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The carbon sequestration potential of China's grasslands

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Citation: Song, J., S. Wan, S. Peng, S. Piao, P. Ciais, X. Han, D.-H. Zeng, G. Cao, Q. Wang, W. Bai, and L. Liu. 2018. The carbon sequestration potential of China's grasslands. Ecosphere 9(10):e02452. 10.1002/ecs2.2452

Abstract. With the consequences of anthropogenic activities such as overgrazing and cropland expansion, grasslands in China suffer severe degradation since the 1980s. The national grassland restoration policy enacted at the beginning of the 21th century has the potential to increase plant growth and productivity and hence regional carbon (C) sequestration. Here, we assessed plant and soil organic C (SOC) stocks for both degraded and restored/non-degraded plots at 802 sites in Northern and Northwest China using pairwise field sampling and quantified the C sequestration potential (CSP) of China's grasslands. A geostatistical model was performed to upscale the field measurements to national scale. Averaged across the 802 paired grassland sites, the mean plant biomass C and SOC density in the top 1 m depth were 0.44 ± 0.17 and 8.82 ± 1.78 kg C/m², respectively. Compared to the degraded grasslands, the restored grasslands had an average of 0.11 ± 0.17 (29.2%) and 1.02 ± 1.28 kg C/m² (12.3%) greater plant biomass C and SOC density, respectively. The geostatistical model produced a total CSP of 17.3 \pm 2.3 Pg C in China's grasslands, with 94% in soils. If the CSP estimated in this study could be achieved, the current grassland SOC stock would increase by 61%, offsetting 11 yr (2000–2010) of national fossil CO₂ emissions.

Key words: carbon cycling; degraded grasslands; Grain for Green Project; grassland management; pairwise field sampling; restored grasslands.

Received 23 January 2018; revised 6 July 2018; accepted 11 July 2018; final version received 28 August 2018. Corresponding Editor: Kristofer D. Johnson.

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INTRODUCTION

As the third largest grassland ecosystem in the world, China's grasslands, spanning from temperate grasslands on the Inner Mongolian Plateau to alpine grasslands on the Tibetan Plateau (Chinese Academy of Sciences 2001), cover 40% of the national land area and 13% of the global grassland area (Liao and Jia 1996, Kang et al. 2007). Vegetation and soils in China's grasslands store a large amount of carbon (C) and play a crucial role in regional and global terrestrial C cycling (Fang et al. 2007, Piao et al. 2009). During the past two decades, numerous studies have quantified plant biomass and soil C density and storage, and evaluated the effects of climate, soil texture, and soil moisture on vegetation and soil C dynamics in China's grasslands using data obtained from China's National Soil Inventory conducted in the 1960s and 1980s and from large-scale soil survey conducted in the early 21th century, as well as satellite-based datasets (e.g., for plant biomass C: Ni 2002, 2013, Piao et al. 2007, Fan et al. 2008, Ma et al. 2010, for soil C: Ni 2002, 2013, Wang et al. 2003, Wu et al. 2003, Xie et al. 2007, Mi et al. 2008, Yang et al. 2008, 2009, 2010*a*, *b*, 2012, Shi et al. 2012). Overall, these studies have demonstrated that plant biomass and soil C stocks of China's grasslands range from 0.05 to 1.60 kg C/m² (0.6–4.7 Pg C) and from 3.90 to 21.40 kg C/m² (16.7–43.0 Pg C), respectively.

Since the 1980s, China's grasslands have experienced serious degradation caused by intensive grazing and conversion to croplands, with up to 90% of the grassland ecosystems being classified as degraded (Akiyama and Kawamura 2007, ARNGM 2010, Zhou et al. 2017). In order to maintain the ecosystem services of the grassland regions, the Grain for Green Project was initiated in 2000 to reduce or exclude grazing and to restore the croplands back to grasslands (Liu et al. 2008, Delang and Yuan 2016). By 2014, the restored grasslands in China have reached 100 million hectares (Appendix S1: Fig. S1a). In addition, it has been well documented that the restoration strategy significantly increases both plant coverage and productivity (ARNGM 2010, Mu et al. 2013, Xiong et al. 2016; Appendix S1: Fig. S1b, c), accelerates the succession of plant communities (Hu et al. 2016a), and subsequently enhances soil C sequestration (Ostwald et al. 2011, Deng et al. 2014, 2017, Shi and Han 2014, Song et al. 2014, Hu et al. 2016b, Pan et al. 2017). Nevertheless, large uncertainties exist in the C budget of China's grasslands, with published estimates ranging from a large loss (3.56 Pg C; Xie et al. 2007) to a small gain of C (0.2 Pg C; Piao et al. 2009) during the last 20 yr. These uncertainties and controversies reflect a lack of a comprehensive assessment of C storage for different grassland management practices and climate regimes covering most of grassland types in China (Wang et al. 2011, Deng et al. 2014, 2017). Quantifying how grassland conservation and management practices affect C storage is needed to better inform the decisions on landbased mitigation strategies (Long et al. 2010, Deng et al. 2014, Conant et al. 2017).

