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RESEARCH ARTICLE

Land use type shapes carbon pathways in Tibetan alpine ecosystems: Characterization of ^{13}C abundance in aggregates and density fractions

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Highlights

- Plantation land on the Tibetan Plateau reduces PAD and slows carbon transfer.
- Aggregate differentiation of organic carbon exists in density fractions but not in SOC.
- Aggregate differentiation of $\delta^{13}C$ and $\Delta^{13}C$ exists only in the density fractions of plantations.
- The direction of $\delta^{13}C$ enrichment from LF to PF to MF indicates carbon transfer in alpine plantations.

Abstract

Insight into the carbon turnover in soil aggregates and density fractions is essential for reducing the uncertainty in estimating carbon pools on the Tibetan Plateau, and how they vary with land use type is unclear. In this study, the effect of land use type on carbon storage and fractionation was quantified based on organic carbon and its ^{13}C abundance at the microscale of soil aggregates and density fractions in Tibetan alpine ecosystems. The sequence of soil aggregate destruction in the land use types of plantation (13.1%)<shrubland (32.7%)<grassland (47.9%)<farmland (61.8%) shows that plantations strengthen the soil structure. Plantation land had a greater contribution of light fraction organic carbon (28.3%) but a lower contribution of mineral-associated organic carbon (40.6%) to the carbon stock compared to farmland (13.5 and 70.3%). Interestingly, plantation land enhanced the aggregational differentiation of organic carbon and ^{13}C in each density fraction, whereas no such phenomenon existed in the soil organic carbon. Carbon isotope analyses revealed that carbon transfer in the plantation land occurred from the light fraction in macroaggregates (–24.9‰) to the mineral-associated fraction in microaggregates (–19.9‰). When compared to the other three land use types, the low transferability of carbon in aggregates and density fractions in plantation land provides a stable carbon pool for the Tibetan Plateau. This study shows that plantations can mitigate global climate change by slowing carbon transfer and increasing carbon storage at the microscale of aggregates and density fractions in alpine regions.

Keywords: land use type, soil aggregate, density fractions, carbon transfer, Tibetan Plateau

1. Introduction

The Tibetan Plateau harbors substantial carbon reserves, but it is particularly vulnerable to both global warming and human activities (Ma *et al.* 2020). The high altitude and low temperatures slow the soil carbon turnover, which has established the plateau as a significant carbon reservoir (Ding *et al.* 2016). Notably, the Tibetan Plateau accounts for 28.5% of the total soil inorganic carbon and 23.4% of the soil organic carbon (SOC) content in China (Yang *et al.* 2010). This region is experiencing a warming trend of 0.25–0.30°C per decade, which is two to three times the global average, making it a "magnifying glass" for global warming (Chen *et al.* 2013). Present estimates of regional carbon stocks on the Tibetan Plateau primarily rely on model simulations and remote

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sensing monitoring, with climate change as the predominant driving factor. However, carbon stocks vary across the region due to differences in vegetation types, temperature gradients, precipitation levels, and grazing disturbance (Xiao *et al.* 2023; Feng *et al.* 2024). Limited field observations and pronounced spatial heterogeneity contribute to significant uncertainties in estimates of SOC reserves on the Tibetan Plateau (Reinhart *et al.* 2014). Therefore, conducting further investigations into the responses of regional carbon dynamics on the Tibetan Plateau is crucial, especially regarding the micro scales and changes in vegetation types.

Soil aggregates exhibit heterogeneity in density, as well as chemical and biological processes, which differentially influence SOC stabilization and carbon stocks (Ma *et al.* 2021). The structure of soil aggregates reflects the stability and breaking behavior of bulk soil, which affects the transport and cycling of nutrients, water, and gases (Rabot *et al.* 2018). In addition, as distinct microenvironments, soil aggregates provide various microhabitats for microorganisms, influencing the degree of microbial utilization and decomposition of organic carbon (Luan *et al.* 2021). Generally, the organic carbon in macroaggregates (>0.25 mm) is primarily derived from plant residues, fungal colonies, and recent organic carbon inputs (Six *et al.* 2004), and it mostly consists of labile substrates (Williams *et al.* 2018). In contrast, microaggregates (<0.25 mm) contain more humified and recalcitrant carbon, which contributes significantly to long-term SOC accumulation (Peng *et al.* 2017). In general, different soil aggregate sizes play distinct roles in carbon sequestration potential. However, carbon transfer within aggregates and fractions remains understudied in alpine regions, particularly regarding the long-term effects of these processes on the stability and sequestration potential of SOC.

Our understanding of carbon stabilization and turnover in "black box" systems has been deepened by the fractionation of SOC (Poeplau *et al.* 2018). Since total SOC responds slowly to environmental changes over short periods, accurately capturing the intrinsic changes in soil quality in a timely manner is difficult. The labile and stable SOC fractions differ significantly in their decomposition rates, turnover, and resilience (Jiménez-González *et al.* 2020). The labile fraction, with a relatively short turnover time, serves as a primary nutrient source for plant and microbial growth and metabolism. It also functions as a sensitive indicator of soil quality and carbon stocks (Wang M *et al.* 2021; Wang *et al.* 2022). In contrast, the stable fraction exhibits a turnover time ranging from hundreds to thousands of years, making it less responsive to global warming and human disturbances (Ghani *et al.* 2022). Hence, isolating soil carbon pools with different turnover rates in alpine ecosystems is essential to further reveal SOC formation and its interaction with the soil matrix.

Carbon stabilization pathways across different aggregate sizes and carbon fractions can be identified using the natural abundance of the stable isotope ^{13}C (Liu *et al.* 2018a; Wang *et al.* 2020). Analyzing fluctuations in the natural ^{13}C abundance of SOC provides valuable insights into carbon decomposition and accumulation, especially during aggregate formation and fragmentation (Atere *et al.* 2020). During the decomposition of soil organic matter (SOM), the lighter ^{12}C isotope is preferentially released as CO_2 through soil respiration. Over time, the heavier ^{13}C isotope becomes enriched in the carbon pool, resulting in natural isotopic variations among different carbon fractions (Conrad *et al.* 2012). Shi *et al.* (2023) observed an increase in plant carbon stocks in aggregates during long-term forest succession, with the carbon flow shifting from larger aggregates to the silt and clay grain levels. Disparities in organic carbon content and ^{13}C abundance are evident across different aggregate sizes and density fractions in various ecosystems (Gunina and Kuzyakov 2014; Liu *et al.* 2018a). Although the natural abundance of ^{13}C is a powerful tool for assessing the stability of organic carbon and tracking its transformation and fate, the heterogeneity of microenvironments and organic carbon pools across systems must also be considered (Werth and Kuzyakov 2008).

Land use types significantly influence the spatial variation of carbon stocks on the Tibetan Plateau (Wiesmeier *et al.* 2014), with distinct sequestration and turnover rates associated with each type. In response to growing awareness of climate change and environmental conservation, extensive afforestation efforts have been implemented on the Tibetan Plateau (Liu *et al.* 2021). Plantations are regarded as an effective strategy for mitigating CO_2 emissions with substantial long-term carbon sink potential, and they also provide ecological, social, and environmental benefits (Justine *et al.* 2015). Research indicates that plantations in lowland regions enhance soil quality by improving soil structure, increasing fertility, reducing erosion, and stimulating microbial activity (Gao *et al.* 2022). While studies on soil carbon pools under different land use types are expanding, quantitative data on the impact of land use types on organic carbon dynamics in the alpine regions of southern Xizang remain limited.

