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Leucaena leucocephala plantations can increase soil organic carbon storage by increasing labile fractions without reducing stability in dry-hot valley savannas

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Abstract

Background Soil organic carbon (SOC) stocks increase under nitrogen-fixing plantations. However, the mechanisms underlying this increase in SOC stocks and the stability in savannas converted to *Leucaena leucocephala* plantations remain unknown. This study explored the dynamic changes in SOC stocks in bulk and labile soil fractions, carbon stability, and their driving factors in *L. leucocephala* plantations across different layers in the top 50 cm of soil in the dry-hot valley of the Jinsha River.

Results *L. leucocephala* plantations significantly increased the bulk SOC stocks and some labile fractions and significantly altered vertical patterns of SOC stocks. Stand age had a strong positive effect on SOC stocks, particularly in the surface soil layer (0–10 cm). SOC stocks and contribution from litter carbon inputs decreased significantly with soil depth. Moreover, the relative proportion of new C in bulk soil, readily oxidizable organic carbon (ROC), and dissolved organic carbon (DOC) stocks and their ratios to SOC stocks were significantly and positively correlated with SOC stocks. Carbon mineralization efficiency exhibited an initial increase followed by a decrease during the growth of *L. leucocephala* and was primarily regulated by soil C:N and the proportion of hot-water extractable organic carbon.

Conclusions *L. leucocephala* plantations increased SOC stocks by increasing labile carbon fractions, with no significant reduction in SOC stability as stand age increased. This study highlights the pivotal role and underlying mechanisms of nitrogen-fixing plantations in achieving and sustaining persistent SOC sequestration in dry-hot valley savannas.

Keywords Carbon stability, Carbon isotope, Labile carbon fraction, Nitrogen-fixing plantation, Vegetation restoration

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Introduction

Soil contains more than three times the amount of carbon (C) stored in the atmosphere (Lal 2004), and the sequestration and stability of soil organic carbon (SOC) is crucial for regulating atmospheric CO₂ levels (Zhang et al. 2015; Bond-Lamberty et al. 2018). Numerous studies have demonstrated that afforestation or reforestation is an effective natural climate solution for mitigating climate change (Nepal et al. 2019), primarily through enhancing SOC sequestration (Bossio et al. 2020). However, available research—both meta-analyses as well as individual survey studies suggests that the SOC sequestration potential of plantations varies considerably across ecosystems and with site characteristics. This variability is mediated by multiple factors, such as background soil C levels prior to land use change (Hong et al. 2020), tree species identity, and management practices (Li et al. 2012). More importantly, stabilizing the C stored in soils affects the retention time of SOC and thereby determines soil C persistence, which has a critical impact on the C sink and its resistance to climate change and anthropogenic disturbances in managed forests. Therefore, quantifying the size and stability of SOC stocks in the plantations is essential for predicting and evaluating the role of plantation forests in achieving C neutrality.

The soil C sequestration effects of plantations depend on tree species selection (Vesterdal et al. 2013; Zhu et al. 2023). As the most widely-employed species in vegetation restoration (Chaer et al. 2011; Zhao and Zhang 2012), nitrogen-fixing trees can increase soil C storage in degraded lands more than other tree species (Forrester et al. 2013; Xiang et al. 2017, 2021; Mayer et al. 2020; Koutika et al. 2021). The soil C sequestration capacity of nitrogen-fixing plantations is mainly influenced by stand age (Deng et al. 2017; Chai et al. 2019) and soil depth (Wiesmeier et al. 2012; Yang et al. 2018). Dynamic changes in SOC stocks are determined by the net balance between C inputs and losses (Schlesinger 1977; De Deyn et al. 2008). Thus, extensive evidence is available to quantify the contribution of C sources and inputs to SOC caused by tree age and soil depth. Alterations to the natural abundances of ¹³C in soils facilitate the exploration of relative change in new C formation and old C decomposition following planting (Deng et al. 2016; Jiang et al. 2019). For example, Deng et al. (2016) calculated the relative proportion of new C in bulk soil (f_{new}) using stable C isotopes to quantify the amount of C inputs from leaf litter to soil organic matter (SOM) during vegetation restoration. Moreover, microbial-driven decomposition of organic matter results in C outputs, and the intensity of this process is usually determined by the activity of extracellular enzymes related to C cycling (Sinsabaugh et al. 2008). However, the fate of C sequestered in soils

has received insufficient attention. Theoretically, the SOC pool consists of labile and recalcitrant C fractions (Cheng et al. 2007), which exhibit high and low decomposability, respectively. Notably, the labile C pool is more sensitive to environmental changes and relatively easy to measure. Thus, the precise amount of C stored in plantation soils that is allocated to labile C pools could potentially influence SOC turnover and stabilization. Previous studies have mostly focused on C stocks in bulk soil pools, leaving the dynamics of labile C pools poorly understood. Therefore, exploring the dynamics of different SOC component pools can reveal the pathways through which they exert their effects and contribute to a better understanding of the role of plantation forests in mitigating global climate change.

SOC stability, here defined as its resistance to decomposition (Stone and Plante 2015), can be characterized by several biological, chemical, and thermodynamic indicators (Hou et al. 2019). For instance, SOC stability has been widely assessed using measures of cumulative CO₂ respiration during soil incubations and the labile fraction of SOC (e.g., dissolved organic carbon or easily oxidizable carbon) (Hou et al. 2019). Additionally, soil C:N ratio serves as a reliable proxy for characterizing SOC stability, as it reflects the recalcitrance of organic matter to decomposition (Conen et al. 2008; Hou et al. 2019). The effects of plantation on SOC stability have attracted increasing attention in recent decades, but findings remain controversial largely due to methodological inconsistencies in quantifying soil C stability. For example, research conducted in a 40-year afforestation project reported lower relative SOC stability, attributed to a smaller proportion of stabilized C in the overall SOC pool (Li et al. 2023). In contrast, other studies have documented positive effects of plantation on SOC stability. Specifically, afforestation on the Loess Plateau significantly enhanced SOC stability, with the heavy fraction of SOC (stable C pool) accounting for a large proportion of sequestered C (Gao et al. 2018). Similarly, long-term afforestation (10–30 years) on the Loess Plateau contributed to SOC stabilization by reducing C mineralization rates (Rong et al. 2021). A previous study further demonstrated that nitrogen-fixing tree species (e.g., *Robinia pseudoacacia*) promoted higher chemical stability of SOC pools (Ye et al. 2022). Notably, a critical limitation of previous studies is the reliance on single-method assessments of SOC stability, which may fail to capture the multifaceted nature of C stabilization processes. Moreover, most studies have focused exclusively on surface soils, despite growing evidence that soil depth strongly influences SOC stability, with deeper soil layers often exhibiting higher C stability than surface soil layers (Ma et al. 2016; Soucémariadin et al. 2018). Therefore, further studies investigating the

impact of plantations on SOC stability across various soil depths are crucial for comprehensively understanding the efficacy of afforestation projects in terms of long-term C sequestration and climate change mitigation.