In this study, a large collection of 4812 plots was sampled to compare plant biomass and soil organic C (SOC) stocks between restored and adjacent degraded plots at 802 sites in the grasslands of Northern and Northwest China in summer of 2009 and 2010 (Fig. 1a). Combined with climate datasets, satellite-derived Normalized Difference Vegetation Index (NDVI) and a model tree ensemble (MTE) algorithm parameterized by these site-scale measurements were used to calculate region-scale plant biomass and SOC stocks as well as the C sequestration potential (CSP) of China's grasslands. Our specific objectives were to (1) assess plant biomass and SOC density and stocks in China's grasslands, (2) quantify the CSP at site and region scales, and (3) identify land use and management options that would allow to best realize most of the CSP of China's grasslands.

MATERIALS AND METHODS

Pairwise experimental design

Based on bioclimatic conditions and soil types, we grouped grassland sites into six major types: meadow steppe, typical steppe, desert steppe, sandy grassland, alpine steppe, and alpine meadow (Fig. 1a). Meadow steppe, typical steppe, desert steppe, and sandy grassland are located in arid and semiarid regions in Northern China (latitude: 39.460–49.206° N, longitude: 109.245–125.511° E, altitude: 127–1516 m) where low precipitation is the predominant limiting factor for plant growth. Alpine steppe and alpine meadow are distributed in the Tibetan Plateau (latitude: 31.155–38.025° N, longitude: 91.650–101.360° E, altitude: 2914–4904 m) where low temperature is the dominant limiting factor.

The Grain for Green Project restoration policy in China's grasslands includes two strategies: (1) excluding and/or reducing grazing pressure in the grasslands and (2) converting croplands cultivated since 1950s back to grasslands (Liu et al. 2008, Delang and Yuan 2016). Therefore, we identified nine possible vegetation pairs for the six major grassland types: P1, grazed/degraded vs. ungrazed/undisturbed grasslands; P2, bare soil vs. disturbed/undisturbed grasslands; P3, shrublands vs. grasslands; P4, oldfield vs. natural grasslands; P5, managed vs. natural/grazed grasslands; P6, croplands/managed grasslands vs. shrublands; P7, croplands vs. undisturbed/grazed grasslands; P8, croplands vs. oldfield grasslands; and P9, croplands vs. managed grasslands. Grazed and degraded grasslands suffered modergrazing and overgrazing, respectively. ate



Fig. 1. (a) Spatial distributions of the six major grassland types in China and the locations of 802 sampling sites in this study. (b) An example for schematic diagrams of pairwise sampling design.

Ungrazed/undisturbed grasslands represented long-term enclosed grasslands. Compared to ungrazed/undisturbed grasslands, vegetation cover of degraded grasslands decreased by more than 30%. Bare soil referred to tillage soil without crops. Shrublands consisted of sparse woody shrubs. Grasslands in P3 and natural grasslands in P4 included both grazed and ungrazed/undisturbed grasslands. Oldfield grasslands represented abandoned agricultural land. Croplands were cultivated land with crops. Managed grasslands were artificial pasture.

In each of the six major grassland types defined above, as many vegetation pairs were selected as possible to measure plant biomass C and SOC stocks in middle summer (July and August) of 2009 and 2010. In order to extrapolate the results of field measurement to a regional scale and to parameterize the model, at least four $20 \times 20 \text{ km}^2$ sampling areas were determined for each vegetation pair in each of the six major grassland types, with the distance between any two adjacent sampling areas larger than 100 km. In each sampling area, six sampling sites were selected with the distance larger than 1 km between any two adjacent sites. At each sampling site, three pairs of sampling plots were determined with the distance between any two adjacent pairs of sampling plots larger than 50 m. In order to minimize spatial heterogeneity, the two $1 \times 1 \text{ m}^2$ sampling plots in each pair with the same slope and elevation were assigned to the degraded and restored vegetation types, respectively, and the distance between the two sampling plots in each pair was <30 m (Fig. 1b).