Studying the variations in organic carbon and its ^{13}C isotopes among density fractions at the aggregate scale under diverse land use types on the Tibetan Plateau is crucial for advancing our understanding of carbon turnover and accumulation in alpine ecosystems. To achieve this, we employed density fractionation methods to separate the aggregates into three key density fractions: light fraction (LF), particulate fraction (PF), and mineral-associated fraction (MF). This analysis focused on four major land use types (farmland, grassland, shrubland, and plantation land) in the southern Tibetan Plateau, and we quantified their natural ^{13}C abundances. We investigated the intra-aggregate dynamics of organic carbon and its ^{13}C abundance within macroaggregates and microaggregates, as well as the inter-aggregate carbon fluxes between the aggregates and density fractions. The goal of this study was to reveal variations in the distribution of organic carbon fractions and their ^{13}C isotopes at the aggregate scale in soils under different land use types on the Tibetan Plateau. Ultimately, this study emphasizes the importance of separating soil aggregates and fractions to reveal SOC dynamics in alpine ecosystems.

2. Materials and methods

2.1. Site description and field sampling

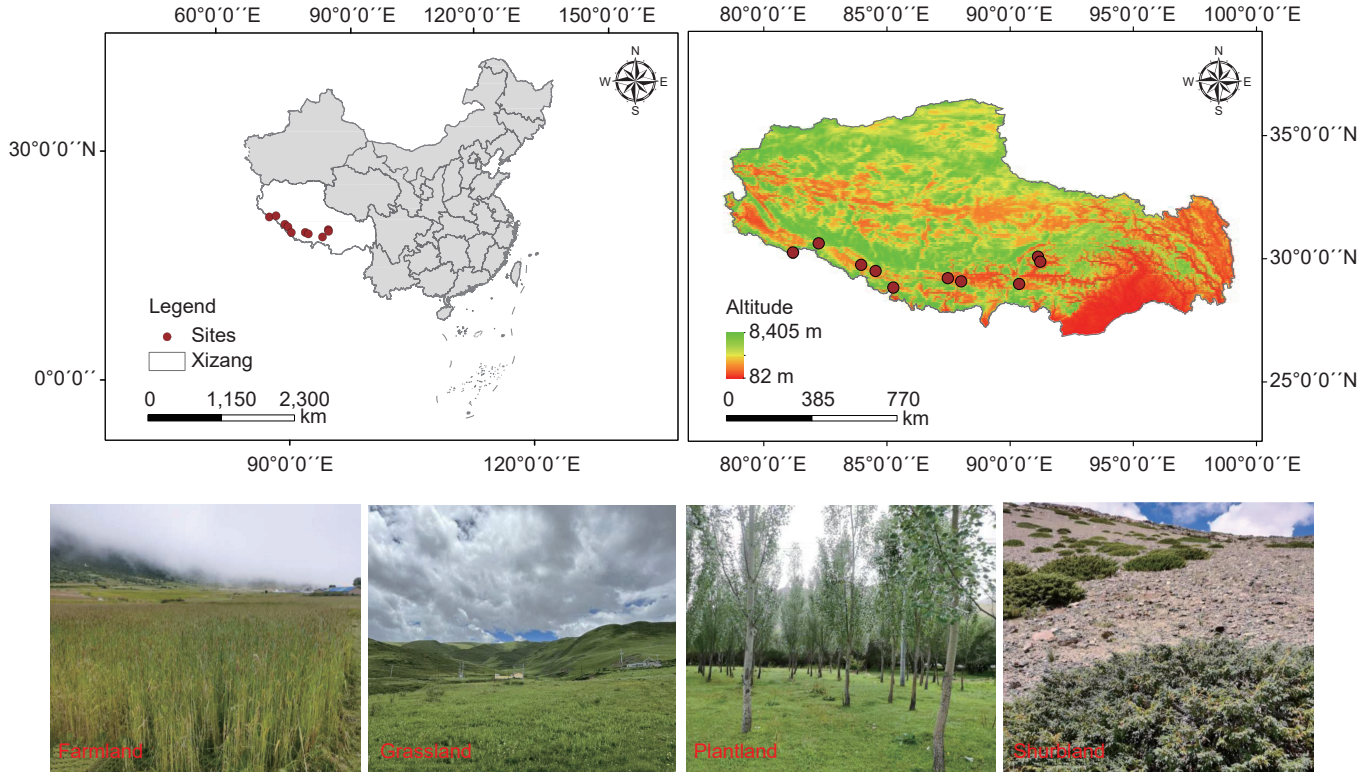
The study area is located in the southern Tibetan Plateau, China (81°19′–91°43′E, 28°41′–30°94′N), encompassing altitudes ranging from 3,300 to 4,800 m and characterized by a temperate plateau climate. The sites exhibit a substantial precipitation gradient, ranging from 72 to 706 mm annually, with mean annual temperatures between 8°C and 16°C. The longitude, latitude, and elevation of each site were recorded using an outdoor hand-held instrument equipped with a global positioning system. This study examined four land use types: farmland, grassland, shrubland and plantation land. In farmland, the primary crops are highland barley (*Hordeum vulgare*) and oilseed rape (*Brassica campestris*). The grasslands are densely vegetated and often covered with grass. The shrubland is a naturally occurring perennial thicket in the area, dominated by incense cedar (*Sabina pingii*) and Changdu caragana (*Caragana changduensis*). The main plant species in the plantation forest is white birch (*Betula platyphylla*). Before afforestation, the primary land use type was characterized by a rocky riverbank.

Soil samples were collected from each of the four land use types (farmland, grassland, shrubland, and plantation) at 10 sites across the study area that were approximately 150 km apart (Fig. 1). According to the Chinese soil classification system, the dominant soil type in the study area is Cryic Aridisols (Appendix A). Before sampling, the apoplastic layer was carefully removed by hand to access the soil. Soil samples were taken from the 0 to 20 cm soil layer using a 5 cm diameter stainless steel soil sampler. For each plot (10 m×10 m), five subsamples were randomly taken and thoroughly mixed to form a composite sample. Larger soil clods were broken down along natural fissures, and visible weeds, roots, stones, and other debris were removed manually. The samples were subsequently air-dried at 25°C. In total, 40 composite soil samples were collected.

2.2. Aggregate size fractionation

Mechanical stabilized aggregate (MSA) was obtained using the Shawinow dry sieve method. Approximately 500 g of air-dried soil was placed on a 0.25 mm aperture sieve with a stainless-steel tray positioned below it to collect the particles passing through the sieve. The sieve was shaken horizontally for 5 min at a consistent force to separate aggregates smaller than 0.25 mm, allowing them to fall into the tray. After sieving, the soil retained on the sieve (>0.25 mm) and particles collected in the tray (<0.25 mm) were gathered, weighed, and stored for subsequent analysis. To prevent cross-contamination during sieving, all equipment was thoroughly cleaned with 75% ethanol.

