

Article

The Aggregate Structure and Organic Carbon Mineralization in Forest Soils Along an Elevation Gradient in the Sygera Mountains of the Southeastern Tibetan Plateau

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Abstract: The distribution of the soil aggregate structure and its associated organic carbon along the elevation gradient remains unclear, but it may be crucial for the stabilization of soil carbon pools in mountainous forests. In this study, we first assessed the changes in aggregate-associated organic carbon and the aggregate structure in the 0–20 cm soil layers of an alpine forest in the Sygera Mountains along an elevation gradient (3000–4200 m). We then conducted an incubation experiment to explore the relationship between aggregates and soil organic carbon mineralization, using the Pearson correlation analysis and RDA. The results indicated that macroaggregates and microaggregates were the predominant forms of aggregates in the Sygera Mountains, contributing significantly to organic carbon (33.57% and 38.29%, respectively). As the elevation increased, the stability of aggregates in mid and high elevations (3600–4200 m) was significantly higher than that in low elevations (3000–3300 m). Aggregate stability and macroaggregate-associated organic carbon were positively correlated with the total soil organic carbon, suggesting that organic carbon is essential for promoting soil aggregation in forest soils. With the rising temperatures, the rate of soil mineralization at different elevation sites significantly increased, and the Q_{10} values were greater at low elevations than at mid and high elevations. This implied that soil carbon pools at low elevations were more sensitive to climate warming. The significant negative correlation between microaggregate-associated organic carbon and soil mineralization suggested that microaggregates contribute to the stabilization of soil carbon pools. Given that the link between aggregates and soil mineralization strengthened with increasing temperatures, the role of aggregates in the stabilization of forest soil carbon pools should be emphasized under a warming trend.

Keywords: mountain forest ecosystem; elevation gradient; soil aggregates; soil organic carbon mineralization; climate warming



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1. Introduction

Soils are the largest reservoir of organic carbon in terrestrial ecosystems, storing more than the atmosphere and biomass combined [1]. Among these, mountain forests comprise over one-fifth of the world's land area and play a crucial role not only in supporting biodiversity, resisting natural disasters, and conserving soil and water but also in sequestering soil carbon and moderating climate change [2,3]. The soil carbon storage in the top 0–20 cm layer can reach up to 57% of the total organic carbon pool within 1 m of the soil depth [4]. However, due to the highly sensitive nature of mountain ecosystems to global climate change, they are susceptible to climate warming, leading to a shift in forest soils from being a carbon sink to a net carbon contributor [5,6]. In mountainous forest regions, the variations in precipitation and temperature across different elevations create distinct vertical zonation [7]. Therefore, the change in ecosystem homeostasis under climate change is considered an ideal subject to study, garnering significant attention and research from scholars [8].

The formation of stable aggregates influences soil function, as it maintains soil porosity, restricts the diffusion of oxygen and water, regulates microbial communities, protects organic matter, and sustains nutrient availability [9]. Based on particle size, aggregates are usually categorized into macroaggregates (>0.25 mm), microaggregates (0.053 – 0.25 mm), and silt and clay fractions (<0.053 mm) [10]. A previous study showed that forest soils receive higher carbon inputs than soils in other ecosystems, which are utilized by microorganisms to form binding agents that facilitate the aggregation of small particles and microaggregates into stable macroaggregates [11]. It can lessen the interaction between organic matter and extracellular enzymes, limit oxygen diffusion, and restrict microbial–substrate interactions [10,12], thereby facilitating organic carbon accumulation in forest ecosystems [13]. However, some studies have also shown that macroaggregates are vulnerable to environmental changes and disturbances, while microaggregate-associated organic carbon is more stable than that associated with macroaggregates or the silt and clay fractions [14–16].

The factors affecting soil organic carbon (SOC) decomposition include temperature, moisture, substrate quality, substrate availability, and microorganisms [17–21]. Among these, temperature is the most critical factor, regulating soil carbon dynamics [22]. The Q_{10} values, which represent the sensitivity of the soil carbon mineralization to temperature, are usually used to assess the intensity of carbon flux feedback between the soil and climate [23]. In recent years, the role of substrate (SOC) availability—such as aggregate protection, mineral associations, or spatial heterogeneity—in regulating soil mineralization has been increasingly emphasized, in addition to carbon quality [24–27]. Growing evidence suggests that its sensitivity to temperature is not solely influenced by carbon quality, and that reducing substrate availability can lower Q_{10} [28–32]. Promoting the physical isolation of organic carbon by soil aggregates or its binding to minerals are both ways to reduce the accessibility of organic carbon to attenuate its Q_{10} [33,34].

In mountain forest ecosystems, the elevation influences the formation of forest belts with different characteristics (e.g., climate, vegetation types, and soil minerals). The variations substantially alter the soil microenvironment, directly or indirectly affecting the structure of soil aggregates [35]. Therefore, with the background of global warming, identifying the effects of soil aggregation on SOC mineralization along an elevation gradient is crucial for accurately forecasting the C–climate cycle feedback. Based on this, we focused on the Sygera Mountains of the southeastern Tibetan Plateau to determine the role of soil aggregates in SOC decomposition along an elevation gradient. Specifically, we first analyzed the structure of soil aggregates at different elevations by the wet-sieving method and then determined the mineralization pattern of soil organic carbon at various temperatures through incubation experiments. Our main objectives were to (i) identify

the distribution and stability of soil aggregates along an elevation gradient; (ii) determine the characteristics of forest soil carbon mineralization under warming; and (iii) analyze the impacts of soil aggregates on SOC mineralization with correlation and redundancy analyses. By elucidating these links, we aimed to provide new insights for optimizing forest soils to enhance their capacity for carbon sequestration in the face of global warming.