Hierarchical scheme for field sampling:

- 1. Grassland Types: 6
- 2. Vegetation Pairs: 9
- 3. Sampling Areas: 4
- 4. Sampling Sites: 6
- 5. Sampling Pairs: 3
- 6. Sampling Plots: 2

Not all vegetation pairs were available for each of the six grassland types. Number of sites selected in the six grassland types was 120 for meadow steppe, 70 for typical steppe, 84 for desert steppe, 114 for sandy grassland, 234 for alpine steppe, and 180 for alpine meadow. In total, there were 802 sites, 2406 sampling pairs, and 4812 plots (latitude: 31.155–49.206° N, longitude: 91.650–125.511° E, altitude: 127–4904 m; Fig. 1a).

All plant materials (including green aboveground biomass and litter) in each plot were collected, oven-dried at 65°C for more than 48 h to constant weight, and weighed. Three soil cores with a diameter of 6–8 cm were taken at the depths of 0–10, 10–20, 20–40, 40–60, and 60– 100 cm in each plot. Soil cores with all the five depths were taken from all the 2328 plots in the four major grassland types in Northern China. However, due to the variability of soil depths, not all depths from all plots in the two major grassland types in the Tibetan Plateau were sampled. A total of 612, 684, 1008, and 180 plots were taken with the depths of 0-100, 0-60, 0-40, and 0-20 cm, respectively. The three soil cores with the same depth were combined into a composite sample. Plant roots were separated from soil by 2-mm mesh, washed, and oven-dried to constant weight to measure root biomass. In addition, the soil samples for C content analysis were air-dried, handpicked to remove fine roots, ground in a ball mill, and sieved through a 0.25-mm mesh. Contents of SOC were analyzed using the Walkley-Black dichromate oxidation procedure (DAHV and CISNR 1994). Soil bulk density was measured for all the soil profiles in order to convert SOC content in g C/g soil to g C/m². Soil samples of bulk density were obtained using a standard container with 100 cm³ in volume (5.5 cm in diameter and 5 cm in height). Rock fragments of the bulk density samples were removed through a 2mm mesh. Gravimetrical water content of the bulk density samples was measured after 48-h desiccation at 105°C. The ratio of the oven-dry soil mass to the container volume was used to calculate soil bulk density. Soils in the degraded grasslands were more compacted and had a higher soil bulk density than intact ones (Appendix S1: Fig. S2), which could offset the potential effects of ecological restoration on soil and ecosystem C stocks. Therefore, mean soil bulk density was calculated for each soil depth between the degraded and restored grasslands. Means and standard deviations were calculated using the values of the three plots in the degraded and restored grasslands, respectively. Weighted means were calculated from the lowest to the highest sampling levels: sampling site, sampling area, vegetation pair, and grassland type.

Using a similar approach as reported in metaanalyses (Hedges et al. 1999, Wan et al. 2001, Gurevitch et al. 2018), the roles of different restoration strategies in affecting plant and soil C stocks in each of and across the six major grassland types were examined. The natural logtransformed response ratio (RR) was calculated to estimate the effect size of the different restoration strategies on plant and soil C stocks: $\ln RR = \ln(\bar{X}_E/\bar{X}_C)$, where \bar{X}_E and \bar{X}_C are the mean values of the restored/non-degraded and degraded treatments, respectively. The statistical software Meta-Win 2.1 (Sinauer Associates, Sunderland, Massachusetts, USA) was used to calculate weighted response ratio (ln RR_{++}) and bias-corrected 95% bootstrap confidence interval. Percentage change (%) induced by the different restoration strategies was evaluated as (exp (ln RR_{++}) – 1) × 100.

Spatial distribution of grassland types in China

A digital map with 1-km resolution of spatial distribution of grassland types in China is obtained from the Department of Animal Husbandry Veterinary (DAHV 1994). The 17 grassland types in this map are classified on the basis of climatic zonation, humidity index, and vegetation type of grassland (Nelson and Sommers 1982, Chen and Fischer 1998). In this study, we grouped the 17 grassland types into six major types, namely meadow steppe, typical steppe, desert steppe, alpine steppe, alpine meadow, and sandy grassland as shown in Fig. 1a.

NDVI data

Normalized difference vegetation index, defined as the ratio of the difference between near-infrared reflectance and red visible reflectance to their sum, is a remote-sensed vegetation index widely used to measure vegetation greenness and photosynthetic activity (Myneni et al. 1997, Zhou et al. 2001, Tucker et al. 2005). The NDVI data used in this study were produced by the Global Inventory Monitoring and Modeling Studies group, derived from the NOAA/AVHRR land dataset at a spatial resolution of 10 \times 10 km² and 15-d interval for the period 1982-2010 (Zhou et al. 2001). In this study, we used NDVI as one of the predictors to estimate plant standing biomass C and SOC stocks of grasslands in China. All the spatial datasets were first gridded to a common 1-km pixel before further analyses.