Water stabilized aggregate (WSA) was separated using the wet sieving method (Elliott 1986). Specifically, 100 g of air-dried soil was placed on a 0.25 mm sieve that was completely submerged in deionized water within a stainless-steel bowl and gently shaken horizontally for 5 min to ensure thorough wetting. The sieve was then moved up and down in the water for 4 min to allow aggregates smaller than 0.25 mm to pass through into the bowl. The materials retained on



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Fig. 1 Distribution of sampling sites and images of the four land use types.

the sieve (>0.25 mm) and in the bowl (<0.25 mm) were transferred to crucibles, dried at 60°C, and weighed to determine their proportions of the total soil mass. To prevent cross-contamination between samples, the equipment was thoroughly cleaned with sterile water. The percent aggregate destruction (PAD) was calculated as follows:

$$PAD=\frac{DR_{>0.25}-WR_{>0.25}}{DR_{>0.25}}\times 100\%$$

where $DR_{>0.25}$ is the percentage (%) of MSA and $WR_{>0.25}$ is the percentage (%) of WSA.

2.3. Soil density fractionation

The widely accepted approach for fractionating and analyzing organic carbon classifies it into three main fractions: light fraction organic carbon (LOC), particulate organic carbon (POC), and mineral-associated organic carbon (MOC). This classification is based on variations in formation, function, and turnover rate (Rui *et al.* 2022). To separate these fractions, the density fractions were obtained from macroaggregates, microaggregates, and bulk soil using the dry sieve method. The methodology for density fractionation was adapted from Gunina and Kuzyakov (2014) and Lavallee *et al.* (2019). Initially, 5.0 g of air-dried soil was added to a 50 mL tube, along with 25 mL of NaI solution (adjusted to a density of 1.85 g cm^{-3}) and 5 mm glass beads. The tube was gently shaken by hand to ensure thorough mixing, followed by continuous shaking on a shaking table for 16 h (25°C, 60 r min^{-1}). The resulting shaken solution underwent centrifugation at 4,000 r min^{-1} for 30 min, and the supernatant (LF, ρ<1.85 g cm^{-3}) was carefully extracted and filtered through a 0.45 μm membrane filter. The filter was repeatedly rinsed with NaI solution to ensure complete transfer of the LF, followed by rinsing with deionized water. Subsequently, 25 mL of NaI solution (density 2.0 g cm^{-3}) was added to the residual material in the tube. The tube was capped tightly, shaken by hand for 3 min, and then placed on a shaker at 120 r min^{-1} for 8 h. The mixture was centrifuged at 4,000 r min^{-1} for 30 min, and the suspension was filtered as previously described to isolate the PF (1.85<ρ<2.0 g cm^{-3}). The remaining precipitate in the tube was broken up and washed with deionized water to obtain the MF (ρ>2.0 g cm^{-3}). After fractionation, the samples were dried and ground to pass through a 100-mesh sieve. To remove carbonates, the samples were treated with an excess of 1 mol L^{-1} HCl solution and left to react for 24 h. The samples were subsequently rinsed with deionized water until neutral, then dried.

2.4. Carbon isotope analyses

The carbon content was assessed with an elemental analyzer, and stable isotope values ($\delta^{13}C$) were obtained *via* a stable isotope mass spectrometer. Carbon isotope ratios are expressed as $\delta^{13}C$ (‰), with reference to the international PDB (Pee Dee Belemnite) tuff standard. Organic carbon storage was quantified by determining the organic carbon content per 500 g of soil for each aggregate size or density fraction.

The flow of carbon between aggregates and density fractions was inferred using the method outlined by Gunina and Kuzyakov (2014). In surface soils, the fixation and decomposition of SOC result in ^{13}C fractionation, leading to an increase in the $\delta^{13}C$ in specific fractions. Fractions with higher $\delta^{13}C$ values are derived from those with lower $\delta^{13}C$ values. C isotope fractionation is used to discern the "sources" and "sinks" of the soil aggregate system fractions. The direction of C flow can be inferred based on the $\Delta^{13}C$ value, where $\Delta^{13}C=\Delta^{13}C_{product}-\Delta^{13}C_{source}$. A larger difference in $\Delta^{13}C$ between two fractions indicates a lower frequency of carbon exchange between them. In this study, the $\Delta^{13}C$ values of the different soils were calculated by subtracting the carbon isotope values of the density fractions in the aggregates from the isotope values of the corresponding bulk soil. Pathways of C flow in soil fractions were deduced by calculating the $\Delta^{13}C$ values. Furthermore, the direction of each arrow represents the flow of C, and the width of each arrow indicates the possibility of C flow in that direction. The arrow width is inversely proportional to the $\Delta^{13}C$ difference between the connected aggregates or carbon fractions.

2.5. Statistical analyses

The experimental data are presented as mean±standard deviation. Statistical analysis of all data was performed using SPSS (version 20.0, IBM, USA). Differences in organic carbon and its ^{13}C abundance in the soil samples among land use types were analyzed using Tukey's honestly significant difference in one-way ANOVA, with a significance level of $P\leq 0.05$. Graphs were generated using Origin 2021 software (Origin Lab, USA).

3. Results

3.1. Influence of land use type on soil aggregates and density fractions

Soil stability is defined as the capacity of soil aggregates to resist both decomposition and erosion. Among the four land use types on the Tibetan Plateau, there are significant ranges of variation in MSA, WSA, and PAD. The MSA macroaggregate proportions ranged from 40.6 to 93.7%, with farmland exhibiting the highest percentage (Fig. 2-A). The WSA microaggregate proportion in plantations (42.8%) was significantly lower than those in farmland (67%), grassland (61.1%), and shrubland (60.3%) (Fig. 2-B). The ranking of PAD across the four land use types was as follows: farmland (61.8%), grassland (47.9%)>shrubland (32.7%)>plantation (13.1%) (Fig. 2-C).

The distributions of different soil fractions (LF, PF, and MF) in both bulk soil and aggregates (>0.25 mm and <0.25 mm) exhibited significant variations among the different land use types. Among these, the proportion of LF in bulk soils was the lowest (2.6 to 5.5%). Notably, grassland had a significantly higher LF proportion (5.5%) compared to the other three land use types (2.5 to 2.9%) (Appendix B). The PF fraction was dominant in plantations, grasslands, and shrublands, comprising 58.9 to 76.6% of the soil density fractions, which were all significantly higher than the proportion in farmland (41%). In contrast, MF was the dominant soil fraction in farmland, accounting for 56.4% of the total, which was a significantly higher proportion than in

other land use types (20.5–38.2%).

