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Aridity influences root versus shoot contributions to steppe grassland soil carbon stock and its stability

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ABSTRACT

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Keywords: Carbon cycle Climate change Dryland Microbial biomass Plant biomass allocation (root/shoot) Soil carbon fraction Grassland soils are globally important sinks for atmospheric CO₂, and their carbon (C) is primarily formed from plant inputs of above- and belowground. Aridity is expected to increase in grassland biomes with climate change, which may influence soil C dynamics through its effects on plant productivity and biomass allocation (i.e., the root/shoot ratio). However, it remains unclear on how aridity controls root versus shoot contributions to soil organic carbon (SOC) pools in grasslands. Here we investigated plant biomass allocation, plant and soil C isotopic signature, soil microbial biomass, SOC stock and its respective heavy versus light factions along a 1500 km aridity gradient (0.47 \leq aridity \leq 0.79) across steppe grasslands in northern China. We identified a central role of aridity in the cascading chain of SOC formation and stability. Both plant biomass and SOC decreased with aridity, but root/shoot ratio increased with aridity. Isotopic and regression analyses revealed that SOC were primarily contributed by shoots in wet grasslands (aridity < 0.61), but more by roots in drier areas (aridity > 0.61). These are consistent with patterns of microbial biomass and its fraction to SOC, both of which decreased with aridity, indicating SOC are more contributed by microbial biomass in wet sites. Similarly, microbial C was also derived mainly from shoots in wet grasslands but from roots in drier areas. Such changes in plant biomass allocation and dominant sources of SOC along increasing aridity explain an elevating fraction of heavy C in SOC, suggesting SOC in drier sites are stabler. Our study thus highlights that aridity strongly controls the pool size and stability of SOC by influencing the relative contributions of roots and shoots to SOC in steppe grasslands. As climate change continues to unfolds, our findings have important implications for predicting steppe SOC stocks and their stability in the future.

inputs, is the largest carbon (C) reservoir in terrestrial ecosystems (Jackson et al., 2017; Lal, 2004). Increasing evidence shows that plant

productivities and chemical compositions are different between roots

1. Introduction

Soil organic carbon (SOC), supplied mainly by plant shoot and root

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and shoots (Hartmann et al., 2020; Xia et al., 2015), which make plant biomass allocation (i.e., the root to shoot ratio) (Chen et al., 2021a; Sanaullah et al., 2012) to be an essential control over SOC storage and stability (Rasse et al., 2005; Sokol et al., 2019a). However, the strategies of plant biomass allocation are complex, which vary with plant species and developmental stages, but also depend on responses to global change, such as warming, drought, and CO₂ enrichment (Luo et al., 2006; Sanaullah et al., 2012; Zhou et al., 2012). Therefore, a better understanding of the effects of plant biomass allocation on soil C processes is essential for modelling C cycles more precisely, at regional and global scales (Freschet et al., 2013; Prentice et al., 2011).

Recently, root exudates from rhizodeposition have been thought as a crucial SOC source (Pausch and Kuzyakov, 2018), which is usually the critical precursor of slow-cycling SOC (Sokol et al., 2019a; Xia et al., 2015). Meanwhile, leaf litter is a comparatively inefficient C source for forming stable SOC (Clemmensen et al., 2013; Mendez-Millan et al., 2010). However, previous studies were conducted mainly at the plot scale within similar experimental conditions. In reality, climate strongly controls plant species composition, biomass production and allocation, and litter decomposition (Freschet et al., 2013; Hartmann et al., 2020). A better understanding of climate effects on plant C inputs into soils will reduce uncertainty on soil C cycling simulation (Cotrufo et al., 2015; Hartmann et al., 2020). For example, harvest residue inputs have limited effects on soil C stocks in subtropical forests (Hu et al., 2014) but significantly affect SOC in temperate forests (Huang et al. (2011). The inconsistent findings are likely due to different climate conditions. High temperatures in subtropical forests can accelerate microbial decomposition and result in plant C releasing quickly into the atmosphere.

