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Changes in soil carbon and nitrogen stocks following degradation of alpine grasslands on the Qinghai-Tibetan Plateau: A meta-analysis

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Abstract

Until now, nearly 90% of alpine grasslands on the Qinghai-Tibetan Plateau (QTP) have been degraded. However, there is currently no consensus on how soil organic carbon (SOC) and soil total nitrogen (STN) stocks vary with the degradation succession of alpine grasslands in this region. Here, a meta-analysis was conducted to quantify the dynamics of SOC and STN stocks in topsoil (0–30 cm) at different degradation stages of alpine grasslands on the QTP. The results showed that grassland degradation led to average losses of 48 and 39% for SOC and STN stocks, respectively. The changes in SOC and STN stocks following grassland degradation did not differ significantly between grassland types, but were significantly affected by grassland degradation stage. The reductions in both SOC and STN stocks increased with the degradation stage, and the highest reductions were all found at extreme degradation stage. The results indicated that the depletion of SOC and STN pools were aggravated with the degradation succession of grassland. The tightly coupled SOC and STN implied that the depletion of SOC stock was closely related to that of STN stock during the process of grassland degradation. Positive relationships were detected between the dynamics of vegetation coverage and that of SOC or STN stock, indicating that vegetation coverage could not only reflect grassland degradation, but might also be a potential indicator of SOC and STN status. The findings suggest that preventing the degradation succession of alpine grasslands is vital to maintain or promote SOC and STN levels on the QTP.

KEYWORDS

alpine region, grassland degradation, meta-analysis, soil carbon, soil nitrogen

1 | INTRODUCTION

As one of the most widespread biomes worldwide, grasslands are essential components of the terrestrial carbon (C) cycle (Scurlock & Hall, 1998). It is estimated that approximately 10–30% of the global soil organic carbon (SOC) are stored in grassland soils, which sequester C at a rate of 0.5 Pg yr^{-1} (Follett & Reed, 2010; Zhou et al., 2017). The rate is almost a quarter of the potential C sequestration in global soils (Follett & Reed, 2010). The dynamics of the SOC pool in grasslands thus plays a significant role in the global C balance and impacts the global climate (Conant, Cerri, Osborne, & Paustian, 2017; Soussana et al., 2004). However, large areas of grasslands have been degraded around the world in recent decades, mainly as a result of human activities and climate change (Akiyama & Kawamura, 2007; Dlamini, Chivenge, Manson, & Chaplot, 2014). Grassland degradation often leads to negative consequences such as reductions in soil basal cover and plant productivity, which may cause SOC losses through aggravating soil erosion and reducing soil organic matter (SOM) inputs (Abdalla, Mutema, Chivenge, Everson, & Chaplot, 2018; Li, Dong, Wen, Wang, & Wu, 2014). In these cases, grassland soils may become a source rather than a sink for atmospheric CO_2 (Abdalla et al., 2018; Mchunu & Chaplot, 2012).

The Qinghai-Tibetan Plateau (QTP), known as the 'Roof of the World' and the 'Third Pole of the Earth', is the largest plateau on the Eurasian continent and a key ecological region with the lowest-latitude permafrost in the world (Dong et al., 2020; Li, Dong, Wen, et al., 2014). Over 85% of the QTP is covered by alpine grasslands (e.g., alpine meadow and alpine steppe), which are important parts of global grassland biomes (Li, Dong, Wen, et al., 2014). Alpine grasslands in this region not only offer fundamental resources of livelihood for local herdsmen, but also provide crucial ecosystem functioning and services such as C sequestration and biodiversity conservation (Genxu, Ju, Guodong, & Yuanmin, 2002; Miehe et al., 2019). Nevertheless, the harsh conditions (e.g., low temperature, low precipitation, and short plant growing season) in the QTP make the grasslands very sensitive to both environmental changes and anthropogenic disturbances (Liu, Zamanian, Schleuss, Zarebanadkouki, & Kuzyakov, 2018). It is estimated that approximately 90% of alpine grasslands on the QTP have been degraded (Li, Dong, Wen, et al., 2014), with 35% being severely degraded into 'black soil beach', where the entire turf layer is totally removed leaving soils uncovered (Shang & Long, 2007). The driving forces of alpine grassland degradation on the QTP are recognized as overgrazing, rodent disturbances, and climate change (Harris, 2010; Shang & Long, 2007). The impact of land degradation on the SOC pool in alpine grasslands of the QTP has been investigated in previous studies, most of which reported that grassland degradation led to depletion of SOC stock (Dong et al., 2012; Li, Dong, Wen, et al., 2014; Wen, Jinlan, Xiaojiao, Shangli, & Wenxia, 2018). However, existing studies mainly used the equivalent soil volume method to calculate SOC stocks in both non-degraded and degraded grasslands, leading to underestimations of SOC depletion after grassland degradation because soil bulk density (BD) was often increased by livestock trampling under the condition of overgrazing (Hiltbrunner, Schulze, Hagedorn, Schmidt, & Zimmmermann, 2012; Zeng, Zhang, Wang, Chen, & Joswiak, 2013; Zhou et al., 2019). As an example, Zhou et al. (2019) found that BD in the 0–10 cm soil layer significantly increased from 0.93 g cm^{-3} to 1.18–1.65 g cm^{-3} after degradation of an alpine steppe in the hinterland of the QTP. To accurately assess the negative feedback of grassland degradation on the terrestrial C cycle, it is desirable to quantify SOC stock based on the equivalent soil mass method, which has been demonstrated to produce more accurate results than the equivalent soil volume method when evaluating the dynamics of SOC stock after the changes in land-use or management practice (Ellert & Bettany, 1995; Lee, Hopmans, Rolston, Baer, & Six, 2009; Wendt & Hauser, 2013). Nevertheless, few studies have employed the equivalent soil mass method to access the impact of grassland degradation on SOC stock not only in the QTP but also in other regions of the world (Dlamini et al., 2014; Li, Dong, Wen, et al., 2014).

