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ORIGINAL ARTICLE

Soil organic carbon sequestration following a secondary succession of agricultural abandonment in the karst region of southwest China

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Abstract
Soil organic carbon (SOC) sequestration is closely linked to global climate change and soil quality. Secondary succession of agricultural abandonment under the Grain for Green Project (GGP) program generally promotes SOC sequestration in the karst region of southwestern China. This study investigated the controlling mechanism of enhancing SOC sequestration during secondary succession of agricultural abandonment, based on soil aggregation, soil erosion, and soil Ca dynamic. In the study area, croplands, shrub-grass lands, and secondary forest lands were regarded as the three stages during the secondary succession of cropland abandonment by the space-for-time substitution method. The proportions of water-stable and different-sized aggregates, SOC contents associated with aggregates, soil Ca contents and Ca/Al ratios, and soil erodibility *K* factors were analyzed in the soils at the 0–10, 10–20, and 20–30 cm depths. The proportions of macro-aggregates at the 0–10 cm depth in the croplands (mean 61.3%) were significantly lower than those in the shrub-grass lands (mean 78.5%) and secondary forest lands (mean 81.6%). The SOC contents associated with macro-aggregates at the 0–20 cm depth in the croplands (mean 30.5 g kg^{-1}) were significantly lower than those in the secondary forest lands (mean 52.2 g kg^{-1}) but were slightly (not significantly) lower than those under the shrub-grass lands (mean 38.6 g kg^{-1}). Soil Ca/Al ratios at the 0–20 cm depth in the croplands (mean 0.087) and shrub-grass lands (mean 0.105) were significantly lower than those under the secondary forest lands (mean 0.63). The proportions of water-stable aggregates increased and the *K* factor decreased after cropland abandonment. These results indicated that under the experiment conditions, soil aggregation increased, soil erosion reduced, and soil Ca accumulated during the secondary succession of agricultural abandonment. A conceptual model for enhancing SOC sequestration during the secondary succession of agricultural abandonment was proposed. This conceptual model suggests that the GGP program has a positive effect on SOC sequestration and soil quality in the karst region.

Keywords Soil organic carbon sequestration · Agricultural abandonment · Secondary succession · Calcareous soils · Karst region

Introduction

Soil stores 1300–2000 Gt C (1 Gt = 10^{15} g), which is the largest C pool in terrestrial ecosystems, larger than the plant C pool (500–600 Gt) and atmospheric C pool (750 Gt) (Lal 2004). The soil C pool consists of the soil organic carbon (SOC) pool and soil inorganic carbon (SIC) pool, in which the SOC pool is relatively active with an uncertain turnover time ranging from several weeks to several hundred years (Schmidt et al. 2011). Even a slight change in the huge SOC pool likely affects the atmospheric CO_2 concentration; thus, SOC dynamics have important implications for global climate change and the human living environment (Yang et al. 2016; Xu et al. 2018). The secondary succession of agricultural abandonment is one of the land-use change types (Clark and Johnson 2011; Bell et al. 2020; Djuma et al. 2020), which has been widely reported as an important factor affecting the SOC dynamic (Kalinina et al. 2019; Bell et al. 2021). Poeplau et al. (2011) reported that SOC storage gradually reduced during several decades after transforming forest and grasslands into croplands but it increased following the secondary succession on the abandoned croplands.

