



Soil microbial CO₂ fixation plays a significant role in terrestrial carbon sink in a dryland ecosystem: A four-year small-scale field-plot observation on the Tibetan Plateau

Hao Chen^{a,1}, Fei Wang^{a,c,1}, Weidong Kong^{a,b,c,*}, Hongzeng Jia^{a,c}, Tianqi Zhou^{a,c}, Ri Xu^{a,b}, Guangjian Wu^{b,d}, Junbo Wang^{b,d}, Jinshui Wu^e

^a Key Laboratory of Alpine Ecology, Institute of Tibetan Plateau Research, Chinese Academy of Sciences (CAS), Beijing 100101, China

^b CAS Center for Excellence in Tibetan Plateau Earth Sciences, Chinese Academy of Sciences, Beijing 100101, China

^c College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

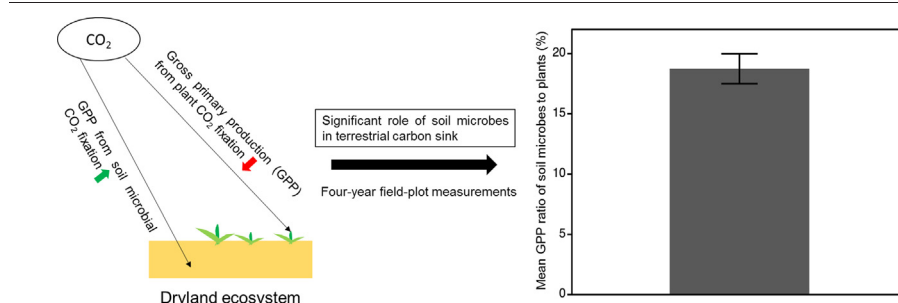
^d Key Laboratory of Tibetan Environment Changes and Land Surface Processes, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China

^e Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China

HIGHLIGHTS

- Four-year field observation of soil microbial and plant GPP was performed.
- Soil microbial GPP accounts for 18.2% of plant GPP.
- Soil microbial GPP has a greater interannual variation than plant GPP.
- Soil microbial CO₂ fixation substantially contributes to GPP in dry grasslands.
- Soil moisture but not temperature drives the GPP ratio of soil microbes to plants.

GRAPHICAL ABSTRACT



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ABSTRACT

Assessment of the global terrestrial carbon (C) sink remains uncertain, and the uncertainty is largely derived from dryland ecosystems. Here we investigated the uncertainty and dynamics of gross primary productivity (GPP) by distinguishing the contributions of soil microbial primary producers and plants to CO₂ fixation during four sequential growing seasons in a fragile dry grassland on the Tibetan Plateau. The results demonstrated that soil microbial GPP consistently accounted for a high proportion of plant GPP (18.2%), and both exhibited similar seasonal patterns during the four-year observation. Soil microbial GPP demonstrated a much greater interannual variation (76.1%) than plant GPP (15.1%), indicating that the interannual GPP uncertainty could be largely from microbial primary producers. Regression analysis indicated that plant GPP had higher sensitivity (demonstrated by slope) than soil microbial GPP to both soil water content and temperature. The GPP ratio of soil microbes to plants also demonstrated a clear seasonal change, and peaked in July in the four-year observation, with a minimum interannual variation (6.8%). The GPP ratio enhanced with increasing soil water content ($P < 0.001$), but did not correlate with soil temperature. Our findings suggest the great potential of soil microbial GPP, and challenge the plant-oriented models of terrestrial C estimation, which account for plant GPP but ignore soil microbial GPP. Thus, a more robust framework needs to incorporate both soil microbial and plant GPPs for accurately assessing C balance.

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* Corresponding author at: Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Building 3, Courtyard 16, Lincui Road, Chaoyang District, Beijing 100101, China.

E-mail address: wdkong@itpcas.ac.cn (W. Kong).

¹ These authors contributed equally to the manuscript.