Climate change can significantly influence plant biomass allocation and microbial activity, and, consequently, SOC stock and its C composition and stability (Hartmann et al., 2020; Jackson et al., 2017). Generally, increasing precipitation and temperature decreases the rootto-shoot ratio (von Fischer et al., 2008). Chen et al. (2021b) concluded that temperature, rainfall, and plant properties (e.g., plant height and coverage) jointly regulated plant biomass allocation between shoots and roots, however, biotic factors can override abiotic ones in regulating plant biomass allocation. This is because climate indirectly controls plant biomass allocation through its effects on plant species composition (Sanaullah et al., 2012; von Fischer et al., 2008). For example, it has been almost confirmed that root-to-shoot ratios of C₃ plants had a higher decreasing rate than C₄ plants (e.g., Angelo & Pau, 2015). Therefore, changes in the C₃/C₄ ratio due to climate change may potentially influence plant biomass allocation. Meanwhile, plant growth response to climate may further affect soil microbial metabolic processes and SOC pools (Brüggemann et al., 2011; Jackson et al., 2017). On the one hand, soil microbes could influence the mineralization of plant litter (Sokol et al., 2019a). On the other hand, microbial products are essential components of SOC (Liang et al., 2019). Further, shoot litter includes more significant quantities of labile components and higher nutrient concentrations than root litter (Abiven et al., 2005; Xia et al., 2015). More shoot inputs can favor soil microbial growth better when other soil conditions keep constant (Abiven et al., 2005). The different production rates between roots and shoots may further affect SOC stocks and labile and stable C composition (Sokol and Bradford, 2019; Xia et al., 2015). At present, studies focus on the influences of plant growth and microbial decomposition, separately, on SOC stock under climate change. Both processes may cascade these effects throughout food webs (Schmidt et al., 2011). Unfortunately, we still poorly understand how climate affects SOC stock and its fractions (Brüggemann et al., 2011). Therefore, it is vital to elucidate the mechanisms underlying plant biomass allocation responses to climate factors and its effect on the microbial metabolic route (Jackson et al., 2017).

Grasslands occupy \sim 22% of the global land area and account for a similar fraction of total SOC (Maestre et al., 2016), where most biogeographical processes are driven by aridity (Maestre et al., 2016; Wang et al., 2014). Aridity index positively correlates with water

availability in drylands and therefore has a substantial impact on C cycling processes such as plant productivity, microbial activity and nutrient concentration (Maestre et al., 2016; Reynolds et al., 2007). It is predicted that grassland will likely increase by ~20% by the end of this century due to increasing aridity (IPCC, 2014). However, it is challenging to quantify the effects of aridity on total SOC in regional grasslands by looking for a slight change in the root versus shoot C inputs to a large, spatially variable stock (Brüggemann et al., 2011; Lehmann et al., 2020). Fortunately, we can use the natural abundance of ¹³C, which is more depleted in leaves than roots (Badeck et al., 2005; Ghashghaie and Badeck, 2014), to track the root versus shoot inputs into SOC (Mendez-Millan et al., 2010).

Here, we present combined estimates of plant biomass allocation, vegetation and soil C isotopic composition, and SOC stock and its fractions along an aridity gradient across regional steppe grasslands in Inner Mongolia, China. We hypothesize that increasing aridity increases plant biomass allocation to roots and further increase root inputs into SOC and the proportion of soil stable C, whereas decreasing aridity makes more C being allocated to shoots and results an increase in shoot contributions to SOC and a lower proportion of soil stable C.

2. Materials and methods

2.1. Site description and sampling

In the summer of 2017, 20 sampling sites, spanning an aridity gradient (0.47 \leq aridity \leq 0.79) along a 1,500-km transect in Inner Mongolia in northern China, have been selected (Fig. 1 and Table S1). At each site, three subplots $(1 \times 1 \text{ m})$, with a distance of >30 m between them, were randomly laid within a 100×100 m area. We identified the dominant species of grass for each subplot. The relative aboveground cover (%) of both C_3 and C_4 grasses were estimated to calculate the relative abundance of C₃ to C₄ grasses. Very few shrubs or woody plants were found anywhere along the transect. We randomly selected three quadrats (25 \times 25 cm) in each subplot for vegetation surveys. All plants were sampled and used for analyses. Plant individuals were carefully hand-sorted into the shoot (mainly foliar) and root samples, both of which were washed with deionized water to remove soil particles. Plant samples were placed in black plastic bags and transported to the laboratory for analysis. Five soil samples (0-20 cm depth) were taken using a soil corer (2.5 cm diameter) and mixed for each subplot. Soil bulk density, which was used to calculate soil C stocks, was determined before soil sampling. The main vegetation types from west to east across the transect were: desert steppe, degraded steppe, typical steppe and meadow steppe, and the soil types were Arenosols, Kastanozems and Chernozems (Hu et al., 2018).

2.2. Climate data

Mean annual temperature (MAT) and precipitation (MAP) at each site were obtained from the WorldClim (http://www.worldclim.org). Aridity index, the ratio of annual precipitation to annual potential evapotranspiration, were obtained from the Global Aridity database (http://www.cgiar-csi.org). Here, aridity is defined as one minus the aridity index, and then higher aridity values indicate more severe aridity (Xiong et al., 2020).