2. Materials and Methods

2.1. Study Area

The Tibetan Plateau, known as the “third pole” of the world, is characterized by its complex and variable elevation, topography, climate, soil, and vegetation, making it a sensitive and ecologically fragile area for global climate change [36,37]. The study area is located in the Sygera Mountains (29°10′–30°15′ N, 93°12′–95°35′ E) in the southeastern Tibetan Plateau, China, with a maximum elevation of 5200 m a.s.l. Given the wide altitude range, the area is characterized by distinct altitudinal zonation [38,39]. The Sygera Mountain, which is situated at the middle and lower reaches of the Yarlung Zangbo River in Southeast Tibet, occupies an area of around 2300 km² [40]. Influenced by the warm and humid monsoon winds of the Indian Ocean, the region is situated in a transition zone between humid and semi-humid climates, with distinct wet and dry seasons. The mean temperature (MAT) ranges from 15.8 to 0.5 °C, with the annual precipitation ranging from 676.6 to 866.0 mm, with the majority occurring from June to September during the growing season. The soil in the study area was classified as Cambisols according to the WRB system. Five experimental sites (30 m × 30 m) were selected at 3000, 3300, 3600, 3900 and 4200 m a.s.l. on the western slopes of the Sygera Mountain (Table 1) [41,42]. The selected sites had similar geographical conditions and slope gradients to minimize variations in the natural factors that influence soil properties.

Table 1. Sampling site information along the elevation gradient in the Sygera Mountains, China.

Sites	Elevation (m)	Level	Lat. (N)	Long. (E)	Climate Zones	Vegetation Zones
E1	3000	Low	29°58′	94.46′	Montane warm temperate zone	Coniferous and broad-leaved mixed forest
E2	3300	Low	29°57′	94.55′	Montane temperate zone	Dark-coniferous forest
E3	3600	Mid	29°56′	94.55′	Montane temperate zone	Dark-coniferous forest
E4	3900	Mid	29°57′	94.58′	Subalpine boreal zone	Dark-coniferous forest
E5	4200	High	29°61′	94.61′	Subalpine boreal zone	Dark-coniferous forest

The Latin names corresponding to ‘Coniferous and broad-leaved mixed forest’ and ‘Dark-coniferous forest’ are *Silva conifera et foliosa* and *Silva conifera umbra*, respectively.

2.2. Soil Sampling

The soil samples were collected in early September 2023 from three parallel plots (1 m × 1 m) at each experimental site, with each plot being approximately 20 m apart. After removing the litter from the soil surface, five soil samples were randomly collected using a soil-coring kit (5 cm in diameter) at a depth of 0–20 cm for each sample plot and mixed into a composite sample. The fresh soil samples were gently separated along natural planes of weakness and passed through a 6 mm sieve to remove large roots, stones, and debris. All samples were transported to the laboratory on the same day and passed through a 2 mm sieve to eliminate visible pieces of stones and roots. Each soil sample was evenly divided into two parts, one stored at 4 °C for SOC mineralization analysis and the other air-dried for the subsequent physicochemical analysis. The water holding capacity (WHC) of the soil was determined according to the method described by Howard et al. [43].

2.3. Analysis of Soil Aggregates

The soil aggregates were separated using the wet-sieving method [44]. Briefly, a 250 µm sieve was nested on top of a 53 µm sieve, and 100 g of the air-dried soil sample was

placed on the 250 μm sieve. Deionized water was added to submerge the sample surface, followed by shaking for 5 min. The nested sieve was then manually moved up and down for 4 min. The soil samples retained on the sieve and those that passed through were collected in separate containers, and excess water from the samples was removed by centrifugation. Finally, the samples were dried at 40 $^{\circ}\text{C}$ to a constant weight, and the weights were recorded to determine the mass of macroaggregates (>0.25 mm), microaggregates (0.053–0.25 mm), and silt and clay fractions (<0.053 mm) in the soil samples. Following the elimination of inorganic carbon using hydrochloric acid, the carbon contents of bulk soil and soil aggregates were analyzed by a Flash 2000HT elemental analyzer (Thermo Fisher Scientific, Waltham, MA, USA).

The soil aggregate stability is expressed by the mean weight diameter (MWD, mm), geometric mean diameter (GMD, mm) and percentage of water-stable aggregates with particle size > 0.25 mm ($\text{WSA}_{>0.25}$, %) [45]. The parameters are calculated as follows:

$$\text{MWD} = \sum_{i=1}^n (\bar{x}_i w_i) \quad (1)$$

$$\text{GMD} = \exp\left(\frac{\sum_{i=1}^n (w_i \ln \bar{x}_i)}{\sum_{i=1}^n w_i}\right) \quad (2)$$

$$\text{WSA}_{>0.25} = M_{T>0.25} / M_T \quad (3)$$

where n represents the number of fractions (>0.25 , 0.053–0.25, <0.053 mm), i represents the i th aggregate, $\bar{x}_i$ represents the mean diameter (mm) of the i th aggregate (1.125, 0.1515, and 0.0265), w_i represents the proportion of the i th aggregate, $M_{T>0.25}$ is the mass of >0.25 mm water-stable aggregates (g), and M_T is the total aggregate mass across varying particle sizes (g).