1. Introduction

Drylands cover more than 40% of the Earth's land surface, constituting the most extensive terrestrial biome, and play a dominant role in terrestrial C sink (Poulter et al., 2014; Ahlström et al., 2015; Le Quéré et al., 2018; Green et al., 2019). Dryland regions, especially where have naturally sparse vegetation but widely distributed soil microbial crusts under water limitation (Belnap, 2003; Reynolds et al., 2007), may greatly introduce uncertainties in assessing ecosystem C dynamics and gross primary production (GPP) (Beer et al., 2010; Ballantyne et al., 2015; Fan et al., 2019; Kheirfam, 2020). Given the accelerated dryland expansion (Huang et al., 2016), a thorough understanding of the GPP uncertainties in dryland ecosystems is urgently required to assess the local and global C stock balance and their responses to climate change.

Terrestrial GPP includes contributions from both plants and soil microbial primary producers (Tang et al., 2020). However, the widely used techniques for estimating GPP are for plant GPP, rather than soil microbial GPP, such as remote sensing-based Earth system models and *in situ* observations (Zhang et al., 2016; Wang et al., 2017; Cui et al., 2019; Fatichi et al., 2019; Pei et al., 2020). Therefore, soil microbial GPP has been seriously ignored, although these primary producers have been evidenced to play a significant role in CO₂ fixation (Maestre et al., 2013; Weber et al., 2016). It has long been recognized that biological soil crusts (BSCs, including mosses, lichens, bacteria, and fungi), a typical type of soil primary producers, play an important role in fixing CO₂ in drylands (Maestre et al., 2013; Su et al., 2013; Huang et al., 2014). Recent studies demonstrate that free microbial primary producers, beside BSC, also sequester abundant amounts of atmospheric CO₂ in diverse soils (Miltner et al., 2004; Yuan et al., 2012; Ge et al., 2013; Zhao et al., 2018). Primary producers and productivity are both sensitive to environmental changes in drylands, for instance, drought decreases vegetation photosynthesis rate and growth, and consequently reduces terrestrial ecosystem productivity (Wolf et al., 2016; He et al., 2018; Stocker et al., 2019). In contrast, soil microbes can better adapt to harsh conditions (such as dry and cold) (Beer et al., 2009), thereby grow faster and have increasing CO₂-fixing efficiency than plants (Usui and Ikenouchi, 1997). The high adaptive capacity of soil primary producers is evidenced by the wide distribution of BSCs and CO₂-fixing genes (e.g. *cbbL* gene) in drylands (Belnap, 2003; Zhao et al., 2018). However, soil microbial GPP has not drawn much attention in large-scale GPP estimations by satellite monitoring, as remote sensing-based methods commonly use information on solar radiation and vegetation greenness and type, but do not take the soil microbial primary producers into account (Fan et al., 2019; Fatichi et al., 2019; Stocker et al., 2019). The individual contributions of soil microbes and plants to terrestrial GPP, and their distinct responses to environmental changes have not been distinguished (Maestre et al., 2013; Chen et al., 2017; Cui et al., 2019).

In this study, an *in situ* field observation of soil microbial and plant GPP was conducted in a dry alpine steppe on the Tibetan Plateau. The objectives were: 1) to evaluate the relative importance of soil microbes, compared to plants, in contributing terrestrial GPP and 2) to investigate their monthly and annually variations in response to temperature and water conditions in the dryland ecosystem. We hypothesized that soil microbial CO₂ fixation would account for a considerable part of plant GPP, and the GPP ratio of soil microbes to plants varies with seasons by altering temperature and water content.

2. Materials and methods

2.1. Description of study site

The study site is located in Nam Co Station for Multisphere Observation and Research, Institute of Tibetan Plateau Research, Chinese Academy of Sciences (N 30°46', E90°59', 4730 m above sea level, Fig. S1). The Nam Co site is at the foot of the Mt. Nyenchen Tanglha and the