Until now, numerous indicators including soil properties (Kimetu et al., 2008), plant characteristics (Ma et al., 2002), and death rate of livestock (White, Murray, & Rohweder, 2000) have been proposed to evaluate the degree of grassland degradation. Since plant characteristics (e.g., vegetation coverage and productivity) not only determines the production of animal husbandry, but also reflects soil fertility, they are widely used to define the degradation stage of grassland worldwide (Dlamini et al., 2014; Liu et al., 2018). The commonly used degradation classification for alpine grasslands on the QTP was proposed by Ma et al. (2002), who divided grasslands into non-degradation, light degradation, moderate degradation, heavy degradation, and extreme degradation according to vegetation coverage, productivity, as well as proportion and height of edible plants (Table S1). In the QTP, although previous studies have compared SOC stocks in alpine grasslands at different degradation stages, it is still difficult to clarify how SOC stock changes with grassland degradation succession because the results differed considerably among individual studies (Dong et al., 2012; Liu et al., 2020; Zhou et al., 2019). The relationships between SOC dynamics and plant characteristics in degraded grasslands are also not well understood. Answering these questions may provide useful information for the large-scale estimation of SOC changes after grassland degradation on the QTP through remote sensing or modeling approach.

Here, a meta-analysis was conducted based on the dataset collected from 36 studies to quantify the changes in SOC stock in topsoil (0–30 cm) at different degradation stages of alpine grasslands on the QTP. Since nitrogen (N) is an essential element affecting both plant growth and the persistence of C sequestration in grassland ecosystems (Luo et al., 2004; Rastetter, Ågren, & Shaver, 1997; van Groenigen et al., 2017), the effect of grassland degradation on soil total N (STN) stock was also assessed to better understand the dynamics of SOC following grassland degradation. Considering grassland degradation could impact on soil BD, the equivalent soil mass method was performed to calculate SOC and STN stocks in this study. The main aims of this study were to: (a) estimate the changes in SOC and STN stocks at different degradation stages of alpine grasslands on the QTP; (b) explore potential factors influencing the dynamics of SOC and STN stocks following grassland degradation. The following hypotheses were tested: (a) both SOC and STN stocks decreased with the degradation succession of grassland; (b) the dynamics of both SOC and STN stocks were related to those of vegetation coverage and productivity.

2 | MATERIALS AND METHODS

2.1 | Data collection

To compile data for meta-analysis, relevant articles published before June 2020 were searched through three databases including ISI Web of Science, Google Scholar, and China National Knowledge Infrastructure (CNKI). The combinations of search terms were 'soil,degradation or degeneration or degraded', 'alpine grassland or alpine meadow or alpine steppe', and 'Qinghai-Tibetan Plateau or Tibetan Plateau or Tibet'. The following criteria were set to determine whether a study would be selected for meta-analysis:

1. The degradation stage of grassland was clearly stated or could be obtained according to the classification of alpine grassland degradation in the QTP (Table S1); (Ma et al., 2002). The control site must be non-degraded grassland to evaluate the impacts of grassland degradation on SOC and STN stocks.
2. Studies should be carried out using paired-site chronosequence, making similar soil and climatic conditions for the non-degraded and degraded sites.
3. Stock of SOC or STN was reported or could be calculated based on soil BD, sampling depth, and content of SOC or STN. Furthermore, soil BD must be presented to perform equivalent soil mass corrections of SOC and STN stocks.
4. The means and sample sizes must be provided for both non-degradation and degradation sites.

Since most collected studies focused on the change in SOC or STN stock in topsoil (0–30 cm) after grassland degradation, the data of soil properties such as SOC stock, STN stock, and soil BD were compiled from 0 to 30 cm soil layer. If one study reported SOC or STN stocks at different depths (e.g., 0–10 cm, 10–20 cm, and 20–30 cm), only stocks measured across the whole sampling depth were used to avoid interdependence of observations (Ma, Chen, Bork, Carlyle, & Chang, 2020). For the same purpose, only soil BD in the uppermost soil layer was collected (Jian et al., 2016). In total, 178 paired observations between degraded alpine grasslands and adjacent non-degraded alpine grasslands from 36 peer-reviewed studies were compiled to evaluate the dynamics of SOC and STN stocks following grassland degradation on the QTP. The grassland types were classified into alpine meadow (AM) and alpine steppe (AS), which are the two major grassland types on the QTP. The degradation stages of grassland were divided into five groups including non-degradation (ND), light degradation (LD), moderate degradation (MD), heavy degradation (HD), and extreme degradation (ED) to assess the effects of grassland degradation stage on SOC and STN stocks (Liu et al., 2018; Ma et al., 2002; Zhang, Xue, Peng, You, & Hao, 2019). The raw data in the selected studies were extracted from graphs using GetData Graph Digitizer v.2.25 (http://www.getdata-graph-digitizer.com/index.php) or directly obtained from tables (Liu et al., 2020). Information on the location, mean annual temperature (°C), mean annual precipitation (mm), and grassland type of each study site was also gathered when it was available (Table S2).