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In previous studies, the enhanced SOC storage during secondary succession of agricultural abandonment was mainly attributed to the elevated organic matter input derived from litterfall and roots due to the increased plant biomass (Ghafoor et al. 2017). However, besides organic matter input, organic matter decomposition is another important factor affecting SOC storage (Jobbagy and Jackson 2000; Xia et al. 2020). In addition to increasing recalcitrant SOC accumulation, enhancing labile SOC stabilization in the soil environment can also slow down the decomposition rate of SOC or turnover rate of the total SOC pool (Juhos et al. 2021). Generally, the unprotected labile SOC has a relatively short residence time in soil ranging from several days to several months, which is not considered to affect global climate change (Wynn et al. 2006). However, with the alteration of soil environment under land-use change, the labile SOC can be stored on a larger time scale, which is also meaningful for global climate change. Chemical protection by association with multivalent cations, clay particles and physical protection by soil aggregates play important roles in enhancing SOC stabilization (Sollins et al. 1996; Wright and Hons 2005; Kleber and Johnson 2010; Schmidt et al. 2011; Lehmann and Kleber 2015; Munoz et al. 2016; Chen et al. 2020; Scott et al. 2021). It is necessary to determine the primary mechanism of SOC stabilization following a secondary succession of agricultural abandonment to understand the SOC sequestration potential during land-use change (Li et al. 2012; Fan et al. 2020; Lan et al. 2020).

In the karst region of southwestern China, long-term and unsustainable agricultural activities have led to severe soil degradation, which is characteristic of soil erosion and nutrient loss (Wang et al. 2019; Zhang et al. 2021; Han et al. 2021; Liu et al. 2022). To restore the karst ecological environment, many sloping croplands with a low crop yield had been abandoned under the Grain for Green Project (GGP) program since the beginning of the twenty-first century (Wang et al. 2017). The changes in SOC contents or storage during secondary succession of agricultural abandonment have been studied in the karst region (Xiao et al. 2018; Han et al. 2020; Lan 2021). Liu et al. (2020) reported that soil macro-aggregates (250–2000 μm) significantly affected SOC sequestration and Li et al. (2017) found that the replenishment of soil Ca was the most important factor enhancing SOC storage. Soil exchangeable Ca^{2+} is the most important cation affecting SOC storage in the calcareous soils, which can combine soil organic matter (SOM) and clay minerals to enhance SOC stabilization (Lützow et al. 2006). Moreover, fine-sized OM–Ca^{2+}–mineral complexes can bind together to form larger-sized soil aggregates, which further enhances the protection for SOC (Six et al. 2000). However, soil erosion can cause a decrease in SOC storage through the loss of dissolved organic carbon (DOC) and particulate organic carbon (POC) (Haring et al. 2013). Furthermore, soil erosion can indirectly affect SOC stabilization by destroying aggregate structure (Liu and Han 2020) and soil Ca^{2+} leaching loss (Li et al. 2017). In the karst region, enhanced SOC sequestration following a secondary succession of agricultural abandonment has been widely studied (Lan et al. 2020; Lan 2021); however, understanding of the mechanism is lacking. The study objectives were to: (1) analyze the effects of soil aggregation, soil erosion, and soil Ca dynamic on SOC content and stabilization and (2) establish a conceptual model for increasing SOC sequestration during secondary succession of agricultural abandonment in the karst region. This research has implications for evaluating the influences of the GGP program on karst ecological restoration and global climate change.

Materials and methods

Study area

The study area is located in a small karst catchment with an area of 1.54 km^2 (Chenqi catchment, 26°15′47–26°16′43″N, 105°46′3–105°46′0.50″E), Puding county, Guizhou province of southwest China. This catchment has a typical karst landform, in which a valley is surrounded by three hills and a seasonal river flows from east to west (Liu et al. 2020). The altitudes of these hills reach up to 1524 m (above sea level) at maximum, while only 1310 m at the valley (Yue et al. 2020). The karst region has a subtropical monsoonal climate, most of the rainfalls (> 80%) occur in the rainy season from May to October, with mean annual precipitation (MAP) of 1315 mm. Season evapotranspiration (mean: 260 mm in spring, 330 mm in summer, 185 mm in autumn, and 115 mm in winter) is much lower than seasonal precipitation (Gao et al. 2016). The lowest and highest air temperatures generally occur in January (3–6 °C) and July (22–25 °C), respectively, with a mean annual temperature (MAT) of 15.1 °C (Zhao et al. 2010). The soil on the hilltops and hillslopes is calcareous, mainly developed from the limestones of the upper and middle part of the Guanling Formation of the middle Triassic (Zhao et al. 2010), and classified as calcic Inceptisols in the soil taxonomy of the USDA (Soil Survey Staff 2014). The soil on the valley floor is a Quaternary deposit, which is mainly materials deposited from surrounding hillslopes by soil erosion (Green et al. 2019). Soil thickness ranges from 0.3 to 0.5 m on the hilltops, 0.5–1 m on the hillslopes, and over 1 m on the valley floor. On the hilltops and hillslopes, the soil surface to 30 cm depth is a humic horizon (O), and the layer below 30 cm to bedrock includes an eluvial horizon (A), illuvial horizon (B), and parent material horizon (C). For the croplands on the valley floor, the soil surface to 30 cm depth is the cultivated horizon. In the catchment, soil pH values range from 6.9 to 7.5