3.2. Influence of land use type on organic carbon fractions at the aggregate scale

The SOC of the Tibetan Plateau followed the order of grassland (35.9 g kg^{-1})>farmland (19.9 g kg^{-1})>shrubland (18.4 g kg^{-1}) and plantation (15.6 g kg^{-1}) (Table 1). The distribution of SOC exhibited a pattern of grassland (43.4 g kg^{-1})>shrubland (29.4 g kg^{-1})>farmland (19.6 g kg^{-1}) and plantation (17.6 g kg^{-1}). In bulk soil, LOC was significantly higher than POC and MOC in all land use types, aligning with the findings of Chen *et al.* (2022). LOC was markedly higher in grassland (107.2 g kg^{-1}) and plantation (97.4 g kg^{-1}) compared to farmland (62.8 g kg^{-1}), whereas it reached its lowest levels in shrubland (28.3 g kg^{-1}) (Fig. 3-A).

3.3. Carbon storage of the density fractions in aggregates among land use types

The Sankey diagrams (Fig. 4) show the distribution of SOC stocks between aggregates and the three fractions among the four land use types. The distribution pattern of SOC stocks at the aggregate scale was consistent among all land use types, with macroaggregates exhibiting higher carbon stocks (3.4 to 45.1 g, 60.0 to 88.6%) compared to microaggregates (0.3 to 14.0 g, 11.4 to 39.3%) (Fig. 4). In both farmland and plantations, the contributions of soil fractions to carbon stocks followed the sequence of MF>PF>LF. Although plantations exhibited the lowest overall SOC content, the carbon stock distribution among the other three fractions was more balanced, with LF storage significantly higher than in farmland.

3.4. ^{13}C characteristics of the density fractions in aggregates among land use types

Carbon isotopes are an effective tool for identifying the sources of various carbon fractions, and they can provide crucial insights into carbon turnover and accumulation within soil ecosystems (Wick *et al.* 2009; Wang *et al.* 2020). In this study, we analyzed carbon isotope differences in the different aggregates and density fractions of the four land use types on the Tibetan Plateau. The $\delta^{13}C$ values ranged from –26.3 to –18.1‰ in LF, –26.9 to –17.1‰ in PF, and –26.2 to –18.4‰ in MF (Fig. 5; Appendix C). The $\delta^{13}C$ contents in soil fractions exhibited a clear trend based on land use type. Notably, a significant correlation between $^{13}C_{MF}$ and land use type was observed at the aggregate scale, but not in bulk soil. Specifically, among the four land use types, $^{13}C_{MF}$ was the highest in microaggregates and the lowest in macroaggregates in plantation. In general, $\delta^{13}C$ and $\Delta^{13}C$ in grassland, shrubland, and plantation ecosystems on the Tibetan Plateau increased with decreasing soil aggregate size (Appendix D). On the contrary, the $\delta^{13}C$ values in farmland ecosystems demonstrated the opposite trend, where the $\delta^{13}C$

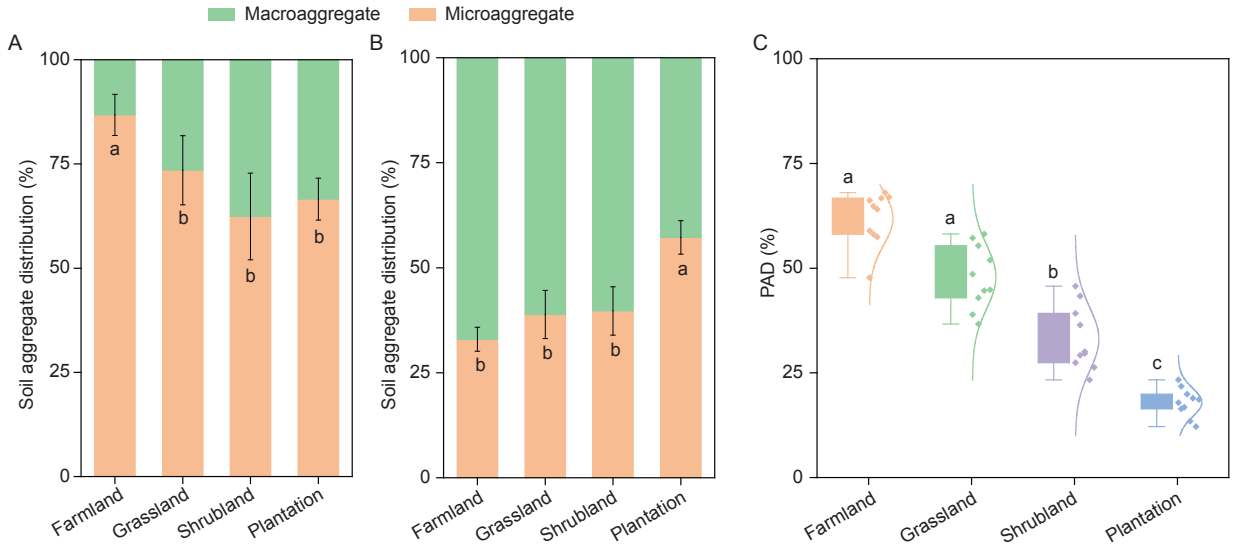


Fig. 2 Soil aggregate distribution (%) and percentage of aggregate disruption (PAD) for the different land use types. A, mechanically stable aggregate size distribution. B, water stable aggregate size distribution. C, percentage of aggregate destruction. Error bars represent standard errors (n=10). Lowercase letters reflect significant differences between land use types (P<0.05).

Table 1 Nutrients in different land use types and SOC in bulk soil, macroaggregates (>0.25 mm) and microaggregates (<0.25 mm)[1)]

Land use type	TC (g kg^{-1})	TN (g kg^{-1})	C/N	SOC (g kg^{-1})		
				Bulk soil	Macroaggregates	Microaggregates
Farmland	19.88±3.83 ab	2.06±0.34 a	9.54±1.33 b	19.57±4.86 b	19.38±4.77 b	20.93±5.7 b
Grassland	35.9±11.96 a	2.15±0.66 a	16.15±2.02 a	43.38±9.98 a	48.51±12.69 a	37.52±7.78 a
Shrubland	18.49±2.96 b	1.23±0.23 b	16.18±2.43 a	29.36±2.31 ab	31.13±2.28 ab	28.8±2.70 ab
Plantation	15.59±0.80 b	1.16±0.17 b	15.33±3.59 a	17.61±4.20 b	18.08±6.44 b	17.77±4.63 b

[1)] TC, total carbon; TN, total nitrogen; SOC, soil organic carbon.
Data are mean±SD (n=10). Different lowercase letters indicate significant differences between land use types (P<0.05).

