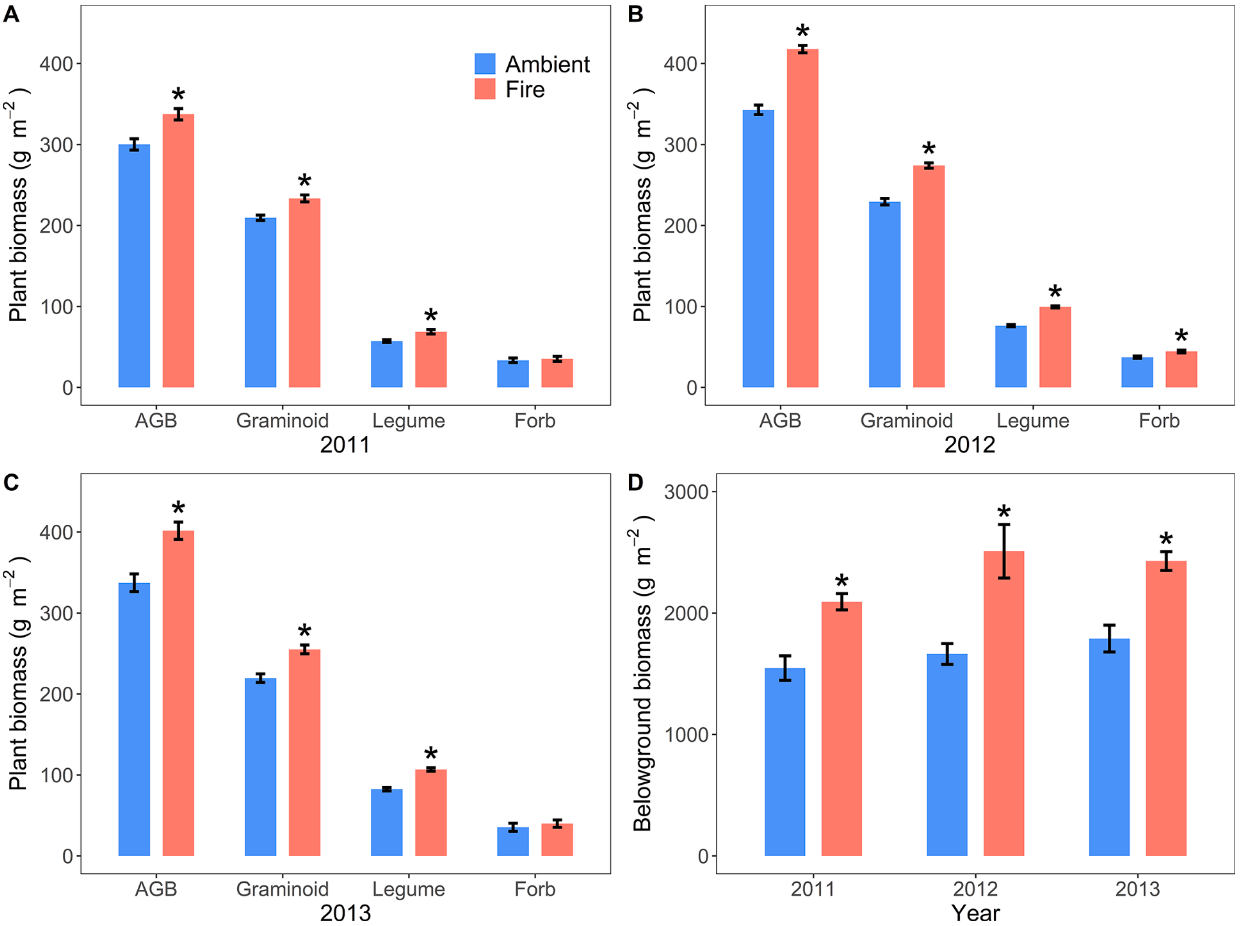

Fig. 1. Annual (A-C) plant functional biomass, total aboveground biomass (AGB) and (D) total belowground biomass in ambient and fire treatments across the three growing seasons. Values are mean ± standard errors for six replicates. Asterisk indicates significant difference at $p < 0.05$.

3.2. Fire effects on ecosystem CO_2 exchange

Across the three growing seasons, fire significantly enhanced GPP by an average of 13%. When separately evaluated in each year, fire significantly enhanced GPP by 16% in 2012 and by 14% in 2013, whereas there was no difference in 2011 (Fig. 4). Fire on average significantly enhanced NEE by 20% across the three growing seasons (i.e. more negative NEE in fire blocks) (Fig. 4). Specifically, fire significantly enhanced NEE by 22% in both 2012 and 2013, but there was no clear effects in 2011 (Fig. 4). Fire significantly raised ER by 11% in 2012 and by 9% in 2013, with an average increase of 9% across the three growing seasons (Fig. 4). There were significant year effects on GPP, ER and NEE, but no interactive effects of fire and year were observed for them (Table 2 and Fig. 3).

3.3. Relations between ecosystem CO2 exchange and biotic and abiotic factors

Seasonal variations in GPP, ER and NEE were closely positively associated with the seasonal variations in soil temperature and soil volumetric moisture, regardless of the fire treatment (Fig. S1). Fire-induced increases in soil temperatures were not directly related to post-fire stimulation of GPP, ER and NEE (Fig. 5). However, reductions in soil moisture significantly positively correlated with the changes in GPP, ER and NEE (Fig. 5). The increases in soil inorganic N were positively and significantly correlated with the increases in GPP and NEE, whereas there was no clear relationship with ER (Fig. 5). In addition, there were no significant relationships between fire-induced changes in microbial biomass C and N and their ratio and the corresponding changes in GPP, ER and NEE (Figs. 5 and S2).