2.4. Analysis of SOC Mineralization

Fresh soil equivalent to 60 g of its dry weight was placed in 500 mL Mason jars and incubated at 60% WHC. The soil was pre-incubated at 25 $^{\circ}\text{C}$ for 7 days to activate the microorganisms. Subsequently, the soils were incubated at temperatures of 5, 15, and 25 $^{\circ}\text{C}$ under dark aerobic conditions. Small beakers (25 mL) containing 5 mL of 0.1 M NaOH solution were placed in each Mason jar to trap the CO_2 from SOC mineralization. The gas samples were collected from the NaOH vials after 1, 8, 16, 25, 33, and 40 days [46,47]. In the presence of BaCl_2 , the NaOH solution was titrated with 0.01 M HCl to pH 8.3 to determine the amount of CO_2 . Compressed air was used to flush the jars to replenish oxygen after each interval and deionized water was added to keep the soil moisture at 60% WHC [48]. The SOC mineralization ratio (SOC %) over 40 days was calculated as follows:

$$\text{Cumulative soil mineralization} = \text{Cumulative } \text{CO}_2 \times \frac{12}{44} \quad (4)$$

$$\text{SOC}\% = \frac{\text{Cumulative soil mineralization}}{\text{SOC}} \times 100\% \quad (5)$$

where SOC % represents the ratio of cumulative soil mineralization (g C kg^{-1}) to total soil organic carbon and SOC represents the content of total organic carbon in bulk soil (g C kg^{-1}).

The Q_{10} value was calculated as follows [49,50]:

$$R = \text{Be}^{KT} \quad (6)$$

$$Q_{10} = \frac{R_{T+10}}{R_T} = \frac{\text{Be}^{K(T+10)}}{\text{Be}^{KT}} = e^{10K} \quad (7)$$

where R and T represent the soil CO₂ emission and temperature, respectively. The coefficient of B represents the respiration rate per unit of organic carbon at 0 °C, while the coefficient of K represents the decay constant.

2.5. Statistical Analysis

The data were analyzed using a one-way analysis of variance (ANOVA) in the SPSS 27.0 software (SPSS Inc., Chicago, IL, USA), with Duncan's multiple comparison method applied to assess the differences in soil aggregate structure, aggregate-associated organic carbon, and SOC mineralization at different elevations. The statistical significance threshold was set at 0.05, and the significance was labeled by letter notation (a, b, c) based on the size of the mean value of the results at each site. Pearson's correlation analysis in SPSS 27.0 was employed to determine the relationship between soil aggregate-related indicators and soil mineralization. A redundancy analysis (RDA) was performed using the Canoco 5 (Biometrics Ltd., Wageningen, Gelderland, The Netherlands) software to assess the explanatory ability of aggregate indicators on SOC mineralization and to identify the dominant influencing factors. The graphs were generated using Origin Pro 2025 (OriginLab Corp., Northampton, MA, USA).

3. Results

3.1. Aggregate Size Distribution and Stability Indexes

Taking the elevation of 3500 m as the boundary, the Sygera Mountains are divided into low and middle–high elevation zones, and there were significant differences in the aggregate contents between the low and middle–high elevation zones (Figure 1, $p < 0.05$). Microaggregates and macroaggregates were the dominant forms of aggregates in the Sygera Mountains. The content of macroaggregates decreased with the elevation in the low and middle–high elevation zones, respectively, with the highest at 3600 m (65.72%). For the microaggregates, the content increased with the elevation at both low and medium-high elevations, with the lowest at 3600 m (26.53%). The variation in silt and clay fractions within the altitude range is similar to that of microaggregates, although the value of silt and clay fractions at 3900 m was slightly higher than that at 4200 m. The trend of soil aggregates along an elevation gradient was consistent in various stability indexes (Figure 2). The average WSA_{>0.25}, MWD and GMD of the aggregates were 39.16%, 0.52 mm, and 0.28 mm, respectively. In general, the soil aggregate stability indexes were significantly higher in E3 and lower in E2 than in other sites ($p < 0.05$). There were no significant differences in soil aggregate stability among E1, E4, and E5.

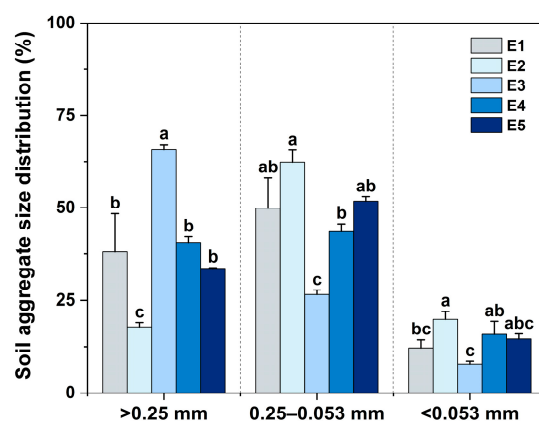


Figure 1. The soil aggregate size distribution along a range of elevations in the Sygera Mountains (%). The significance was labeled by letter notation (a, b, c) based on the size of the mean value of the results at each site ($p < 0.05$).