terrain here is flat. The region represents a typical dry steppe (You et al., 2007; Wei et al., 2014, 2015). The region is under the control of the Indian Monsoon in summer and the Westerlies in the rest seasons. Over the past four decades, the average annual precipitation is 415 mm (with large interannual variation ranging from 295 to 550 mm), of which 80%–90% occurs in growing seasons from May and September. The average annual temperature is −0.6 °C. The region has long, cold winters and short, cool summers, with strong solar radiation (max: 317 W m^{−2} in May) and low air pressure at 571 h Pa. The dominant vegetation species are *Stipa Purpurea* and *Kobresia Pygmaea* with total coverage of 60–80%. Other vegetation species included *Oxytropis microphylla*, *Leontopodium pusillum*, *Androsace tapete*, *Sibbaldia adpressa*, *Potentilla* spp., *Saussurea stoliczkai*. The heights of the plants ranged from 1 to 10 cm (Lu et al., 2009; Zhu et al., 2015; Wang et al., 2020). The well-developed biological soil crusts are inlaid among the plants, with dominant types of lichens (Fig. S1). In our previous investigation, soil autotrophic microbial communities in the biological soil crusts were classified as *Cyanobacteria*, *Rhizobiales* and *Actinobacteria* (Zhao et al., 2018). The soil is sandy silt at an early stage of weathering with soil organic C of 1.5%, cation exchange capacity of 54.4 mmol kg^{−1}, and pH value of 7.8 (Wei et al., 2014). The research site has history of moderate grazing in recent decades, and has been fenced for scientific use since 2005.

2.2. Field experimental design

The field experimental design is shown in Fig. S1. The experiment contained two treatments (with plants and without plants for gross primary productivity, GPP). The plots (10 in total) were distributed with five randomized blocks in a uniform area of 6 × 10 m. The size of each plot was 50 × 50 cm with a minimum buffer distance of around 2 m between plots. We did not select a further distance with the concern that the heterogeneity would affect the degree of accuracy of the plant GPP calculation (as shown in Section 2.3). The treatment without plants was maintained by removing aboveground plants one day before the measurement during growing seasons using scissors.

2.3. Gross primary production measurements

To measure the GPP, stainless steel collars (50 × 50 cm) were installed at depth of 5 cm in all plots two weeks before the initial measurements in 2016, and kept in place during the entire observation period. The aim of installing the collars at depth of 5 cm was to avoid the risk of air leakage from the sandy topsoil when conducting GPP measurements. The images showing the collars and the process of the GPP measurement were shown in Fig. S1.

Static chamber method has been widely used for *in situ* measuring ecosystem CO₂ flux (Novis et al., 2007; Niu et al., 2013; Su et al., 2013; Huang et al., 2014; Chen et al., 2015), and was used for the GPP measurements in the current study. The measurement processes were briefly shown in Fig. S1. GPP was calculated by the following equation:

$$\text{GPP} = \text{RE} - \text{NEE}$$

where RE is ecosystem respiration (RE, in mg CO₂ m^{−2} h^{−1}) and NEE is net ecosystem CO₂ exchange (NEE, in mg CO₂ m^{−2} h^{−1}). NEE was measured using a transparent chamber (50 × 50 × 50 cm) made of acrylic sheets, and RE was measured using a lightproof cloth to cover the transparent chamber. The chamber was attached to an infrared gas analyzer (LI-840A, LI-COR Inc. Lincoln, NE, USA) with an electric pump to circulate gas via inlet and outlet tubes (4 mm inner diameter) at a flow rate of 500 ml min^{−1}. The CO₂ flux (including both RE and NEE) was calculated as shown in the following equation:

$$F_i = \rho_i \cdot (V/A) \cdot (P/P_0) \cdot (T_0/T) \cdot (dC_i/dt)$$

where F_i is the flux rate in $\text{mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, ρ_i is the density at standard condition, V is the chamber volume, A is the chamber base area, P is the air pressure, P_0 is the standard air pressure, T is the air temperature, T_0 is the standard temperature, and dC_i/dt is the change rate of the gas concentration. Soil microbial GPP was measured in plots where plants were removed by scissors prior to *in situ* measuring the CO_2 flux, while plant GPP was calculated by the following equation:

$$\text{Plant GPP} = \text{GPP in plot with plants} - \text{soil microbial GPP}.$$

The CO_2 flux measurement was extensively conducted for each month of the growing seasons in 2016 (from May to October) and 2018 (January and from June to October). Aiming to illuminate the monthly variation of CO_2 flux between years and possible soil microbial GPP in Winter seasons, CO_2 flux was measured for specific months of 2017 (April, October, November and December) and 2019 (May and September). The CO_2 flux was measured every 2 h from sunrise to sunset in a typical sunny day in each measuring month. For each time, the entire measurement for all plots was done in half an hour. Daily CO_2 flux was calculated as the average hourly CO_2 flux throughout the day, and annually CO_2 flux was calculated as the average daily CO_2 in each month.