Significant positive relationships were consistently observed between fire-induced changes in aboveground biomass, graminoid biomass and legume biomass and fire-induced changes in GPP, ER and NEE (Fig. 6). However, there was no clear relationship between fire-induced changes in forb biomass and the corresponding changes in GPP, ER and NEE (Fig. 6).

Table 2

Linear mixed-effects models of variance for year, fire and their interactive effects on gross primary production (GPP), ecosystem respiration (ER) and net ecosystem exchange (NEE).

Variable	Treat	numDF	denDF	F-value	p-value
GPP	Intercept	1	20	2878.664	<.0001
	Burn	1	10	11.361	0.007
	Year	2	20	65.353	<.0001
	Burn * Year	2	20	1.995	0.162
ER	Intercept	1	20	3071.626	<.0001
	Burn	1	10	5.286	0.044
	Year	2	20	63.936	<.0001
	Burn * Year	2	20	1.715	0.205
NEE	Intercept	1	20	2514.774	<.0001
	Burn	1	10	20.969	0.001
	Year	2	20	21.349	<.0001
	Burn * Year	2	20	0.680	0.518

numDF: numerator degrees of freedom. denDF: denominator degrees of freedom. Linear mixed-effects models were conducted separately for GPP, ER and NEE. Fire, year and their interaction (Fire * Year) were considered as fixed factors, while block was considered as a random factor.

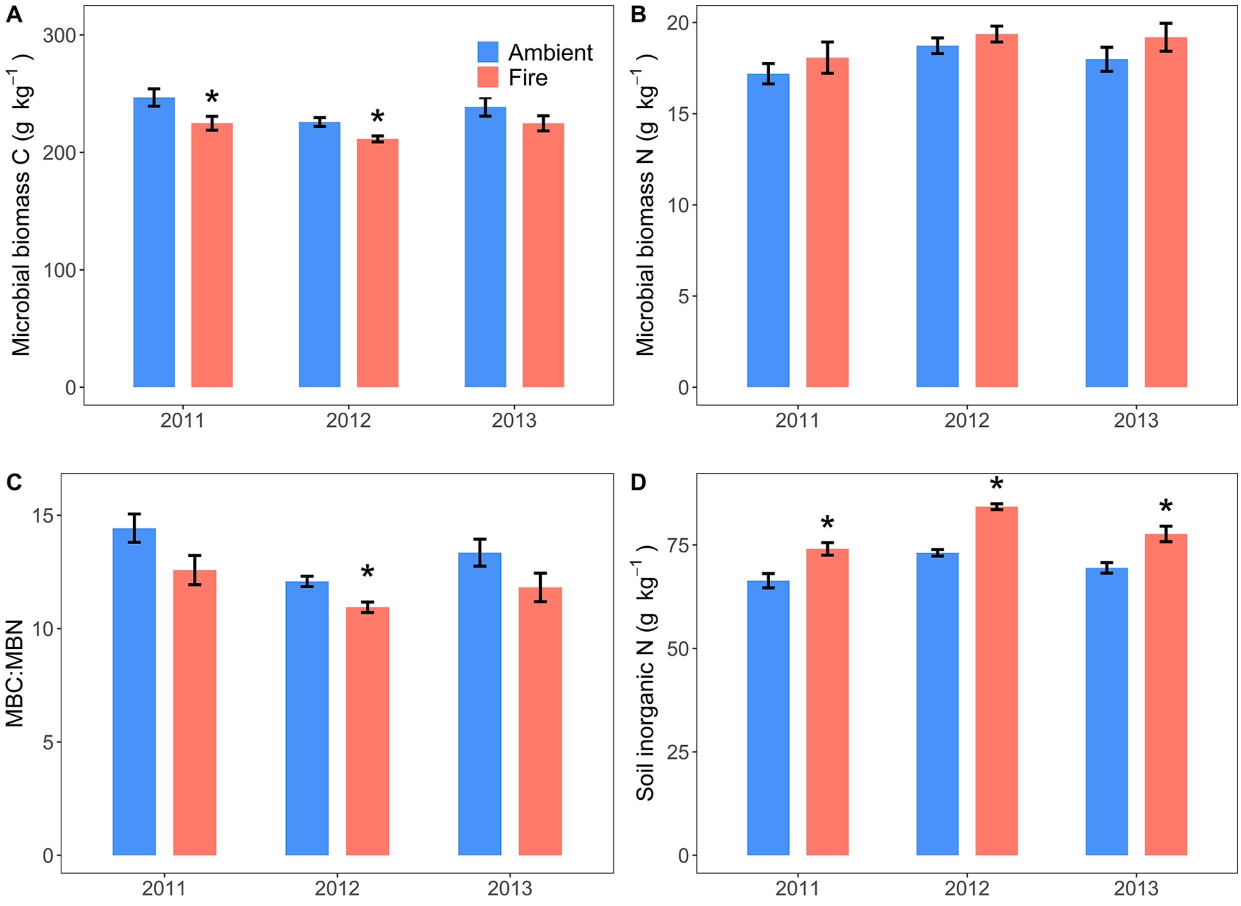

Fig. 2. Annual average (A) microbial biomass carbon (MBC), (B) microbial biomass nitrogen (MBN), (C) MBC:MBN and (D) soil inorganic nitrogen in ambient and fire treatments across the three growing seasons. Values are mean ± standard errors for six replicates. Asterisk indicates significant difference at $p < 0.05$.