Climate data

The monthly temperature and precipitation averaged over the period of 1950–2000 were obtained from WorldClim Global Climate Data (http://www.worldclim.org/current; Hijmans et al. 2005). The climate datasets were generated at 1-km spatial resolution through interpolation of average monthly temperature and precipitation from 24542 and 47554 weather stations, respectively.

Model tree ensemble

Model tree ensemble is a machine-learning algorithm, which predicts a target variable based on a set of explanatory variables. Model trees are constructed using the observed data. Once the model tree is built, it can be applied to predict the target variable given the explanatory variables. Model trees can be understood as a hierarchical functional classification of the target variable. We applied MTE method to predict plant biomass C and SOC density using the plots from 802 sampling sites (Jung et al. 2009).

Estimations of current plant biomass C and SOC density

First, we constructed MTE models to predict plot-level measurements of plant biomass C and SOC stocks, using grassland types, site-specific NDVI, and a number of climate variables as predictors. All the 4812 plots from 802 sampling sites including both disturbed and undisturbed samples were used to develop the MTE models. Climate variables employed in the prediction included mean annual temperature/precipitation, growing season (April-October) temperature/ precipitation, and spring (March–May), summer (June–August), autumn (September–November), and winter (December-February) temperature/ precipitation. The predictive power of the MTE models is 46% and 76% for plant biomass C and SOC, respectively (Fig. 2a, b). Second, to scale up the plot-level measurements to regional-scale estimate of plant standing biomass C and SOC stocks, we applied the MTE models to the spatial-specific NDVI and climate datasets, together with a digital map of grassland types in China. In contrast with previous estimates based on limited and biased sampling in less-disturbed grasslands (Fang et al. 2010), our study combined the pairwise field sampling with climate and NDVI datasets of high spatial resolution, which can address the detailed spatial heterogeneity of grassland C stocks.

Predictions of the potential plant biomass C and SOC density and C sequestration potential

Assuming that all the degraded grasslands can be restored to achieve pre-disturbed conditions through effective grassland management, the CSP of China's grasslands can be evaluated as the difference in C stocks between potential and current



Fig. 2. Scatterplots of C density predicted from the model tree ensemble models vs. plot-scale measurements. (a) Predicted plant biomass C density vs. measured plant biomass C density based on all the 4812 plots. (b) Predicted soil organic C (SOC) density vs. measured SOC density based on all the 4812 plots. (c) Predicted plant biomass C density vs. measured plant biomass C density based on 2406 undisturbed plots. (d) Predicted SOC density vs. measured SOC density based on 2406 undisturbed plots. The dash line is the 1:1 line.

status. Here, we took the restored plots as indicative of potential status and developed the MTE models to predict potential C stocks with the 2406 undisturbed plots from 802 sampling sites, using grassland types and a number of climate variables (as listed above) as predictors. Note that we did not include satellite-derived NDVI as predictors, since they include information about the disturbance of current human activity on plant canopy. The MTE models explained 82% and 80% of the variations in plant biomass C and SOC stocks, respectively (Fig. 2c, d).

To scale up the plot-level measurements to regional-scale estimates, we combined the MTE models with gridded climate datasets and a digital map of grassland types and obtained the potential plant biomass C and SOC stocks of China's grasslands. The CSP was calculated as the difference between potential and current C stocks (Appendix S1: Table S1). Note that for some pixels, potential plant biomass C and/or SOC density were estimated to be lower than that of current status, probably resulting from agricultural practices to maintain and enhance production (e.g., irrigation, fertilization). For this end, the total CSP of China's grasslands was calculated by summing up only pixels in which potential plant biomass C or SOC density exceeded current status.