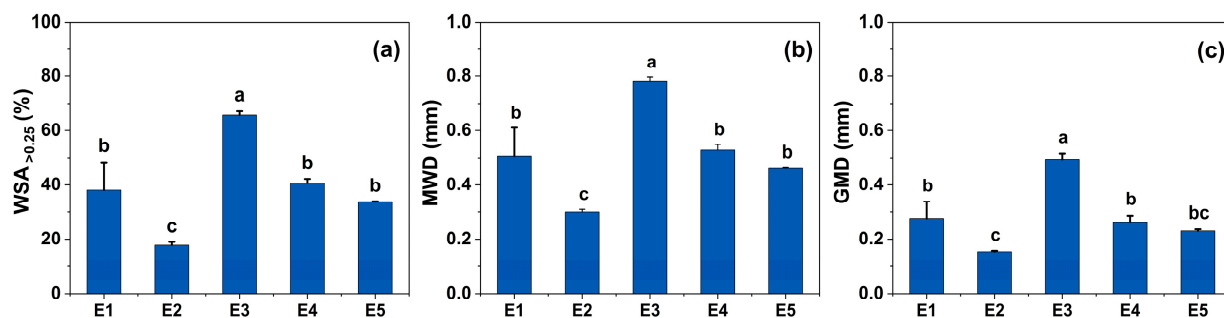


Figure 2. Soil aggregate stability indexes along an elevation gradient: WSA_{>0.25} (a), MWD (b), and GMD (c). The significance was labeled by letter notation (a, b, c) based on the size of the mean value of the results at each site ($p < 0.05$). WSA_{>0.25}, MWD, and GMD are the content of water-stable aggregate of >0.25 mm in diameter, mean weight diameter, and geometric mean diameter, respectively.

3.2. SOC Concentration

Soil organic carbon was significantly altered by elevation gradients in the Sygera Mountains ($p < 0.001$, Table 2). The concentration of SOC at the five sites ranged from 6.35 to 55.22 g kg^{−1}, with the following order of concentration: E3 > E5 > E1 > E4 > E2. The macroaggregate-associated organic carbon accounted for about 33.57% of soil organic carbon, and the trend of macroaggregate-associated OC distribution along the altitude gradient was consistent with that of SOC. E3 was significantly higher in macroaggregate-associated OC than that at other sites, with a concentration of 23.04 g kg^{−1}. As the main form of soil organic carbon, microaggregate-associated OC accounted for about 38.29% of the total. The concentrations of microaggregate-associated OC at E5 and E1 were significantly higher than that at other sites, about 15.44 g kg^{−1} and 9.88 g kg^{−1}, respectively. There was no significant difference in microaggregate-associated OC concentrations at E2, E3, and E4. The content of carbon in the silt and clay fractions ranged from 0.82 to 4.28 g kg^{−1}, accounting for an average of about 11.19% of the total organic carbon.

Table 2. The SOC concentration of bulk soil and aggregates (g kg^{−1}) along an elevation gradient (mean value ± standard error).

Elevation (m)	Bulk Soil	Aggregate Fractions (mm)		
		>0.25 mm	0.25–0.053 mm	<0.053 mm
E1 (3000)	29.30 ± 2.58 c	8.69 ± 2.85 bc	9.88 ± 1.20 b	3.13 ± 0.81 ab
E2 (3300)	6.35 ± 0.30 e	1.42 ± 0.29 d	4.67 ± 0.66 c	0.82 ± 0.04 c
E3 (3600)	55.22 ± 1.03 a	23.04 ± 0.86 a	6.19 ± 1.98 c	1.63 ± 0.04 bc
E4 (3900)	12.28 ± 1.01 b	5.91 ± 0.56 c	4.63 ± 0.26 c	2.40 ± 0.79 bc
E5 (4200)	43.82 ± 2.28 d	11.32 ± 0.72 b	15.44 ± 0.62 a	4.28 ± 0.44 a

Different lowercase letters indicate significant differences among various elevation gradients ($p < 0.05$).

3.3. Soil Organic Carbon Mineralization

Except for E3, the trends of soil mineralization rates at the three different temperatures (5, 15 and 25 °C) were generally consistent (Figure 3). At all three temperatures, the average soil mineralization rate initially increases and then decreases with increasing elevation, and E3 and E4 exhibited relatively high average soil mineralization rates. As the incubation temperature rises, the soil mineralization rates at various elevations increased significantly, with an average increase of 52.77% for every 10 degrees in temperature. Correspondingly, the cumulative CO₂ production increased with rising temperature, with average values of 2.08, 3.39, and 4.96 g kg^{−1} at 5, 15, and 25 °C, respectively (Figure 4). During the incubation period, the total CO₂ production at E3 and E4 was significantly higher than that at other sites. There was no significant difference in cumulative CO₂ production among E1, E2,

and E5 at 5 °C, which ranged from 1.00 to 1.56 g kg⁻¹. When the temperature increased to 15 °C, the total CO₂ production at E2 increased by 94.45%, whereas E1 and E5 exhibited the lowest production. At 25 °C, the decreasing order of total CO₂ production along the elevation gradient was E3 > E4 > E2 > E1 > E5.