4. Discussion

Our results revealed post-fire co-stimulation of GPP and ER in an alpine meadow grassland on the Tibetan Plateau. The larger stimulation of GPP than ER led to a net increase in NEE after fire and thus turning this ecosystems into a post-fire net C sink. Fire-induced changes in GPP, ER and NEE were not fully explained by the corresponding changes in soil temperature, soil moisture, or soil microbial biomass. Rather, post-fire stimulation of GPP, ER and NEE were closely associated with fire-induced increases in graminoid biomass, legume biomass and soil inorganic N content. Our results underscore how complete knowledge of GPP, ER and NEE can provide mechanistic understanding of post-fire ecosystem CO_2 exchange.

4.1. Fire effects on microclimate, microbial biomass and soil inorganic N

Our study found that fire significantly increased soil temperature but decreased soil moisture (Table 1). Changes in soil temperature and soil moisture were consistent with results from other studies (Dore et al., 2012; Ma et al., 2004). Removal of plant residuals and dead debris by fire reduced surface albedo, which could increase soil temperature and decrease soil moisture (Dore et al., 2012; McCarthy and Brown, 2006; Obrist et al., 2003). Increases in soil temperature and decreases in soil moisture held true in the second and third year after fire (Table 1), when we observed larger canopy cover from the fire than the ambient blocks (Fig. 1). One explanation is that it takes time for the surface litter accumulation in the fire blocks, even though the rapid recovery of canopy cover. Meanwhile, the higher water demand associated with the enhanced post-fire plant growth could further reduce the soil moisture content.

Fire significantly reduced soil microbial biomass C, while having no effect on microbial biomass N (Fig. 2). Post-fire changes in microbial biomass C and N were reported from many other studies, but the results were equivocal (Certini, 2005; Dooley and Treseder, 2012; Holden and Treseder, 2013). Reductions in microbial biomass C might be related to the adverse effects caused by the high temperatures, reductions in soil moisture, or losses in soil labile C substrates (Dooley and Treseder, 2012; Wüthrich et al., 2002). The absence of significant fire effects on microbial biomass N may be due to the net balance between the increased microbial N immobilization and mineralization processes (Turner et al., 2007). In addition, fire significantly decreased microbial biomass C:N, which indicated the possible changes in microbial community composition (Wang et al., 2012). For example, fire significantly reduced gram positive and negative bacterial abundance in California annual grasslands (Docherty et al., 2012).

Fire significantly increased soil inorganic N content (Fig. 2), consistent with previous findings (Certini, 2005; Docherty et al., 2012). Three mechanisms may contribute to the post-fire increases in soil inorganic N content. First, microbial ammonium immobilization could play crucial roles in securing post-fire N supply (Wan et al., 2001). Results from the Greater Yellowstone ecosystem showed substantial microbial immobilization of ammonium immediately after fire, which could provide N sources during post-fire recover stage (Turner et al., 2007). Second, enhanced N mineralization could partly contribute to the higher soil inorganic N content (Certini, 2005; Wan et al., 2001). For example, previous study have found that prescribed fire significantly increased N mineralization and nitrification rates in a suburban forest ecosystem of subtropical Australia (Zhang et al., 2018b). Third, ash inputs after fire might also contribute to increasing soil inorganic N content (Grogan et al., 2000), but such ash impacts were not examined in the study site.

4.2. Fire effects on plant functional type biomass

Fire significantly increased graminoid biomass, legume biomass and total aboveground biomass in our study (Fig. 3). Post-fire shifts in plant functional type biomass were widely observed in many ecosystems (Bernhardt et al., 2011; Koerner and Collins, 2014; Wang et al., 2015). Legume is able to fix atmospheric N through symbiotic relationships with soil-dwelling bacteria and acquire phosphorus by maintaining relative active soil phosphatase activity (Png et al., 2017; Vance, 2001). The strong N and phosphorus acquisition capabilities will enable legume to outcompete other species after fire (Png et al., 2017; Simms et al., 2006). Graminoid is the dominant species on the study site, which has evolved a range of functional traits (e.g., the needle leaf) to adapt to the low soil temperature and low soil moisture (Chen et al., 2020; Dorji et al., 2013; Klein et al., 2004). In addition, the belowground bud banks associated with graminoid could probably provide another pathway for their survival after fire disturbance (Wang et al., 2018).

On the contrary, fire had no effect on forb biomass (Fig. 3), despite forb only accounted for 11% of the total aboveground biomass. One explanation might be that forb is more likely limited by fire-induced lower soil moisture due to the shallower root systems compared to other species (Chen et al., 2020; Chen et al., 2016b; Klein et al., 2004). In addition, fire significantly increased belowground biomass (Fig. 3). This might be related to the post-fire enhanced C allocation belowground (Certini, 2005; Neary et al., 1999). Alternatively, dead roots were not excluded when measuring belowground biomass in this study, which might overestimate belowground biomass in the fire treatments.