2.2 | Data calculation

In this study, the minimum equivalent soil mass method was applied to perform soil mass corrections of SOC and STN stocks. This method adjusts soil mass to the lightest soil mass across study sites in individual studies and has been proved to be a better choice than the maximum equivalent soil mass method when estimating the changes in SOC and STN stocks in grassland ecosystems (Lee et al., 2009). The detailed procedure of the minimum equivalent soil mass method was described in Bárcena et al. (2014) and Liu, Sheng, et al. (2020). In brief, the first step of this method was to calculate the mass per unit area of the soil according to the fixed depth at non-degradation and degradation sites for each study:

$$M_f = \mathrm{BD} \times h \times 100, \tag{1}$$

Where: M_f (Mg ha^{-1}) is the dry mass of soil to a fixed depth; BD (g cm^{-3}) is the bulk density; and h (cm) is the thickness of soil layer. After that, the M_f at different sites was compared to select the site with the lightest soil mass, which was regarded as the reference soil. A certain quantity of soil mass (M_s, Mg ha^{-1}) had to be subtracted from the heavier soils to obtain the equivalent soil mass (M_e, Mg ha^{-1}):

$$M_s = M_f - M_e. \tag{2}$$

The stocks of SOC and STN in equivalent soil mass (S_e, Mg ha^{-1}) were then calculated according to the following equations:

$$S = C \times M \times 0.001, \tag{3}$$

$$S_e = S_f - S_s, \tag{4}$$

Where: S is the stock of SOC or STN (Mg ha^{-1}); C is the content of SOC or STN (g kg^{-1}); M is the dry mass of soil (Mg ha^{-1}); S_f is the stock of SOC or STN (Mg ha^{-1}) to a fixed depth; and S_s is the stock of SOC or STN (Mg ha^{-1}) calculated for M_s. If the content of SOM was reported, the following equation was used to convert content of SOM to that of SOC (Don, Schumacher, & Freibauer, 2011):

$$\mathrm{SOC} = \mathrm{SOM} \times 0.58. \tag{5}$$

2.3 | Meta-analysis

In the present meta-analysis, the natural log-transformed response ratio (lnRR) was used as the effect size to evaluate the differences in soil BD and stocks of SOC and STN between non-degraded and degraded grasslands (Dlamini, Chivenge, & Chaplot, 2016; Lam, Chen, Norton, Armstrong, & Mosier, 2012):

$$\ln(\mathrm{RR}) = \ln\left(\frac{X_{\mathrm{nd}}}{X_d}\right), \quad (6)$$

Where: X_{nd} and X_d indicate the mean values of soil BD, SOC stock and STN stock at non-degraded grasslands and degraded grasslands, respectively. The response ratios were transformed to percent changes ([RR − 1] × 100) to present the dynamics of soil BD, SOC stock, and STN stock after grassland degradation (Liu, Sheng, et al., 2020; Zhang et al., 2019). Positive values implied increases in soil BD, SOC stock, and STN stock after grassland degradation, whereas negative values indicated that grassland degradation decreased soil BD, SOC stock, and STN stock.

In general, the effect sizes were unweighted (Shi et al., 2016), weighted by the inverse of pooled variances (Jian et al., 2016; Zhang et al., 2019) or replications (Dlamini et al., 2016; Lam et al., 2012; Ma et al., 2020; Xia et al., 2018) from previous meta-analyses. Since not all the compiled studies presented the standard deviations of the means, and variance-based weighting function might cause extreme weights (van Groenigen, Osenberg, & Hungate, 2011), the effect sizes were thus weighted by a function of replications in this study:

$$W = \frac{N_{\mathrm{nd}} \times N_d}{N_{\mathrm{nd}} + N_d}, \quad (7)$$

Where: W is the weight; N_{nd} and N_d are the numbers of replications at non-degraded sites and degraded sites, respectively.

The Q test was conducted to assess whether the compiled studies were homogeneous (Soma & Garamszegi, 2011). The results indicated that there was no heterogeneity among studies for soil BD, SOC stock, and STN stock (Table S3). Publication bias was examined using funnel plots. Given that most compiled studies did not report sampling variance, the funnel plots were plotted as the effect sizes against their sample sizes (Ma et al., 2020). Begg's rank test and Egger's regression test were applied to evaluate the potential asymmetry of the funnel plots (Ma et al., 2020; McDonald, Lawrence, Kendall, & Rader, 2019). The results showed that there was no publication bias in the present meta-analysis (Table S3 and Figure S1). Mean effect sizes and 95% confidence intervals were used to identify the effects of grassland degradation on soil BD, SOC stock, and STN stock (Xia et al., 2018). Moreover, the differences in effect sizes between grassland types or among degradation stages were assessed based on between-group heterogeneity (Q_b) test (Waqas et al., 2020). When 95% confidence intervals did not overlap with zero, it implied that grassland degradation resulted in significant changes in soil BD, SOC stock, or STN stock. The means of different subgrouping categories were deemed significantly different from one another if their 95% confidence intervals did not overlap (Lam et al., 2012; Zhang et al., 2019). All statistical analyses were performed using the Metafor package in R v.4.0.2 (R core team, 2020; Viechtbauer, 2010).

3 | RESULTS

3.1 | Grassland degradation impacts on soil BD

Across all the observations compiled in this study, soil BD significantly increased by 24% (95% confidence interval, 17–31%) after degradation of alpine grasslands on the QTP (Figure 1). For AM, land degradation significantly increased soil BD by 27%. The degradation of AS led to an increase of 10% for soil BD, whereas the overlapped 95% confidence interval and zero indicated that the change was not significant. Although the increase in soil BD after the degradation of AM was approximately 2.6-times higher than that after the degradation of AS, no significant difference was detected between them (Q_b = 0.85, p > 0.05; Table 1). Soil BD significantly increased at all degradation stages of grassland. The increases of soil BD were 14, 22, 26, and 37% at the stage of LD, MD, HD, and ED, respectively. Similar to soil depth and grassland type, grassland degradation stage did not affect the dynamics of soil BD after grassland degradation as well (Q_b = 0.89, p > 0 .05; Table 1).

