







RESEARCH ARTICLE

Patterns and drivers of the degradability of dissolved organic matter in dryland soils on the Tibetan Plateau

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Abstract

1. Dryland soils consistently exhibit a low capacity for the long-term accumulation and storage of organic matter, which has been primarily attributed to low plant biomass inputs under drought suppression. Whether, and how, soil organic matter (SOM) compositions contribute to the consistently low SOM storage have been puzzling. A fundamental understanding of this mechanism is particularly essential to achieve the aspiration of '4 per mille Soils for Food Security and Climate'.
2. By screening the molecular composition of dissolved organic matter (DOM), the gatekeeper of SOM decomposition, we explored the transformation processes among the pools of SOM, DOM and microbial biomass carbon (MBC) in soils along a precipitation gradient on dryland grasslands of the Tibetan Plateau.
3. The results revealed that the number and mean weight of DOM molecules significantly decreased, and the soil DOM composition gradually shifted to be more labile along the transition from meadow, steppe, to desert with decreasing precipitation, coinciding with the substantial reduction in SOM. Compared with meadow soils, DOM degradability increased by 8.7% in steppe soils and by 23.4% in desert soils. The ratio of soil MBC to total organic carbon was threefold higher in desert than in meadow, and positively correlated with DOM degradability, indicating that labile DOM accelerated microbial growth and SOM decomposition in desert soils. Structural equation model and correlation analyses demonstrated that the DOM degradability was primarily controlled by soil dissolved nitrogen and soil organic C and soil DOC/DN ratio.
4. *Synthesis and application.* This study at a molecular level provides a novel insight into the important role of the degradability of dissolved organic matter in carbon

accumulation in dryland soils with consistently low organic matter storage. The findings will inform better global managements of soil organic matter under consideration of both food security and climate change.

KEYWORDS

carbon storage, degradability, dissolved organic matter, dryland soil, microbial activity, molecular composition, Tibetan Plateau

1 | INTRODUCTION

Drylands cover more than 40% of the Earth's land surface and are predicted to expand further under climate change (Ahlström et al., 2015; Huang et al., 2016; Poulter et al., 2014). The carbon loss from soil organic matter (SOM) can substantially accelerate global warming (IPCC, 2013; Lal, 2004; Li et al., 2020; Schmidt et al., 2011). Dryland soils consistently exhibit low long-term organic matter storage, which has typically been attributed to the low plant biomass inputs to soils under drought suppression. However, SOM storage depends on the balance between biomass inputs and decomposition (Lehmann & Kleber, 2015; Liang, 2020), with the formation process of SOM a continuum of microbial transformations of organic compounds (Lehmann & Kleber, 2015; Ma et al., 2018; Paul, 2016), including *in vivo* turnover via microbial anabolic assimilation, and *ex vivo* extracellular modification via microbial enzymes (Liang et al., 2017, 2019). Generally, most plant-derived residues are recalcitrant due to their low nitrogen (N) and high lignin content (Adair et al., 2008; Melillo et al., 1982). In contrast, although it could be protected by minerals, microbial-derived compounds chemically have a lower C/N ratio than plant compounds and appear to be more labile (Miltner et al., 2012; Schmidt et al., 2011; Soong et al., 2020; Wang et al., 2020). Once the microbial-derived compounds are released from mineral protected fraction into soil solution, it would be easier to be decomposed by microbes. SOM compounds are chemically diverse, varying with microbial and plant physiology and community structure (Kögel-Knabner, 2002; Schmidt et al., 2011). Therefore, the contributions of soil microbes and plants to SOM formation are a fundamental question during ecosystem development with climate change (Khan et al., 2020; Liu et al., 2016), and are of particular concern in dryland soils due to their low organic carbon but possibly high carbon storage potential (Cotrufo et al., 2015; Kallenbach et al., 2016; Schmidt et al., 2011).

The formation process of SOM primarily controls its intrinsic composition and, in turn, determines SOM quality and subsequent decomposition. Labile components in SOM can stimulate microbial growth and activity, and subsequently accelerate the microbial decomposition of recalcitrant compounds through priming effect (Kuzyakov et al., 2000). While priming effect has been observed in various ecosystems (Chen et al., 2019), its impacts on SOM storage during ecosystem development remain largely unknown.

Dissolved organic matter (DOM), which represents the most active SOM fraction that micro-organisms can access, acts as the 'hotspot' and 'gatekeeper' for SOM dynamics (Marschner & Kalbitz, 2003). Therefore, DOM offers a bridge between SOM storage and microbial decomposition and allows a better understanding of the microbial-mediated SOM continuum. Degradation of DOM plays a key role in regulating accumulation and stabilization of SOM (Liu et al., 2021; Zhang et al., 2019). Due to the complex sources and drivers of the SOM pool, DOM likewise contains a myriad of different compounds that vary vastly in their intrinsic composition (Cotrufo et al., 2015; Kaiser & Kalbitz, 2012; Kalbitz et al., 2000). Besides the dissolution of SOM, DOM pool can be directly derived from the dissolution of plant residues during microbial transformations, and from microbial biomass and necromass (Ding et al., 2020). Soil DOM can be affected by the environmental conditions and soil properties, such as soil C/N ratio, pH (Li, Chen, et al., 2019; Li, Sun, et al., 2018). A recent study reported that aridity can greatly affect the DOM chemical composition via influencing microbial processes (Ding et al., 2020). However, due to a lack of comprehensive consideration of plant and microbial variations, the underlying mechanisms of soil DOM chemistry in dryland soils remain unclear.