Savannas are important ecosystems in the tropical and subtropical zones of Africa, Australia, and Asia (Sankaran et al. 2005), supporting vast biodiversity and performing numerous ecological functions (Bastin et al. 2019; Hanan and Swemmer 2022). These savannas are frequently converted to plantations, primarily driven by economic benefit and the goal of enhancing C sequestration (Rüegg et al. 2019). Specifically, tree-planting strategies in these ecosystems have been proposed as a potential measure to increase C sequestration, which could contribute to global efforts to mitigate climate change (Hanan and Swemmer 2022). However, how this land-use conversion alters SOC stocks, stability, and the contribution of soil C sequestration to C neutrality in plantations remains poorly understood (Zhou et al. 2023). Savannas are represented by natural shrub–grass communities in the dry-hot valley of the Jinsha River, which play an irreplaceable role in maintaining the regional ecological security barrier in southwest China. Despite this, their ecosystem functions are inefficient and unstable, often remaining in a degraded state (Jin and Ou 2000; Peng et al. 2013). To address this issue, plantations of *Leucaena leucocephala* have been successfully established in the dry-hot valleys to prevent land degradation and soil erosion, while also improving local environmental conditions and enhancing overall ecological functioning (Gong et al. 2022). Previous studies on *L. leucocephala* plantations in this region have mainly focused on soil quality (Peng et al. 2013), soil nutrient availability (Lin et al. 2019), above- and belowground C sequestration (Gong et al. 2019), and soil nitrogen accumulation (Gong et al. 2022). However, information on how soil C dynamics and fate of sequestered C vary with *L. leucocephala* stand age and soil depth is scarce. In this study, we selected *L. leucocephala* plantations of different stand ages and adjacent natural shrub–grass plots in the dry-hot valley of the Jinsha River, and hypothesized that (1) stand age and soil depth would affect the dynamics of bulk SOC and labile SOC fractions and (2) an increase in labile SOC fractions would reduce overall SOC stability with the growth of *L. leucocephala* plantations.

Materials and methods

Site description and experimental design

This study was conducted in the dry-hot valley in Yuanmou County, Yunnan Province, China (101°36′–102°07′E, 25°31′–26°07′N), with all study plots located at the Yuanmou Desert Ecosystem Research Station. At the end of the twentieth century, study area was dominated

by farmlands and severely degraded lands, which resulted from intense grazing disturbance and was characterized by exposed soil surfaces and severe gully erosion. After human activities had been excluded, afforestation with *L. leucocephala* was implemented to promptly reverse land degradation trends and restore vegetation. Owing to the high seed production and long-distance dispersal capability of *L. leucocephala*, these trees could rapidly propagate and continuously spread into natural savanna communities, eventually leading to the establishment of a series of *L. leucocephala* plantations (Luo et al. 2022). Based on this vegetation restoration series, we selected three *L. leucocephala* stands (nitrogen-fixing plants and C3 plants) and adjacent savanna plots dominated by natural shrub–grass communities (C4 plants). Four replicate plots were established for each of the four developmental stages for investigation and soil sampling (Fig. S1), resulting in a total of 16 plots. Plot sizes were 20 m × 20 m for the young (SL, 5 years old), middle-aged (ML, 10 years old), and mature (LL, 25 years old) stand and 5 m × 5 m for the natural shrub–grass plots (CK). Additional details on climate, soil type, and dominant species at this site are available in our previously published papers (Luo et al. 2022; Jin et al. 2024).

Litter and soil sampling

Prior to soil sample collection, we measured tree height and diameter at breast height (DBH) of all *L. leucocephala* individuals in each plantation plot. Aboveground biomass (AGB) was then calculated using the species-specific allometric growth equation reported by Liu et al. (2018ab). Following leaf litter collection in each plot, four replicate samples were taken in an S-shape from each of four soil layers (0–10, 10–20, 20–30, and 30–50 cm) using a soil borehole sampler (5 cm inner diameter). In total, 64 soil composite samples (4 treatments × 4 soil layers × 4 replicates) and 16 leaf litter samples were obtained. After removing stones and fine roots, soil was divided into air-dried and fresh portions. The fresh portion was stored at 4 °C for determination of soil dissolved organic carbon (DOC), microbial biomass carbon (MBC), carbon mineralization efficiency (CME), and C cycle-related enzyme activity. The air-dried portion was used to determine soil properties, the content and $\delta^{13}\text{C}$ value of SOC, and several labile SOC fractions, including, readily oxidizable organic carbon (ROC), particulate organic carbon (POC), hot-water extractable organic carbon (HWEOC), and light fraction organic carbon (LFOC).

Soil properties, soil bulk, and labile C analysis

Soil pH was measured using a glass electrode meter (Sartorius PB-10; Sartorius, Shanghai, China) in a suspension of soil and water at a ratio of 1:2.5. Soil total nitrogen

(TN) and total phosphorus (TP) were determined using a fully automated interrupted chemical analyzer (CleverChem, Germany) after digestion with sulfuric acid and hydrogen peroxide. Soil available phosphorus (AP), nitrate nitrogen (NO_3^- -N), and ammonium nitrogen (NH_4^+ -N) were extracted using a fully automated interrupted chemical analyzer (CleverChem, Germany) after extraction with 0.5 mol/L NaHCO_3 and 1 mol/L KCl. Soil bulk density (BD) was calculated using the ring knife method. SOC content was determined using the external heating method with potassium dichromate. SOC and labile C stocks were quantified based on C content, bulk density, and thickness of the soil layer (Zhou et al. 2006). ROC, DOC, MBC, POC, HWEOC, and LFOC represent the active components of SOC in various aspects. ROC was determined using an ultraviolet–visible spectrophotometer (Blair et al. 1995). DOC and HWEOC were extracted using distilled water and determined using a TOC/TNb analyzer (Bongiorno et al. 2019). POC and LFOC levels were measured as previously described (Yang et al. 2009). Briefly, air-dried soil was mixed with deionized water, shaken, and passed through a 53 μm sieve to separate coarse organic particles, after which the filtrate was centrifuged and the pellet dried and retained to quantify POC fractions. LFOC was separated via density fractionation using a 1.6 g/cm³ sodium polytungstate. Soil MBC was determined using the chloroform fumigation extraction method (Vance et al. 1987). Soil and leaf litter $\delta^{13}\text{C}$ values were determined using an isotopic mass spectrometer, after which we calculated the fraction of new C (f_{new}) in three stand stages using the mass balance equation (Del Galdo et al. 2003): $f_{\text{new}} = (\delta_{\text{new}} - \delta_{\text{old}}) / (\delta_{\text{veg}} - \delta_{\text{old}})$, where δ_{new} and δ_{old} are the $\delta^{13}\text{C}$ value of soil samples from the *L. leucocephala* plantations and CK plots, respectively, and δ_{veg} is the $\delta^{13}\text{C}$ value of litter samples in the plantations. AGB and soils properties for the natural shrub–grass plots and the three stand ages are shown in Table 1.

C cycle-related enzyme activity and mineralization efficiency analysis

Four hydrolytic enzymes, α -glucosidase (AG), β -1,4-glucosidase (BG), cellobiohydrolase (CB), and β -1,4-xylosidase (XS), were measured using an automatic microplate reader at 365 nm excitation and 450 nm emission (DeForest 2009). The activities of two soil oxidases, soil polyphenol oxidase and catalase (POX and CAT), were measured using an automatic microplate reader at an absorbance of 460 nm (DeForest 2009). After correcting for negative controls and quenching, enzyme activities were expressed in units of $\text{nmol h}^{-1} \text{g}^{-1}$.