2.4. Soil temperature and water content measurements

The soil temperature and water content were recorded by a portable thermometer (L99-TWS-3, Lupu Corp., China) with sensors installed at 2 cm deep in topsoil when CO_2 flux was measured. We selected a depth of 2 cm because the soil surface layer was considered to be the most relevant when studying the responses of soil microbial and plant photosynthetic CO_2 fixation to the soil conditions.

2.5. Statistical analysis

The normality of the data was checked using Kolmogorov-Smirnov test in SPSS software (version 20.0; SPSS Inc., Chicago, IL), and all of the P values were greater than 0.05. Other statistical analyses were conducted using R software (version 3.5.3). Data are expressed as mean \pm SE (standard error). Differences between treatments and months were tested using the Student's t -test. Correlation analyses (Spearman correlation) were used to investigate the relationship between GPPs and soil water content and temperature.

3. Results

3.1. Monthly dynamics of soil microbial and plant gross primary production (GPP)

Soil microbial GPP exhibited a marked seasonal change (Fig. 1). In 2016, soil microbial GPP significantly ($P < 0.001$) increased from May ($8.1 \pm 2.7 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) to the highest in July ($69.3 \pm 13.9 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) by 7.5 fold, and then gradually decreased to the original level in October. Similarly, in 2018 soil microbial GPP significantly ($P < 0.001$) increased from June ($5.3 \pm 0.8 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) to the highest in August ($57.9 \pm 6.1 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) by 10.0 fold, and then decreased to the original level in October. The soil microbial GPP exhibited similar monthly patterns over the growing seasons in 2016 and 2018. In contrast, yearly average GPP was $43.5 \pm 10.6 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in 2016 and $24.7 \pm 8.6 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in 2018, and showed a substantial interannual variation by 76%. We then selected several months in 2017 and 2019 to check the monthly variation of the soil microbial GPP across the four years. The soil microbial GPP in October of 2017 and in May and September of 2019 were very similar to those observed in the same months of 2016 and 2018. Soil microbial GPP did not show CO_2 -fixing activity in late autumn and winter months (from October to April).

Plants had significantly higher GPP than soil microbial primary producers ($P < 0.001$, Fig. 1). Plant GPP exhibited similar monthly patterns to soil microbial GPP, in particular, the lowest and the highest GPP occurred in the same months in 2016 and 2018. In 2016, plant GPP dramatically increased from May ($38.4 \pm 9.9 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) to the highest in July ($276.3 \pm 33.1 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) by 6.2 fold, and then substantially decreased to $2.2 \pm 0.9 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in October. The value significantly ($P < 0.001$) increased in 2018 from June ($45.9 \pm 1.9 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) to the highest in August ($247.0 \pm 34.6 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) by 4.4 fold, and then substantially decreased back to $135.7 \pm 18.7 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ in October. The averaged values of plant GPP in 2016 and 2018 were $141.2 \pm 36.4 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ and $122.7 \pm 32.3 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, respectively, with little interannual variation (15.1%). The selected measuring months in 2017 and 2019 also demonstrated similar GPP values as to the 2016 and 2018.