The constituents of DOM can be screened by a recently developed technology, Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS) (Fang et al., 2017; Kramer et al., 2004; Ohno et al., 2010; Zhang et al., 2016), offering the opportunity to assess the quality and degradability of DOM in soils. In the current study the molecular composition of DOM and the pools of SOM and microbial biomass carbon (MBC) were explored in 10 grassland sites along a SOM gradient in meadow, steppe and desert grasslands on the Tibetan Plateau. Along this gradient, SOM pools and precipitation gradually decrease together (see Tables S1 and S2). By investigating DOM composition and the pools of SOM and soil microbial carbon, we aimed to elucidate the role of carbon composition in SOM transformation in soils with consistently low SOM storage. We hypothesize that apart from the impact of low plant biomass inputs, the low SOM storage could be attributed to high DOM degradability, which stimulates microbial growth and hampers SOM accumulation. This fundamental understanding is particularly essential to achieving the goal of '4 per mille Soils for Food Security and Climate' initiative which aspires to increase global SOM stocks by 4 per 1,000 (or 0.4%) per year as a compensation for the global emissions of greenhouse gases by anthropogenic sources (Minasny et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Study site description

The study sites were located in grassland ecosystems across the Tibetan Plateau of China between 82.9103~92.1504°E and 32.3801~33.3974°N (Table S1). We did not need permission for this fieldwork. The plateau experiences a continental monsoon climate, with mean annual temperature (MAT) ranging from -3.1 to 4.4°C, with the lowest mean monthly temperature in January and the highest in July (Wu et al., 2019). The mean annual precipitation (MAP) gradually decreases from the southeast meadow area (~800 mm) to the northwest desert grassland area (~200 mm), about 85% of which occurs from July to September. The vegetations vary westward from alpine meadow (dominated by *Kobresia pygmaea*, *K. humilis* and *Carex moorcroftii*) to alpine steppe (dominated by *Stipa purpurea*, *S. capillacea* and *S. subsessiliflora* var. *basiplumosa*), and to desert grassland (dominated by *S. purpurea*, *Ceratoides latens* and *S. glareosa*). The soils across all the study sites are classified as Borolls, according to US Soil Taxonomy. For this study, after a thorough field investigation, 10 representative sites along the climatic gradient from meadow (four sites), to steppe (three sites), and desert grassland (three sites) were selected. Within each site, five 1 m × 1 m plots were established at 20 m intervals along a 100 m long sample transect.

2.2 | Climate data collection, plant survey and soil sampling

Climate data, including air temperature, cumulative precipitation and aridity index (dividing precipitation by evaporation), were collected from meteorological stations at each site for the growing season (May–September). Sampling was conducted in July 2017. Within each plot, all living plants were harvested with plant shoot biomass stored in an envelope. Root samples were randomly collected by taking five soil cores (7 cm diameter, 0–20 cm depth) and processed by washing and the manual removal of all soil, pebbles and other debris. We select the depth of 20 cm because we found that most of roots were distributed in the top 20 cm across all the study sites. Plant shoot and root samples were dried at 65°C for 48 hr and weighed to obtain biomass. The climate and plant biomass properties are shown in Table S1.

Five composite soil samples (depth 10 cm) were collected in each plot at the 10 sites. Following field sampling, soils were sieved (2 mm) and separated into three portions. One portion was air-dried for physicochemical analyses, a second portion was kept at 4°C for the measurement of microbial biomass, and the remaining soil was frozen at -20°C for DOM analyses. In total, 50 soil samples were taken for subsequent analyses (10 sampling sites × 5 replicates). All sampling work was done within 1 month to reduce the influence of seasonality. All soil samples were shipped to the ITPCAS laboratories in Beijing (China) for the subsequent laboratory analyses.

2.3 | Soil physicochemical and microbial biomass analyses

For all soil samples, we measured pH, total organic C (TOC), dissolved organic C (DOC), dissolved nitrogen (DN), ammonium, nitrate and MBC (Table S2). Soil physicochemical analyses were performed using standardized protocols (Zhao et al., 2018). Briefly, soil pH was determined in a water/soil suspension with a mass-volume ratio of 1:2.5. Soil TOC was determined using a TOC-L analyser (Shimadzu, Japan). Soil DOC and DN were determined using a TOC-N auto-analyser (multi N/C 3100; Jena, Germany) after extraction in 2 M KCl (soil:solution ratio, 1:4). Soil MBC was determined using fumigation extraction method (Chen et al., 2018; Vance et al., 1987).

2.4 | Extraction of soil DOM and analysis of FT-ICR MS

The preparation and measurement of FT-ICR MS samples (50 in total) are described elsewhere (Li, Sun, et al., 2018; Roth et al., 2019). Briefly, freeze-dried soil (3 g) was placed in polypropylene centrifuge tubes with 15 ml Milli-Q water (i.e. 1:5 w/v). The samples were centrifuged (at 2,800 g) for 10 min after 8 hr shaking (170 rpm, at 80°C) (Guigue et al., 2014). The supernatant was filtered through a 0.45 µm cellulose ester membrane. The filtered sample was then isolated with cartridges (Bond Elut PPL, 500 mg, 6 ml; Agilent) under the condition of pH 2. The cartridges were then rinsed with 20 ml of acidified water (pH 2) and dried with ultrapur N₂ gas. DOM was collected from the cartridges by elution with methanol (5 ml). Samples were then placed in acid washed glass vials and stored frozen (-20°C) in the dark until FT-ICR MS measurement.