4.3. Net ecosystem CO_2 uptake after fire

Fire significantly increased GPP more than ER, resulting in enhanced NEE across the three years (Figs. 3 and 4). Seasonal variations in GPP, ER and NEE were within the range reported by other studies on the Tibetan Plateau (Abaker et al., 2018; He et al., 2014; Luo et al., 2015). However, GPP, ER and NEE were rarely simultaneously measured under fire treatments, limiting our comparison with other studies.

Three mechanisms may contribute to the post-fire stimulation of GPP, ER and NEE.

First, shifts in plant functional type biomass after fire could drive the changes in ecosystem CO_2 exchange (Chen et al., 2016b; Ward et al., 2007). This explanation is supported by the positive relationships between fire-induced increases in graminoid and legume biomass and the corresponding changes in GPP, ER and NEE (Fig. 6). In our study site, legume has larger leaf area and graminoid is generally taller than other species, which could enable their competition for light and photosynthesis (Chen et al., 2020; Chen et al., 2016b). Moreover, various plant species may differ in their photosynthesis and respiration capabilities (Bagchi and Ritchie, 2010; Lavorel and Garnier, 2002). For example, fire-induced one unit increase in legume or graminoid biomass corresponded to roughly a 12 and 14 unit increases in NEE, respectively (Fig. 6). Thus, relatively large increases in graminoid and legume biomass appeared to drive increased net ecosystem CO_2 uptake after fire. In addition, increases in legume biomass within a community could increase soil and leaf N content due to their N fixation capability, which could help stimulate ecosystem photosynthesis and primary production (Adams et al., 2016; Lee et al., 2003).

Second, post-fire-induced increases in soil inorganic N content were positively related to increased GPP and NEE, but not ER (Fig. 5). These results suggest that post-fire stimulation of NEE to N pulses are primarily driven by increased GPP (Homann et al., 2011; Muqaddas et al., 2019). Increased soil inorganic N content after fire could promote plant and microbial metabolic activities and ecosystem CO_2 exchange processes (Certini, 2005; Grogan et al., 2000; Neary et al., 1999). This explanation is supported by other manipulative N addition studies near the study site, in which additional N significantly enhanced GPP, ER and NEE on the Tibetan Plateau (Fang et al., 2012; Ma et al., 2018). Increases in soil inorganic N content might also increase ecosystem CO_2 uptake through a range of indirect processes, for example, water use efficiency, shifts in plant phenology and changes in plant functional traits (Palmroth et al., 2014; Zhang et al., 2018a).