3.2 | Grassland degradation impacts on SOC stock

As illustrated in Figure 2, the degradation of alpine grasslands induced a negative impact on SOC sequestration on the QTP. A significant reduction of 48% for SOC stock (95% confidence interval, −56 to −40%) was observed following grassland degradation across all the observations. Significant losses of SOC stock were observed after the degradation of both AM and AS. The reduction in SOC stock was 51%

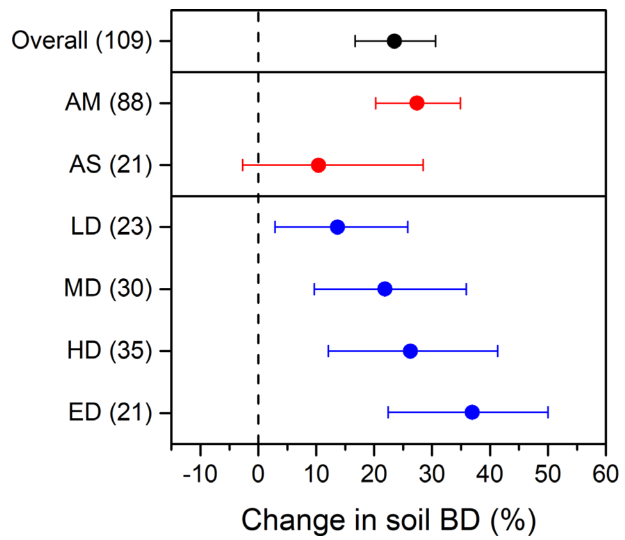

FIGURE 1 Percent changes in soil bulk density (BD) (mean ± 95% confidence intervals) after grassland degradation categorized by grassland type and degradation stage. The sample sizes of each group are shown in the parentheses. AM, AS, LD, MD, HD, and ED represent alpine meadow, alpine steppe, light degradation, moderate degradation, heavy degradation, and extreme degradation, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Between-group heterogeneity (Q_b) of the categorical variables that were examined in the meta-analysis

	Soil BD		SOC stock		STN stock	
Factor	Q_b	*p*	Q_b	*p*	Q_b	*p*
Grassland type	0.85	.36	1.46	.23	0.49	.48
Degradation stage	0.89	.83	**20.54**	**<.001**	**15.52**	**<.01**

Notes: BD, SOC, and STN represent bulk density, soil organic carbon, and soil total nitrogen, respectively; bold values indicate the differences are significant.

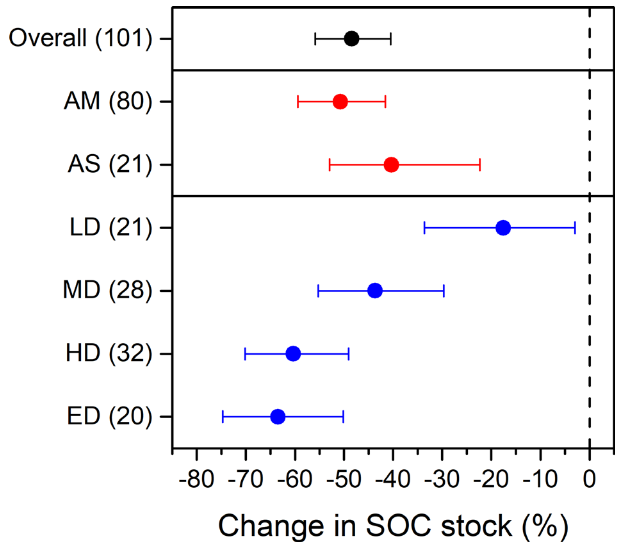

FIGURE 2 Percent changes in soil organic carbon (SOC) stock (mean ± 95% confidence intervals) after grassland degradation categorized by grassland type and degradation stage. The sample sizes of each group are shown in the parentheses. AM, AS, LD, MD, HD, and ED represent alpine meadow, alpine steppe, light degradation, moderate degradation, heavy degradation, and extreme degradation, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

after the degradation of AM, which was nearly 1.3-times higher compared to that after the degradation of AS (−40%). However, the changes in SOC stock did not differ significantly between the two grassland types (Q_b = 1.46, $p > 0.05$; Table 1). In contrast, significant differences in SOC variations were observed among different degradation stages of grassland (Q_b = 20.54, $p < 0.001$; Table 1). The losses of SOC stock gradually increased with the degradation stage of grassland. Specifically, the depletion rates of SOC stock were 18, 44, 60, and 63% at the stage of LD, MD, HD, and ED, respectively. The losses of SOC stock were significantly higher at the stage of HD and ED compared to that at the stage of LD ($p < 0.001$).

3.3 | Grassland degradation impacts on STN stock

Similar to SOC stock, STN stock also showed a decreasing trend following degradation of alpine grasslands on the QTP (Figure 3). On

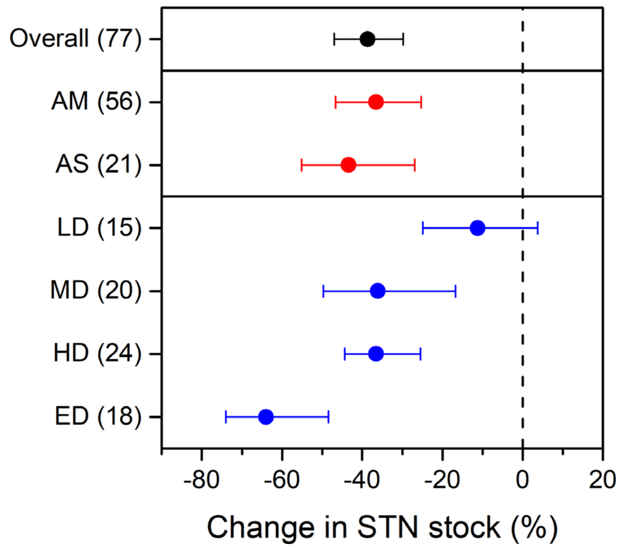

FIGURE 3 Percent changes in soil total nitrogen (STN) stock (mean ± 95% confidence intervals) after grassland degradation categorized by grassland type and degradation stage. The sample sizes of each group are shown in the parentheses. AM, AS, LD, MD, HD, and ED represent alpine meadow, alpine steppe, light degradation, moderate degradation, heavy degradation, and extreme degradation, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