Briefly, 20 g of fresh soil was placed in a 250 mL culture bottle, and the soil moisture content was adjusted

to 60% of the field capacity. At the same time, empty culture bottles without soil samples were used as blank controls. Bottles were then placed in a biochemical incubator (Shanghai Yiheng Scientific Instruments Co., Ltd.) and cultured at 25 °C. Headspace CO_2 concentrations were measured after 1, 2, 4, 5, 7, 9, 13, 17, 21, 25, 29, and 39 days. Gas concentration was analyzed using gas chromatography (GC-2014, Shimadzu). CME was calculated as the cumulative CO_2 efflux divided by SOC content (Dong et al. 2022).

Statistical analysis

One-way analysis of variance (ANOVA) was used to examine the differences in SOC stocks (0–50 cm soil depth), labile C stocks, and the ratio of labile C fractions to SOC stocks in natural shrub–grass plots and the three stand ages of *L. leucocephala*. Two-way ANOVA was used to analyze the effects of stand age and soil depth on soil chemical characteristics, SOC stocks, labile C stocks, f_{new} , enzyme activities, and CME. Regression analysis was used to analyze the correlations among SOC stocks, labile C stocks, soil C:N, the ratio of labile C stocks to SOC stocks, CME, and f_{new} . ANOVA was performed using IBM SPSS Statistics 20 (IBM, Armonk, New York, USA), and regression analysis and figures were created using Origin 9.0. Structural equation modeling (SEM) was used to better understand the direct and indirect factors driving variation in SOC stock and CME using R software (version 4.0.3 with package *lavaan*).

Results

SOC stocks in bulk and labile fractions

SOC stocks in the top 50 cm of soil were 21.19%, 66.86%, and 94.14% higher in the SL, ML, and LL stages of *L. leucocephala* plantations, respectively, compared to CK (Fig. 1a). The SOC stocks in the bulk soil were significantly affected by stand age ($P < 0.05$), soil depth ($P < 0.05$), and their combined effects ($P < 0.05$, Fig. 1a). In CK plots, SOC stocks increased significantly with soil depth, whereas we found the opposite trend in the *L. leucocephala* plantation soil (Fig. 1a). SOC stocks in the 0–10 cm and ratio of this value to whole-profile stocks also increased significantly with stand age, whereas the percentage of SOC contained in the 30–50 cm soil layer decreased (Fig. 1b).

Labile C stocks in the top 50 cm were significantly affected by the stand stage of *L. leucocephala* plantations (Fig. 2). LFOC stocks initially decreased before increasing with advancing stand age (Fig. 2a). POC, ROC, and DOC stocks in the 0–50 cm layer increased significantly under artificial vegetation restoration (Fig. 2b, c and e). MBC and HWEOC stocks (0–50 cm) were highest in CK and lowest in the SL and ML stages (Fig. 2d and f). The

Table 1 AGB and soils properties of natural shrub–grass and different stand ages of *L. leucocephala* plantation (mean ± standard error; $n = 4$)

Age	Depth (cm)	AGB (g/m ²)	TP (g/kg)	TN (g/kg)	NH ₄ ⁺ -N (mg/kg)	NO ₃ ⁻ -N (mg/kg)	AP (mg/kg)	Bulk density (g/cm ³)	pH	Soil C:N
CK	0–10	328.93 C	0.42 ± 0.02 Aa	0.91 ± 0.12 Ba	1.65 ± 0.23 Ba	0.27 ± 0.09 Ca	2.96 ± 0.35 Aa	0.72 ± 0.00 Cd	8.14 ± 0.05 Ab	12.89 ± 3.71 Ba
	10–20		0.42 ± 0.02 Ca	0.72 ± 0.04 Aa	1.27 ± 0.21 Bab	0.55 ± 0.09 Aa	2.24 ± 0.25 Aab	1.73 ± 0.00 Aa	8.26 ± 0.11 Aab	7.78 ± 1.10 Aa
	20–30		0.32 ± 0.03 Ab	0.75 ± 0.06 Aa	1.05 ± 0.08 Cab	0.54 ± 0.09 ABa	1.82 ± 0.28 Ab	1.24 ± 0.00 Dc	8.34 ± 0.03 Aa	13.50 ± 3.29 a
	30–50		0.44 ± 0.03 Aa	0.78 ± 0.06 Aa	1.21 ± 0.06 ab	0.61 ± 0.17 ABa	1.60 ± 0.34 Ab	1.30 ± 0.00 Bb	8.41 ± 0.01 Aa	8.85 ± 2.00 Ba
SL	0–10	2158.83 BC	0.30 ± 0.03 Ba	0.65 ± 0.03 Ca	4.17 ± 1.20 Aa	3.33 ± 0.51 Aa	0.89 ± 0.12 Ba	1.36 ± 0.02 Ab	7.82 ± 0.28 Aa	23.24 ± 6.71 ABa
	10–20		0.14 ± 0.01 Cb	0.54 ± 0.05 Bb	2.25 ± 0.51 ABab	0.66 ± 0.10 Ab	0.94 ± 0.12 Ca	1.45 ± 0.02 Ba	7.65 ± 0.22 Ba	18.82 ± 9.70 Aa
	20–30		0.07 ± 0.01 Dc	0.47 ± 0.02 Bbc	1.74 ± 0.22 Bb	0.30 ± 0.06 Bb	1.01 ± 0.12 Ba	1.48 ± 0.02 Aa	7.71 ± 0.21 Ba	8.49 ± 2.18 Aa
	30–50		0.08 ± 0.01 Dc	0.43 ± 0.02 Bcc	1.94 ± 0.51 ABab	0.26 ± 0.05 Bb	1.09 ± 0.15 Aa	1.51 ± 0.03 Aa	7.81 ± 0.09 Ba	10.58 ± 2.42 Ba
ML	0–10	3291.35 B	0.35 ± 0.01 Ba	0.75 ± 0.05 BCa	5.05 ± 0.68 Aa	2.28 ± 0.68 ABa	2.67 ± 0.56 Aa	1.25 ± 0.00 Ba	8.15 ± 0.11 Ab	27.39 ± 1.95 Aa
	10–20		0.31 ± 0.01 Bb	0.73 ± 0.01 Aa	2.53 ± 0.27 Ab	0.20 ± 0.03 Bb	1.58 ± 0.19 Bb	1.19 ± 0.00 Da	8.38 ± 0.07 Aab	16.48 ± 1.78 Ab
	20–30		0.14 ± 0.01 Cc	0.55 ± 0.04 Bb	2.48 ± 0.10 Ab	0.24 ± 0.05 Bb	1.46 ± 0.18 ABb	1.33 ± 0.00 Ca	8.40 ± 0.10 Aab	16.00 ± 1.98 Ab
	30–50		0.17 ± 0.01 Cc	0.49 ± 0.03 Bb	2.41 ± 0.33 Ab	0.64 ± 0.32 ABb	1.11 ± 0.06 Ab	1.37 ± 0.00 Ba	8.52 ± 0.06 Aa	18.94 ± 3.98 ABb
LL	0–10	5882.11 A	0.44 ± 0.02 Aa	1.38 ± 0.07 Aa	4.03 ± 0.17 Aa	1.11 ± 0.37 BCa	3.06 ± 0.40 Aa	1.32 ± 0.03 Aab	8.02 ± 0.10 Aa	24.12 ± 3.26 ABa
	10–20		0.27 ± 0.04 Bb	0.61 ± 0.04 ABC	1.72 ± 0.08 ABb	0.20 ± 0.06 Bb	1.89 ± 0.14 ABb	1.31 ± 0.01 Cb	8.14 ± 0.27 ABa	18.67 ± 3.42 Aab
	20–30		0.22 ± 0.02 Bb	0.86 ± 0.06 Ab	1.35 ± 0.07 BCbc	0.78 ± 0.15 Aab	1.46 ± 0.23 ABb	1.40 ± 0.04 Ba	8.27 ± 0.26 Aa	11.07 ± 3.17 Ab
	30–50		0.29 ± 0.03 Bb	0.31 ± 0.08 Cd	1.01 ± 0.27 Bc	0.94 ± 0.13 Aa	1.41 ± 0.19 Ab	1.36 ± 0.03 Bab	8.29 ± 0.25 Aa	22.51 ± 4.33 Aab
Age	P	< 0.01	< 0.001	< 0.001	0.01	< 0.001	< 0.001	< 0.001	< 0.001	0.01
Depth	P	–	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.27	< 0.05
AgeDepth	P	–	< 0.001	0.15	< 0.001	< 0.001	0.034	< 0.001	0.98	0.40