2.3. Shoot and root biomasses and carbon isotopes

Root and shoot samples were dried at 60 $^{\circ}$ C to a constant mass to measure belowground biomass (BGB) and aboveground biomass (AGB). The plant biomass allocation was calculated as the ratio of BGB/AGB, and total plant biomass was calculated as the sum of BGB and AGB (Chen et al., 2021b). Both shoot and root samples were ground in a ball mill and stored in plastic bags in a refrigerator at 4 $^{\circ}$ C until further analysis. About 3 mg of shoot and root samples were loaded into a capsule to



Fig. 1. Geographical distribution of sampling sites and ecosystem landscape. A 1500 km transect in the grasslands of northern China was sampled in Inner Mongolia (a). Soils were sampled from 20 sites with three replicates at each site across four types of grassland: (b), meadow steppe; (c), typical steppe; (d), degraded steppe; (e), desert steppe. Symbols of sites in close proximity overlap on the map.

determine C isotope ratios using an Elementar Vario EL Cube analyser (Elementar Analysis system GmbH, Hanau, Germany), which was interfaced to a Thermo Scientific Delta V isotope ratio mass spectrometer (Thermo Fisher Scientific, MA, USA), with an overall precision greater than 0.20 ‰. C isotope ratios were presented as: δ^{13} C (‰) = ($R_{sample} / R_{standard} - 1$) × 1000‰, where *R* is the molar ¹³C to ¹²C ratio and standard is the Vienna Pee Dee Belemnite standard (VPDB).

2.4. Bulk soil, light and heavy fraction carbon pools and isotopes

Fresh soil samples were passed through a 2.0 mm sieve and stored in a refrigerator at 4 °C until further analysis. Soil moisture was measured gravimetrically. Using a modified version of the density fractionation method of Huang et al. (2011), the soil samples were physically separated into two pools: light and heavy fractions. Briefly, 10 g of air-dried soil was placed in a centrifuge tube with 50 mL of NaI (Fisher Chemical, UK) with a density of 1.70 g cm⁻³. A reciprocating shaker shook the tubes for one hour, then centrifuged at 1000 rpm for 15 min. The floating material and the material remaining at the bottom of the tube were washed onto a separate funnel and then rinsed repeatedly with deionised water. They were designated the light and heavy fractions, respectively. Both the light and heavy fractions were dried at 60 °C for 48 h and then ground in a mortar and pestle for analysis.

Following the method described by Harris et al. (2001), all soil samples for isotope and chemical analysis were treated with 150 mL of 0.5 M HCl to remove carbonate before analysis. Total C concentration and δ^{13} C values (in ‰ relative to VPDB) were determined on bulk soil samples and light and heavy soil fractions. There were about 65 mg of soil (depending on SOC content) placed in silver cups coated with tin cups and analyzed for their isotopic composition. Soil C concentration was measured by an Elementar Vario TOC analyser (Elementar Analysis system GmbH, Hanau, Germany). The determination of δ^{13} C was made using a Thermo Scientific Delta V isotope ratio mass spectrometer by following the same method used for measuring C isotope ratios of plant samples. Two acetanilide standards were analysed with every 12 samples.

2.5. Soil microbial biomass carbon

Three homogenized soil samples for each site were selected and their

microbial biomass C concentration measured using the fumigationextraction method (Vance et al., 1987). Two subsamples of soil (5 g dry weight equivalent) from each sample were shaken in 0.5 M K₂SO₄ for 4 h in tubes. One subsample was exposed to chloroform-fumigation while the other served as a nonfumigated control. After shaking, the supernatant from each tube was poured through grade 42 Whatman filter paper. Liquid extracts were analyzed for total C on a total organic C analyser (Shimadzu Corp., Kyoto, Japan). The microbial biomass C pool was calculated as the difference between organic C extracted from the K₂SO₄ extracts of fumigated and unfumigated samples, divided by a correction factor of 0.45 (Beck et al., 1997).

2.6. Statistical analysis

All analyses were performed using the statistical software R v. 3.4.3 (R_Core_Team, 2017). We fitted linear and non-linear regressions to the relationships between all our ecosystem variables and aridity. The Akaike information criterion (AIC) was used to decide the model that provided the best fit in each case. In general, differences in AIC higher than 2 indicate that the models are different (Hastie, 2017). Based on Berdugo et al. (2020), we explored the presence of thresholds only when non-linear models were a better fit to the data compared to linear models. As plant δ^{13} C values may reflect plant water use efficiency and growth (Angelo and Pau, 2015; Cernusak et al., 2013), segmented regression analyses, using the "segmented" package in R (Muggeo, 2008), were used to fit the apparent non-linear relationships between the $\delta^{13}C$ content and estimated aridity for both root and shoot compartments. The breakpoint corresponds to the aridity value at which root or shoot δ^{13} C can be 'broken' into two linear regressions with different slopes or even opposite signs (Fig. 4a). We then used a likelihood ratio test to test the significance of the goodness of fit of the non-linear relationships compared with linear model fits, which confirmed a breakpoint at aridity = 0.61. Yet, we discussed related phenomena in the discussion section.