Results

Estimations of carbon density and CSP of China's grasslands with pairwise field sampling

The pairwise plot-level comparisons of plant biomass C and SOC up to 1 m depth between the degraded and restored/non-degraded grasslands were conducted for the six major grassland types. Across all the degraded and restored grasslands, plant biomass C and SOC density were, on average, 0.44 ± 0.17 and 8.82 ± 1.78 kg C/m², respectively (Fig. 3). There were substantial variations of plant biomass C and SOC density among the different grassland types. The most productive grassland in Northern China in terms of plant biomass C density was typical steppe (1.15 ± 0.16 kg C/m²), and the least productive one was sandy grasslands (0.24 ± 0.07 kg C/m²; Fig. 3a). Alpine meadow in the Tibetan Plateau had the largest SOC density (15.32 ± 4.00 kg C/m²), whereas sandy grasslands showed the lowest

value ($4.99 \pm 0.77 \text{ kg C/m}^2$; Fig. 3b). In addition, the majority of the C storage was in soils (95.2%). Moreover, the proportions of SOC stocks in the surface soil layer (0–20 cm) to the total SOC stocks declined with increasing soil sampling depth from 54.3% in the topsoil layer (0–40 cm) to 34.2% in the 1-m soil layer under the degraded conditions and from 57.0% to 35.6% under the restoration (Appendix S1: Fig. S3). Furthermore, the proportion differences between the restored and degraded grasslands were much lower at the 0–100 cm sampling depth (1.37) than those at the 0–60 cm (3.59) and 0–40 cm depths (2.76).

Results from the pairwise field samples showed that the restored grasslands had a higher



Fig. 3. (a) Plant biomass C and (b) soil organic C density under degraded and restored conditions in the six major grassland types of China. The numerical values above the bars represent the numbers of pairs.

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C density than the degraded grasslands, on average, by 0.11 ± 0.17 kg C/m² (29.2%) for plants and 1.02 ± 1.28 kg C/m² (12.3%) for SOC at the top 1 m depth (Fig. 3; Appendix S1: Table S1). The CSP differed among grassland types (Table 1) but did not depend on the initial C storage of degraded grasslands (Appendix S1: Fig. S4). For example, degraded alpine meadow had a moderate plant biomass C and SOC density but the largest CSP (8.01 kg C/m²). However, degraded sandy grasslands had the lowest plant biomass C and SOC density but the second highest CSP (1.08 kg C/m²).

Effects of restoration practices and grassland types on the CSP of China's grasslands

We assessed the effects of different restoration practices on C stocks. All the restoration practices involving natural grasslands at 461 sites (P1, grazed/degraded vs. ungrazed/undisturbed grasslands; P2, bare soil vs. disturbed/undisturbed grasslands; P3, shrublands to grasslands; and P4, oldfield vs. natural grasslands) significantly enhanced both plant biomass C (122.6-1004.0%) and SOC stocks (46.7–71.1%), except for that the restoration of shrublands to grasslands slightly stimulated SOC (12.6%), but reduced plant biomass C density by 28.8% (Fig. 4). The more severe the previous disturbance intensity (P2 > P4 > P1 > P3), the larger was the CSP. By contrast, all the five restoration practices that convert croplands back to grasslands or shrublands (P5, managed vs. natural grasslands; P6, croplands/managed grasslands vs. shrublands; P7, croplands vs. natural grasslands; P8, croplands vs. oldfield grasslands; and P9, croplands vs. managed grasslands) tended to reduce C density (Fig. 4). In addition, the C stock enhancements caused by the four restoration practices involving natural grasslands were always greater than the reductions by the five strategies involving croplands. Even the same restoration practice had contrasting impacts on C stocks in different grassland types. For example, cropland expansion (P7) stimulated plant biomass C stocks in the meadow and desert steppe (Appendix S1: Fig. S5a, c) and SOC stocks in the alpine steppe (Appendix S1: Fig. S6e) but reduced them in the typical steppe (Appendix S1: Fig. S5b) and alpine meadow (Appendix S1: Fig. S6f).

The quantification of CSP of China's grasslands with model simulations

We used an MTE-based machine-learning algorithm to scale up the pairwise plot-level measurements of C stocks and CSP to regional-scale estimates. A total plant biomass C stock in China's grasslands was 1.8 ± 0.1 Pg C $(0.54 \pm 0.04$ kg C/m²; Fig. 5a). Plant biomass C density was relatively high in the eastern parts of Inner Mongolia and eastern Tibetan Plateau (>1 kg C/m^2) that receive higher precipitation, and low plant biomass C density (<0.5 kg C/m²) in the drier steppe of Northwest China and western Qinghai-Tibet Plateau were simulated (Fig. 6a). For SOC stock, total SOC in the top 1-m soil was 27.0 \pm 2.1 Pg C $(8.23 \pm 0.64 \text{ kg C/m}^2; \text{ Fig. 5b})$. Similar to the pattern of plant biomass C density, a relatively high SOC density was found in the eastern part of Inner Mongolia and Tibetan Plateau (>10 kg C/m²) where meadow steppe and alpine meadow prevail (Fig. 6b). Intermediate SOC density was obtained in alpine steppe and typical steppe in the central area of Inner Mongolia and Northwest China (5–10 kg C/m²), and particularly low SOC density was found in desert steppe and sandy grasslands (0–5 kg C/m^2).