Different uppercase letters indicate significant differences between the natural shrub–grass (CK) and different stand ages of *L. leucocephala* plantations ($P < 0.05$). Different lowercase letters indicate significant differences between soil depths for each treatment ($P < 0.05$). SL, ML and LL were the young, middle-aged and mature stands of *L. leucocephala*

AGB: aboveground biomass; TP: total phosphorus; TN: total nitrogen; AP: available phosphorus

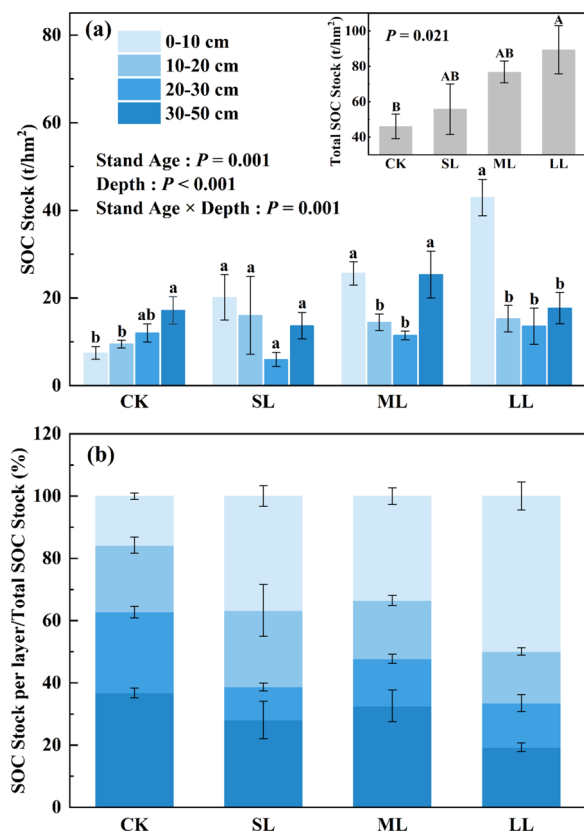


Fig. 1 SOC stock (a) and the proportion of SOC stock at different depths to total profile SOC stock (b) at natural shrub–grass and different stand ages of *L. leucocephala* plantations. Mean values are shown with standard error ($n = 4$). Different uppercase letters indicate significant differences between natural shrub–grass and different stand ages of *L. leucocephala* plantations ($P < 0.05$). Different lowercase letters indicate significant differences between different soil depths in each treatment ($P < 0.05$). CK: natural shrub–grass; SL, ML, and LL were the young, middle-aged and mature stands of *L. leucocephala*

sizes of most labile C pools were significantly affected by stand age, soil depth, and their combination (Fig. 2). The lowest labile C stock was measured in the 0–10 cm layer in CK, whereas the highest labile C stock was recorded in the 0–10 cm layer in the SL to LL stages (Fig. 2a–f). Ratios of soil labile C (POC, ROC, and DOC) to total SOC stocks were significantly higher in the SL, ML, and LL stages compared to CK (Fig. 3b, c and e). The ratio of LFOC to SOC stocks did not change (Fig. 3a), whereas the ratios of MBC and HWEOC to SOC stock decreased significantly following restoration of *L. leucocephala* plantations (Fig. 3d and f).

f_{new} and C cycle-related enzyme activity

Soil depth and stand age had a significant effect on the f_{new} value in the development of *L. leucocephala* plantations ($P < 0.001$; Fig. 4). Values of f_{new} were not

significantly different across stand ages in any soil depth other than the 20–30 cm layer. We measured significantly lower f_{new} with increasing soil depth, with the highest value occurring in the 0–10 cm layer (64.83%–76.88%) (Fig. 4). Both soil depth and stand age significantly affected BG and CB, and stand age significantly affected POX and CAT (Fig. S2). Soil depth had a significant effect on AG and XS (Fig. S2). AG, BG, CB, and XS activities at 0–10 cm layer were all significantly higher in the natural shrub–grass plots and across the three stand age categories (Fig. S2).

Influencing factors for SOC stock

LFOC, ROC, and DOC stocks were significantly and positively correlated with SOC stocks, whereas POC and MBC stocks were not across *L. leucocephala* plantations (Fig. 5a). HWEOC stocks were significantly and negatively correlated with SOC stocks (Fig. 5a), whereas f_{new} was significantly and positively correlated with SOC stocks (Fig. 5b). SEM analysis indicated that interactions between soil depth and *L. leucocephala* plantation explained 72% of the total variance in SOC stocks (Fig. 5c). Soil depth negatively affected SOC stocks and was indirectly affected by f_{new} , soil enzyme activities, soil properties, and labile C stocks (Fig. 5c). *L. leucocephala* plantations positively affected SOC stocks and were also indirectly affected by their effects on AGB, soil properties, f_{new} and labile C stocks (Fig. 5c). Labile C stocks and f_{new} directly and positively affected SOC stocks (Fig. 5c). Standardized total effects suggest that soil depth and ROC were the predominant factors influencing SOC stocks, negatively and positively, respectively (Fig. 5d).

SOC stability and its influencing factors

The CME varied significantly between the natural shrub–grass plots and the three stand ages (Fig. 6a). Compared to values in the natural shrub–grass plots, CME first increased in the SL stage before decreasing in the ML and LL stages (Fig. 6a). CME did not vary significantly across the three stand ages of *L. leucocephala* plantations (Fig. 6a). CME showed significant nonlinear changes in *L. leucocephala* plantations. When *L. leucocephala* plantations were newly introduced, CME exhibited an initial increase, but subsequently, the CME gradually decreased. We did not record a significant overall decrease in CME during the growth of *L. leucocephala* (Fig. 6a). Soil depth and its interactions with stand age did not have a significant influence on CME (Fig. 6c). CME in natural shrub–grass plots significantly decreased with soil depth, whereas it did not exhibit significant changes with soil depth in *L. leucocephala* plantations (Fig. 6d).