Based on Hu et al. (2020), piecewise structural equation modelling (SEM) was performed to test the direct and indirect effects of aridity and plant growth on SOC stock. We first evaluated the effects of aridity and plant growth on SOC stock by fitting linear mixed-effects models (LMMs), which enabled us to identify the best predictors for use in the SEM analysis. Finally, we used grass community composition (C_3/C_4)

abundance), total plant biomass and plant biomass allocation (BGB/ AGB) to reflect plant growth. Each predictor variable was standardized and Z-score transformed, and the parameter estimates and relative effect size (defined here as the parameter estimate and confidence interval obtained from the LMM) of each predictor on SOC were reported. We evaluated the hypothesis that aridity is the primary driver of variation in grass community composition, total plant biomass and plant biomass allocation, and total plant biomass and plant biomass allocation further influence SOC stock. Path diagrams were created to represent the relationship between measured variables with arrows that represent the unidirectional relationships between those variables, with significance set to $\alpha = 0.05$. Standardized effect sizes and coefficients of determination (R^2) were calculated and used to scale the arrows. The SEM was conducted using "piecewiseSEM" package (Lefcheck, 2016) in R.

To evaluate fraction contribution of each hypothesized driver on SOC, we firstly used a two end-member mixing model coded in R. An assumption of such a two end-member mixing model is that each soil sample consists of C from two end-members in varying proportions. The two end-member model, adapted from Fritz et al. (1976), was given by:

$$\widehat{c} = f_1 E_1 + f_2 E_2 \tag{1}$$

where \hat{c} is the δ^{13} C content of the different soil C components within each group of sample sites, E_1 and E_2 are the respective δ^{13} C contents of roots and shoots, respectively. f_1 and f_2 are the proportional contributions of two different C sources, which are assumed to sum to 100% (f_1 $+ f_2 = 100\%$). The Stable Isotope Mixing Models in the R package "simmr" (Parnell et al., 2013) were used to estimate the relative contributions of potential C sources (roots and shoots) to ¹³C samples of soil. Food-web specific functions from the mass balance, such as trophic enrichment factors or preferential source contributions, were omitted, following the procedure used in previous studies (Dean et al., 2020). Although microbial decomposition of plant materials may cause some isotopic fractionation and possibly impact the above- and belowground contributions to SOC, the resulting SOC still bears the isotopic signature of the parent vegetation (Brüggemann et al., 2011; Mendez-Millan et al., 2010). Many previous studies have found no evidence that such effects are important (Angelo and Pau, 2015; von Fischer et al., 2008). Thus, isotopic fractionation may have limited effects on the $\delta^{13}\text{C}$ signatures of SOC in this regional study.

Additionally, we calculated the relative importance of BGB and AGB on SOC stock or soil microbial biomass C by fitting LMMs coded in R. In these calculations, we used the above- and belowground biomass, as appropriate, as the only fixed-effects term. Sampling location was used as a random term in the LMMs, as our dataset contains multiple observations at specific sites with similar AI. To check for multicollinearity, we calculated variance inflation factors (VIFs) for all predictors in the models. None of the VIFs was higher than 2, far below 5: the VIF value generally believed to cause concern (Dormann et al., 2013). Following the protocol of Hu et al. (2020), LMMs were conducted using the "Ime4" package in R, and the model coefficients were tested using the "ImerTest" package. To present the results of LMMs graphically, we used partial residual plots to demonstrate the relative effects of the BGB and AGB on soil C stocks or microbial biomass C.