with minor spatial variation (Liu et al. 2019). Soil inorganic carbon (SIC) contents range from 0.83 to 42.03 g kg^{-1}, and the soils close to bedrock generally have a high SIC content (Liu et al. 2020).

In addition to the ecological and environmental fragility of the Guizhou karst landform itself, long-term and unsustainable agricultural management had further exacerbated soil degradation (Wang et al. 2019; Liu et al. 2020; Zeng and Han 2020). To alleviate and remediate the ecological problem of soil degradation, the GGP program has been carried out in the karst region (Wang et al. 2017). In the study area, the secondary forest lands on the hillsides were converted from terraced croplands 50 years ago, the shrub-grass lands at the foot of the hills have been transformed from terraced croplands for 3–8 years, and only the croplands on the valley floor remain in conventional cultivation (Liu et al. 2020). Thus, the zone of croplands, shrub-grass lands, and secondary forest lands show a vertical distribution in the catchment. In the croplands, the main crops of maize (*Zea mays*), oilseed rape (*Brassica napus*), potato (*Solanum tuberosum*), and peanut (*Arachis hypogaea*) are planted in rotation from spring to autumn, while the fields lie fallow in winter. N–P–K fertilizer and urea provide about 300 kg ha^{-1} yr^{-1} N, 85 kg ha^{-1} yr^{-1} P, and 6 kg ha^{-1} yr^{-1} K for crop production, and farm manures are applied irregularly and non-quantitatively (Li et al. 2018). In the shrub-grass lands, the main plant species are herbaceous plants including *Imperata cylindrical*, *Setaria viridis*, and *Miscanthus sinensis*, and low shrubs or trees including *Berchemia sinica*, *Ilex macrocarpa*, and *Pyracantha fortuneana*. In the secondary forest lands, the main plant species are tall evergreen trees including *Litsea pungens*, *Padus racemosa*, *Pinus tabuliformis*, *Cinnamomum camphora*, *Camellia japonica*, and *Cyclocarya paliurus*. In this study, the shrub-grass lands and secondary forest lands are regarded as the different stages following the secondary succession of abandoned croplands by the space-for-time substitution method (Blois et al. 2013). The photographs of the three stages were shown by Liu et al. (2020).

Soil sampling

Soil sampling was carried out in the Chenqi catchment in June 2016. At present, the proportional area of croplands, shrub-grass lands, and secondary forest lands within the Chenqi catchment is approximate 50, 20, and 30%, respectively. In total, 18 sampling sites from different land-use types were randomly selected relative to the proportional area of within the catchment: 8 sites were in the croplands, 5 sites were in the shrub-grass lands, and 5 sites were in the secondary forest lands, as shown by Liu et al. (2020). Distance between any two different sites under the same land-use type was 50–100 m. A soil pit (0.5 × 0.5 × 0.5 m) was dug at each site, and three duplicate soil samples were chosen from the three sides of the pit. Soil samples were collected from the top to the bottom at the 0–10, 10–20, and 20–30 cm depth. In total, 162 soil samples were collected. The duplicate samples in each pit at the same depth were mixed as one composite sample.