The CME was significantly and positively correlated with LFOC/SOC, POC/SOC, ROC/SOC, MBC/SOC,

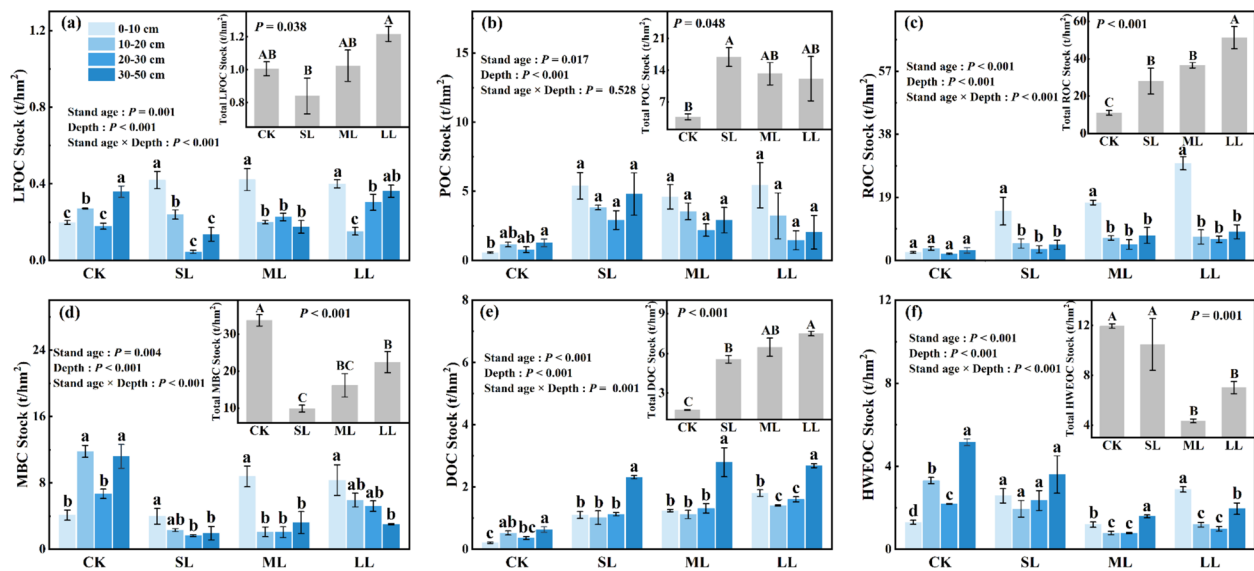


Fig. 2 Labile C stocks at natural shrub-grass and different stand ages of *L. leucocephala* plantation. Different uppercase letters indicate significant differences between CK and different stand ages of *L. leucocephala* plantations ($P < 0.05$)

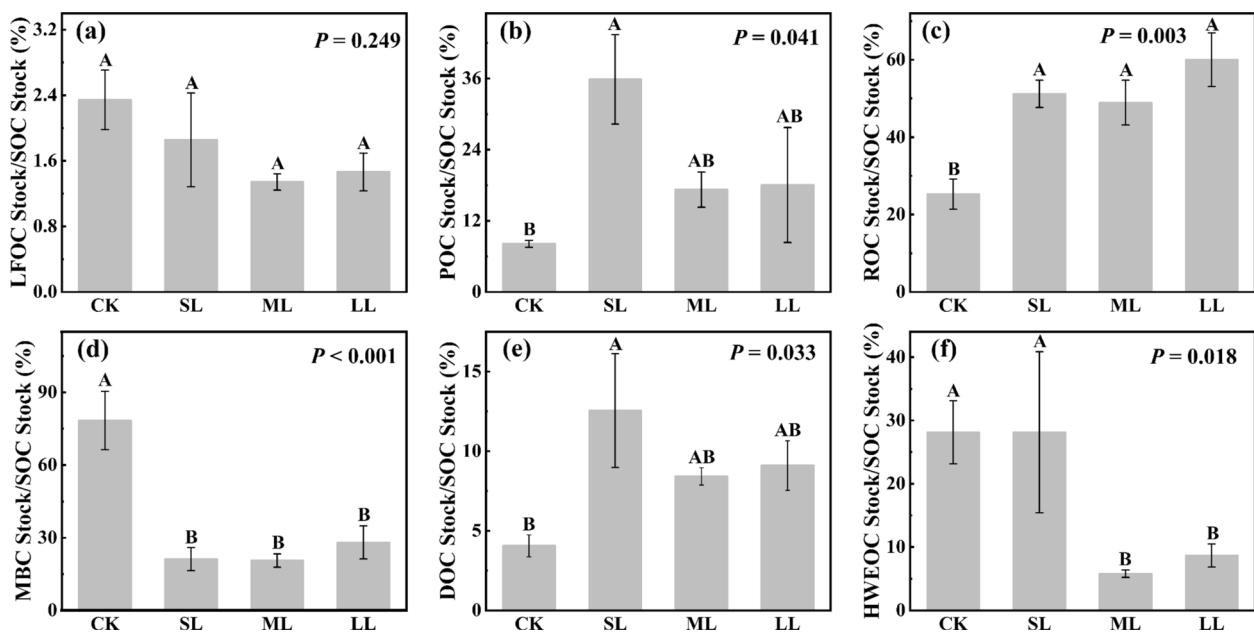


Fig. 3 Proportion of labile C stocks to total SOC stock at natural shrub-grass and different stand ages of *L. leucocephala* plantation. Different uppercase letters indicate significant differences between CK and different stand ages of *L. leucocephala* plantations ($P < 0.05$)

DOC/SOC, and HWEOC/SOC (Fig. 6c). CME was significantly and negatively correlated with soil C:N (Fig. 6d). Soil C:N was significantly and negatively correlated with LFOC/SOC, POC/SOC, MBC/SOC, DOC/SOC, and HWEOC/SOC but not with ROC/SOC (Fig. S3). SEM analysis indicated that interactions between soil depth and *L. leucocephala* plantation explained 89%

of total variance in CME. Soil depth negatively affected SOC stocks and was indirectly affected by labile C stocks and the ratio of labile C to SOC stocks (Fig. 6g). *L. leucocephala* plantations positively affected CME and were also indirectly affected by their influence on soil enzyme activities, soil properties, labile C stock, soil C:N, labile C stocks, and the ratio of labile C to SOC stocks. The ratio

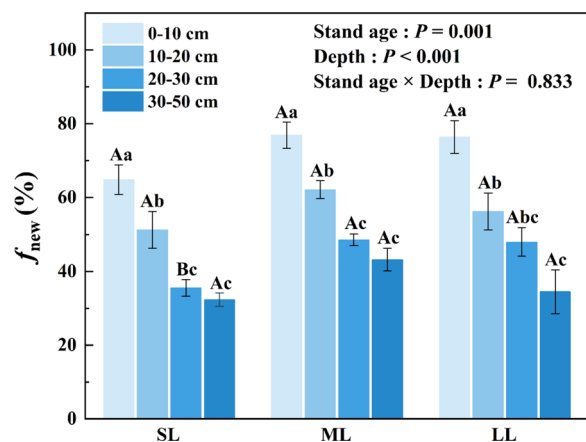


Fig. 4 f_{new} values at different stand ages of *L. leucocephala* plantation. Different uppercase letters indicate significant differences between natural shrub–grass and different stand ages of *L. leucocephala* plantations in each soil depth ($P < 0.05$). Different lowercase letters indicate significant differences between different soil depths in each stand stage ($P < 0.05$)

of labile C to SOC stocks positively and directly affected CME. Standardized total effects suggest that HWEOC/SOC, soil C:N, and pH were the predominant factors influencing CME, both positively and negatively (Fig. 6h).