3. Results

3.1. Variation in climate variables, plant biomass allocation and soil carbon and their relationships

The results showed that aridity increased from southwest to northeast along the transect (Fig. 1), and that soil moisture content was significantly negatively correlated with aridity ($R^2 = 0.55$, P < 0.001; Fig. S2). Both BGB ($R^2 = 0.66$, P < 0.001) and AGB ($R^2 = 0.81$, P < 0.001) were negatively correlated with aridity, but the ratio of BGB to AGB was positively correlated with aridity ($R^2 = 0.76$, P < 0.01; Fig. 2a, b). The C₃ grass dominated across the whole transact, with C₃ coverage $\sim 80\%$ at all sites (2c, d). The % C₃ cover decreased with aridity when aridity < 0.61, but it increased with aridity when aridity ≥ 0.61 . However, the relationship between % C₄ cover and aridity was reversed compared with % C₃ cover. The ratio of C₃/C₄ significantly positively decreased with aridity. The SOC stock ($R^2 = 0.77$, P < 0.001; Fig. 2e, f) and its light fraction ($R^2 = 0.70$, P < 0.001) was negatively correlated with aridity. Soil heavy fraction was the primary component of bulk soil, but this fraction was positively correlated with aridity ($R^2 = 0.70$, P < 0.001). Soil microbial biomass C ($R^2 = 0.76$, P < 0.001; Fig. 2g, h) and the ratio of microbial biomass C to SOC ($R^2 = 0.66$, P < 0.001) were negatively correlated with aridity.

We used SEM to examine the potential influence of plant biomass allocation (BGB/AGB) on soil C responses to aridity. The analysis revealed that aridity exerted indirect control on SOC stock by regulating grass species composition, total plant biomass and allocation (Fig. 3). Total plant biomass directly positively controlled SOC stock, while plant biomass allocation directly negatively controlled SOC stock.

3.2. The relative contribution of shoots and roots to soil carbon and its fractions

We found that neither root nor shoot δ^{13} C exhibited a simple linear correlation with aridity (Fig. 4a). Instead, both root ($R^2 = 0.74$, P < 0.01) and shoot ($R^2 = 0.66$, P < 0.01) δ^{13} C showed a hump-shaped relationship with the maximum at aridity = 0.61. However, the δ^{13} C of bulk soil ($R^2 = 0.77$, P < 0.001; Fig. 4b) and its light ($R^2 = 0.66$, P < 0.001; Fig. 4c) and heavy fractions ($R^2 = 0.81$, P < 0.001) were positively correlated with aridity (Fig. 4b, c). Our vegetation survey shows that C₄ species abundance was highest in middle of the climate transect (Fig. 2d). As the δ^{13} C values of C₃ plant tissues (-27.8%) are distinct from C₄ plants (-14.0%; Prentice et al., 2011; von Fischer et al., 2008), changes in the community composition of C₃ and C₄ plants with aridity may result in the hump-shaped relationship between the plant δ^{13} C value and aridity.

The isotope mixing models applied indicated that the relative contribution of shoots to SOC was higher than that of roots in wet areas with aridity <0.61 (73% vs. 27%; Fig. 5a). However, the pattern was reversed in drier areas with aridity \geq 0.61, where the root contribution to SOC was higher than the shoot contribution (71% vs. 29%; Fig. 5b). The relative contributions of roots to the soil light fraction were lower than those of shoots at all sites, with the estimates of root and shoot sources being 30% vs. 70% in the wet areas and 24% vs. 76% in the drier areas (Fig. 5c, d). The variation of plant C sources into soil heavy fraction was very similar to that of bulk soil. In detail, the relative contributions of roots to soil heavy fraction were 29% vs. 71% in the wet grasslands and 63% vs. 37% in the drier grasslands (Fig. 5e, f).

3.3. Effects of plant biomass allocation on soil carbon and microbial biomass carbon

The LMMs showed that AGB was a better predictor of variation of SOC stocks than BGB in wet areas with aridity <0.61 (partial $R^2 = 0.43$, P < 0.01 vs. partial $R^2 = 0.00$, P > 0.05; Fig. 6a, b). At drier sites (aridity ≥ 0.61) the variation of SOC stocks was better explained by BGB rather than AGB (partial $R^2 = 0.41$, P < 0.01 vs. partial $R^2 = 0.00$, P > 0.05; Fig. 6c, d). Similarly, our results also indicated that in wet areas the variation of microbial biomass C was better explained by AGB than by BGB (partial $R^2 = 0.40$, P < 0.01 vs. partial $R^2 = 0.00$, P > 0.05; Fig. 7a, b), while at drier sites it was better explained by BGB (partial $R^2 = 0.35$, P < 0.01 vs. partial $R^2 = 0.00$, P > 0.05; Fig. 7c, d).

In summary, the dominant controls of SOC and microbial biomass C by shoot inputs versus root inputs as revealed by LMM are consistent with two end-member mixing analyses. All evidence consistently points towards SOC being derived more from shoots than roots in wet grasslands, with the reverse being true in drier grasslands.