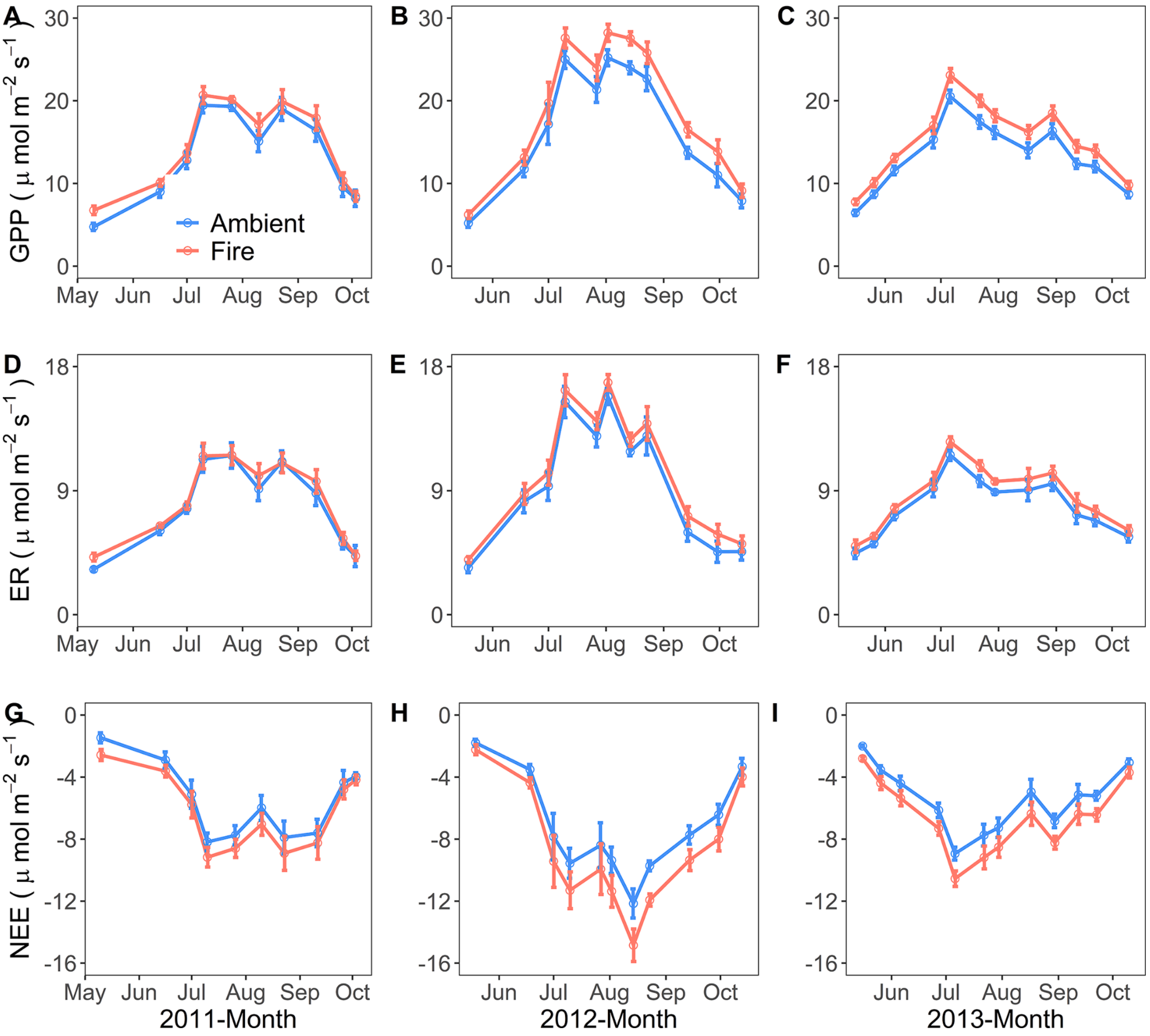

Fig. 3. Seasonal variations of (A, B and C) gross primary productivity (GPP), (D, E and F) ecosystem respiration (ER) and (G, H and I) net ecosystem exchange (NEE) in ambient and fire treatments. Values are mean ± standard errors for six replicates. Negative values of NEE represent net ecosystem C uptake.

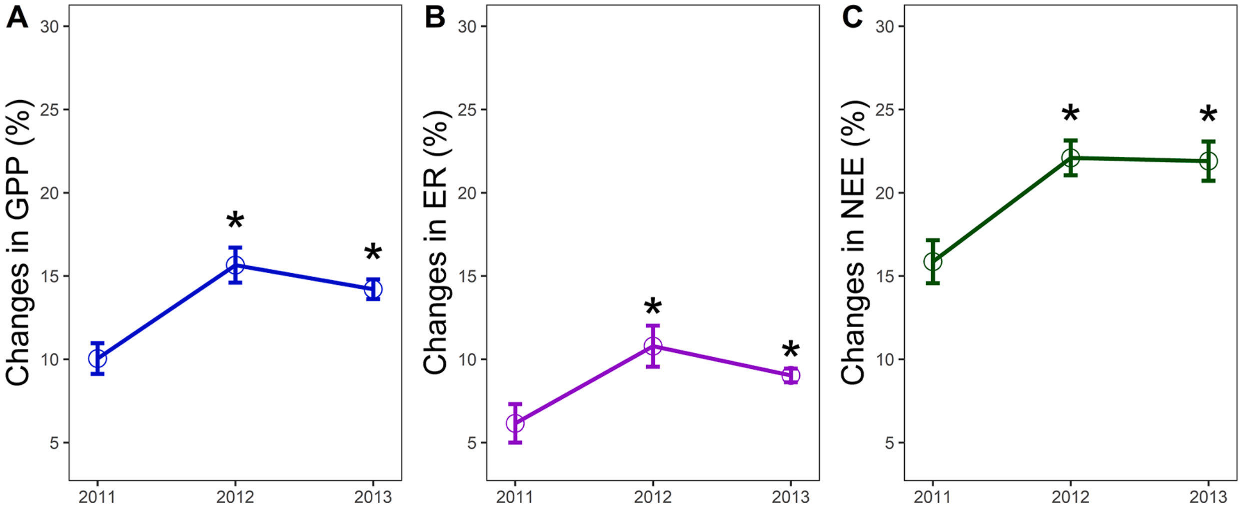

Fig. 4. Annual average changes in gross primary productivity (GPP), ecosystem respiration (ER) and net ecosystem exchange (NEE) across the three growing seasons in ambient and fire treatments. Values are mean ± standard errors for six replicates. Asterisk indicates significant fire effect at $p < 0.05$.