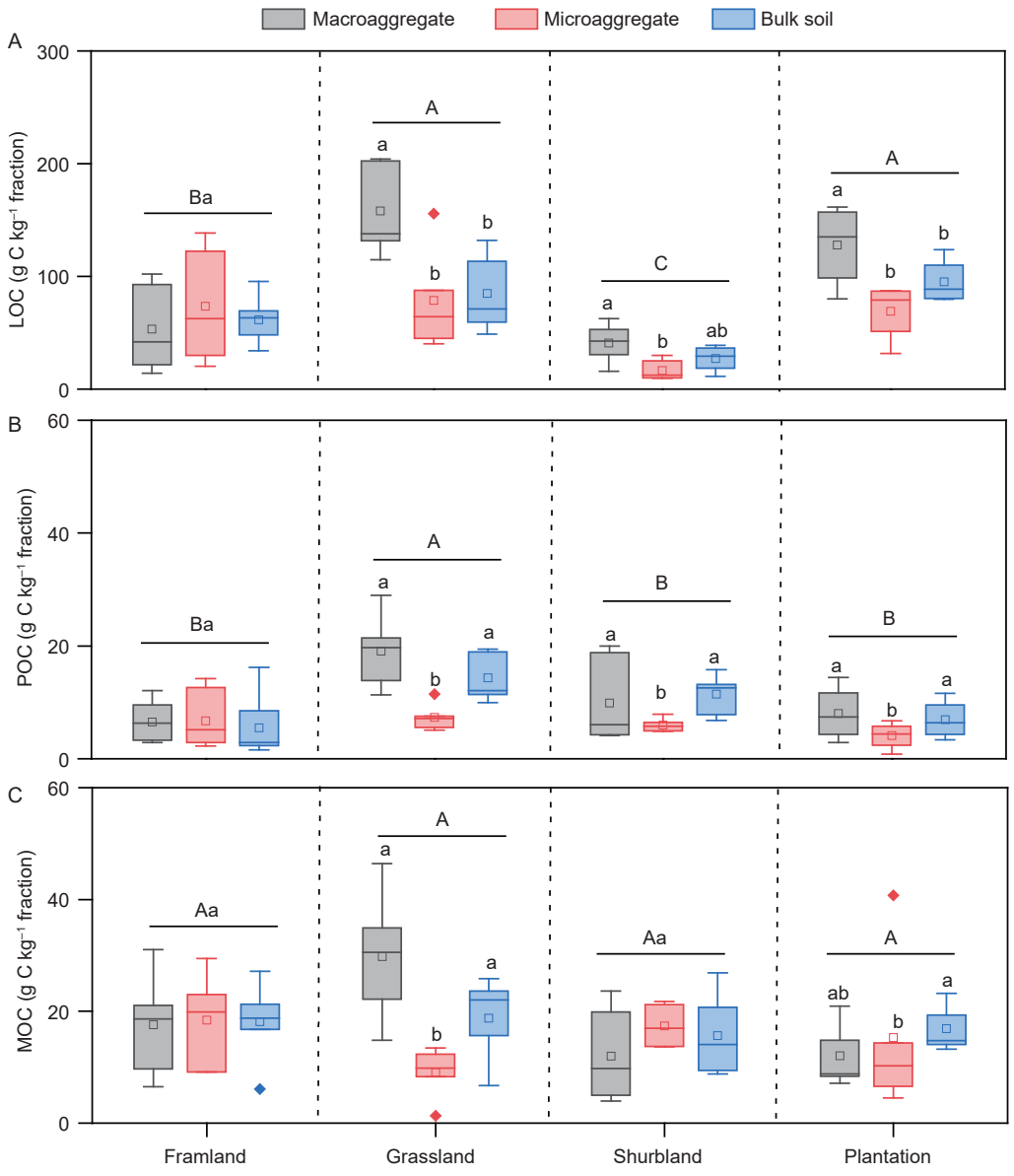


Fig. 3 Organic carbon contents of density fractions in bulk soil and aggregates under different land use types. A, organic carbon content of light fraction organic carbon (LOC). B, organic carbon content of particulate organic carbon (POC). C, organic carbon content of mineral-associated organic carbon (MOC). Different lowercase letters indicate significant differences (P<0.05) among bulk soil and aggregates in a specific fraction for the same land use type. Different capital letters indicate significant differences (P<0.05) between land use types for the same particle size of aggregates.

values in density fractions slightly increased with aggregate size (Fig. 5). Interestingly, significant isotopic fractionation of the density fractions was observed in plantation soils, with microaggregates exhibiting higher $\delta^{13}C_{LF}$, $\delta^{13}C_{PF}$ and $\delta^{13}C_{MF}$ values compared to macroaggregates (Fig. 5).

3.5. Carbon flow between organic carbon fractions in aggregates by land use type

The complexity of carbon transfer processes among different land use types on the Tibetan Plateau is illustrated in four carbon flux diagrams (Fig. 6). Distinct carbon pathways are evident in both soil aggregates and density fractions. In grassland, shrubland, and plantation soils, the overall $\Delta^{13}C$ of soil aggregates increases from macroaggregates to microaggregates, while the opposite trend is observed in farmland. Meanwhile, the transfer of carbon within soil density fractions in alpine ecosystem plantations follows a sequence from light to heavy (i.e., flow from LF to PF to MF) (Fig. 6), suggesting that the SOC in the heavier fraction is from microbial carbon utilization and transformation (Chen *et al.* 2022). In grassland and shrubland soils, carbon flows begin at the same point as in plantations, i.e., the LF (with no inflow) in the macroaggregate (Fig. 6). However, the carbon flow directions in grassland and shrubland differ from that in plantations, with a higher probability of flowing to LF than MF in the microaggregates.

The widths and predicted directions of the arrows indicate a lower probability of carbon transfer in aggregates and