average, grassland degradation significantly reduced STN stock by 39% (95% confidence interval, −47 to −30%), which was lower than the depletion rate of SOC stock. The reduction in STN stock was higher following the degradation of AS (−43%) compared to that following the degradation of AM (−36%), whereas no significant difference was detected between them (Q_b = 0.49, $p > 0.05$; Table 1). With the degradation succession of grassland, the reductions in STN stock also showed an increasing trend. The depletion rate of STN stock ranged between −64 and −11% at different degradation stages of grassland. Nevertheless, the reduction in STN stock was not significant at the stage of LD, as indicated by the overlapped 95% confidence interval and zero. This was a major difference between the change in SOC stock and that of STN stock following grassland degradation. Like SOC stock, the change in STN stock was also significantly influenced by the degradation stage of grassland (Q_b = 15.52, $p < 0.01$; Table 1). The reductions in STN stock at the stage of HD and ED were significantly higher than that at the stage of LD as well ($p < 0.01$).

3.4 | Relationships between SOC and STN stocks at different grassland degradation stages

As presented in Figure 4a, the effect sizes of SOC stock were unrelated to those of STN stock at the stage of LD (r^2 = 0.24, $p > 0.05$). In contrast, the effect sizes of SOC stock and those of STN stock were positively correlated at the rest of the degradation stages (r^2 = 0.34–0.72, $p < 0.05$ or 0.001; Figure 4b–d). It was observed that

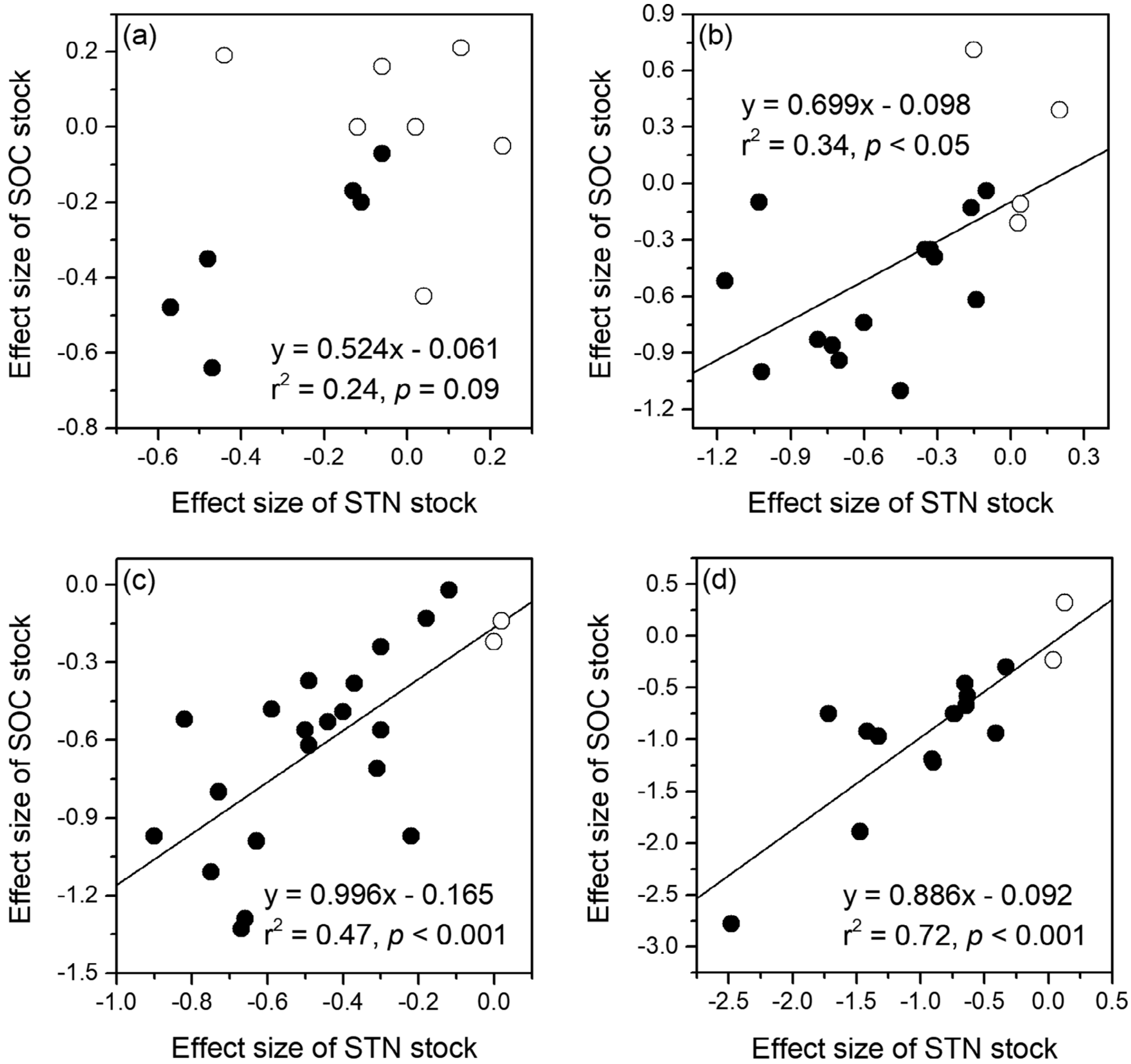

FIGURE 4 Relationships between the effect sizes of soil organic carbon (SOC) stock and those of soil total nitrogen (STN) stock at different grassland degradation stages: (a) light degradation (LD); (b) moderate degradation (MD); (c) heavy degradation (HD); and (d) extreme degradation (ED). The black circles indicate that both SOC and STN stocks decreased after grassland degradation

the r^2 values gradually increased with the degradation stage of grassland, and the highest r^2 value was observed at the stage of ED ($r^2 = 0.72$, $p < 0.001$; Figure 4d). At the stage of LD, only 54% observations showed reductions in both SOC and STN stocks, whereas the others reported increases in SOC stock, STN stock, or both of them after grassland degradation. In contrast, both SOC and STN stocks exhibited decreasing trends in most observations at the stage of MD (78%), HD (91%), and ED (88%).