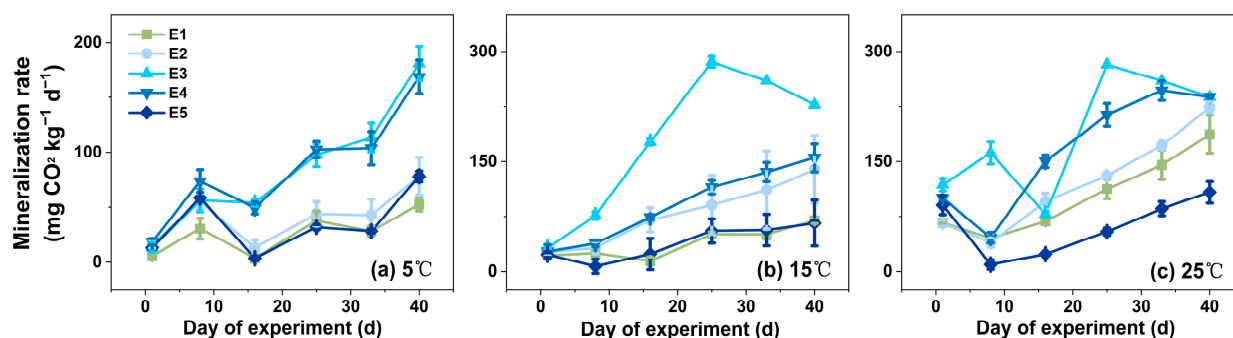


Figure 3. Soil mineralization rates from five elevation gradients of the Sygera Mountains incubated under 5 °C (a), 15 °C (b), and 25 °C (c).

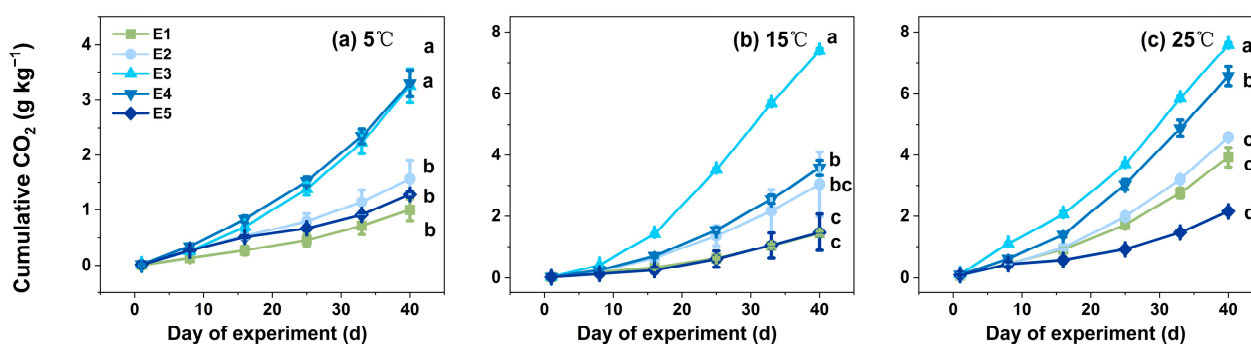


Figure 4. Cumulative soil mineralization from five elevation gradients of the Sygera Mountains incubated under 5 °C (a), 15 °C (b), and 25 °C (c). The significance was labeled by letter notation (a, b, c, d) based on the size of the mean value of the results at each site ($p < 0.05$).

Among the five sites, E2 and E4 exhibited the highest ratio of soil organic carbon mineralization, while E5 had the lowest with an average of 1.01% in the SOC. During the incubation period, the SOC mineralization ratio at 5 °C along the elevation gradient ranged from 0.80% to 7.44% (Table 3). When the temperature increased to 25 °C, the ratio of organic carbon mineralization rose from 1.34% to 19.71%. The increase in the SOC mineralization ratio due to warming decreases with increasing elevation. In the study region, the Q_{10} values of soil ranged from 1.35 to 2.30. The Q_{10} values in the low elevation zones were significantly higher than those in the middle–high elevation zones. Within the elevation range of 3000 to 3600 m, the Q_{10} values decreased with increasing elevation, while no significant differences were observed at altitudes from 3600 to 4200 m (Figure 5).

Table 3. SOC mineralization ratio (SOC %) over 40 days at 5 °C, 15 °C, and 25 °C along an elevation gradient (mean value $\pm$ standard error).

Elevation (m)	SOC _(5°C) %	SOC _(15°C) %	SOC _(25°C) %
E1 (3000)	0.96 $\pm$ 0.24 b	1.36 $\pm$ 0.09 b	3.71 $\pm$ 0.46 c
E2 (3300)	6.64 $\pm$ 1.28 a	13.25 $\pm$ 4.73 a	19.71 $\pm$ 0.64 a
E3 (3600)	1.60 $\pm$ 0.13 b	3.65 $\pm$ 0.06 b	3.75 $\pm$ 0.07 c
E4 (3900)	7.44 $\pm$ 0.93 a	8.05 $\pm$ 0.97 ab	14.73 $\pm$ 1.10 b
E5 (4200)	0.80 $\pm$ 0.04 b	0.89 $\pm$ 0.33 b	1.34 $\pm$ 0.02 d

Different lowercase letters indicate significant differences among various elevation gradients ($p < 0.05$).

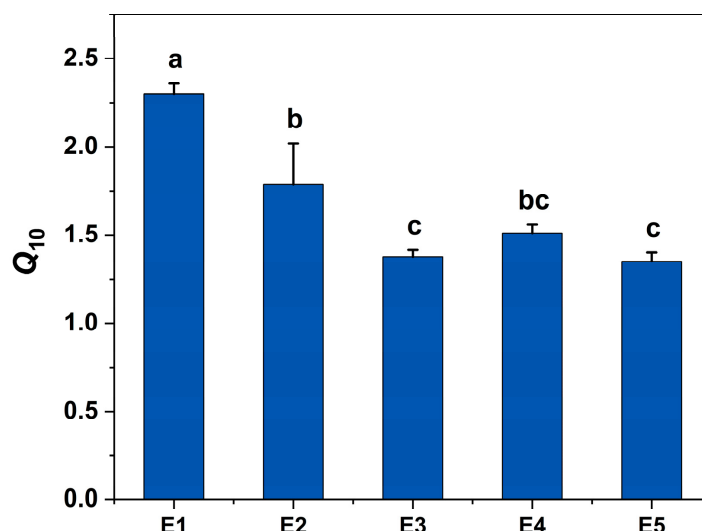


Figure 5. Temperature sensitivity of soil carbon decomposition (Q_{10}) along elevation. The significance was labeled by letter notation (a, b, c) based on the size of the mean value of the results at each site ($p < 0.05$).