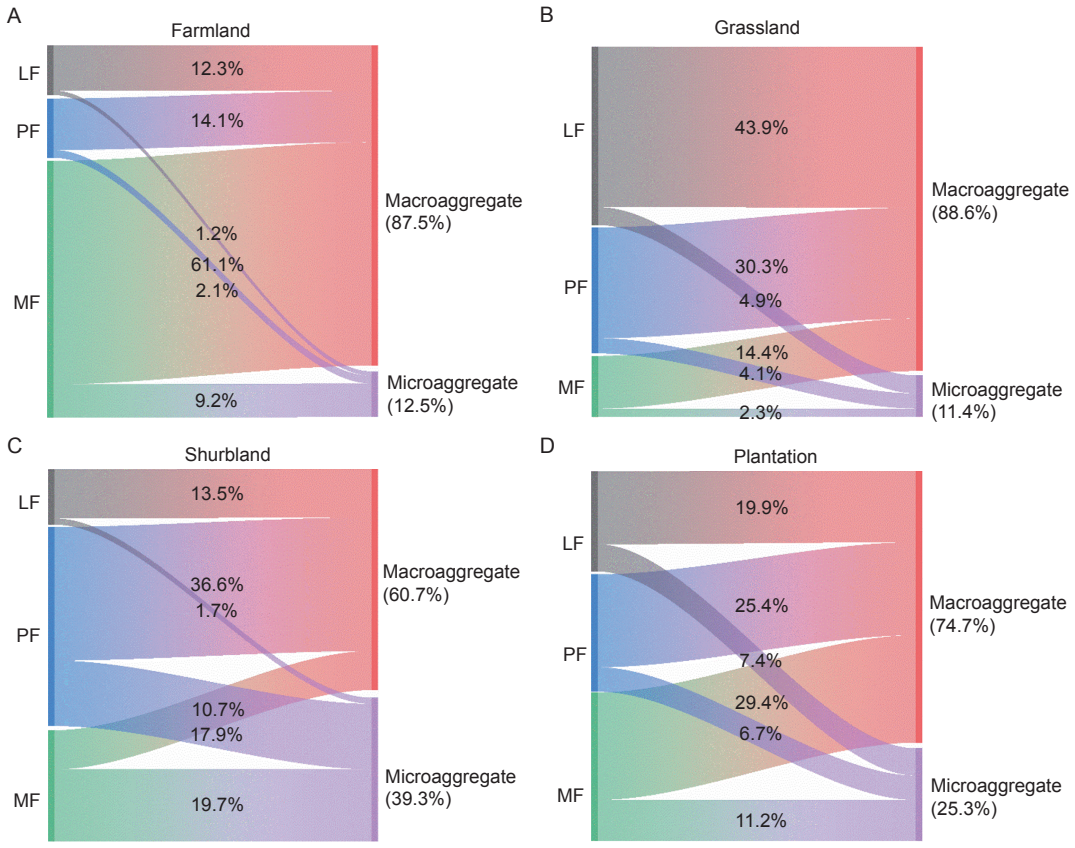


Fig. 4 Occurrences of carbon storage in different density fractions and aggregates. A, farmland. B, grassland. C, shrubland. D, plantation. LF, light fraction; PF, particulate fraction; MF, mineral-associated fraction. Box height indicates the percentage of total occurrences, and the width of each line indicates the amount of stock.

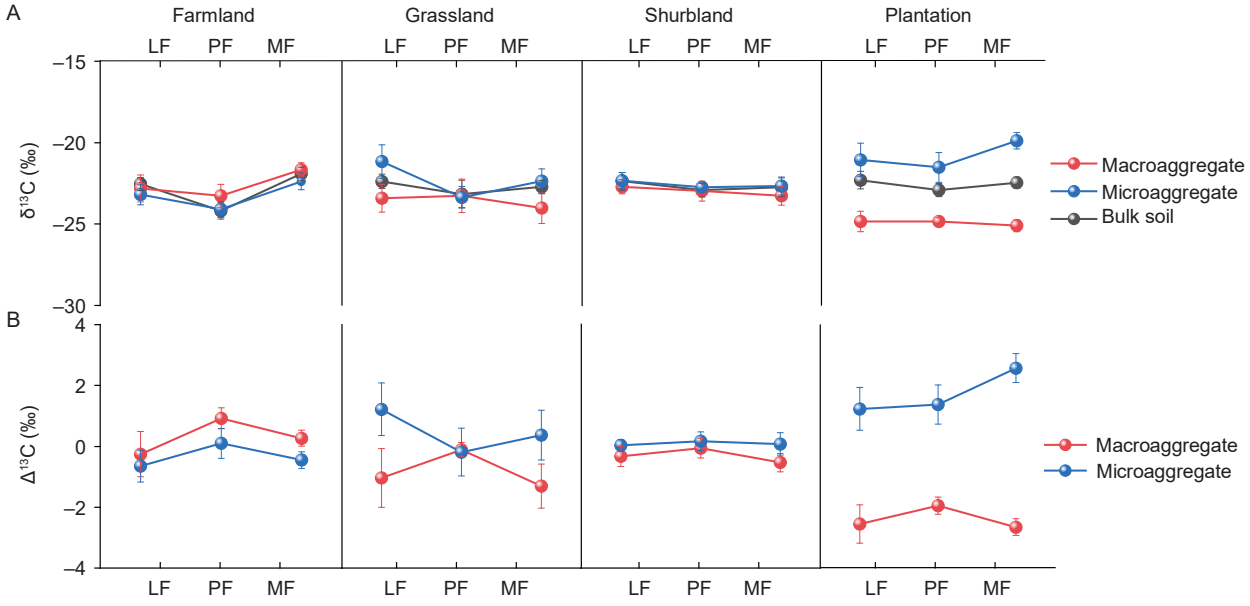


Fig. 5 Values of $\delta^{13}C$ and $\Delta^{13}C$ for the density fractions in bulk soil and aggregates under different land use types. A, $\delta^{13}C$ of density fractions. B, $\Delta^{13}C$ of density fractions. LF, light fraction; PF, particulate fraction; MF, mineral-associated fraction. The $\Delta^{13}C$ value of each density fraction in an aggregate was obtained by subtracting the $\delta^{13}C$ of the aggregate from that of the corresponding bulk soil.

density fractions under plantations compared to the other three land use types. This emphasizes the crucial role of plantations in maintaining carbon cycle stability in the Tibetan alpine ecosystem (Reinhart *et al.* 2014; Wang C *et al.*

2021). In addition, carbon flow paths in plantations between aggregates and density fractions show a movement from LF in macroaggregates (–24.9‰) to MF in microaggregates (–19.9‰) (Fig. 6).

4. Discussion

4.1. Land use types affect soil aggregate stability on the Tibetan Plateau

In grassland, shrubland, and forest ecosystems, fresh litter is a significant source of organic matter from plant origin, and it positively influences soil aggregates (Doetterl *et al.* 2015). Carbon substrates released during the decomposition of apoplastic litter are crucial for promoting the formation of substantial aggregates, thereby improving soil structure stability and mitigating aggregate fragmentation (Yang *et al.* 2024). However, farmland exhibits higher mechanical stability but lower water stability and increased PAD. This is attributed to the abundance of clay and silt particles in farmland, which tend to compact and aggregate during cultivation, resulting in soil particle clumping. Such compaction not only hinders water infiltration but also increases the susceptibility of soil particles to fragmentation, thereby compromising the long-term stability of the soil structure (Polakowski *et al.* 2021). In general, soil aggregates derived from dry sieving in farmland are larger but less stable, due to the complex interplay of soil composition, tillage practices, and compaction.

This study revealed a higher prevalence of PF in the plantation, grassland, and shrubland soils, indicating enhanced sequestration of labile organic carbon in these systems. The proportion of PF in different ecosystems plays a crucial role in enhancing soil health through multiple mechanisms. High PF content improves soil productivity by increasing the organic matter content, enhancing microbial diversity, and accelerating organic matter decomposition. As a result, nutrient cycling, water retention, soil structure, and resistance to erosion and compaction are significantly improved (Li *et al.* 2022; Shi *et al.* 2023). Conversely, the predominance of MF in