Soil analysis

Soil samples were air-dried (25 °C) after removing obvious gravel and fresh coarse roots. A part of the samples was crushed by hand to make all particles pass through a 10 mesh-steel sifter, which was stored as the sample of bulk soil (< 2 mm). The remaining soil samples were not crushed and were used for soil aggregate separation by the improved wet sieving method (Six et al. 1998). In detail, the dried soil samples were slowly wetted by capillary water absorption, then naturally disintegrated into a series of small-sized fractions. These different-sized fractions were passed sequentially through the 2000, 250, and 53 μm sifters in pure water. The aggregates over 2000 μm in diameter were crushed by a tweezer until all aggregates passed through the 2000 μm sifter. Macro-aggregates (250–2000 μm) and micro-aggregates (53–250 μm) were collected after passing through 250 and 53 μm sifters, respectively. The silt + clay sized fractions (< 53 μm) were extracted from the residual mixed liquid by centrifugation. The moist aggregate samples were dried in an oven at 55 °C until constant weight and then weighed to calculate their mass percent. The aggregates separated by the wet sieving method are water-stable aggregates (Emadi et al. 2009); thus, the proportion of water-stable aggregates is the summation of macro-aggregate and micro-aggregate proportions (Liu and Han 2020).

The samples of bulk soils and different-sized aggregates or fractions were ground in an agate mortar until all fine particles pass through a 200 mesh-nylon sifter. The powder samples (< 75 μm) were soaked in 0.5 mol L^{-1} diluted hydrochloric acid for 24 h to remove carbonates (Midwood and Boutton 1998). The acid-treated samples were washed repeatedly with pure water until neutral liquid, and then dried (65 °C) and ground into powder (Liu et al. 2021c). The SOC contents of bulk soil, different-sized aggregates, or fractions were measured by a total organic carbon analyzer (Vario TOC cube, Elementar, Germany) in the Surficial Environment and Hydrological Geochemistry Laboratory, China University of Geosciences (Beijing). Standard soil substances (OAS B2152) were repeatedly measured to monitor reproducibility. The relative standard deviations were less than 3%. Actual SOC content should be calibrated because of mass loss during removing carbonates, i.e., the measured SOC content is multiplied by the ratio of the sample mass after and before treatment (Liu et al. 2021b).

To analyze Al and Ca contents of bulk soil, 50 mg powder sample was digested with a mixing solution including 3 mL pure nitric acid, 3 mL pure hydrofluoric acid, and 1 mL pure perchloric acid in a Teflon crucible (heat to 140 °C) for 3 days (Liang et al. 2021). The digested solution was diluted to 25 mL in a glass volumetric flask with 2% nitric acid, used for the analyses of Al and Ca concentrations by an inductively coupled plasma-optical emission spectrometry (ICP-OES, Optima 5300DV, Perkin Elmer, USA) in the Center Laboratory for Physical and Chemical Analysis, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences. Blank samples and standard substance (GBW07404) of limestone soil were digested and measured similarly to the normal sample to monitor the recovery rate (over 97%) during the digestion procedure and the precision (±0.1%) and accuracy during the analysis test procedure. The Al and Ca concentrations in the liquid used for analysis should be transformed into the contents in bulk soil (Liu et al. 2021a).