3.5 | Relationships between SOC or STN stock and plant characteristics

The relationships between SOC or STN stock and vegetation coverage, aboveground biomass, as well as belowground biomass were illustrated in Figure 5. A positive relationship was detected between the effect sizes of vegetation coverage and those of SOC stock ($r^2 = 0.26$, $p < 0.001$; Figure 5a). Similarly, the effect sizes of vegetation coverage were positively correlated to those of STN stock as well ($r^2 = 0.23$, $p < 0.001$; Figure 5b). In contrast, there was no relationship between the variations of aboveground biomass and those of SOC ($r^2 = 0.01$, $p > 0.05$; Figure 5c) or STN stock ($r^2 = 0.001$, $p > 0.05$; Figure 5d). Similar to vegetation coverage, the effect sizes of belowground biomass were also positively related to those of both SOC ($r^2 = 0.56$, $p < 0.001$; Figure 5e) and STN stocks ($r^2 = 0.26$, $p < 0.05$; Figure 5f).

4 | DISCUSSION

4.1 | Effect of grassland degradation on soil BD: Implications for estimating C and N stocks

Soil BD is a necessary parameter for the estimation of SOC and STN stocks (Throop, Archer, Monger, & Waltman, 2012). Some studies also found a close relationship between soil BD and SOM content (Perie &

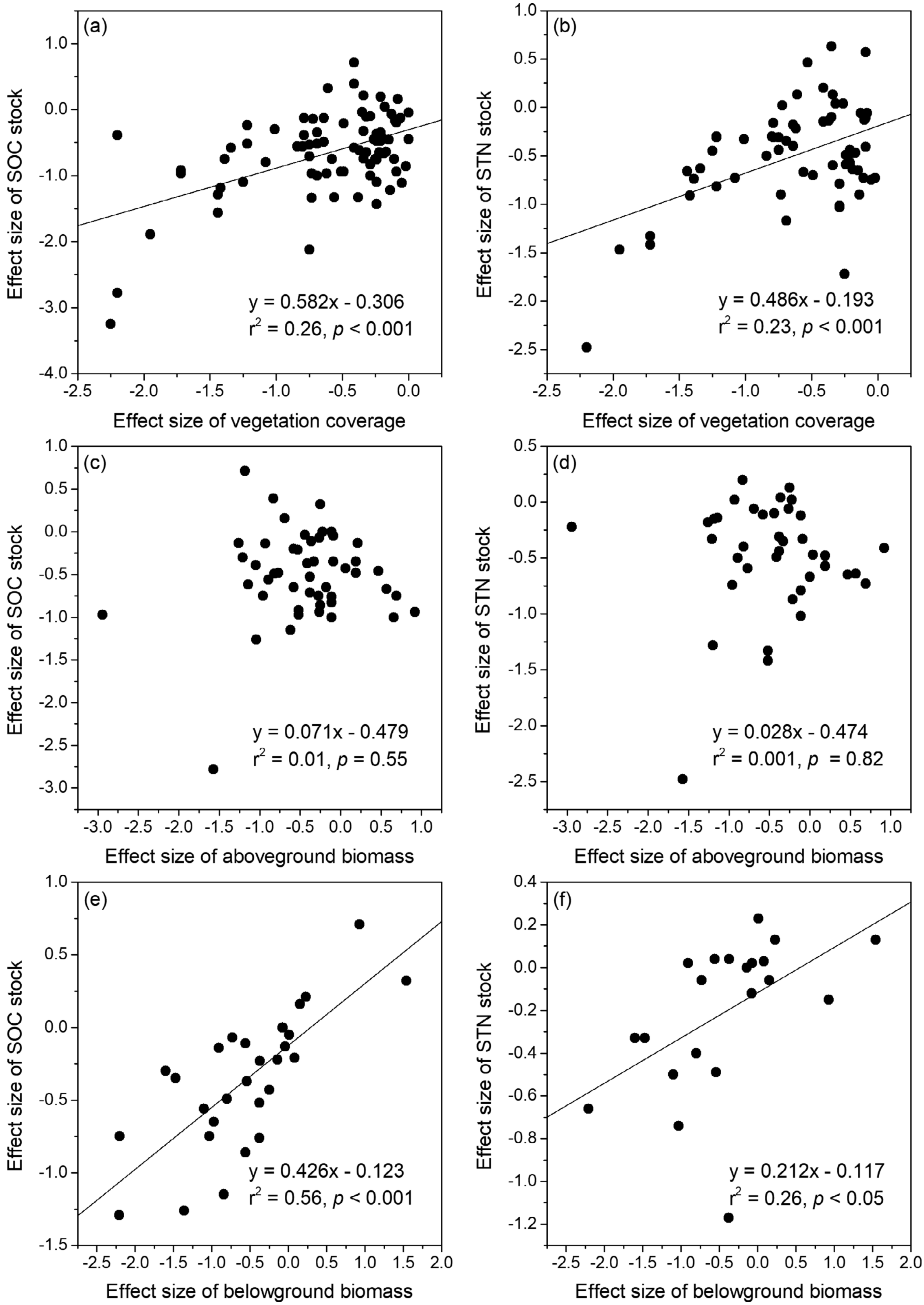

FIGURE 5 Relationships between the effect sizes of soil organic carbon (SOC) or soil total nitrogen (STN) stock and those of vegetation coverage, aboveground biomass, or belowground biomass