Bruker Apex Ultra FT-ICR MS was used to perform ultrahigh resolution mass spectrometry analysis of DOM samples. To compare the relative intensities of MS spectra in various samples, deuterated stearic acid (C₁₈D₃₅H₁O₂; Sigma-Aldrich) was added as an internal standard (Fang et al., 2017). Ammonium hydroxide was added prior to electrospray to increase the ionization efficiency (Ohno et al., 2010). Samples (180 µl/hr) were injected into the electrospray source. Spectra were acquired over 128 scans (with an ion accumulation time of 0.6 s; ion flight time into the ICR cell of 0.0012 s, and a *m/z* range of 150–1,200). PPL extraction blanks and solvent blanks were prepared and analysed to check for contamination and carry-over; peaks found in the blank were removed from the profiles obtained for the DOM samples.

Molecular formulas of DOM were calculated using a custom software (Fang et al., 2017). Detected mass peaks with S/N greater than 6 were exported to datasheets for processing. Elemental combinations were limited to molecular formulas containing ¹²C_{0–100}, ¹H_{0–200}, ¹⁴N_{0–4}, ¹⁶O_{0–30}, ³²S_{0–2} and mass measurement errors <1. Each assigned class species was extended in double bond equivalence (DBE) values (with a mass interval of 2 Da) and C numbers

(CH₂ unit, with a mass interval of 14 Da) by an automatic retrieval within a tolerance of ± 0.001 Kendrick mass defect (KMD) (Zhang et al., 2012). Through the application of these criteria, formulas were ascribed with a high level of confidence, and only formulas that were physically possible were permitted.

Each sample was technically measured three times, and only mass peaks that were detected more than twice of the three replicates were retained for down-stream data analysis (Lucas et al., 2016). Relative abundance of moieties was determined through normalization of the sum of all FT-ICR MS signal intensities of each mass of the respective DOM formulas. Compound groups were delineated by aromaticity index (AI), oxygen to carbon ratio (O/C) and hydrogen to carbon ratio (H/C) cutoffs. O/C and H/C ratio can be used to describe the degree of oxygenation and hydrogenation, respectively, and AI can be used to identify aromatic (AI > 0.5) and condensed aromatic (AI \geq 0.67) compounds (Antony et al., 2014; Feng et al., 2016; Koch & Dittmar, 2006; Li, Sun, et al., 2018; Lv et al., 2016). The detailed delineation of compound groups is as follow: lipids (O/C = 0–0.3, H/C = 1.5–2.0), protein/amino sugars (O/C = 0.3–0.67, H/C = 1.5–2.2, N/C \geq 0.05), carbohydrates (O/C = 0.67–1.2; H/C = 1.5–2), unsaturated hydrocarbons (O/C = 0–0.1, H/C = 0.7–1), lignins (O/C = 0.1–0.67, H/C = 0.7–1.5, AI < 0.67), condensed aromatics (O/C = 0–0.67, H/C = 0.2–0.7, AI \geq 0.67) and tannins (O/C = 0.67–1.2, H/C = 0.5–1.5, AI < 0.67).

2.5 | Statistical analyses

All statistical analyses were performed in the R environment. Significant differences in measurements among grassland types were analysed using ANOVA ($p < 0.05$). The DOM molecular composition was visualized using redundancy analysis (RDA) based on the relative abundance of individual molecules using the 'VEGAN'

package. The DOM molecules with significant difference in relative abundance (the marker molecules) among grassland types were determined by linear discriminant analysis (LDA) effect size (LEfSe) (Lucas et al., 2016; Segata et al., 2011). The threshold on the LDA score for discriminative features was set at 1.5, and the Kruskal–Wallis tests were performed at a significance level of $p < 0.1$. The implementation of LEfSe was performed in the Galaxy framework with online analysis tools at <http://huttenhower.sph.harvard.edu/lefse/>. To link the LEfSe analysis results to degradability among grassland types, we then calculated DOM degradability. Based on the principle developed by Flerus et al. (2012), the sum of intensities of POS correlating compounds containing relatively more H and less C (C₁₃H₁₈O₇, C₁₄H₂₀O₇, C₁₅H₂₂O₇, C₁₅H₂₂O₈ and C₁₆H₂₄O₈) was used to indicate DOM degradability in this study. Structural equation model (SEM) was constructed using AMOS (SPSS Inc.). In the SEM, all factors were standardized based on the equation before model analysis: $(\text{rawValue} - \min(\text{rawValue})) / (\max(\text{rawValue}) - \min(\text{rawValue}))$, where min = minimum value and max = maximum value across all samples.

3 | RESULTS

3.1 | Change in soil TOC and the ratio of MBC to TOC across the three grassland types

The concentration of soil TOC significantly decreased from meadow (4.6%) to steppe (0.8%) and desert grassland (0.9%) ($p < 0.05$, Figure 1a). This was accompanied by decreasing plant shoot and root biomasses across the three grassland types (Table S1). Interestingly, although the concentration of soil MBC decreased with shifts of grassland types, its ratio to TOC (MBC/TOC ratio) significantly increased from meadow (0.01) to steppe (0.02) and desert grassland (0.03) ($p < 0.05$, Figure 1b).