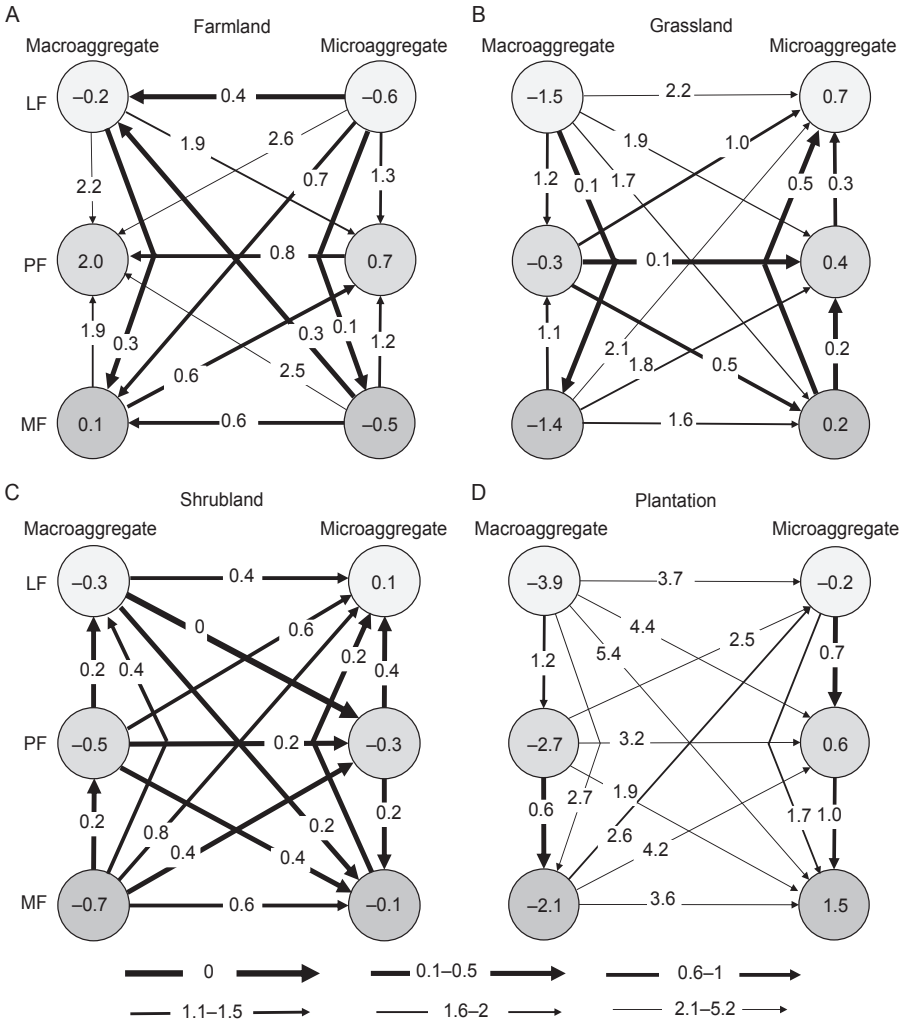


Fig. 6 Carbon flows within the aggregate size classes and density fractions of soil according to land use types. A, farmland. B, grassland. C, shrubland. D, plantation. LF, light fraction; PF, particulate fraction; MF, mineral-associated fraction. The numbers in circles represent the $\Delta^{13}C$ values of the soil, which were obtained from the differences ($\Delta^{13}C$) between the $\delta^{13}C$ of the respective density fractions and the $\delta^{13}C$ of bulk soil. The direction of an arrow indicates the direction of C transfer (from lower $\Delta^{13}C$ values to higher values). The numbers on the arrows are based on differences in $\Delta^{13}C$ values between density fractions. Smaller differences correspond to wider arrows and represent more possible C flow paths.

agricultural lands indicates that frequent disturbances, such as tillage, enhance the mineralization of organic matter, thereby increasing the association of carbon with mineral particles. This transformation highlights the critical influence of land management on the carbon sequestration potential of agroecosystems in contrast to natural systems. Among the various land use types, soil density fractions of the two soil aggregates exhibited similar trends to those of the bulk soil, consistent with findings in other ecosystems (Atere *et al*. 2020). In rice cropping systems, aggregates at all grain levels (>250 μm, 53–250 μm, and <53 μm) showed significantly higher MF compared to several other density fractions (Chen *et al.* 2022). The main reason for this is that fertilization increases MF in the soil by adding elements such as nitrogen, phosphorus, and potassium. Moreover, frequent farming accelerates mineral redistribution and soil erosion, thereby reducing the soil's carbon storage capacity.

4.2. Land use type effects on the carbon storage of density fractions at the aggregate scale

Numerous studies have highlighted the significant impact of land use type on the organic matter dynamics of soil ecosystems (Tan *et al*. 2007). This study addresses the knowledge gap regarding how land use types in alpine regions influence SOC dynamics at the micro-scale (aggregates). Our findings indicated that land use type significantly influences the LOC and POC, likely due to differences in the susceptibility of these fractions to microbial decomposition. In contrast, the minimal effect on MOC suggested that this fraction is relatively recalcitrant and less responsive to changes in land use. This differential response may be attributed to the strong adsorption of MOC onto mineral surfaces, which provides greater physical protection against microbial enzymatic activity, thereby enhancing its persistence within the soil system (Six *et al.* 1998; Zhang *et al.* 2023). Studies on the impact of farming practices on organic carbon fractions in aggregates indicate that LOC and POC are more susceptible, while MOC shows less fluctuations in both topsoil and subsoil (Six *et al.* 1998; Zhang *et al.* 2023).

In this study, soil density fractions in plantations, grassland and shrubland exhibited aggregational differentiation. This is primarily due to the dense packing of large soil aggregates, which restricts access to easily decomposable organic carbon for microbial decomposition (Tan *et al.* 2007), thereby contributing to heterogeneity among the aggregates. In addition, variations in organic matter, oxygen, and moisture within soil aggregates result in an uneven distribution of the functional microorganisms associated with organic carbon degradation at the aggregate scale (Tisdall and Oades 1982; Zhang *et al.* 2018). In general, both land use type and soil structure exert distinct influences on soil carbon turnover and microbial diversity (Chen *et al.* 2023a). This aligns with the concept of an aggregate hierarchy, where organic binders from plant litter and microaggregates contribute to macroaggregates, resulting in a higher SOC content in macroaggregates (Tisdall and Oades 1982; Yu *et al.* 2020). The prevalence of macroaggregates significantly contributes to their dominance in total organic carbon storage. Our findings extend the theory that large aggregates are major contributors to soil carbon storage in the grasslands, shrublands and plantations in alpine ecosystems (Mohamed *et al.* 2021; Zhang *et al.* 2021).

The contributions of various soil fractions to carbon stocks differ among land use types at the aggregate scale (Volk *et al.* 2018). The notable increase in LF organic content in plantation soil was attributed to enhanced biomass input, signifying a positive impact on SOC and its associated fractions. This enhancement contributes to a significant increase in soil carbon sequestration efficiency with vegetation recovery (Li *et al.* 2022; Shi *et al.* 2023). The impacts of land use types primarily result from the inputs of biotic residues and soil carbon decomposition. Previous studies have indicated that plantations can enhance the SOC content and quality by modifying soil structure, increasing soil fertility, reducing soil erosion, and promoting microbial activity (Yang *et al.* 2022). However, since plantations in southern Xizang are primarily used for rehabilitating degraded soils and are often established for short durations, the accumulation of plant-derived carbon in the soil remains relatively low, resulting in a less pronounced improvement in soil quality (Park *et al.* 2022). Shi *et al.* (2023) reported that the recovery of soil quality is slower in the early stages of forest succession. In summary, the analysis of carbon fractions under different land uses indicates that plantations exert active ecological effects on SOC in the Tibetan Plateau (He *et al.* 2021).