Ouimet, 2008; Ruehlmann & Körschens, 2009). The equivalent soil volume method, which calculates SOC or STN stock through multiplying SOC or STN content with soil BD to a fixed soil depth, is a widely used method to quantify the changes in SOC and STN stocks following grassland degradation on the QTP (Dong et al., 2012; Li, Dong, Wen, et al., 2014; Wen et al., 2018). However, this method has been shown to introduce substantial errors when soil BD changes following grassland degradation (Ellert & Bettany, 1995; Lee et al., 2009). For example, if grassland degradation decreases SOC content while increasing soil BD, the reduction in SOC stock after grassland degradation is likely to be underestimated using this method (Huo et al., 2013; Wendt & Hauser, 2013). In the present meta-analysis, the results showed that grassland degradation significantly increased soil BD by 24% across all the observations (Figure 1), indicating that soil compaction occurred following grassland degradation. The findings were consistent with those of previous studies that were conducted in grasslands of other regions around the world (Dlamini et al., 2014; Hiltbrunner et al., 2012). As an example, Dlamini et al. (2014) observed significant increases in soil BD after degradation of a sub-tropical humid grassland in South Africa. The increased soil BD were mainly attributed to livestock (e.g., yak and Tibetan sheep) trampling, which resulted in mechanical stress imposed on the soils and then induced the collapse of soil structure (Hiltbrunner et al., 2012; Zhou, Gan, Shangguan, & Dong, 2010). In addition, grazing or rodent activities could decrease the amount of aboveground biomass and limit the development of root system, leading to a reduction in SOM inputs (Bai et al., 2015; Pang & Guo, 2018). This was another reason for the increased soil BD because SOM is a loose and porous material that not only serves as the major component of soils (Arvidsson, 1998; Ruehlmann & Körschens, 2009), but also plays an important role in the formation of soil aggregates (Piccolo & Mbagwu, 1999). Based on these results, it is suggested that the equivalent soil mass method should be employed rather than the equivalent soil volume method to accurately quantify the impacts of alpine grassland degradation on SOC and STN stocks on the QTP (Lee et al., 2009; Wendt & Hauser, 2013).

4.2 | Underlying mechanisms responsible for the depletion of SOC and STN stocks following grassland degradation

In the past several decades, the negative consequences caused by grassland degradation have attracted much attention because of the deteriorating environment of grassland ecosystems worldwide (Abdalla et al., 2018; Galdino et al., 2016; Nesper et al., 2015; Wang, Deng, Song, Li, & Chen, 2017). Existing studies have demonstrated that grassland degradation can lead to depletion of SOC and STN stocks, but the results differed considerably in individual studies (Abdalla et al., 2018; Dlamini et al., 2014; Dong et al., 2012). For instance, in an alpine grassland of the QTP, Dong et al. (2012) observed that grassland degradation significantly reduced SOC and STN stocks by 55 and 49%, respectively. Higher depletion rates were reported by Abdalla et al. (2018), who conducted a research in South Africa and found that SOC and STN stocks in non-degraded grasslands were 754 and 167% higher compared to those in highly degraded grasslands, respectively. In a recent meta-analysis, Dlamini et al. (2016) found that grassland degradation reduced SOC stock by an average of 9% on the global scale. They also pointed out that the depletion of SOC stock following grassland degradation was strongly linked to climatic conditions, soil properties, and the degradation stage of grassland. Therefore, the impacts of grassland degradation on SOC and STN stocks should also be evaluated from a regional perspective due to the spatial heterogeneity of climatic conditions, soil types, and grassland biomes. The results of this study showed that on average, grassland degradation induced significant reductions of 48 and 39% for SOC and STN stocks, respectively (Figures 2 and 3), demonstrating that alpine grassland degradation led to losses of both SOC and STN in topsoil on the QTP. There are multiple potential mechanisms responsible for the depletion of SOC and STN stocks after grassland degradation. First, livestock grazing and rodent activities (e.g., burrowing) could negatively impact the growth of plants, reducing both above- and belowground productivity of the plant community (Bai et al., 2015; Li, Dong, Wen, et al., 2014; Pang & Guo, 2018). In this case, the inputs of SOM from plants (e.g., plant residues and root exudates) would be decreased. The positive relationships between the dynamics of SOC or STN stock and those of belowground biomass partly supported this assertion (Figure 5e,f). Nevertheless, it was unexpected that the dynamics of aboveground biomass was unrelated to those of SOC and STN stocks (Figure 5c,d). This was possibly due to the presence of poisonous plants because some compiled studies reported that aboveground biomass of plant community was considerably increased by poisonous plants (e.g., *Ligularia virgaurea* and *Stellera chamaejasme* L.), which may become the dominant species if grasslands are heavily or extremely degraded (Qi, 2005; Ren, Shang, Long, Hou, & Deng, 2013). Although the increased aboveground biomass could enhance SOM inputs, substantial losses of SOC and STN induced by grassland degradation were difficult to offset in the short term (Li et al., 2014; Ren et al., 2013). For example, Ren et al. (2013) observed that aboveground biomass in four heavily degraded alpine meadows were 60–152% higher than that in non-degraded alpine meadows due to the spread of poisonous plants. However, vegetation coverage, as well as SOM and STN contents in degraded alpine meadows, was still lower compared to those in non-degraded alpine meadows. Second, the physical protection of SOM could be weakened by external disturbances, especially by livestock trampling under overgrazing conditions due to the destruction of soil aggregates (Dong et al., 2020; Wiesmeier et al., 2012). This would stimulate the decomposition of SOM and result in the depletion of SOC and STN stocks (Abdalla et al., 2018; Dong et al., 2020). Third, grassland degradation reduced soil cation exchange capacity because of the decreased clay and SOM contents and the increased soil pH (Wang, Wang, Li, & Cheng, 2007; Wu & Tiessen, 2002). Under this condition, soil nutrients (e.g., NO_3^- and NH_4^+) could easily be lost through leaching (Liu et al., 2018; Wu & Tiessen, 2002). The fourth reason for the reduced STN stock was that the number of leguminous species declined with grassland degradation which then decreased N contents that were derived from biological N fixation (Li et al., 2015; Wang et al., 2015). However, the relative importance of these mechanisms in inducing the depletion of

SOC and STN stocks is still unclear and should be paid closer attention in future studies.