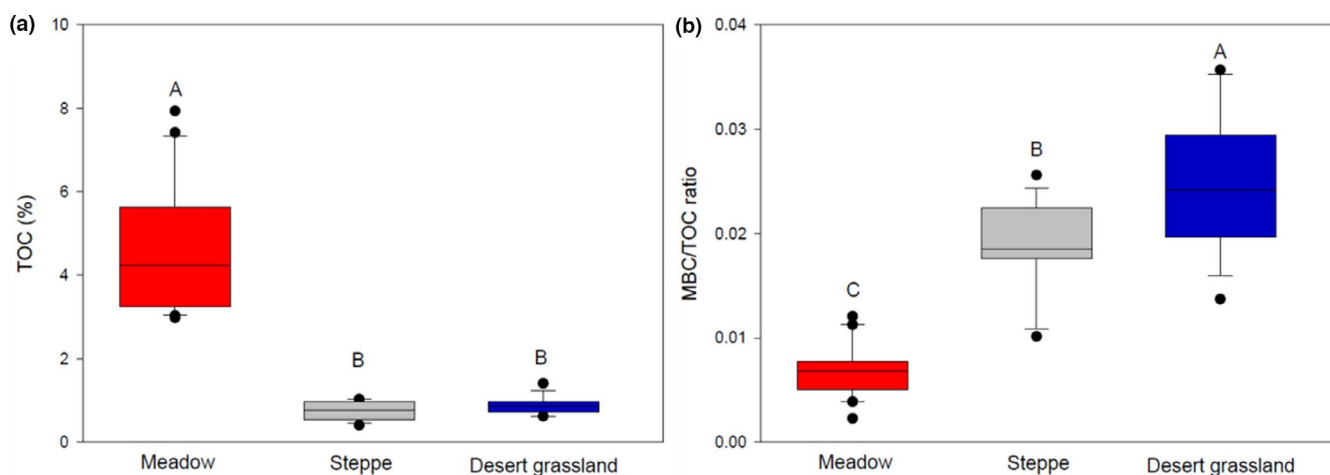


FIGURE 1 Total organic carbon concentration (TOC, a) and the ratio of microbial biomass carbon to TOC (MBC/TOC ratio, b) in soils of meadow, steppe, and desert on the Tibetan Plateau. Different uppercase letters indicate significant differences among the three grassland types ($n = 20$ for meadow and $n = 15$ for steppe and desert grassland)

3.2 | Changes in composition of soil DOM across the three grassland types

With the decreasing concentration of soil DOC (Table S2), the number of soil DOM molecules also significantly decreased from meadow (3,577) to steppe (2,729) and desert grassland (2,435) ($p < 0.05$, Figure S1a). Similarly, the mean molecular weight significantly decreased, ranging from 404.8 in meadow, to 394.7 in steppe and 382.1 in desert grassland ($p < 0.05$, Figure S1b). Furthermore, RDA revealed that DOM molecular composition was dependent of grassland types (Figure S1c).

The shift of DOM composition pattern across grassland types was associated with a set of environmental factors (Figure S1c). The factors driving the shift towards desert grassland (MAT, AI, soil pH and MBC/TOC ratio) were positively correlated with DOM molecules that have relatively lower O/C and higher H/C ratio ($p < 0.05$, Figure S2a–d). Inversely, the factors driving the shift towards meadow (TOC, DOC, DN, DOC/DN ratio, plant shoot and root biomasses) were positively correlated with DOM molecules that have relatively higher O/C and lower H/C ratio ($p < 0.05$, Figure S2e–i). The molecules were classified into six categories, among which, the total relative abundance of lipids, proteins and lignins significantly increased with the transition of meadow, steppe and desert grassland. By contrast, the relative abundance of carbohydrates, condensed aromatics and tannins significantly decreased with grassland transition (all $p < 0.05$, Figure S3).

3.3 | Changes in degradability of soil DOM across the three grassland types and its relationship with MBC/TOC ratio

Linear discriminant effect size (LefSe) analysis showed individual molecules that were significantly enriched in each grassland type (Figure 2a). In meadow, there were 379 DOM molecules being enriched. These molecules had relatively higher O/C ratio and lower H/C ratio. By contrast, there were 306 DOM molecules being enriched in desert grassland. These molecules had relatively lower O/C ratio and higher H/C ratio. As a transition region between meadow and desert, steppe showed few (37) significantly enriched DOM molecules. The calculated DOM degradability index significantly increased by 23.4%, ranging from 0.32 in meadow, 0.35 in steppe and 0.40 in desert grassland ($p < 0.05$, Figure 2b). The calculated DOM degradability showed significantly positive correlation with MBC/TOC ratio ($R^2 = 0.350$, $p < 0.001$, Figure 3). By categories, the MBC/TOC ratio was positively correlated with lipids, proteins and lignins, and was negatively correlated with carbohydrates, condensed aromatics and tannins (All $p < 0.05$, Figure S4).