Discussion

SOC stock dynamics and their influencing factors

Nitrogen-fixing tree plantations have been shown to significantly increase SOC stocks in various ecosystems (Xiang et al. 2017; Koutika et al. 2021). We identified larger SOC stock in the top 50 cm of soil in *L. leucocephala* plantations (Fig. 1a), consistent with our first hypothesis and aligned with previous findings in artificially restored nitrogen-fixing tree plantations. Specifically, similar increases in SOC stocks have been reported for *Robinia pseudoacacia* (Qiu et al. 2010; Lu et al. 2013; Hoogmoed et al. 2014; Xiang et al. 2021) and *Caragana microphylla* (Deng et al. 2017; Chai et al. 2019; Jia et al. 2022) plantations in the arid and semi-arid areas of northern China. These results suggest that plantations of nitrogen-fixing species can rapidly promote soil C sequestration in degraded ecosystems in the ecologically fragile semi-arid regions of southwest China. Moreover, SOC stocks usually increase with increasing stand age, but the rate of soil C sequestration probably decreases with forest maturity because of the gradual reduction in soil nitrogen availability (Hoogmoed et al. 2014). Our study indicates that *L. leucocephala*, with constant nitrogen fixation characteristics, can sustainably improve soil C sequestration in the dry-hot valleys of southwest China.

Consistent with our first hypothesis, soil depth also had a significant effect on SOC stocks across *L. leucocephala* stand ages (Fig. 1a). SOC stocks increased with soil depth, indicating that a larger proportion of C was stored in the subsoil at the natural shrub–grass stage. As stand growth progressed, the surface soil layer (especially 0–10 cm) accumulated relatively more C, which drove a significant negative association between SOC stocks and soil depth. Specifically, the upper 30 cm of soil stored more than half of the total C in the 0–50 cm profile in *L. leucocephala* plantations (Fig. 1b). This finding reveals that plantations had a stronger effect on SOC stocks in surface soils than in subsoils, which is consistent with previous reports (Jiang et al. 2019). Collectively, these results demonstrate that establishing nitrogen-fixing plantations profoundly alters the vertical patterns of SOC sequestration. This alteration is likely closely linked to the relatively higher root biomass characteristic of surface layers (Jobbagy and Jackson 2000) and increased C release from floor litter. These findings further suggest that the encroachment of *L. leucocephala* into typical savanna shrub-grassland communities may substantially reshape the SOC profile by affecting ecological processes in surface soil.

Fundamentally, the magnitude of SOC stocks is determined by the dynamic balance between C inputs and decomposition (Schlesinger 1977). Our SEM results revealed that SOC stocks were influenced not only by the depth-mediated positive effects of enzyme activities and f_{new} but also by the stand-mediated positive effects of AGB, soil properties, active C fractions, and f_{new} (Fig. 5). AGB is a potential source of C inputs to the soil, while f_{new} specifically quantifies the proportion of new C inputs to the soil from litter (Del Galdo et al. 2003). Activity of C cycle-related extracellular enzymes was positively correlated with the decomposition of SOC (Sinsabaugh et al. 2008). Together, these observations indicate that SOC dynamics of *L. leucocephala* plantations can be explained by the underlying mechanisms governing changes in both C input and output processes.

AGB significantly affects the soil C content (Huang and Spohn 2015; Wang et al. 2019). In our study, increases in AGB and f_{new} with stand age contributed to the gradual accumulation of SOC stocks in *L. leucocephala* plantations. This pattern is possibly driven by relatively higher C inputs from higher root biomass and floor litter with tree growth (Wang et al. 2019). Indeed, our SEM results further confirmed that f_{new} exerted a significant direct positive effect on SOC stock (Fig. 5). This finding underscores the key role of leaf litter in SOC accumulation in *L. leucocephala* plantations. Notably, our study also revealed a clear decline in f_{new} values with increasing soil depth (Fig. 4). Across all three *L. leucocephala* stand

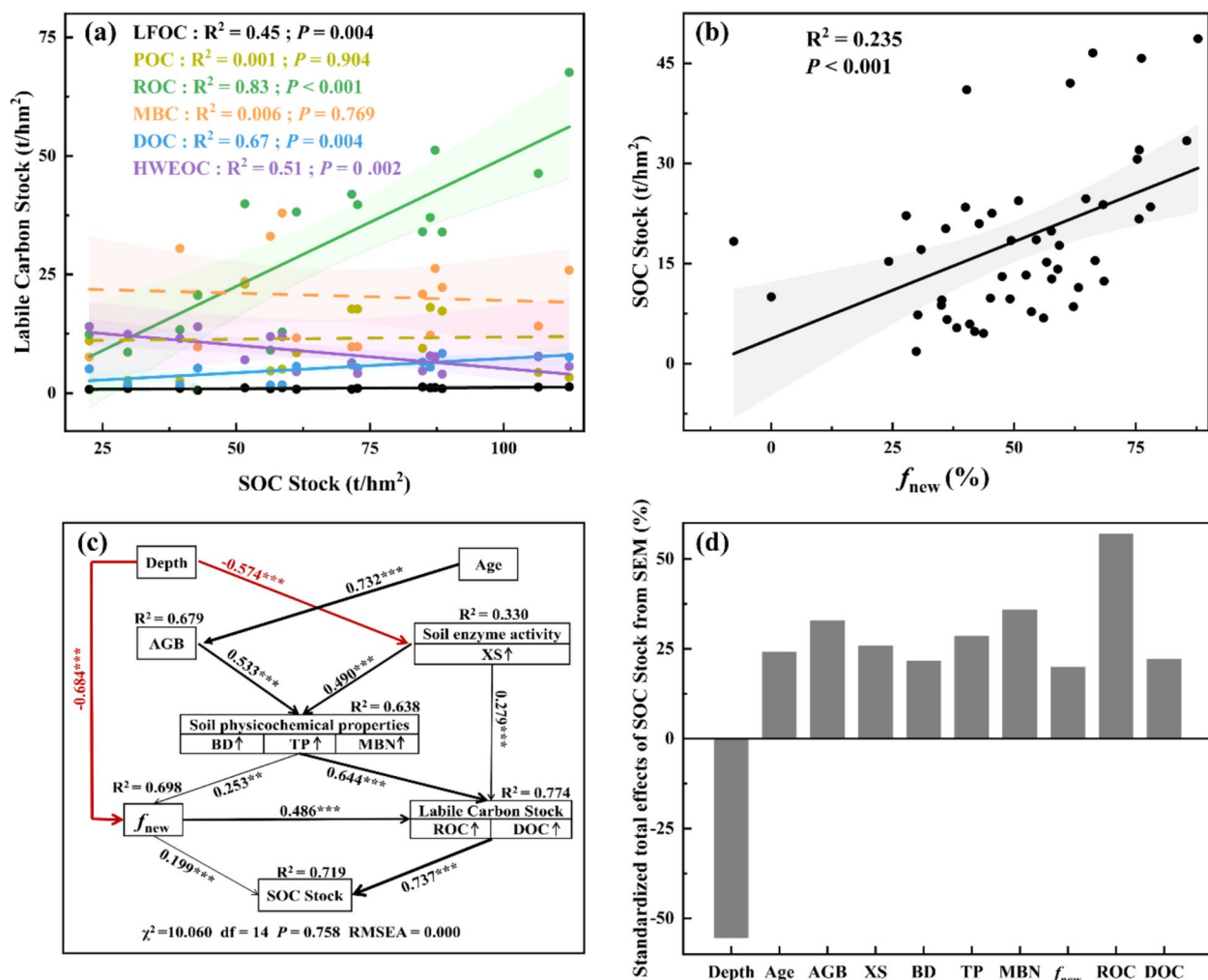


Fig. 5 Regression analysis of labile C stocks and f_{new} with SOC stocks (a, b), and structural equation modelling (SEM) for SOC stocks (c). Black and red arrows represent positive and negative pathways respectively. The widths of the arrows are proportional to the strength of the relationship, with the numbers near the arrows indicating the standard path coefficients. Asterisks (*) indicate significant effects (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The goodness-of-fit statistics for the model are shown below. The standardized total effects were derived from the SEM (d)