Fig. 2. Variations of soil carbon and plant growth along the aridity gradient. Plant belowground biomass (BGB) and aboveground biomass (AGB, a), the ratio of BGB/ AGB (b), percent C_3 and C_4 cover (c) and the ratio of C_3/C_4 (d), soil organic carbon (SOC, e), soil light fraction (LF) and heavy fraction (HF) composition (f), soil microbial biomass carbon (MBC, g), and the ratio of MBC/SOC (h). Data points represent observations for individual sites (n = 20), and regression lines show the influence of each variable on the carbon loss rate in the linear model. *** indicates P < 0.001.



Fig. 3. Piecewise structure equation models (SEM) showing the direct and indirect effects of aridity, plant community composition (C_3/C_4 abundance), total plant biomass and plant biomass allocation (root/shoot ratio) on soil organic carbon stock. All fitted coefficients are significant at $\alpha = 0.05$. Only significant effects are listed. Numbers besides arrows show standardized coefficients (r). Black numbers are coefficients of determination (R^2). Blue solid lines and orange dashed lines are the positive associations and negative associations, respectively. Plant allocation is the ratio of below- to aboveground biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We found that aridity mediated the relative contributions of aboveand belowground C input into SOC, in agreement with our hypothesis. Specifically, a larger proportion of SOC was derived from plant shoots in wet grasslands (aridity < 0.61), while root inputs were the primary source at drier sites (aridity \geq 0.61). This finding is supported by our analyses of both a two end-member mixing model (Fig. 5) and an LMM (Figs. 6, 7). This is because plant biomass allocation (as indicated by the ratio of below- to aboveground biomass) increased with aridity, which may influence root and shoot C inputs into soil and further soil microbial ecology of C cycling processes.

The contrast in δ^{13} C between roots and shoots allowed for calculation of the root/shoot ratio from δ^{13} C of SOC with a two end-member mixing model. The results indicated that aridity influenced soil C sources of plant inputs, where SOC was derived more from shoot parts at wet sites but roots inputs were the primary source at drier areas (Fig. 5). We separated drier sites versus wet areas using an aridity value of 0.61, which linked to a community compositional shift in C₃/C₄ abundance as aridity changes. Our study sites were dominated by C₃ grasses (with >80% coverage), and % C₃ cover showed a "V" shape along the aridity gradients with the lowest value at aridity = 0.61. C₃ plant productivity and biomass allocation have typically been found to be more sensitive to changes in aridity in comparison with those of C₄ species (Angelo and Pau, 2015; von Fischer et al., 2008; Zhou et al., 2012). Moreover, our value was close to the predicted aridity value of \sim 0.54 that there was a sharp decline in vegetation productivity and photosynthetic activity in global drylands (Berdugo et al., 2020). Further, faster rate of decomposition of C₄-derived C compared with C₃-derived C have been previously observed (Wynn and Bird, 2007). Ecosystem attributes are highly interconnected (Berdugo et al., 2020); therefore, changes in plant community composition induced by increases in aridity may trigger sequential changes in plant C source contributions to SOC. Although the δ^{13} C value of bulk soil was lower than that of shoot and root at most sampling sites, the value was a little higher than δ^{13} C of both sources at the higher end of aridity. This may produce uncertainties when we used a two end-member mixing model to trace soil C from plant C source. This pattern may relate with the ¹³C fractionation during SOC decomposition, and the quantification of soil age resulting isotopic shift between vegetation and SOC (Wittmer et al., 2010) and leading to further relative enrichment of ¹³C SOC (von Fischer et al., 2008). Here our analysis was restricted to the topsoil (0-20 cm), and further fractionations have been thought to be negligible when we traced plant C through ¹³C natural signature within this depth (von Fischer et al., 2008; Wittmer et al., 2010; Wynn and Bird, 2007). In the topsoil, both aboveground and root biomass contribute to SOC (Wynn and Bird, 2007), and ~70% of root biomass is there (Ma et al., 2008). In addition, 80 % of C in the top 20 cm of soil has a residence time of 50 years in Inner Mongolia (Wittmer et al., 2010), indicating that our soils are accurately reflecting the current vegetation. Furthermore, our studies conducted at fine scales where C₃ and C₄ species coexist would be the most informative to answer questions about resource partitioning. It will help us determine if aboveground and belowground patterns influence soil C inputs when competition is occurring across aridity gradients.