3.4 | Environmental factors driving degradability of DOM in Tibetan grassland soils

The structural equation model revealed that the direct drivers for DOM degradability were soil organic C and DN (Figure 4). DOM

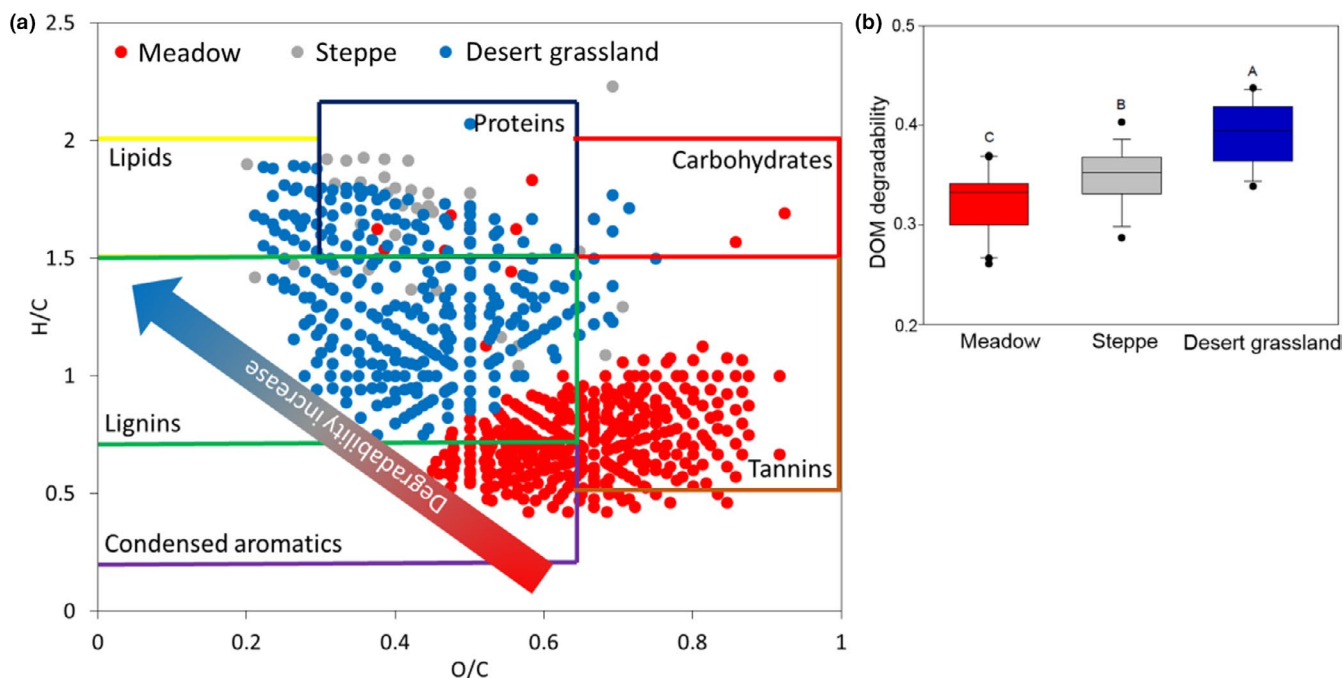


FIGURE 2 Dissolved organic matter (DOM) molecules (a) identified by linear discriminant effect size analysis (LefSe) and DOM degradability (b) in the three types of Tibetan grassland soils. (a) Red, grey and blue points indicate molecules that are significantly ($p < 0.05$) enriched in meadow, steppe and desert grassland soils respectively ($n = 379$, 37 and 306 respectively). Rectangles with different colours separate DOM categories on the diagram. (b) Different uppercase letters indicate significant differences among the three grassland types ($n = 20$ for meadow and $n = 15$ for steppe and desert grassland)

degradability was positively driven by soil DN ($r = 0.913$, $p < 0.01$), and negatively driven by soil organic C ($r = -1.060$, $p < 0.05$). Furthermore, MBC/TOC ratio was negatively driven by soil organic C ($r = -0.839$, $p < 0.001$) and positively driven by pH ($r = 0.776$, $p < 0.001$) and soil DN ($r = 0.588$, $p < 0.01$). Additionally, both soil organic C and DN were positively driven by root biomass but with different effect sizes ($r = 0.268$ for soil organic C and $r = 0.955$ for soil DN, $p < 0.05$). Soil organic C was also positively driven by shoot biomass ($r = 0.103$, $p < 0.05$), which was further positively driven by root biomass ($r = 0.614$, $p < 0.001$). Soil pH was negatively driven by soil organic C ($r = -0.710$, $p < 0.001$) and shoot biomass ($r = -0.276$, $p < 0.001$).