ages, the highest f_{new} values were consistently observed in the 0–10 cm soil layer (64.83–76.88%), while the lowest f_{new} values occurred in the 30–50 cm layer (24.25–34.48%). This implies a gradual decrease in new C inputs with increasing soil depth. Interestingly, the activity of C cycle-related extracellular enzymes exhibited a similar depth-dependent decline (Fig. S2), which resulted in a comparable vertical distribution of C decomposition potential between natural shrub-grasslands and *L. leucocephala* plantations. Consequently, the observed shift in the vertical pattern of SOC—from an increasing trend in the natural shrub-grassland to a decreasing trend across stand developmental stages—is likely attributable to differences in aboveground C inputs. Additionally, variation in soil properties (BD, TP, and MBN) with stand age have

also been identified as factors impact dynamic changes in SOC stocks (Deng et al. 2016).

As a more active and sensitive fractions of SOC, labile C stocks were significantly influenced by both soil depth and stand age (Fig. 2). For example, DOC and ROC exhibited a pattern similar to that of bulk SOC with increasing stand age, whereas HWEOC and POC showed more complex trends (Fig. 2). The observed increase in labile C stocks with stand age may be attributed to the accumulation of greater litter with a lower C:N (Manzoni et al. 2010; Chen et al. 2016; Guo et al. 2017), which decomposes easily and can form activated C reservoirs. Strikingly, we did not find consistent associations between the six measured labile C pool metrics and SOC stocks (Fig. 5a). Specifically, SOC stocks were positively

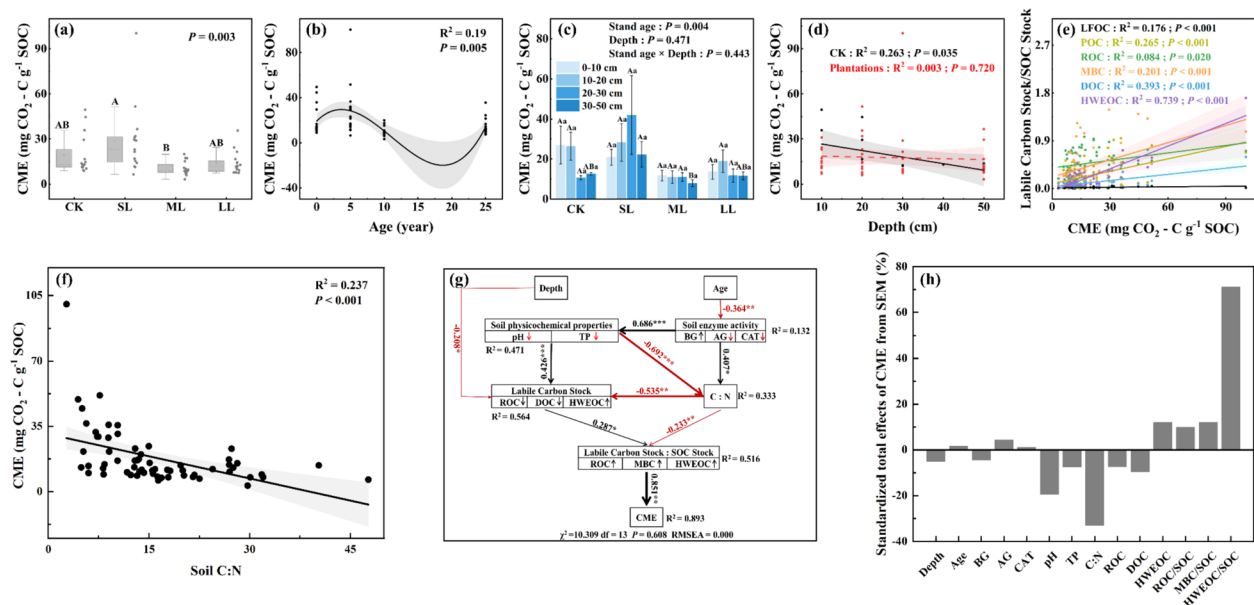


Fig. 6 C mineralization efficiency (CME) at natural shrub–grass and different stand ages of *L. leucocephala* plantation (a, c). Different uppercase letters indicate significant differences between natural shrub–grass and different stand ages of *L. leucocephala* plantations ($P < 0.05$). Different lowercase letters indicate significant differences between different soil depths in each treatment ($P < 0.05$). Regression analysis of stand ages (b), soil depth (d), proportions of labile C stocks to SOC stocks (e) and soil C:N (f) with CME, and structural equation modeling (SEM) for CME (g). Black and red arrows represent positive and negative pathways respectively. The widths of the arrows are proportional to the strength of the relationship, with the numbers near the arrows indicating the standard path coefficients. Asterisks (*) indicate significant effects (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The goodness-of-fit statistics for the model are shown below. The standardized total effects were derived from the SEM (h)

correlated with LFOC, ROC, and DOC, but showed no significant correlations with POC or MBC stocks (Fig. 5a). This finding implies that LFOC, ROC, and DOC are reliable indicators for assessing SOC changes under vegetation restoration in semi-arid dry-hot valleys. These results provide new evidence that not all labile C pools can be used to infer how SOC stocks respond to environmental changes and that comprehensive consideration is needed in future studies. Furthermore, SEM analysis explicitly revealed that increases in ROC and DOC were strongly associated with promoted SOC stocks during the development of *L. leucocephala* plantation (Fig. 5c). This suggests that soil C sequestration can be enhanced by targeting the accumulation of these active C components (DOC and ROC), which represents a potential approach to C sequestration enhancement in *L. leucocephala* plantations.

SOC stability and its driving factor

Compared to SOC storage, SOC stability is of greater importance in the context of vegetation restoration because it is closely related to nutrient mineralization and the persistence of sequestered C stocks. In other words, it is crucial for predicting the sustainability of C sequestration in artificial forests, which is important for understanding feedbacks between terrestrial ecosystems

and the atmosphere (Yang et al. 2020). SOC stability can be measured in several ways (Hou et al. 2019). For example, the relative proportion of labile versus recalcitrant C fractions characterizes the chemical stability of SOC. Soils with a higher ratio of labile C to total SOC (labile C/SOC) are more susceptible to microbial decomposition and mineralization (Cheng et al. 2007), thereby indicating lower SOC stability (Dong et al. 2022). Alternatively, the soil C:N ratio, which reflects the quality of soil substrate, is often tightly associated with the degree of SOC decomposition (Conen et al. 2008; Hou et al. 2019). Given that different stability indicators target unique properties of SOC fractions, clarifying the relationship between these metrics is essential for a comprehensive assessment of SOC stability. As expected, our analysis revealed a significant negative association between CME and soil C:N ratio (Fig. 6f). This finding confirms that high-quality SOM (lower C:N ratio) facilitates microbial decomposition, thereby reducing overall SOC stability. Additionally, we identified a positive correlation between CME and labile C fractions. The higher R^2 value of HWEOC/SOC reflects the relatively greater explanatory power of CME compared to other labile C fractions (Fig. 6e).