Further, our study indicated that plant biomass allocation may explain the relative amounts of above- and belowground plant C inputs into soils at different environmental conditions (Fig. 6). Plant biomass allocation generally reflects the balance between the acquisition of resources belowground (water and nutrients) and aboveground (light and CO₂; Angelo & Pau 2015; Chen et al. 2021b). The optimal partitioning theory predicts that allocation to belowground organs is favored over aboveground ones when facing soil resource limitations (Bloom et al., 1985). It will help plant growth to relieve constraints imposed by the most limiting resource, such as soil water (Hartmann et al., 2020). SEM analysis indicated that aridity had an indirect effect on soil C through its negative effects on total plant biomass and positive effects on plant biomass allocation (Fig. 3). Chen et al. (2021a) suggested that temperature and precipitation exerted an indirect control on topsoil C through its positive effects on plant C input in steppe grasslands. Specifically, our results indicated that soil C stocks were more influenced by shoot



Fig. 4. Variations of δ^{13} C in soil and plant parts along the aridity gradient. Roots and shoots (a), bulk soil (b) and its light fraction (LF) and heavy fraction (HF) of the 0–20 cm soil layer (c). The vertical dashed line is the regression breakpoint at aridity = 0.61. *** indicates *P* < 0.001, and ** indicates *P* < 0.01.



Fig. 5. Relative source contributions to soil carbon. Mean proportion of root and shoot contribution to organic carbon in bulk soil (a-b), soil light fraction (c-d), and heavy fraction carbon (e-f) of the 0–20 cm soil layer.

biomass at wet grasslands, but it reversed to root biomass at drier sites, because plant biomass allocation may influence plant C inputs into SOC pools through controlling the root and foliar litter production and root exudates (Abiven et al., 2005; Freschet et al., 2013; Rasse et al., 2005). Cotrufo et al. (2015) demonstrated that a fifth of shoot litter is not mineralized to CO2 in grasslands, but instead transferred into SOC via biochemical and physical pathways. The vegetation in our studies areas is mostly composed of perennial grasses with ungrazed foliage senescing and forming shoot litter at the end of the growing season (Prentice et al., 2011; Wittmer et al., 2010). Although roots biomass generally higher than shoot biomass in steppe grasslands, the C turnover time of roots is often longer than that of shoots (Sokol et al., 2019a) due to the plants are mostly perennial grasses (Dai et al., 2018; Hu et al., 2018). To some extent, this may decrease root C contributions into soil. Meanwhile, as shoot biomass increased with water availability (Fig. 2b), it may explain a greater production of shoot litter in wetter grasslands (von Fischer et al., 2008). As aridity decreases, more dissolved organic C from shoot litter (both fresh and decaying litter) leachate permeated into the mineral soil during precipitation evens (Kaiser and Kalbitz, 2012; Sanderman and Amundson, 2008). In high-leaching areas, dissolved organic C

can contribute up to 89% of new input soil C (Sanderman and Amundson, 2008). Indeed, we found that soil dissolved organic C deceased with aridity (Fig. S3), which was in line with our leaching hypothesis. Except for that, the temperature was lower at wet grasslands than that at drier sites, which may benefit shoot C input into soil at wet grasslands (Dai et al., 2018). Dai et al. (2018) suggested that low temperature inhibited litter decomposition and therefore may result more shoot C being transformed into soil in our study regions. However, in drier grasslands with sparse plant cover, shoot litter decomposition is mainly controlled by photodegradation with most C being returned to the atmosphere (Austin and Vivanco, 2006). Thus, root litter and root exudates are clearly an important C input to SOC in dry grasses (Pausch and Kuzyakov, 2018; Sanaullah et al., 2012). Although root litter and exudates may strongly influence SOC throughout the growing season at wet areas, shoot C inputs should be more efficient. In grasslands, root C enters into a spatially constrained area of the soil, with ~ 2 mm around the root (Nguyen, 2003). In contrast to root inputs, dissolved organic C from shoot litter enters the mineral soil as more irregular and widely distributed pulses of C (Sokol et al., 2019b). This may explain why SOC contains more shoot derived C in wet areas, but more root derived C in



Fig. 6. The relative importance of plant belowground biomass (BGB) and aboveground biomass (AGB) on soil carbon stocks at different environmental conditions. The green dots represent sampling sites with aridity < 0.61 (a-b), while the brown dots indicate sampling sites with aridity \ge 0.61 (c-d). The shaded areas indicate 95% confidence intervals. ** indicates *P* < 0.01, and ns denotes a non-significant trend (*P* > 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drier ones.