The DOC/DN ratio significantly ($p < 0.05$) decreased by 40.5% from meadow (3.7) and steppe (3.3) to desert grassland (2.2, Figure 5a). Meanwhile, the relative abundance of nitrogen

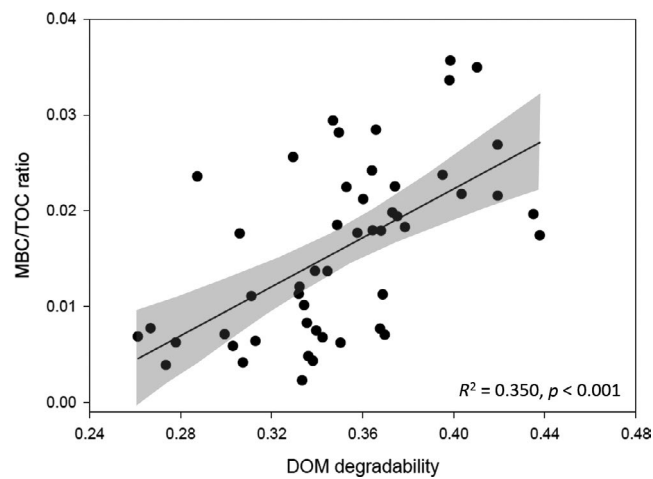
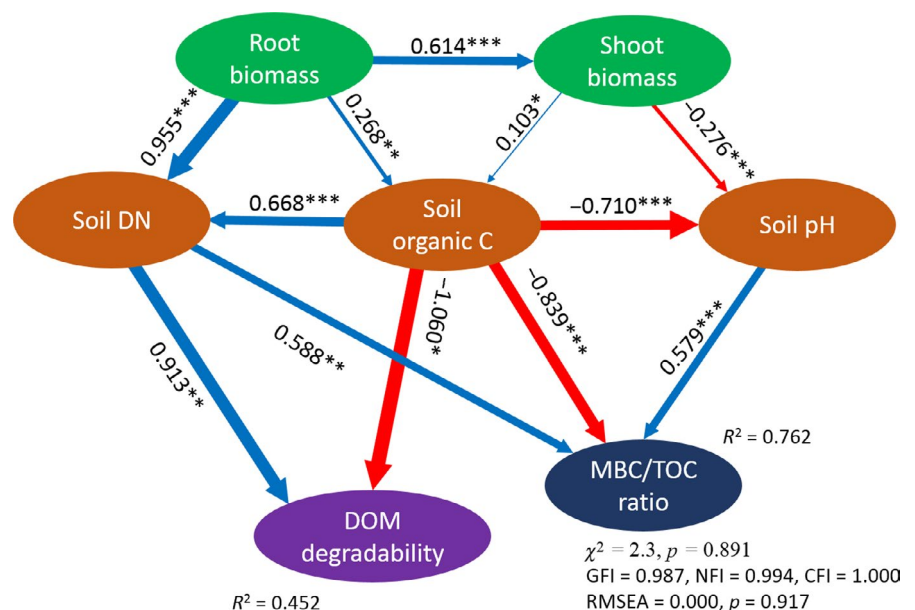


FIGURE 3 The degradability of soil dissolved organic matter (DOM degradability) positively correlated with the ratio of microbial biomass carbon to total organic carbon (MBC/TOC ratio). Lines and shaded areas indicate the predictions and their 95% confidence intervals respectively

FIGURE 4 Structural equation model showing the effects of soil and plant variables on soil dissolved organic matter (DOM) degradability. DN, dissolved nitrogen; MBC, microbial biomass carbon; TOC, total organic carbon. The factor 'soil organic C' is the average of the standardized soil total organic C and dissolved organic C. Numbers adjacent to arrows indicate the effect size of the relationship at different levels of significance (* < 0.05 , ** < 0.01 , *** < 0.001). R^2 denotes the proportion of variance explained



(N)-containing DOM compounds significantly increased by 27.1%, ranging from 41.3% in meadow, 48.5% in steppe and 52.6% in desert grassland ($p < 0.05$, Figure 5a). The N-containing compounds was negatively correlated with the DOC/DN ratio ($p < 0.001$, Figure 5c), and the DOM degradability with positively correlated with the N-containing compounds ($p < 0.001$, Figure 5d). Furthermore, the DOC/DN ratio was negatively correlated with the relative abundance of lipids ($R^2 = 0.118$, $p = 0.015$) and proteins ($R^2 = 0.205$, $p = 0.001$), and was positively correlated with condensed aromatics ($R^2 = 0.285$, $p < 0.001$) and tannins ($R^2 = 0.269$, $p < 0.001$, Figure S5).

4 | DISCUSSION

4.1 | New insight on low SOM storage in desert grasslands

Soil TOC, together with plant biomass, decreased along the precipitation gradient from meadow to steppe and desert grasslands (Figure 1a, Table S1), indicating that the SOM reduction can be attributed to the reduced plant-derived inputs induced by drought suppression. Furthermore, the increased soil MBC/TOC ratio with aridity (Figure 1b) indicates relatively faster microbial metabolism of TOC pool, by which a relatively higher proportion of reduced SOM is derived from microbial decomposition. Therefore, our finding supports a new insight that soil microbial growth plays an important role in determining the low SOM storage of desert soils, which is consistent with the concept that the balance between SOM formation and decomposition determines the SOM pool size (Lehmann & Kleber, 2015; Liang et al., 2017).