To predict the potential plant biomass C and SOC stocks under undisturbed conditions, we trained the MTE statistical model for the restored plots only and use climate and grassland types as predictors. We obtained a plant biomass CSP

Table 1. Carbon sequestration potential (kg C/m^2) of plant and soil for the six grassland types estimated from the 802 sampling sites.

	Meadow steppe	Typical steppe	Desert steppe	Sandy grasslands	Alpine steppe	Alpine meadow
NSS	120	70	84	114	234	180
Biomass	-0.34 ± 0.19	0.29 ± 0.16	-0.06 ± 0.06	0.001 ± 0.07	0.20 ± 0.04	0.86 ± 0.11
Soil	0.27 ± 0.64	0.47 ± 0.47	0.41 ± 0.27	1.08 ± 0.68	-0.20 ± 0.92	8.01 ± 2.68

Note: NSS, number of sampling sites.



Fig. 4. Percent changes (Mean \pm 95% confidence interval) in (a) plant biomass C and (b) soil organic C density induced by different ecological restoration strategies across the six major grassland types of China. P1, grazed/ degraded vs. ungrazed/undisturbed grasslands; P2, bare soil vs. disturbed/undisturbed grasslands; P3, shrublands vs. grasslands; P4, oldfield vs. natural grasslands; P5, managed vs. natural/grazed grasslands; P6, croplands/managed grasslands vs. shrublands; P7, croplands vs. undisturbed/grazed grasslands; P8, croplands vs. oldfield grasslands; and P9, croplands vs. managed grasslands. Numerical value above each bar represents the number of comparison pairs.

of 1.0 ± 0.1 Pg C (Fig. 5a). Substantial increases in plant biomass C density were shown in eastern Inner Mongolia, Altai and Tianshan Mountains, and the eastern Tibetan Plateau (Fig. 6c, e). Across the six grassland types, meadow steppe and alpine meadow had relatively large plant biomass CSP per unit area in the MTE model. The mean potential plant biomass C density was 67% and 78% higher than the current plant biomass C density, respectively. The CSP of soils was of 16.3 ± 2.3 Pg C (Fig. 5b), which was 16 times larger than the CSP of plant biomass. The largest CSP of soils was mainly found in western Inner Mongolia, Altai Mountains, Tianshan Mountains, and Tibetan Plateau (Fig. 6d, f). Among the six grassland types, alpine meadow had the largest soil CSP per unit area (≈ 10 kg C/m²), with an average potential SOC density increase by 79%, comparing to the other five grassland types (2–4 kg C/m²).



Fig. 5. (a) Current and potential stocks for plant biomass C and its sequestration potential in China's grasslands. (b) Current and potential stocks for soil organic C and its sequestration potential in China's grasslands.

This result was consistent with that of plot data (Appendix S1: Table S1). The total CSP of grasslands in China was estimated as 17.3 ± 2.3 Pg C, of which the CSP of soils represents 94%, which was close to the plot-data estimation (95.2%).

Discussion

Assessments of C density and CSP of China's grasslands

Plant biomass C density in grassland estimated from our pairwise field sampling and the MTE model was mostly in the range of previous estimates (0.05–1.60 kg C/m² and 0.60–4.70 Pg C; Ni 2002, 2013, Piao et al. 2007, Fan et al. 2008, Ma et al. 2010, 2016). But in alpine meadow, our field sampling estimation (0.17–1.26 kg C/m²) was lower than that in a previous study conducted in the Qinghai Plateau (0.04–2.80 kg C/m²; Liu et al. 2016), probably due to that the present study included more degraded plots with lower plant productivity. The estimation of SOC density (ranged from 3.50 kg C/m² in sandy grasslands to 23.58 kg C/m² in alpine meadow by pairwise field sampling and $8.23 \pm 0.64 \text{ kg C/m}^2$ and 27.00 ± 2.10 Pg C using the MTE model) was also similar to the observations of several previous studies (3.90-21.40 kg C/m² and 16.70-43.00 Pg C; Ni 2002, 2013, Wang et al. 2003, Wu et al. 2003, Xie et al. 2007, Mi et al. 2008, Yang et al. 2008, 2009, 2010a, b, 2012, Shi et al. 2012, Liu et al. 2016, Ma et al. 2016). The mean SOC density in China's grasslands was comparable to that in China's paddy (1.20–22.60 kg C/m²; Pan et al. 2004). The SOC density in desert steppe and sandy grasslands (3.50–6.18 kg C/m^2) was within the range of previous observations (0.59-9.57 kg C/m^2 ; Wang et al. 2014).