The soils in the study area are developed from weathering of limestone (mainly calcites and a few impurities). The chemical reaction ($CaCO_3 + CO_2 + H_2O = Ca^{2+} + 2HCO_3^-$) determines the decrease in weathered rock (or soil parent material) mass during weathering. Thus, the contents of all elements in soils are variable during the rock weathering and soil formation processes. In geochemistry, the change in absolute content of one element does not confirm whether the accumulation or depletion of the element occurs during rock weathering and soil formation processes. However, the ratio of the element content relative to another nonmigratory element can eliminate the effects of rock weathering and soil formation processes on the element's dynamic (Balls et al. 1997). Generally, Ca is an easily migratory element in soils and other environments (Gao et al. 2021; Wang et al. 2021). In the study area, besides the effects of land-use change on soil Ca depletion or enrichment, soil Ca content is also affected by the limestone weathering and soil formation processes (Li et al. 2021). Aluminum is nonmigratory during the limestone weathering and soil formation processes, therefore the ratio of soil Ca content to Al content (i.e., soil Ca/Al ratio) can indicate soil Ca accumulation or depletion during the secondary succession of agricultural abandonment.

Statistical analyses

Shapiro–Wilk (S–W) test was performed to detect normality for the proportions of different-sized aggregates or fractions, aggregate-associated SOC contents in bulk soils, SOC/SON ratios, soil Ca contents, and Ca/Al ratios in the soils at the different depths under different land-use types. Data should be transformed by logarithmic transformation to meet the normal test if necessary. One-way ANOVA with the Least Significant Difference (LSD) test was performed to determine the differences in the proportions of different-sized aggregates, SOC contents associated with different-sized aggregates, soil Ca contents, soil Ca/Al ratios, microbial residue C stock, and *K* factor in the same depth layer among different land-use types at the significance level of $P < 0.05$. The relationships of SOC contents with macro-aggregate proportions and soil Ca contents under different land-use types were determined by linear regression analysis, showing coefficients of *r* and associated *P*-value.

Results

Soil aggregate proportion

In the calcareous soils, macro-aggregates accounted for the largest proportion (> 60%) in all aggregates and fractions (Table 1). In the soils at 0–10 cm depth, the proportions of macro-aggregates (mean 61.3%) in the croplands were significantly lower, while the proportions of micro-aggregates (mean 15.8%) and silt + clay sized fractions (mean 22.9%) were significantly greater, than those in the shrub-grass lands (mean 78.5, 9.2, 12.3%, respectively). Moreover, the proportions of macro-aggregates (mean 81.6%), micro-aggregates (mean 8.1%), or silt + clay sized fractions (mean 10.3%) in the secondary forest lands were not significantly different compared to those in the shrub-grass lands.

Micro-aggregate proportions in the soils at the 10–30 cm depth under the shrub-grass lands were not significantly different from those under the secondary forest lands and croplands. The proportions of macro-aggregates in the soils at the 20–30 cm depth and the proportions of silt + clay sized fractions in the soils at the 10–30 cm depth were not significantly different among the three land-use types. These results showed that the proportion of soil macro-aggregates increased but the proportions of micro-aggregates and silt + clay sized fractions decreased during the secondary succession of agricultural abandonment. Moreover, the variations of different-sized aggregates and fractions under different land-use types gradually weakened with increasing soil depth.

Water-stable aggregates accounted for 77–90% (wt.%) of all aggregates or fractions. The proportions of water-stable aggregates in the soils at the 0–10 cm depth under the croplands were significantly lower than those under the shrub-grass lands and secondary forest lands but were not significantly different among the three land-use types in the soils at the 20–30 cm depth. This result showed that water-stable aggregates in the undisturbed surface soils significantly increased after 3 years of cropland abandonment.

Table 1 The proportions of different-sized aggregates in the soils at different depths under different land-use types