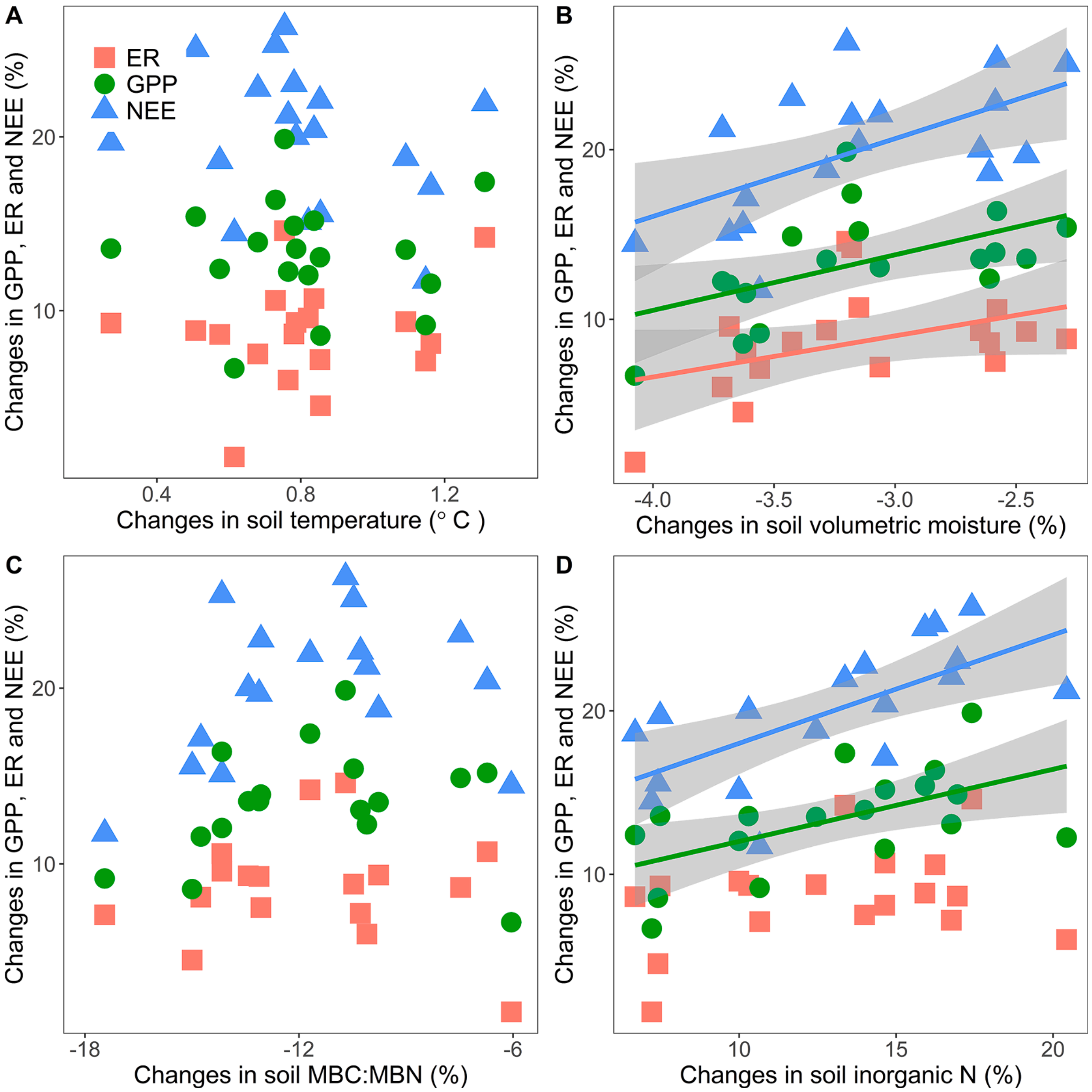

Fig. 5. Relationships of changes in gross primary production (GPP), ecosystem respiration (ER) and net ecosystem exchange (NEE) with the corresponding changes in (A) soil temperature, (B) soil volumetric moisture, (C) microbial biomass carbon:nitrogen and (D) soil inorganic nitrogen. Positive relationships were observed between changes in soil volumetric moisture and changes in GPP ($Y = 3.271\ X + 23.616$, $R^2 = 0.288$, df $= 16$, $F = 6.456$, $p = 0.0218$), ER ($Y = 2.424\ X + 16.300$, $R^2 = 0.172$, df $= 16$, $F = 3.321$, $p = 0.087$) and NEE ($Y = 4.583\ X + 34.401$, $R^2 = 0.350$, df $= 16$, $F = 8.615$, $p = 0.010$). Positive relationships were observed between changes in soil inorganic nitrogen and changes in GPP ($Y = 0.441\ X + 7.601$, $R^2 = 0.328$, df $= 16$, $F = 7.799$, $p = 0.013$) and NEE ($Y = 0.663\ X + 11.385$, $R^2 = 0.459$, df $= 16$, $F = 13.570$, $p = 0.002$).

Third, seasonal variations in GPP, ER and NEE were positively related to the soil temperature and soil moisture (Fig. S1), suggesting the important roles of soil temperature and soil moisture in modulating ecosystem CO_2 exchange on the Tibetan Plateau (Felton et al., 2019; Luo, 2007; Niu et al., 2013; Yang et al., 2018). However, there were no direct links between fire-induced changes in soil temperature and the changes in GPP, ER and NEE (Fig. 5). On the contrary, increases in GPP, ER and NEE were positively correlated with changes in soil moisture (Fig. 5), suggesting that fire-induced reductions in soil moisture might not necessarily limit ecosystem CO_2 sequestration. It is likely that reductions in soil moisture did not reach the threshold that limited plant growth during the experimental periods. One supporting evidence might be that we observed larger precipitation during the experimental periods than the long-term historical records. Alternatively, post-fire increases in soil inorganic N content could enhance ecosystem water use efficiency as the majority regions on the Tibetan Plateau were also limited by soil N availability (Fang et al., 2012; Ma et al., 2018).

4.4. *Rapid recovery of ecosystem C sequestration*

When analyzed separately for each growing season, post-fire stimulation of GPP and NEE were much greater in the second and the third year after fire than in the first year after fire (Fig. 4). Our results suggest rapid recovery of ecosystem C sequestration after fire disturbance in the meadow grassland, which is consistent with studies from other grasslands (Beringer et al., 2007; Fellows et al., 2018). Four mechanisms may account for the rapid recovery of ecosystem C sequestration in our study site.