3.4. Effects of Soil Aggregates on Soil Mineralization

Soil mineralization exhibited significant negative correlations with aggregate-associated organic carbon along the elevation gradients in the Sygera Mountains ($p < 0.05$, Table 4), of which the OC in microaggregates and macroaggregates significantly affect it at 5 °C and 25 °C, respectively ($p < 0.01$). The OC in the silt and clay fractions showed significant negative correlations with soil mineralization at 15 °C and 25 °C. The soil aggregate stability did not show significant correlations with soil mineralization. For the Q_{10} values, both the aggregate stability indexes and the aggregate-associated OC exhibited a negative correlation with it, although not statistically significant. A redundancy analysis (RDA) was employed to investigate the influence of soil aggregates on soil mineralization at different temperatures (Figure 6). Different soil aggregates factors exhibited significant differences in their contributions to cumulative CO₂ production. Collectively, the soil aggregate factors can explain 85.90% of the variations in soil mineralization, of which the soil aggregate-associated OC and aggregate stability accounted for 48.00% and 37.90%, respectively (Table 5). The microaggregate-associated OC and GMD exhibited highly significant effects on soil mineralization ($p < 0.01$) and could explain 44.30% and 31.90% of the variations in the ratio of SOC mineralized at different temperatures, respectively.

Table 4. Pearson correlation coefficients for the relationship between soil aggregates with soil mineralization.

Variable	WSA _{>0.25}	MWD	GMD	OC _{Macro}	OC _{Micro}	OC _{Silt+Clay}
SOC _(5°C) %	−0.35	−0.36	−0.39	−0.58 *	−0.64 **	−0.43
SOC _(15°C) %	−0.41	−0.41	−0.35	−0.49	−0.58 *	−0.54 *
SOC _(25°C) %	−0.49	−0.50	−0.48	−0.68 **	−0.72 **	−0.56 *
Q_{10}	−0.29	−0.29	−0.26	−0.36	−0.09	−0.04

SOC_(5°C) %—SOC mineralization ratio over 40 days at 5 °C; SOC_(15°C) %—SOC mineralization ratio over 40 days at 15 °C; SOC_(25°C) %—SOC mineralization ratio over 40 days at 25 °C; Q_{10} —temperature sensitivity of soil carbon decomposition; MWD—mean weight diameter; WSA_{>0.25}—percentage of water-stable aggregates greater than 0.25 mm; GMD—geometric mean diameter; OC_{Macro}—macroaggregate-associated organic carbon; OC_{Micro}—microaggregate-associated organic carbon; OC_{Silt+Clay}—silt and clay-associated organic carbon. Levels of significance indicated: * significant at $p \leq 0.05$, ** significant at $p \leq 0.01$.

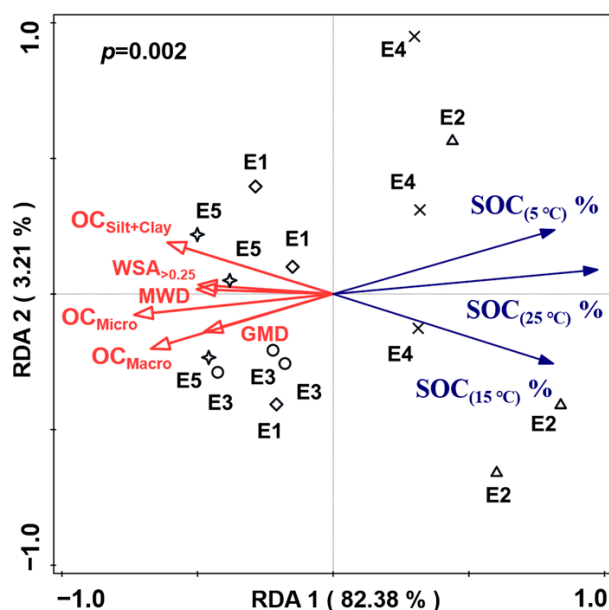


Figure 6. Redundancy analysis ordination diagram illustrating the relationships of soil aggregates with soil organic carbon mineralization. $SOC_{(5^{\circ}C)}\%$ —the percentage of SOC mineralized at 5 °C; $SOC_{(15^{\circ}C)}\%$ —the percentage of SOC mineralized at 15 °C; $SOC_{(25^{\circ}C)}\%$ —the percentage of SOC mineralized at 25 °C; MWD—mean weight diameter; $WSA_{>0.25}$ —percentage of water-stable aggregates greater than 0.25 mm; GMD—geometric mean diameter; OC_{Macro} —macroaggregate-associated organic carbon; OC_{Micro} —microaggregate-associated organic carbon; $OC_{Silt+Clay}$ —silt and clay-associated organic carbon.

Table 5. Importance ranking and significance test of soil aggregate factor explanation.