3.2. Monthly dynamics of GPP ratio of soil microbes to plants

Similar to the monthly GPP pattern, GPP ratio of soil microbes to plants also exhibited a monthly pattern (Fig. 2). In 2016, the GPP ratio of soil microbes to plants gradually but significantly ($P < 0.001$)

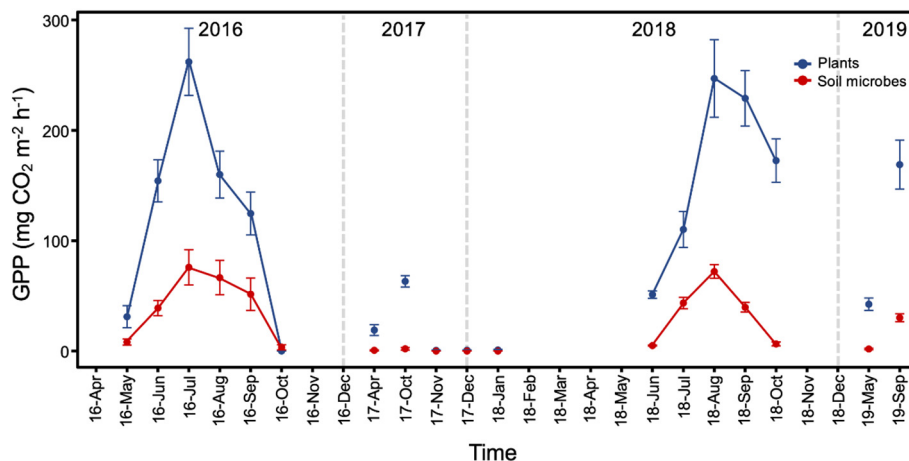


Fig. 1. Seasonal dynamics in gross primary production (GPP) of soil microbial primary producers and plants during 2016–2019. Soil microbial and plant GPP demonstrated similar seasonal patterns in the four-year field observation. Note that in the x axis the time line is equally spaced for the years 2016 and 2018 but not for 2017 and 2019.

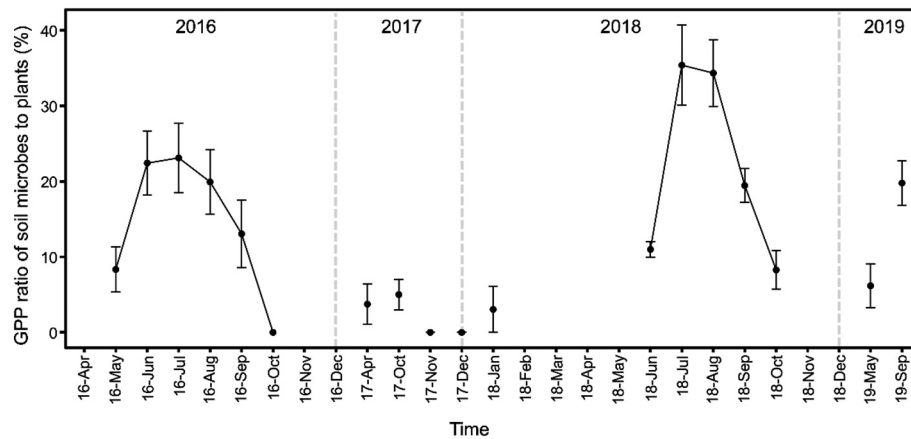


Fig. 2. Seasonal dynamics in gross primary production (GPP) ratio of soil microbes to plants during 2016–2019. The GPP ratio of soil microbes to plants gradually increased from May to July and then decreased to the original levels. Note that in the x axis the time line is equally spaced for the years 2016 and 2018 but not for 2017 and 2019.

increased from May ($8.0 \pm 2.8\%$) to the highest in July ($21.9 \pm 4.1\%$) by 1.7 fold, and then gradually decreased to the original level in October. In 2018, the GPP ratio significantly ($P < 0.001$) increased from June ($10.3 \pm 0.9\%$) to July ($35.7 \pm 4.7\%$) by 2.5 fold, and then gradually decreased to $7.6 \pm 2.3\%$ in October. The ratios in selected months of 2017 and 2019 were similar to those in the same months of 2016 and 2018. The averaged GPP ratio was $17.6 \pm 3.3\%$ in 2016, similar to that in 2018 ($18.8 \pm 5.4\%$, Fig. S2), with very little interannual variation (6.8%).