4.3 | Depletion of SOC and STN stocks after grassland degradation in different grassland types and degradation stages

AM and AS are two major grassland biomes on the QTP, both of which have strong ability to sequester C into soils (Genxu et al., 2002; Yang et al., 2008). Therefore, the degradation of AM and AS in this region may lead to substantial losses of SOC and STN, which are inadequately addressed in previous studies and need to be quantified. The results of this meta-analysis indicated that the reductions in both SOC and STN stocks following grassland degradation did not differ significantly between AM and AS (Table 1). Nevertheless, the average losses of SOC and STN stocks induced by the degradation of AM (24.19 and 1.73 Mg ha^{-1} for SOC and STN stocks, respectively; Table S4) were considerably higher compared to those resulted from the degradation of AS (7.90 and 0.43 Mg ha^{-1} for SOC and STN stocks, respectively; Table S4). Considering AM generally stores higher SOC and STN than AS and is the dominant grassland type on the QTP (Genxu et al., 2002; Yang et al., 2008), the degradation of AM may cause greater adverse impacts on the global climate than that of AS on the QTP. Moreover, it should be noted that studies regarding the impacts of grassland degradation on SOC and STN stocks in subsoil (>30 cm) remain scarce on the QTP. Recently, there is increasing evidence that SOC and STN pools in subsoil can be also influenced by land degradation (Dlamini et al., 2014; Huo et al., 2013). For instance, Huo et al. (2013) observed that SOC stock in the 30–50 cm soil layers decreased by 13% after degradation succession from swamp to meadow in Zoige County of the Northeastern QTP. Consequently, the responses of SOC and STN stocks in subsoil to grassland degradation should also be considered in the future to better understand the impacts of grassland degradation on the C and N cycles on the QTP.

Vegetation coverage is one of the most commonly used indicators for classifying the degradation degree of grasslands (Dlamini et al., 2014; Ma et al., 2002). For instance, Dlamini et al. (2014) chose four grasslands that had different vegetation coverage (75–100%, 50–75%, 25–50%, and 0–5%) to evaluate the impacts of land degradation on SOC and STN stocks in a sub-tropical humid grassland in South Africa. Their results showed that both SOC and STN stocks decreased with vegetation coverage, implying that the depletion of SOC and STN stocks were exacerbated with the retrogressive succession of grasslands. Similarly, the results of present meta-analysis indicated that the reductions in both SOC and STN stocks increased with the degradation stage of grassland (Figures 2 and 3), which was mainly divided by vegetation coverage. As illustrated above, the reduction in SOM inputs, the destruction of soil aggregates, the leaching of soil nutrients, and the loss of leguminous plant species were likely mechanisms responsible for the depletion of SOC and STN stocks following grassland degradation (Dong et al., 2020; Li et al., 2015; Piñeiro, Paruelo, Oesterheld, & Jobbágy, 2010). Empirical evidence has shown that grasslands with high vegetation coverage generally have high net primary productivity, rich plant diversity, and well-structured soils, all of which are favorable for SOC and STN accumulations (Fayiah et al., 2019; Pérès et al., 2013; Wiesmeier et al., 2012). Also, the results of this study suggested that vegetation cover played a crucial role in affecting SOC and STN stocks, as indicated by the positive relationships between the dynamics of vegetation coverage and that of SOC or STN stock (Figure 5a,b). Consequently, it is suggested that vegetation coverage is not only an important indicator of land degradation, but also can reflect SOC and STN status in alpine grasslands of the QTP. Moreover, the results of this study indicated that the coupling relationship between SOC and STN became closer with the degradation succession of grassland (Figure 4). Empirical evidence has indicated that N is a key element limiting SOC accumulations in grassland ecosystems, especially during the restoration of degraded grasslands (Deng, Shangguan, Wu, & Chang, 2017; Fornara, Banin, & Crawley, 2013; Luo et al., 2004; Piñeiro et al., 2010). For example, a recent synthesis reported that the accretion of STN could not meet the demand of SOC increase at the later recovery stage of degraded grasslands which then limited SOC sequestration (Deng et al., 2017). Hence, STN may play a key role in determining the capacity of SOC sequestration during the restoration of degraded alpine grasslands on the QTP (Liu, Sheng, et al., 2020; Yu, Chen, Sun, & Huang, 2019).

5 | CONCLUSIONS

The results of this meta-analysis showed that the degradation of alpine grasslands on the QTP led to significant reductions in both SOC and STN stocks in topsoil. The depletion of SOC and STN stocks following grassland degradation were likely resulted from the reduction in SOM inputs, the destruction of soil aggregates, the leaching of soil nutrients, and the loss of leguminous plant species. The changes in SOC and STN stocks did not differ significantly between grassland types, but were significantly affected by grassland degradation stage. The reductions in both SOC and STN stocks increased with the degradation stage of grassland, indicating that the losses of SOC and STN stocks worsened with continued grassland degradation. The depletion of SOC stock was closely related to that of STN stock at most grassland degradation stages, as indicated by the strongly coupled SOC and STN. The positive relationships between the dynamics of vegetation coverage and that of SOC or STN stock suggested that vegetation coverage was not only an important indicator of grassland degradation, but might also reflect the dynamics of SOC and STN stocks in alpine grasslands of the QTP. Considering the significant role of alpine soils in influencing the global climate, methods of preventing the degradation succession of alpine grasslands are thus of great importance to maintain or promote SOC and STN levels on the QTP.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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