As aridity increases, changes of soil C sources also affect soil C compositions and potentially SOC stability. We found that the ratio of labile SOC (i.e., soil light fractions) decreased with aridity, while recalcitrant SOC (i.e., soil heavy fractions) having an increase pattern (Fig. 2f). Meanwhile, root inputs were the primary source to the heavy fraction in the dry grasslands, but shoot inputs were the major contribution at wetter sites (Fig. 5e, f). Generally, aboveground residues include greater quantities of more labile components (e.g., nonstructural carbohydrates, cellulose and soluble phenolics) compared with root litter (Bird et al., 2008; Xia et al., 2015). Based on the microbial efficiency-matrix stabilization framework, easily degradable and accessible components are the dominant source of microbial products, because they are utilized more efficiently by microbes compared with low quality substrates (Cotrufo et al., 2013). In our study, as the ratio of root/shoot biomass increased with aridity, both microbial biomass C and its fraction to SOC decreased (Fig. 2g, h). Thus, higher soil microbial abundance in wet grasslands could increase the chance of plant C inputs being assimilated, anabolized and then transformed to SOC as microbial products (Bradford et al., 2013; Miltner et al., 2012). These microbial products of decomposition would mainly contribute to stable SOC by promoting aggregation and through strong chemical bonding to the mineral soil matrix (Cotrufo et al., 2013). However, the soil microbial and nematode density was low at drier grasslands (Xiong et al., 2020), and there is also less leaf litter (Hu et al., 2018). Root litter generally represents important recalcitrant and stable C components, and then stable SOC formation may primarily occur through the direct sorption of root C components to mineral surfaces at drier sites (Sokol et al., 2019b). This was supported by our results that the variation of microbial biomass C was better explained by AGB in wet areas (aridity < 0.61), while being better explained by BGB in drier grasslands (aridity \geq 0.61) (Fig. 7). Finally, soil heavy fraction accounted for the majority of total SOC, with a proportion of 79% on average in our study (Fig. 2f). Therefore, the soil C sources of heavy fraction changed with aridity also supported our hypothesis.

Our results collectively point to the importance of the change of soil C source in controlling SOC stock and its stability along aridity gradients. We highlight two key areas for future work, based on our results. Firstly, due to the different biomass allocation between below- and aboveground plant parts, shoot and root C inputs into soil change with aridity and such a shift may affect SOC formation rate with consequences for SOC stock. SOC formation is largely due to physicochemical and biological influences from the surrounding environment that mediate plant biomass allocation and affect microbial transformation (Hartmann et al., 2020; Rasse et al., 2005). Such relationships indicate that the effective simulation of soil C accumulation may require a mechanistic understanding of spatial changes in plant community composition and biomass allocation as aridity increases (Lehmann et al., 2020). Second, the input of roots to shoots into soil C plays an important role in determining SOC composition and stability. We found that greater formation of soil heavy fraction with shoot inputs decreased the proportion of heavy fraction at wet grasslands whereas greater formation of heavy fraction with root inputs increased the proportion of heavy fraction at drier sites. It indicates the need for combination of many theories on SOM formation, with specific attention to climate. The stability of soil C should not only be described by compound chemistry or the level of 'recalcitrance', but should also be described by quantifiable environmental characteristics governing soil C sources of plant inputs (Lehmann et al., 2020; Schmidt et al., 2011). In consistent with Schmidt et al. (2011), our study indicated that chemical recalcitrance is less



Fig. 7. The relative importance of plant belowground biomass (BGB) and aboveground biomass (AGB) on microbial biomass carbon. The green dots represent sampling sites with aridity < 0.61 (a-b), while the brown dots indicate sampling sites with aridity ≥ 0.61 (c-d). The shaded areas indicate 95% confidence intervals. ** indicates P < 0.01, and ns denotes a non-significant trend (P > 0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

critical in determining SOC stability than previously thought. This approach holds great promise for unravelling the fate of plant-derived inputs in soil, determining how their dynamics vary between sites and predicting climate change feedback.

5. Conclusions

Our discovery suggested that SOC was more derived from shoots at wet sites (aridity < 0.61), but shoots were the primary source in drier areas (aridity ≥ 0.61) in steppe grasslands. To our knowledge, this is one of the first studies providing strong evidence to improve understanding of the role of aridity on influencing plant contributions to SOC stocks and their stability in a steppe grassland ecosystem at the regional scale. Understanding the specific dynamics underpinning plant inputs and microbial byproducts to mineral soil will be important for future regional scale predictions of C feedbacks as climate change progresses and drylands expand globally. Thus, more studies are needed for elucidating plant and microbial responses to climate change to reduce uncertainties in predictions of soil C cycling and to support the formulation of credible land management policy, particularly in areas likely to cross the identified aridity thresholds in the future.

Declaration of Competing Interest

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

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Authors' contributions

ZH, and YL designed the research, ZH, Jie-M, HX, and YZ performed the experiments, ZH and MW analysed the data. ZH wrote the first draft of the manuscript and all authors contributed to revisions.

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Appendix A. Supplementary data

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