3.3. Effects of soil water content and temperature on microbial and plant GPP and their ratio

Soil water content and temperature had positive effects on soil microbial GPP and its ratio to plants (both $P < 0.05$, Table S1). Linear regressions revealed that soil microbial and plant GPP both positively correlated with soil temperature (both $P < 0.001$), and plant GPP showed a higher regression slope than soil microbial GPP (Fig. S3). Similarly, soil microbial and plant GPP both positively correlated with soil water content (both $P < 0.01$), and plant GPP showed a higher slope compared to soil microbial GPP. GPP ratio of soil microbes to plants positively correlated with soil water content ($P < 0.001$), while there was no significant correlation with soil temperature (Fig. 3).

4. Discussion

4.1. Importance of soil microbial CO_2 fixation in dryland ecosystems

This study conducted an *in situ* observation comparison between soil microbial and plant GPP in the field. The detected soil microbial GPP ($33.0 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, equal to $0.21 \mu\text{mol m}^{-2} \text{ s}^{-1}$) in the present study was in the range of previously reported GPP of field observations in various drylands in China and global drylands (Novis et al., 2007; Su et al., 2013; Huang et al., 2014). The plant GPP ($131.1 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, equal to $0.83 \mu\text{mol m}^{-2} \text{ s}^{-1}$) was also similar to those observed in grassland ecosystems on the Tibetan Plateau (Chen et al., 2015). Compared to widely recognized plant CO_2 fixation, our findings demonstrated that soil microbial CO_2 fixation also substantially contributed to GPP in the dry grasslands (Figs. 1, 2 and S1), which strongly supported our first hypothesis. The importance of soil microbial CO_2 fixation has been evidenced by previous incubation studies using isotopic labelling in laboratories (Miltner et al., 2004; Yuan et al., 2012; Ge et al., 2013; Zhao et al., 2018), and in field observations of BSC in dryland regions (Novis et al., 2007; Su et al., 2013; Huang et al., 2014). Here our results showed a consistently high proportion (on average 18.2%) of soil microbial to plant GPP and extended the previous recognitions.

Over the past decades, strong integrations of biogeochemistry, plant physiological ecology and remote sensing studies have substantially advanced our understanding of terrestrial GPP (Farquhar et al., 1980; Sellers et al., 1997; Beer et al., 2010). Remote sensing-based methods