Previous studies often sample shallow soil and rarely reach a depth of 1 m (e.g., Yang et al. 2008, 2010b, Ma et al. 2016). Our field investigation into 1 m depth of the soil could greatly reduce uncertainties for the estimation of SOC stocks. In addition, the greater proportion differences in SOC density between the restored and degraded grasslands at the 0-60 cm and 0-40 cm depths than that at the 0–100 cm sampling depth indicate that the restoration efforts mainly lead to accumulate soil C in the surface horizons (ARNGM 2010, Mu et al. 2013, Xiong et al. 2016; Appendix S1: Fig. S1b, c). The result was due to increased root and aboveground biomass inputs to soil C pools that supported by a previous synthesis that has focused on the changes in SOC stocks resulted from China's Grain for Green Program (Deng et al. 2014).

That more than 16 times C stocks in soils than in vegetation found in our study (94% of C stocks in soils) was in line with other several studies in China (92.0–96.6% of C stocks in soils; Fang et al. 2010, Wen et al. 2013, Liu et al. 2016, Ma et al. 2016), and suggested the importance of soils in sequestering C in response to the restoration efforts (Long et al. 2010). Given that plant biomass is the most important C input to soils especially in arid and semiarid ecosystems (Jobbágy and Jackson 2000, Austin 2002, Epstein et al. 2002), much more C stocks in soils than those in vegetation in China's grasslands could be attributed to low litter decomposition in the grasslands.



Fig. 6. (a) Spatial distribution of current plant biomass C density (kg C/m^2). (b) Spatial distribution of current soil organic C (SOC) density. (c) Spatial distribution of potential plant biomass C density. (d) Spatial distribution of potential SOC density. (e) Spatial distribution of plant biomass C sequestration potential (CSP). (f) Spatial distribution of soil CSP.

Temperature in alpine grasslands on the Tibetan Plateau and water availability in the temperate grasslands on the Inner Mongolian Plateau limited decomposition of plant litters and thus accumulated a large amount of C in soils (Liu et al. 2009, Yang et al. 2009).

The pairwise field sampling used in this study is an effective method to assess ecosystem C stocks under land-use change and human disturbances, providing a direct evidence of the positive effects of grassland restoration policy and the Grain for Green Project. Based on our pairwise field sampling, the CSP in alpine meadow was higher than that in the other five grassland types, which could be due to the higher net primary productivity in the ecosystem. This result was supported by the higher C density of plant biomass and the longer turnover time of C in the soil (Fig. 3; Conant and Paustian 2002, Henderson et al. 2015, Ma et al. 2016). In comparison with the assessments of C storage capacity (0.10-0.20 kg C/m²) in semiarid grasslands of Northern China in a previous study that primarily focused on the degraded grasslands and only collected the topsoil (0–10 cm) samples (Wiesmeier et al. 2015a), this study provided a more comprehensive CSP assessment (0.76 kg C/m^2) of vegetation and soil C stocks up to the top 1 m depth. Although substantial differences were observed in the CSP among the six grassland types, there was no correlation between the CSP and the initial C storage of degraded grasslands in our study. Our results were supported by a global synthesis showing that warming-induced changes in soil C losses were not related to standing C stocks (van Gestel et al. 2018). However, these observations were contrary to the findings in England and Wales, where a negative linear correlation between the rate of soil C losses and original organic C content mediated by climate change rather than land-use change was found (Bellamy et al. 2005). Diverse environmental conditions or soil properties in different regions may result in the differential results of the dependence of soil C dynamic upon standing C stocks (van Gestel et al. 2018). In addition, caution should be taken when extrapolating our findings as the datasets were collected in 2009-2010 and grassland management/restoration measures may substantially change with time. SOC calculations in further studies should be conducted based on an equivalent soil mass approach to more accurately quantify the difference in SOC stocks between restored and degraded regions (Wiesmeier et al. 2015b).