Variations	Explains %	Contribution %	Pseudo-F	p
OC_{Micro}	44.3	51.6	10.4	0.006 **
GMD	31.9	37.1	16.1	0.002 **
$OC_{Silt+Clay}$	2.7	3.2	1.4	0.256
$WSA_{>0.25}$	1.8	2.1	0.9	0.386
OC_{Macro}	1.0	1.1	0.5	0.594
MWD	4.2	4.8	2.4	0.162

Levels of significance indicated: ** significant at $p \leq 0.01$.

4. Discussion

4.1. Characteristics of Soil Aggregates in the Sygera Mountains

It is widely acknowledged that a higher proportion of macroaggregates in soil correlates with increased aggregate stability, which contributes to the physical protection of soil organic carbon [51]. Soil aggregate stability is usually evaluated by indices such as $WSA_{>0.25}$, GMD, MWD, with larger values representing a better aggregate stability [45,52,53]. In this study, the proportion of macroaggregates in middle–high elevations was found to be greater than that in low elevations. This indicated that elevation regulated the distribution of aggregates in the Sygera Mountain forest ecosystem, with the mid and high elevations promoting the aggregates. It was in line with the findings of Wu et al. [8] and Li et al. [54] regarding forest soil aggregates in the Helan Mountains and Qilian Mountains in China, respectively. However, unlike those studies, our research indicated that in both low and middle–high elevation zones, the proportion of macroaggregates and aggregate stability decreases with increasing elevation. The elevation of mountain ecosystems is typically associated with variations in the meteorological environment such as precipitation and temperature [6]. This can result in the development of various soil types

and the emergence of different plant species and microbial communities, thereby influencing aggregate formation and stability [6,17,55]. Additionally, during the soil aggregation process, fungal hyphae facilitate macroaggregate formation. Research has indicated that the content of macroaggregates measured in high-altitude areas was connected to higher fungal abundance and increased metabolic activity [56]. Yang et al. [40] found significant differences in the structure and function of soil bacterial communities between two forest types (shrubland and coniferous forest) at the tree line in the Sygera Mountains, leading to the inconsistent microbial decomposition of soil organic carbon across different sites, which provided a unique explanation for soil carbon variation in forested areas. Furthermore, the macroaggregates were extremely vulnerable to alterations and disruptions in the surroundings [14]. At the lower elevations of 3000 and 3300 m in the Sygera Mountains, frequent human activities may contribute to the lower content of soil macroaggregates in these areas [57].

Soil organic carbon serves as an important binding agent to enhance soil aggregate formation and stability [58–60]. Variations in soil vegetation types due to regional climatic differences influence the distribution of SOC, as increased vegetation canopy and plant biomass can enhance the input of organic matter from litter and root exudates [8]. The vertical zonation of vegetation communities in the Sygera Mountains is distinct, encompassing a range of types from low to high elevations, including mixed coniferous–broadleaf forests (*Silva conifera et foliosa*), dark-coniferous forests (*Silva conifera umbra*), shrub meadows (*Pratum fruticosum*), and sparse vegetation zones (*Pratum vegetatio sparsa*) [41,42]. In this study, significant differences in SOC were observed along the altitude gradient, with the highest concentration found at 3600 m in the mid-elevation region. This finding was consistent with the results of Han et al. [41], which indicated that the soil in the mid-elevation zone of the Sygera Mountains possessed substantial nutrients and organic matter, demonstrating strong land productivity and rapid vegetation growth. Moreover, a significant positive correlation was identified between SOC and macroaggregate-associated OC (Table 6). This aligns with the findings of Jastrow et al. [12], which highlighted the critical role of SOC in binding microaggregates and facilitating their transformation into macroaggregates. Furthermore, our results indicated that SOC also affected aggregate stability. It has been shown that organic carbon significantly influences aggregate stability and the K factor, with organic carbon exerting a direct positive impact on $WSA_{>0.25}$ and MWD, underscoring the crucial part that organic matter plays in maintaining soil structure [61]. This was attributed to SOC acting as a binding material that enhanced the hydrophobicity and particle cohesion of aggregates, thereby reducing the dissipative effects on aggregates and minimizing fragmentation [62]. Consequently, the distribution of SOC along the elevation gradient in the Sygera Mountains was an essential factor regulating the structure of aggregates.

Table 6. Pearson correlation coefficients for the relationship between soil organic carbon (SOC) with soil aggregates and Q_{10} .

Variable	$WSA_{>0.25}$	MWD	GMD	OC _{Macro}	OC _{Micro}	OC _{Silt+Clay}	Q_{10}
SOC	0.66 **	0.67 **	0.70 **	0.88 **	0.49	0.33	−0.33

Levels of significance indicated: ** significant at $p \leq 0.01$.

4.2. Linking SOC Mineralization with Soil Aggregates

Soil respiration is the course in which soil microorganisms decompose organic carbon to release CO_2 , representing a primary pathway for the depletion of soil carbon pools [63]. As the most important factor affecting soil respiration, substrate decomposition, as well as root and microbial activity, is constrained by soil temperature [64,65]. In this study, as temperatures increased, soil respiration rates at five elevation sites significantly increased,

with an average increase of 52.77% for every 10 °C rise in temperature. Yu et al. [66] reported that rising temperatures can shift the dominant microbial communities in the soil from k-strategists to r-strategists. Soil r-strategy microorganisms exhibit faster turnover rates and higher activity compared to k-strategists [66]. Generally, warm forest soils devote more carbon to respiration and less to biomass development than cold forest soils [37]. The soil Q_{10} value is commonly used as an important indicator of the sensitivity of soil microbial respiration to temperature variations [67]. In this research, we found that the Q_{10} values at low altitudes were higher than those at middle and high altitudes. Li et al. [68] attributed this to the decrease in stocks of soil organic matter (SOM) in the high-elevation regions. Since SOM is the main substrate for soil respiration, its quantity and quality strongly influence the composition of microbial communities. Nevertheless, there were no significant links between SOC and Q_{10} (Table 6). This may have resulted from the fact that the factors regulating Q_{10} were not only the quantity of organic carbon but also its accessibility [69].