Land-use types	CL	SG	SF
Soils at the 0–10 cm depth			
Water-stable aggregate proportion (%)	77.1 (5.7) b	87.7 (2.2) a	89.7 (4.4) a
Macro-aggregate proportion (%)	61.3 (5.8) b	78.5 (3.7) a	81.6 (5.9) a
Micro-aggregate proportion (%)	15.8 (2.1) a	9.2 (1.8) b	8.1 (1.6) b
Silt + clay sized fraction proportion (%)	22.9 (5.7) a	12.3 (2.2) b	10.3 (4.4) b
Soils at the 10–20 cm depth			
Water-stable aggregate proportion (%)	81.2 (10.0) a	87.8 (1.6) a	90.3 (3.1) a
Macro-aggregate proportion (%)	66.3 (14.8) b	79.3 (3.1) ab	82.6 (3.9) a
Micro-aggregate proportion (%)	15.0 (5.9) a	8.5 (2.3) ab	7.7 (1.4) b
Silt + clay sized fraction proportion (%)	18.8 (10.0) a	12.2 (1.6) a	9.7 (3.1) a
Soils at the 20–30 cm depth			
Water-stable aggregate proportion (%)	78.1 (15.7) a	85.8 (2.9) a	88.6 (5.2) a
Macro-aggregate proportion (%)	64.0 (18.6) a	76.0 (3.7) a	81.2 (5.9) a
Micro-aggregate proportion (%)	14.1 (5.1) a	9.8 (1.0) ab	7.4 (1.7) b
Silt + clay sized fraction proportion (%)	21.9 (15.70) a	14.2 (2.9) a	11.4 (5.2) a

The results are expressed as mean with standard deviation. Different lowercase letters indicate significant differences in the proportions of different-sized aggregates among land-use types, based on the one-way ANOVA with LSD test at the level of $P < 0.05$

CL cropland, *SG* shrub-grass land, *SF* secondary forest land

Aggregate-associated SOC content in bulk soil

The SOC contents associated with macro-aggregates at the 0–20 cm depth under the secondary forest lands (mean 52.2 g kg^{-1}) were significantly greater than those under croplands (mean 30.5 g kg^{-1}), moreover, but neither was significantly different from those under the shrub-grass lands (mean 38.6 g kg^{-1}) (Fig. 1). However, the SOC contents in