Impacts of restoration practices and grassland types

Our results of greater C density/CSP caused by the restoration practices involving natural grasslands in the regions with more severe disturbance were consistent with those in European grasslands where C sink increases with increasing utilization intensity (Soussana et al. 2007). On the contrary, decreased C density/CSP resulting from the five restoration practices associated with conversions from croplands back to grasslands or shrublands was similar to the results of a resampling study and meta-analysis, which revealed that afforestation in former croplands can decrease SOC stocks (Bárcena et al. 2014*a*, Fujisaki et al. 2015), probably due to the accelerated decomposition of SOC caused by fresh C inputs (Fontaine et al. 2004). These findings challenge a widely accepted consensus that croplands generally have lower organic matter accumulation and consequently lower SOC stocks than natural ecosystems due to crop harvest (Post and Kwon 2000, Wiesmeier et al. 2011, 2012, 2014, Qiu et al. 2012, Conant et al. 2017). Compared to natural grasslands, a large amount of water and nutrient inputs in croplands can enhance crop growth, biomass production, and soil C, which may be the reason that farmland carbon density is higher than that of natural ecosystems.

Nevertheless, crop planting in the grassland regions does not necessarily increase C sequestration because crop harvesting always leaves the soil bare without plant or residual cover in nongrowing seasons, which can not only result in severe wind erosion and consequently C losses from surface soil (Yan et al. 2005, Mulitza et al. 2010, Chappell et al. 2012, 2016), but also change soil texture via decreasing silt- and clay-sized particles and thus reduce C sequestration capacity (Wiesmeier et al. 2015a). For example, extensive evidences from model simulations (Arora and Boer 2010, Bachelet et al. 2015, Fuchs et al. 2016, Houghton and Nassikas 2018), meta-analyses (Guo and Gifford 2002, Don et al. 2011, Bárcena et al. 2014b, Kopittke et al. 2017), large-scale SOC field inventories (Wertebach et al. 2017), and manipulative experiments (Del Galdo et al. 2003) have demonstrated that cropland expansion can reduce whereas grassland and forest expansion can increase SOC sequestration. One study, however, found that afforestation cannot change SOC stocks in 0- to 50-cm soil layer (DeGryze et al. 2004). The different responses of SOC stocks to conversions from croplands to natural ecosystems may result from the difference in conversion time as suggested in two previous studies, which demonstrated that SOC stocks are reduced during the early restoration stage and enhanced during the late stage (Hu et al. 2008, Deng et al. 2014). Furthermore, the lower magnitudes of the reductions in C stocks induced by the five strategies involving croplands than the enhancements due to the four restoration practices involving natural grasslands suggested that, if not cultivated for crops or forage grasses, appropriate grassland management practices could sustain

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both the demand for grassland products and the soil C storage.

In addition to the contrasting responses of C stocks to different restoration practices, the same restoration measures can also result in various effects on ecosystem C stocks in different grassland types. For example, the conversion from croplands to grasslands reduced plant biomass C stock in meadow and desert steppe whereas enhanced it in typical steppe. In addition, cropland expansion increased SOC stock in alpine steppe, but decreased it in alpine meadow. The non-uniform effects of the conversion from croplands to grasslands on ecosystem C stock among the six grassland types in China's grasslands may be attributed to difference in climate and conversion time (Hu et al. 2008, Deng et al. 2014). Temperature and soil moisture may have different impacts on soil SOC decomposition in different climate conditions, and conversion time may influence plant litter accumulation and its contribution to soil SOC. Further studies are needed to explore the mechanisms underlying different C budget responses to land-use practices among the six grassland types in China's grasslands. Overall, these findings indicate that the CSPs in China's grasslands are dependent upon both restoration strategy and grassland type.

Based on an unprecedented database with pairwise field sampling and estimations using a geostatistical model, we came to a conclusion that grasslands in China have great CSP. Under current climate conditions, the potential to sequester atmospheric CO₂ can be achieved through effective management policies and practices, including grassland enclosure to reduce grazing intensity (Conant et al. 2001, Liu et al. 2008, Abberton et al. 2010, Mu et al. 2013, Smith 2014, Delang and Yuan 2016). Once this CSP is realized, it would lead to considerable climate mitigation benefits by offsetting 100% of China's total fossil fuel CO₂ emissions from 2000 to 2010 (IEA 2012). However, considering future climate change, the C cycle and different C component pools of grassland ecosystems are expected to vary with changes in temperature and precipitation regime as well as atmospheric CO₂, presenting both opportunities and challenges to grassland management. Future research that combines long-term monitoring and ecosystem modeling is needed to predict grassland C dynamics under different climate and management scenarios to inform effective policy-making and actions.

Acknowledgments

The authors thank two anonymous reviewers for their constructive comments and suggestions in improving the manuscript, and Prof. Dafeng Hui for polishing English. This study was supported by the National Natural Science Foundation of China (31430015) and Chinese Academy of Sciences (KZCX2-YW-Q1-06).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2. 2452/full