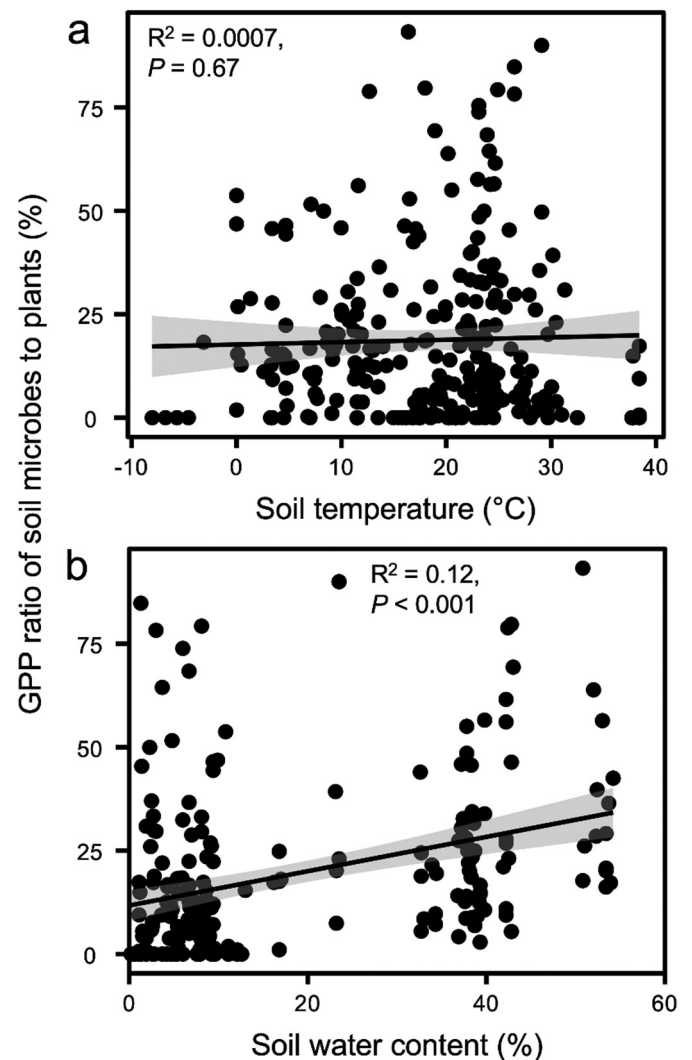


Fig. 3. Regressions of gross primary production (GPP) ratio of soil microbial primary producers to plants with soil temperature (a) and soil water content (b). The GPP ratio positively correlated with soil water content, but not with soil temperature. Lines and shaded polygons indicate the predictions and their 95% confidence intervals, respectively.

for estimating terrestrial GPP have greatly counteracted the 'missing sink' observed previously (Magney et al., 2019; Ryu et al., 2019; Stocker et al., 2019). However, these methods mainly focus on plant photosynthesis (Wang et al., 2017; Fatichi et al., 2019), and cannot account for the soil microbial CO₂ fixation. The lack of incorporating soil microbial GPP has been proposed to result in substantial uncertainties in dryland and even global C balance (Maestre et al., 2013; Weber et al., 2016; Rodriguez-Caballero et al., 2018).

Our estimation of soil microbial GPP across the Tibetan Plateau and global drylands based on the *in situ* observation showed a considerable C sink potential that can not be ignored (Zhang et al., 2002; Huang et al., 2016, Table S2). The global importance of soil microbial GPP is expected to substantially increase due to the accelerated dryland expansion under climate change (half of the global land surface by the end of this century, Huang et al., 2016). Additionally, the dramatically higher interannual variation of soil microbial GPP than plant GPP might also contribute to increase the substantial variability in global dryland C assessment. It should be noted that upscaling from a field-plot study to global would be far from reality due to the spatial variation of dryland ecosystem (Beer et al., 2010; Ahlström et al., 2015). Thus, the current case study has its limitation on large-scale estimation but provides insights into how comprehensively understand ecosystem C sink in drylands and even in humid regions. In the future, more long-term observation-based studies in different ecosystems may be needed to broaden the regional recognition of relative importance of soil microbial and plant GPP as well as their relationships. Further, since the most remote sensing-based models solely address vegetation production (Wang et al., 2019), our results suggest an urgent need to develop a more robust theoretical framework for modelling terrestrial GPP, in which the soil microbial GPP should be taken into account. This is particularly concerned in ecologically fragile ecosystems, such as drylands, where Zhao et al. (2018) reported that soil microbial CO₂ fixation rate negatively correlated with plant biomass and soil nutrients, indicating the more important role of microbial GPP in oligotrophic soils.

4.2. Responses of soil microbial and plant GPP to soil water content and temperature

Soil microbial and plant GPP both substantially changed with the growing seasons, and the highest GPP occurred in July and August. This is in agreement with that season influences soil microbial and plant activity by altering soil temperature and soil moisture (Chen et al., 2018; Fan et al., 2020). This was evidenced by the strong positive correlations of soil microbial and plant GPP with soil temperature and moisture (Fig. S3, Table S1). Soil temperature directly facilitated microbial and plant growth and activity, particularly in yearly cold regions, such as Tibetan Plateau (Bai et al., 2020; Dong et al., 2020). Similarly, the facilitating effect of soil moisture could be both direct and indirect through affecting the availability of substrates, nutrients, and oxygen (Schimel et al., 2007; Singh et al., 2010). It has long been recognized that vegetation activity mainly drives the seasonal variations of atmospheric CO₂ (Magney et al., 2019; Ryu et al., 2019). Our findings further extended the concept that soil microbial CO₂ fixation could also persistently and substantially affect atmospheric CO₂ across seasons.