The DOM characterization would reveal the mechanism behind the higher microbial growth (MBC/TOC) in desert soils, since DOM represents the most active SOM fraction that soil micro-organisms can access (Marschner & Kalbitz, 2003). We speculated that the

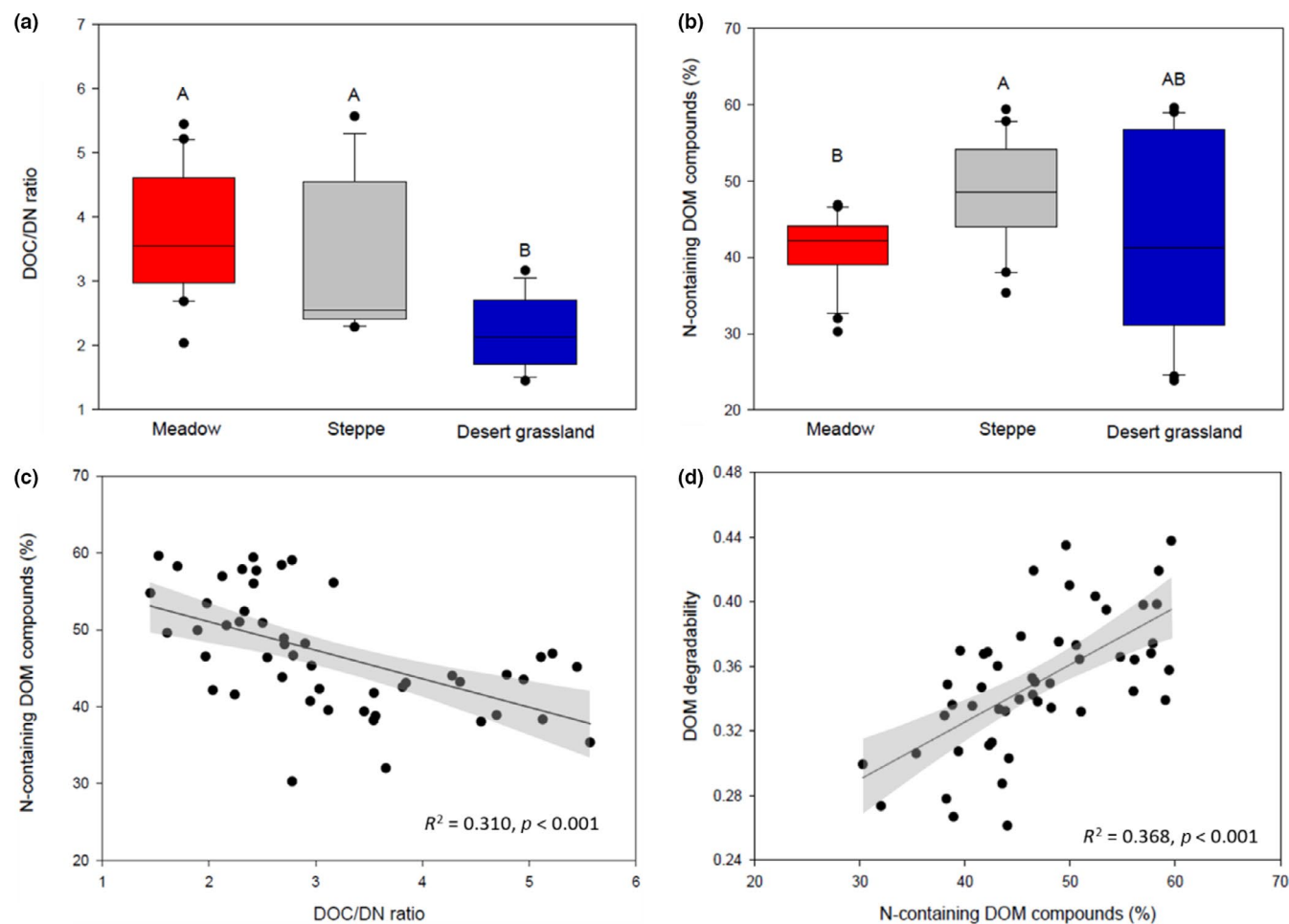


FIGURE 5 The ratio of dissolved organic carbon to dissolved nitrogen (DOC/DN ratio) (a), the relative abundance of nitrogen (N)-containing dissolved organic matter (DOM) compounds (N-containing DOM compounds) (b), and the correlations between DOC/DN ratio and N-containing DOM compounds (c), as well as between N-containing DOM compounds and DOM degradability (d). In (a) and (b), the uppercase letters indicate significant differences among the three grassland types ($n = 20$ for meadow and $n = 15$ for steppe and desert grassland). In (c) and (d), lines and shaded areas indicate the predictions and their 95% confidence intervals respectively

DOM quality (composition and degradability) could play a central role in facilitating microbial growth in desert soils, which eventually reduced the amount of SOM (Cotrufo et al., 2015; Kaiser & Kalbitz, 2012; Kalbitz et al., 2000).

Redundancy analysis revealed that DOM molecular composition gradually shifted along the transition between meadow, steppe and desert grassland (Figure S1c), and the number of different types of soil DOM molecules as well as the mean molecular weight also significantly decreased (Figure S1a). These results indicate that the DOM diversity decreased and the molecules became simpler (Malik et al., 2012; Monreal et al., 1997; Ohno et al., 2010).