As mentioned earlier, the increase in SOC promotes soil aggregation and its stability [70]. In turn, soil aggregates influence the turnover and stability of organic carbon by physical protection mechanisms [71]. It has been demonstrated that the accessibility of OC affects the microbial utilization of SOC more than its biochemical recalcitrance (C-quality) [72]. The physical mechanism of soil aggregates can shield organic matter against microbial and enzymatic degradation through occlusion, interlayer silicate layer encapsulation, hydrophobicity, and the encapsulation of organic macromolecules, thereby allowing organic carbon in the soil to resist rapid decomposition [73]. This finding supports the negative correlation observed between soil aggregates and Q_{10} in this study. However, we also found that aggregates were not the main controlling factor in regulating the temperature sensitivity of SOC in forest soils of the Sygera Mountains. This may be due to the fact that, in addition to being physically protected by aggregates, the accessibility of OC in soils can be limited by soil minerals [74]. Chemical protection by minerals can directly or indirectly influence the variation in Q_{10} by altering microbial activity [37].

Moreover, the structure of aggregates and their associated OC influence SOC mineralization, but different aggregate fractions play distinct roles in the stability of SOC [8,75]. While the OC associated with each aggregate fraction exhibited a negative correlation with soil mineralization, the redundancy analysis indicated that soil microaggregate-associated OC had the most significant impact on the ratio of SOC mineralization, whereas macroaggregates had the least influence. The result aligned with the research conducted by Adnan et al. [75], who reported a higher degree of mineralization of OC in macroaggregates compared to microaggregates. Six et al. [73] posited that despite the higher concentration of OC in macroaggregates, the OC in microaggregates is less conducive to microbial decomposition and utilization, thereby promoting soil carbon sequestration. In addition to aggregate-associated OC, geometric mean diameter (GMD) also significantly influenced soil mineralization. Furthermore, our study demonstrated that the linkage between the aggregate-associated OC and SOC mineralization was strengthened when the temperature increased to 25 °C. This underscored the importance of the physical protective role of aggregates in the context of climate warming, particularly for forest soils rich in organic carbon.

4.3. Implications

It should be noted that in this study, we did not observe a linear relationship between SOC concentration or its mineralization and altitude. Instead, we found alternating high and low values across the elevation gradients. When assessing the stability of SOC at different sites using 'SOC %', the results at sites E2 and E4 were significantly higher than those at other sites, representing a very high vulnerability of the soil carbon pool at these

locations. This might be related to the fact that E2 and E4 are transition zones of the mountain climate (Table 1). Variations in temperature and precipitation not only affect the vegetation composition of coniferous and broadleaf forests but also alter the types of low shrubs and moss species in forest ecosystems. These changes successively influence the soil's physicochemical properties, the quality of organic carbon inputs, and the diversity of the microbial community, ultimately impacting organic carbon turnover [42,76–78]. Referring to the findings of Zheng et al. [79] and Wei et al. [80], on other forest soils of the Tibetan Plateau, the high values of SOC % are not incidental. Therefore, this phenomenon warrants further investigation into its potential causes, such as compositional differences in organic carbon pools at different sites, the mineralization characteristics of soil aggregates, and the role of soil minerals to provide deeper insights into enhancing the stability of forest soil carbon pools. Furthermore, CO₂ release due to the decomposition of detritus in the soil should not be underestimated. According to a study by Smagin et al. [81], the presence of organic debris as a major component of peat soils can lead to very rapid biodegradation processes, especially during the early stages of decomposition, when 50%–60% of organic matter can be lost. Although we made every effort to remove plant residues in this study, debris may not be completely removed by picking and sieving due to the continuous input of abundant litter from forest ecosystems over the years, which could introduce experimental errors. Additionally, the carbonate content in the soil might interfere with the measurement results. This suggests that soil pre-treatment methods, such as removing plant residues (e.g., heavy liquid separation, water washing, mechanical separation) and carbonates (e.g., acid treatment), in conjunction with modern measurement devices, are essential for improving measurement accuracy in future studies of forest carbon pools.

5. Conclusions

The results revealed that the proportion of macroaggregate and aggregate stability at mid–high elevations are superior to those at low elevations, and with lower Q_{10} values. Under the influence of the vertical climatic variations, SOC concentration varied significantly along the altitudinal gradient of the Sygera Mountains, but did not follow a linear trend with altitude. Nevertheless, SOC had a notable impact on the structure and stability of soil aggregates. Furthermore, the distribution of soil aggregates was closely linked to organic carbon mineralization. The soil mineralization rates were significantly elevated with increasing temperature at different elevations, implying that the soil organic carbon in the Sygera Mountains is vulnerable to warming. Overall, GMD and microaggregate-associated organic carbon significantly influenced the ratio of SOC mineralization, with the effect of aggregate indicators on SOC mineralization enhancing with rising temperatures. This emphasizes the important role of soil aggregates in mountain forest ecosystems for SOC preservation in response to global warming.

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