Besides the similarities, the soil microbial and plant GPP also exhibited different responses to the seasons. Linear regressions showed higher sensitivities of plant GPP than soil microbial GPP to soil temperature and moisture over seasons (Fig. S3). As positive effects of temperature and moisture on both plants and soil microbes have long been recognized (Yao et al., 2017; Zhou et al., 2018; Winkler et al., 2019), higher sensitivity of plant GPP could be due to that plants have phenology, but soil microbes do not (Piao et al., 2019). In contrast, soil microbial GPP appeared to be more heavily driven by soil factors (*i.e.* water content and temperature), despite of strong positive interactions between plant and soil microbial growth (Wardle et al., 2004). The absence of phenology in soil microbes was also evidenced by the large

differences of soil microbial and plant GPP at early growing season. For example, in May of 2016 and June of 2018, soil microbes did not fix CO₂ because of low soil temperature and moisture. In contrast, plant GPPs reached up to 23.3 and 25.4 mg CO₂ m⁻² h⁻¹ in May and June, due to the plants usually start greening in May and June, even in harsh environments. In addition, phenology partly explained the lower interannual variation of plant GPP than that soil microbial GPP (Shen et al., 2013; Cao et al., 2018).

GPP ratio of soil microbes to plants, with the average of 18.2%, exhibited a clear seasonal pattern, and the highest GPP ratio occurred in July (Fig. 2). This finding supports the differences between soil microbial and plant GPP in response to climatic conditions, and is in agreement with our second hypothesis that relative contribution of soil microbial GPP would change with seasons. We observed a positive relationship between the GPP ratio of soil microbes to plants and soil water content, while the ratio did not significantly correlate with soil temperature (Fig. 3). This highlights the significant role of soil water, consistent with that more significant effect of soil moisture than temperature on soil microbial activity in dryland ecosystems (Scola et al., 2018; León-Sobrinho et al., 2019). Soil microbes usually better adapt to drought than plants (Beer et al., 2009), and respond faster to increasing moisture and have higher C-fixing efficiency in response to moisture (Usui and Ikenouchi, 1997). Drought impacts on terrestrial GPP are usually underestimated by satellite monitoring methods, which has recently received much attentions (Stocker et al., 2018; Green et al., 2019; Stocker et al., 2019). Here our finding indicates that the relative importance of soil microbial and plant GPP changed with soil moisture, thus provides further information on the underestimation of terrestrial GPP in relation to climate change. Further, recent studies suggests that different types of soil biocrusts can also affect plant communities by changing the microenvironment and surface soil nutrients, indicating the possible occurrence of complicated interactions between plants and soil microbial GPP (Xu et al., 2020). Due to the significance of soil microbial GPP, the differentiation and interactions of soil microbial and plant physiological ecology in relation to terrestrial GPP deserves to be appreciated in diverse dryland ecosystems in the context of changing climate.

5. Conclusion

This study *in situ* investigated the soil microbial and plant GPP, and their temporal variations during growing seasons in a dryland ecosystem on the Tibetan Plateau. Soil microbial GPP had similar change patterns as plant GPP over seasons, but exhibited a greater interannual variation. The high GPP ratio of soil microbes to plants (18.2%) indicates that soil primary producers substantially contributed to terrestrial C sink in the dryland ecosystem. The GPP ratio of soil microbes to plants exhibited the highest in July and enhanced with increasing soil water content but not temperature. These findings challenge the current plant-oriented Earth system models of terrestrial GPP estimation. We call for more *in situ* observations in soil microbial contribution to terrestrial C sink in dryland ecosystems, which could be integrated into models for reducing uncertainties of terrestrial C balance. Further, more attentions should be drawn on the responses of plants and soil microbial GPP to the changing climate in different dryland ecosystems and the mechanisms underlying it.

CRediT authorship contribution statement

Hao Chen: Methodology, Formal analysis, Visualization, Writing - original draft. **Fei Wang:** Methodology, Formal analysis, Data curation, Writing - review & editing. **Weidong Kong:** Conceptualization, Supervision, Project administration, Validation, Writing - review & editing. **Hongzeng Jia:** Resources, Investigation. **Tianqi Zhou:** Resources, Investigation. **Ri Xu:** Resources, Funding acquisition. **Guangjian Wu:** Resources, Investigation. **Junbo Wang:** Resources, Investigation. **Jinshui Wu:** Validation, Writing - review & editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.143282>.

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