Consistent with the above findings, specific DOM molecules were significantly enriched in different grassland types (Figure 2a), and the DOM degradability gradually increased along the transition from meadow to desert. Molecules enriching in meadow soils are considered to be recalcitrant due to higher O/C but lower H/C ratios, including condensed aromatics, tannins and a part of lignins with relatively high O/C and low H/C (Antony et al., 2014; Li, Chen,

et al., 2019). By contrast, molecules enriching in desert soils were more labile due to relatively lower O/C but higher H/C ratios, including lipids, proteins and lignins with relatively low O/C and high H/C (Frostegård & Bååth, 1996; Haider, 1992). These results were in agreement with the change in relative abundance of all DOM categories (Figure S3). The lignins enriched in desert soils could be due to the suppression of microbial decomposition of plant residues by water limitation (Curiel Yuste et al., 2007; Peyton Smith et al., 2017). The DOM degradability index significantly increased from meadow to steppe and desert soils (Figure 2b), and was positively correlated with MBC/TOC ratio ($R^2 = 0.350, p < 0.001$, Figure 3). By DOM category, the MBC/TOC ratio was positively correlated with the relative abundance of lipids, proteins and lignins, but negatively correlated with that of carbohydrates, condensed aromatics and tannins (all $p < 0.05$, Figure S4). Collectively, these results indicate that desert soils exhibited a higher DOM degradability, which accelerated microbial growth, compared with meadow and steppe soils.

The above results are in agreement with the widely recognized fact that soil micro-organisms prefer consuming organic substrates with low molecular weights (Wen et al., 2019). The enrichment of labile DOM compounds in desert soils enhances microbial growth and activity, and may further accelerate the microbial decomposition of the total SOM by intensifying the priming effect (Feng & Zhu, 2021; Kuzyakov, 2010). A stronger priming effect may occur in desert than meadow and steppe soils due to the greater amount of labile DOM molecules, highlighting the important role of DOM composition in SOM decomposition. DOM serves as the intermediate pool for and hotspot of SOM decomposition, bridging the transition between SOM and MBC pools. Our finding provides a novel insight and supplements the notion that SOM reduction is primarily caused by decreased plant biomass input to soils in ecosystems with less vegetation (Berg & McLaugherty, 2010; Lehmann & Kleber, 2015).

4.2 | Drivers of soil DOM molecular composition and degradability across grassland ecosystems

Soil DOM composition patterns significantly shifted along the gradient of meadow, steppe and desert, and was highly associated with a set of environmental factors (Figure S1c, Figure S2). These high associations were in agreement with the linear correlations between environmental factors and the relative abundance of DOM categories (Figure S2). The driving factors were consistent with previous studies (Li, Sun, et al., 2018; Roth et al., 2015; Zhao et al., 2018). Drought and high pH impede the vegetation growth, and consequently reduce the plant-derived compounds into DOM pool. In contrast, soil microbes can better adapt to harsh conditions, thereby contribute relatively more microbial-derived compounds (Beer et al., 2010). Positive relationship between labile DOM molecules and MBC/TOC showed the evidence that MBC could affect DOM composition (Figure S2d). Part of labile DOM molecules may be microbial originated since MBC is a labile SOM fraction and could potentially release into DOM pool.

However, we did not observe the impact of MBC/TOC on DOM degradability in the SEM model. The SEM revealed the soil organic C and DN played central roles in driving DOM degradability (Figure 4). The DOC/DN ratio significantly decreased from meadow and steppe to desert grassland (Figure 5a), which could be attributed to reduced plant biomass inputs into soils, for plants have a relatively high C/N ratio as compared to SOM (Soong et al., 2020). The correlations between DOC/DN ratio and DOM categories (Figure S5), together with the relative abundance of N-containing DOM compounds (Figure 5b) and its correlations (Figure 5c,d), collectively indicated that DOC/DN plays a central role in controlling the DOM composition and its degradability. This is consistent with a previous study reported that DOM with higher organic carbon content may have higher relative abundance of polyphenolic compounds which may be attributed to the high hydrophilicity of some polyphenolic

molecules (Ding et al., 2020). Also, our results agreed a recent finding in the same region that nitrogen limitation becomes stronger in grassland ecosystems on the Tibetan Plateau (Kou et al., 2020). Furthermore, the finding supports the long-standing belief that soil C/N ratio controls SOM decomposition (Bengtsson et al., 2003; Nicolardot et al., 2001), because soil micro-organisms would prefer high N-containing DOM, including carbohydrates, proteins, etc. (Ohno et al., 2014). More recently, N addition was shown to promote microbial decomposition of SOM in an N-limited Tibetan meadow (Du et al., 2020; Li, Li, et al., 2018). The importance of N for C sequestration has drawn increased attention in natural and managed ecosystems since C and N cycles are coupled (Davies et al., 2021; Soares & Rousk, 2019).

5 | CONCLUSIONS

Our findings demonstrated that increased soil DOM degradability accelerates SOM loss by stimulating microbial growth in desert grasslands. This is of particular significance for climate change and food security, as SOM dominates the release of greenhouse gas emissions and maintains soil nutrients for crop production and agricultural sustainability (Cambardella & Elliott, 1992; Schmidt et al., 2011). We provide a novel insight into the SOM storage and maintenance, supplementing the long-standing notion that low SOM storage can be primarily attributed to low plant biomass inputs. The soil dissolved nitrogen and DOC/DN ratio plays a central role in driving the microbial growth, DOM quality and SOM storage. In regions where the soil is relatively carbon saturated but nitrogen deficient, nitrogen inputs may accelerate microbial decomposition of SOM (Castellano et al., 2015; Li, Tian, et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

W.K. conceived the ideas and designed the methodology; H.C. collected and analysed the data; H.C. and W.K. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Zenodo Digital Repository <https://doi.org/10.5281/zenodo.4942382> (Chen et al., 2021).

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SUPPORTING INFORMATION

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