First, the mean annual temperature and the total annual precipitation during the experimental periods were higher than the long-term averaged historical records, providing optimum conditions for post-fire plant re-growth, especially in the cold and arid Tibetan Plateau (Chen et al., 2016a; Chen et al., 2019). From this standpoint, the rapid post-fire stimulation of GPP and NEE might be site-specific. Thus, cautions are required when interpreting our results with other studies from

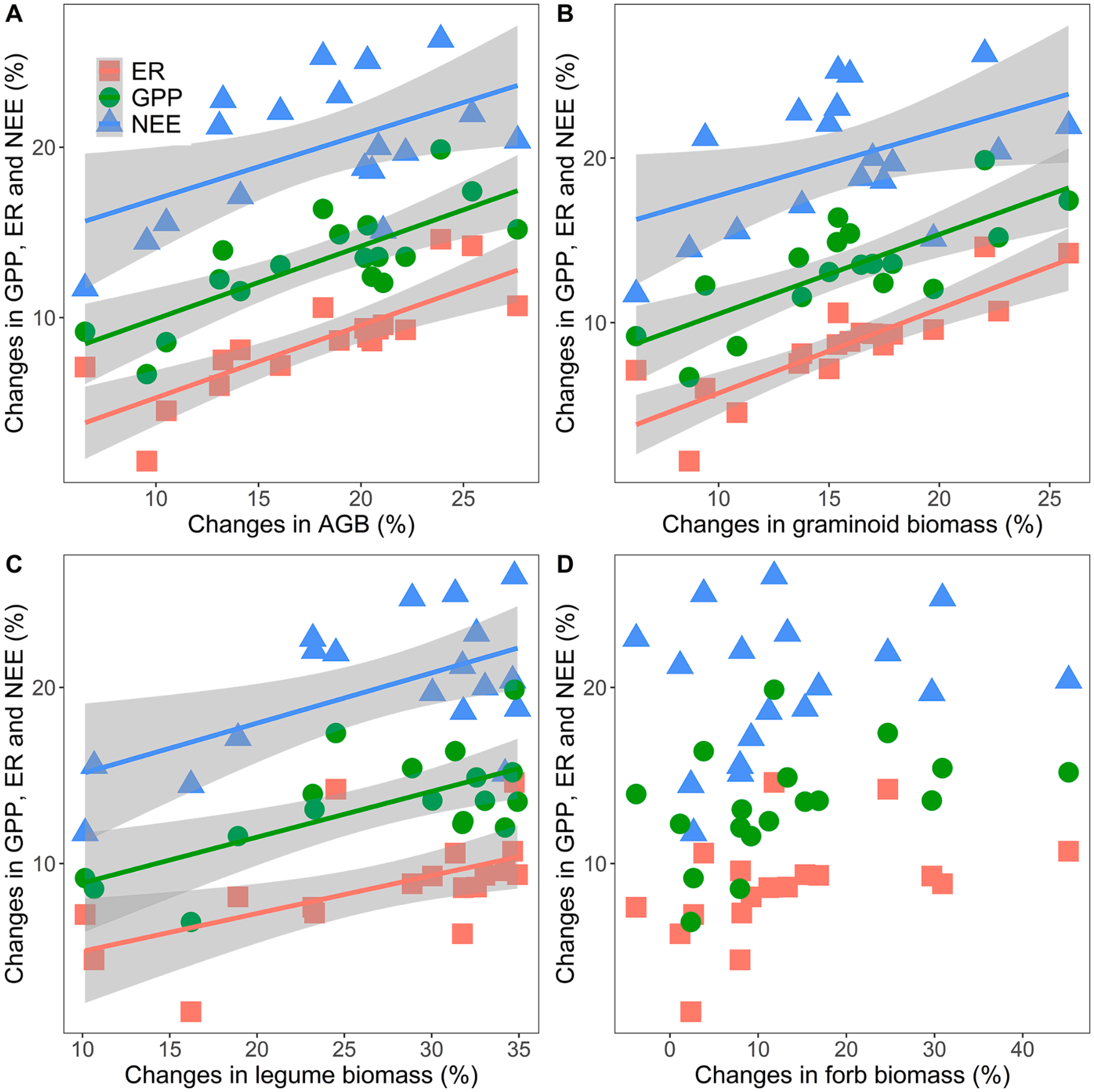

Fig. 6. Relationships of changes in gross primary production (GPP), ecosystem respiration (ER) and net ecosystem exchange (NEE) with the corresponding changes in (A) changes in aboveground biomass (AGB), (B) changes in graminoid biomass, (C) changes in legume biomass and (D) changes in forb biomass. Positive relationships were observed between changes in aboveground biomass and changes in GPP ($Y = 0.427\ X + 5.665$, $R^2 = 0.596$, df = 16, $F = 23.630$, $p < 0.001$), ER ($Y = 0.425\ X + 1.052$, $R^2 = 0.644$, df = 16, $F = 28.880$, $p < 0.001$) and NEE ($Y = 0.378\ X + 13.188$, $R^2 = 0.290$, df = 16, $F = 6.536$, $p = 0.021$). Positive relationships were observed between changes in graminoid biomass and changes in GPP ($Y = 0.483\ X + 5.692$, $R^2 = 0.588$, df = 16, $F = 22.870$, $p < 0.001$), ER ($Y = 0.513\ X + 0.587$, $R^2 = 0.720$, df = 16, $F = 41.180$, $p < 0.001$) and NEE ($Y = 0.389\ X + 13.831$, $R^2 = 0.236$, df = 16, $F = 4.944$, $p = 0.041$). Positive relationships were observed between changes in legume biomass and changes in GPP ($Y = 0.260\ X + 6.297$, $R^2 = 0.454$, df = 16, $F = 11.790$, $p = 0.003$), ER ($Y = 0.215\ X + 2.865$, $R^2 = 0.338$, df = 16, $F = 13.310$, $p = 0.002$) and NEE ($Y = 0.285\ X + 12.262$, $R^2 = 0.339$, df = 16, $F = 8.216$, $p = 0.011$).