Consequently, our study demonstrates that CME and HWEOC/SOC are the most robust predictors of variability in SOC stability across *L. leucocephala* plantations in the dry-hot valley.

There was a significant nonlinear relationship between CME and plantation age (Fig. 6b). Specifically, the CME increased significantly at the early stages of development of *L. leucocephala* plantations relative to the shrub–grasslands, indicating a decline in SOC stability. This early-stage reduction in stability may be attributed to the soil priming effect, which is likely triggered by higher aboveground C inputs from nitrogen-fixing trees (Liu et al. 2020; Fu et al. 2025). Several studies have reported that nitrogen-fixing plantations would decrease SOC stability (Tang and Li 2013; Tang et al. 2013; Liu et al. 2018a, b). In contrast to our second hypothesis, CME tended to decrease slightly during the late growth stage of *L. leucocephala* plantations (Fig. 6a), suggesting a potential recovery in SOC stability. Variation in HWEOC/SOC was almost identical to that of CME across developmental stages of the *L. leucocephala* plantations, decreasing in the ML and LL stages relative to the natural shrub–grass plots (Fig. 3f). These findings suggest that SOC stability did not decline markedly in the late stages of growth and development of *L. leucocephala* plantations.

In addition to stand age, soil depth also had a significant impact on CME across vegetation types (Fig. 6d). In particular, CME decreased significantly with increasing soil depth in natural shrub–grass plots, consistent with previous reports (Rumpel and Koegel-Knabner 2011). This suggests that deeper soils under natural vegetation dominated by shrub and grass in the dry-hot valley not only store more SOC, but also harbor more stable SOC. Together, these findings reveal the critical role of deep soils in long-term C sequestration in savanna communities. Nevertheless, CME did not vary significantly with soil depth in the *L. leucocephala* plantations (Fig. 6d). This finding indicates that nitrogen-fixing plantations altered the vertical pattern of SOC stability by lowering it in the deep soil layers.

SEM results further demonstrate that the non-significant changes in SOC stability across soil profiles in *L. leucocephala* plantations were mainly due to changes in labile C fractions, soil C:N ratio, and soil properties (Fig. 6g and h). First, both labile C fractions and soil C:N ratio are strongly related to the decomposition potential of SOM (Marschner and Kalbitz 2003) and the degree of microbial accessibility (Conen et al. 2008; Hou et al. 2019). The accumulation rate of SOC pool far exceeded that of the soil N pool during the growth of *L. leucocephala* plantations. This imbalance led to a significant increase in soil C:N ratio with stand age (Table 1). The C:N ratio exerted a significant negative effect on CME

(Fig. 6h), indicating that an increasing soil C:N ratio probably enhanced SOC stability. This positive regulatory role of soil C:N primarily revealed that SOC stability during the development of nitrogen-fixing plantations was predominantly regulated by substrate degradability. As expected, these variables were assumed to be the most important factors explaining variations in SOC stability. This finding further highlights the potentially synergistic variation between the biological/chemical structure of SOC and substrate quality. Second, soil pH also has an important and negative impact on SOC stability, which may be due to the fact that lower soil pH limits SOC decomposition (Dong et al. 2022).

Conclusions

L. leucocephala plantations significantly increased bulk soil C stocks and active C stocks in the 0–50 cm layer compared to the natural shrub–grass plots. The *L. leucocephala* plantations had a stronger effect on soil C stocks, especially in the surface soil layer (0–10 cm). SOC stocks and contributions from litter C inputs (f_{new}) decreased significantly with soil depth. Furthermore, SOC stock dynamics were regulated by f_{new} , labile C fractions, and C-related cycling enzymes. CME and HWEOC were robust predictors of SOC stability. SOC stability did not decrease significantly in the late stages of development in *L. leucocephala* plantations. Our study shows that nitrogen-fixing plantations in a dry-hot valley can promote the accumulation of soil C but that it does not significantly lower SOC stability with increasing stand age. This study highlights the importance of nitrogen-fixing plantations to C sequestration and sink enhancement in dry-hot valleys. Therefore, suitable management measures should be implemented in the future for nitrogen-fixing forests in semi-arid regions to promote stand development, thereby enhancing C sink sustainability to fully exploit the potential of C neutrality.

Abbreviations

SOC	Soil organic carbon
ROC	Readily oxidizable organic carbon
DOC	Dissolved organic carbon
f_{new}	Relative proportion of new C in bulk soil
CK	Natural shrub–grass plot
SL	Young <i>L. leucocephala</i> stand
ML	Middle-aged <i>L. leucocephala</i> stand
LL	Mature <i>L. leucocephala</i> stand
DBH	Diameter at breast height
AGB	Aboveground biomass
POC	Particulate organic carbon
MCB	Microbial biomass carbon
HWEOC	Hot-water extractable organic carbon
LFOC	Light fraction organic carbon
$\delta_{\text{new}}^{13}\text{C}$	$\delta^{13}\text{C}$ value of soil samples in the plant
$\delta_{\text{old}}^{13}\text{C}$	$\delta^{13}\text{C}$ value of soil samples in the CK plot
$\delta_{\text{veg}}^{13}\text{C}$	$\delta^{13}\text{C}$ value of litter samples
AG	α -glucosidase
BG	β -1,4-glucosidase

CB	Cellobiohydrolase
XS	β -1,4-Xylosidase
POX	Polyphenol oxidase
CAT	Catalase
BD	Bulk density
TP	Total phosphorus
AP	Available phosphorus
TN	Total nitrogen
CME	Carbon mineralization efficiency

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-025-00656-3>.

Supplementary Material 1: Fig. S1 Map of study site and sampling plots in the Yuanmou ecological station. Fig. S2 Soil C cycling-related enzyme activity at natural shrub grass and different stand ages of *L. leucocephala* plantation. Different uppercase letters indicate significant differences between natural shrub grass and different stand ages of *L. leucocephala* plantations ($P < 0.05$). Different lowercase letters indicate significant differences between different soil depths in each treatment ($P < 0.05$). Fig. S3 Regression analysis of the proportion of labile C stocks to total SOC stocks with soil C:N.

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Author contributions

Defeng Feng, Wei Li, Yongyu Sun, Chenggang Liu and Yanqiang Jin conceived and designed the study; Jun Jin, Mingmo Luo and Jiajia Zhang collected the data; Mingmo Luo, Jun Jin and Jiajia Zhang contributed field sampling; Wei Li, Jun Jin, Mingmo Luo performed the analysis; Erxiong Zhu put forward construction suggestions for the revision of the paper; Defeng Feng, Wei Li, Jiajia Zhang and Jun Jin wrote the paper.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors approved the manuscript for publication in *Ecological Processes*.

Competing of interests

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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