4.3. Aggregational differentiation of ^{13}C from density fractions vary among land use types

Analyzing the natural ^{13}C abundance of SOC in different aggregates and within each density fraction can provide evidence for the carbon transfer and stabilization pathways among aggregates and density fractions (Chen *et al.* 2022). This study identified significant differences in the density fractions among plantations, grassland, and shrubland, although these distinctions were not evident in the SOC among the four land use types (Fig. 5). Subsequent analysis revealed significant aggregational differentiation in the ^{13}C isotopic composition of the density fractions within plantations. Heterogeneity in $\delta^{13}C$ among various aggregates or density fractions has been also revealed in non-alpine regions (Luo *et al.* 2017; Atere *et al.* 2020). Fresh organic matter preferentially enters macroaggregates, resulting in a higher fresh carbon content in macroaggregates compared to microaggregates (Liu *et al.* 2018b). In addition, macroaggregates act as physical barriers that protect SOC from microbial decomposition. The microbial communities associated with macroaggregates further stabilize SOM by producing binding agents like polysaccharides (Chen *et al.* 2022). When macroaggregates break down, they release microaggregates and processed SOM particles (Liu *et al.* 2018a). These microaggregates store more mineralized organic carbon, contributing to the relatively high $\delta^{13}C$ levels found in them.

The ^{13}C from density fractions showed aggregational differentiation only in plantations. This emphasizes the importance of relatively undisturbed ecosystems in promoting carbon stabilization through aggregate structure (Liu *et al.* 2018b). Generally, macroaggregates act as the source or

initial reservoir of fresh organic carbon, whereas the SOC in microaggregates results from microbial decomposition (Gunina and Kuzyakov 2014; Liu *et al.* 2018a). Moreover, the microbial community composition varies with aggregate size, representing a significant factor in the observed aggregational differentiation in $\delta^{13}C$. Substantial evidence indicates that fungi play a crucial role in nutrient and energy redistribution in soil ecosystems through their mycelia, which dominate the decomposition of plant residues (Liu *et al.* 2022). Fungi with higher substrate utilization efficiency are more prevalent in macroaggregates, enabling the decomposition of a greater proportion of ^{13}C-depleted stable carbon (Chen *et al.* 2023b). The macroaggregates also possess more macropores or elongated pores, promoting a rapid microbial response and enhanced decomposition of plant residues (Toosi *et al.* 2017). In summary, the analysis of ^{13}C in various density fractions of soil aggregates on the Tibetan Plateau revealed that the dependence of $\delta^{13}C$ on aggregate size varies with land use type. While existing studies on carbon fractions often concentrate on bulk soil or exclusively explore carbon stabilization pathways at the aggregate scale, our findings indicate the need to examine soil fractionation at the aggregate scale for a comprehensive understanding of the soil carbon cycle. This study presents a unique pattern of aggregate fractionation of organic carbon in the primary land use types within the alpine region of the Tibet Plateau. Notably, an enrichment of $\delta^{13}C$ from macroaggregates to microaggregates occurs in plantations within the alpine ecosystems.

4.4. Influence of land use type on the carbon transfer pathways in soil aggregates and density fractions

The results of this study highlight important differences in carbon transfer pathways among land use types, particularly in alpine ecosystems. In grassland, shrubland, and plantation systems, the carbon transfer from macroaggregates to microaggregates reflects the process of organic matter decomposition, where fresh plant residues first enter macroaggregates and are subsequently processed and stored in microaggregates. This finding supports the theory that macroaggregates serve as the primary storage sites for fresh organic matter, with the carbon becoming increasingly stabilized as it transitions into microaggregates (Six and Paustian 2014; Chen *et al.* 2022).

In this study, we extended the concept that “carbon flows between aggregates follow a large-to-small pattern” to alpine ecosystems (Fig. 5). Similarly, Atere *et al.* (2020) observed a greater tendency for carbon to flow from macroaggregates to microaggregates in subtropical soil. However, the probability of carbon transfer between aggregates was significantly lower in plantations than in grassland and shrubland (Fig. 5). This suggests that while all three soil types on the Tibetan Plateau can reduce soil erosion and conserve both nutrients and water, there are significant differences in the patterns of carbon flow among these aggregates (Wang *et al.* 2023). Grassland and shrubland have relatively shallow root systems, so they are more susceptible to freeze-thaw cycles in alpine regions. These cycles exacerbate the fragmentation of macroaggregates, thereby increasing the probability of carbon transfer between aggregates. Freeze-thaw cycling has been shown to significantly affect soil structure, leading to the breakdown of aggregates in alpine meadows on the Tibetan Plateau (Li *et al.* 2020; Dong *et al.* 2023). Soils with shallow root systems are less resistant to physical disturbances such as freeze-thaw processes, so they are more prone to erosion and structural changes. Indeed, Xiao *et al.* (2020) found that the mean weight diameter of soil aggregates was higher under freeze-thaw conditions in oil pine woodlands on the Loess Plateau of China (Xiao *et al.* 2020). In contrast, farmland exhibited the opposite trend, with carbon flow occurring from microaggregates to macroaggregates. However, the transfer probability in farmland remained much higher than in plantations (Fig. 5-A and D). This difference may be attributed to the periodic plowing in farmland, which accelerates the breakdown of soil aggregates and reduces their protection against the microbial decomposition of SOM. Thus, periodic plowing not only accelerates the loss of SOC but also significantly increases the probability of carbon transfer between aggregates (De Clercq *et al.* 2015).

The reduced carbon transfer observed in plantations emphasizes their crucial role in stabilizing soil carbon. The lower transfer rate and higher stability of soil aggregates in plantations slow carbon decomposition, thus extending soil carbon storage (Wang *et al.* 2021b). The stable soil structure and reduced carbon flux in plantations are essential for maintaining the carbon sink function of alpine ecosystems (Reinhart *et al.* 2014). Overall, this study provides new insights into the carbon dynamics of alpine soils, particularly in plantation systems, and highlights the importance of considering both aggregate size and density fractions when evaluating soil carbon cycling and stabilization processes. The findings contribute to a deeper understanding of how land use influences carbon storage and turnover in high-altitude ecosystems, with implications for enhancing the carbon sink function in these regions.

5. Conclusion

Based on organic carbon content and its ^{13}C abundance, this study demonstrated that carbon storage and transfer between soil aggregates and density fractions varies across land use types on the Tibetan Plateau. The lowest PAD for plantations among the four land use types indicated that plantations improve soil stability in alpine areas. Carbon fraction analyses at the aggregate scale revealed that plantations exert positive ecological effects on carbon storage on the Tibetan Plateau. The study also found that in grassland, shrubland, and plantations, carbon transfer follows a pathway from macroaggregates to microaggregates, in contrast to farmland. Notably, the ^{13}C from density fractions has aggregational differentiation only in plantations. The carbon flow analysis indicates that plantations exhibit a lower carbon transfer probability compared to the other land use types, with carbon transitioning from LF to PF to MF and from macroaggregates to microaggregates. In conclusion, this study quantified land use type effects on carbon turnover and cycling in the aggregate and density fraction microscales, suggesting that plantations contribute to maintaining the

ecological balance in alpine regions, and they also provide a natural solution for mitigating global climate change.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in scientific writing

During the preparation of this manuscript, the authors used ChatGPT 4.0 to assist in improving the clarity and readability of the language. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

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