different climatic regions. Second, rapid increases in canopy cover immediately after fire could reduce the non-productive evaporative losses of soil moisture (Dore et al., 2012; Obrist et al., 2003), thereby providing more available water for transpiration and supporting the large increases in GPP and NEE in the second and third year after fire. This explanation is confirmed by the diminished fire-induced reductions in soil moisture over time after fire (Table 1). Although enhanced plant growth could increase water consumption, this can be partly compensated by the larger precipitation during the experimental periods. Third, removal of aboveground litter and dead debris by fire could significantly increase radiation inputs and soil temperature (Dore et al., 2012; Ma et al., 2004), especially during the early stage after fire disturbance. Higher soil temperature could accelerate the melting of frozen soils and the release of nutrients in the study site, which may advance plant phenology and regrowth potential (Chen et al., 2020). Fourth, the entire study site was fenced during the experimental period, excluding the grazing by sheep, yak and other animals (Chen et al., 2018). This will support the rapid post-fire ecosystem recovery, especially for the annual meadow grassland. In addition, there were no interactive effects of fire and year on ER, which was caused by the contrasting responses of the sources components of ER after fire (Chen et al., 2019). Specifically, fire decreased the contribution of soil respiration to ER, while increasing the proportion of aboveground plant respiration to ER (Chen et al., 2019).

4.5. *Uncertainties and implications*

Our study consisted of three-year continuous observations of ecosystem CO_2 exchange after one prescribed fire disturbance on the

Tibetan Plateau. However, fire effects on ecosystem CO_2 exchange are closely related to the vegetation type or fire regimes (e.g., time, intensity and frequency) (Bowman et al., 2009; Westerling et al., 2006). For example, a minimum of five years were required to recover aboveground C stock lost due to the combustion in mesic sagebrush ecosystems (Fellows et al., 2018), while it took 30 years or more in boreal forests (Amiro et al., 2000). Thus, cautions are required when comparing our results to studies from other vegetation types or different fire regimes (Gough et al., 2007; Katherinep et al., 2006; Turetsky et al., 2015). To our best knowledge, fire effects on ecosystem CO_2 exchange are insufficiently investigated on the Tibetan Plateau, partly due to the harsh physical working environment. This limits our comparison to other studies conducted under similar vegetation types. Considering the increased fire frequency and intensity on the Tibetan Plateau as well as their crucial roles on ecosystem CO_2 exchange, more research from the Tibetan Plateau are warranted. For example, the interactive effects of fire and local herbivory grazing managements should be investigated for future sustainable grassland managements on the Tibetan Plateau.

Our results stress the novel links between fire-induced changes in plant functional type biomass and ecosystem CO_2 exchange. However, changes in plant functional type biomass are not well considered in current Earth Systems Models (Atkin et al., 2015; Lavorel and Garnier, 2002). Due to the accompanied shifts in plant functional type biomass with global climate change or anthropogenic disturbance (Bjorkman et al., 2018; Chen et al., 2020; Klein et al., 2004), we may over- or under-estimate ecosystem CO_2 exchange if shifts in plant functional type biomass are not explicitly considered (Asaf et al., 2013; Wolz et al., 2017). The uncertainties may be more evident for long-term studies because shifts in plant functional type biomass are more likely to occur in long-term studies (Bjorkman et al., 2018). Thus, more research on fire-induced changes in plant functional type biomass and their implications for ecosystem CO_2 exchange dynamics should be a future research priority.

5. Conclusion

Our study demonstrates that fire significantly stimulates GPP more than ER on the Tibetan Plateau, highlighting that NEE has the capacity to rapidly respond to fire treatment in this ecologically sensitive region, driving the post-fire system towards a net C sink. Despite reductions in soil moisture being weakly positively related to the post-fire changes in GPP, ER and NEE, changes in soil moisture and soil temperature cannot fully explain the variations in ecosystem CO_2 exchange. Furthermore, fire-induced increases in graminoid biomass, legume biomass and soil inorganic nitrogen content are strongly positively associated with changes in GPP, ER and NEE. The stimulating effects from shifts in plant functional type biomass outweigh the negative effects associated with the reduced soil moisture. Our study suggests that comprehensive post-fire documentation of GPP, ER and NEE can provide a novel and valuable perspective to advance the understanding of ecosystem CO_2 exchange. More studies from other ecosystems and representation of post-fire co-stimulation of GPP and ER in Earth System Models will further elucidate the role of fire in ecosystem C exchange dynamics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was funded by Aarhus University Research Foundation AUFF Starting Grants (AUFF-E-2019-7-1) and Marie Skłodowska-Curie Individual Fellowship H2020-MSCA-IF-2018 (No. 839806).

Authorship

JC, YL, LC and JC designed the study. JC, DW and YFZ collaborated on the field observation, data synthesis and interpretation. JC, DW and AJF wrote the manuscript. All authors contributed substantially to revisions.

Data availability

All data used in this study are available from the figshare (https://figshare.com/s/058298a1a0134cfaa9a1) or from the online supplementary file.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108388.

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