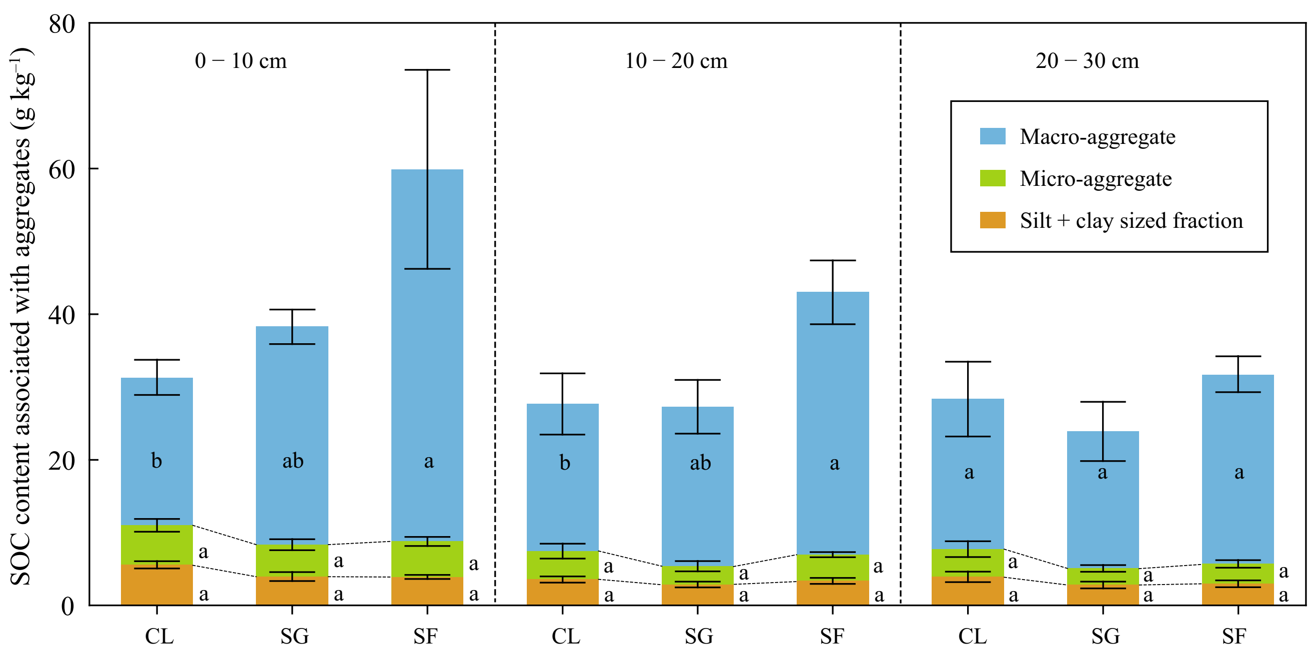

Fig. 1 SOC contents associated with different-sized aggregates in the soils at different depths under different land-use types. The error bar is the standard error (SE). Different lowercase letters indicate significant differences in SOC contents associated with different-sized aggregates among different land-use types, based on the one-way ANOVA with LSD test at the level of $P < 0.05$. *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

the soils at the 20–30 cm depth were not significantly different among the three land-use types. Similarly, the SOC contents associated with micro-aggregates and silt + clay sized fractions at all soil depths were not significantly different among the three land-use types. Additionally, the proportions of macro-aggregates significantly positively correlated with the SOC contents in bulk soils and the SOC contents of macro-aggregates in the croplands, and positive correlations (not significant) between them occurred in the shrub-grass lands and secondary forest lands (Fig. 2). These results showed that the SOC of macro-aggregates was more sensitive than that associated with micro-aggregates and silt + clay sized fractions in response to the secondary succession of agricultural abandonment.

Soil Ca content and Ca/Al ratio

The Ca contents in the soils under the secondary forest lands at the 0–20 cm depth (mean 33.1 g kg^{-1}) were significantly greater than those under the shrub-grass lands (mean 8.0 g kg^{-1}) and croplands (mean 6.9 g kg^{-1}) but were not significantly different among the three land-use types in the soils at the 20–30 cm depth (Fig. 3a). In the soils at the 0–20 cm depth, soil Ca/Al ratios under the secondary forest lands (mean 0.63) were also significantly greater than those under the shrub-grass lands (mean 0.105) and croplands (mean 0.087), and the ratios in the shrub-grass lands were slightly (not significantly) greater than those in the croplands (Fig. 3b). Additionally, soil Ca contents and Ca/Al ratios were significantly positively correlated with the SOC contents in bulk soils under the three land-use types (Fig. 4).

Discussion

In the karst region, SOC sequestration is generally enhanced during the secondary succession of agricultural abandonment, which has been widely reported in previous research (Yang et al. 2016; Liu et al. 2020). Increasing SOC sequestration is characteristic of increases in SOC storage and turnover time, and these are closely associated with the changes in SOC content and stabilization (Cotrufo et al. 2019). In the current study, the effects of soil aggregation, soil erosion, and soil Ca dynamic on SOC content and stabilization are discussed to improve the mechanistic understanding of increasing SOC sequestration during the secondary succession of agricultural abandonment.

Enhancing soil aggregation

Soil aggregate formation and stabilization can significantly affect SOC dynamics after land-use changes or under different land-use management (Huang et al. 2010; Six and Paustian 2014; Zeng et al. 2018). The proportions of macro-aggregates significantly increased during the secondary succession of agricultural abandonment (Table 1). This result indicates that soil aggregation gradually increases after cessation of agricultural disturbances, for example, tillage. Aggregates physically protect the SOC within them due to the role of aggregates in isolating oxygen, water, and microorganisms, which is crucial to enhancing SOC stabilization (Six et al. 1998; Oades and Waters 1991; Zhu et al. 2021). However, long-term tillage leads to mechanical fragmentation of macro-aggregates, resulting in more SOC being exposed to the air and directly attacked by microorganisms

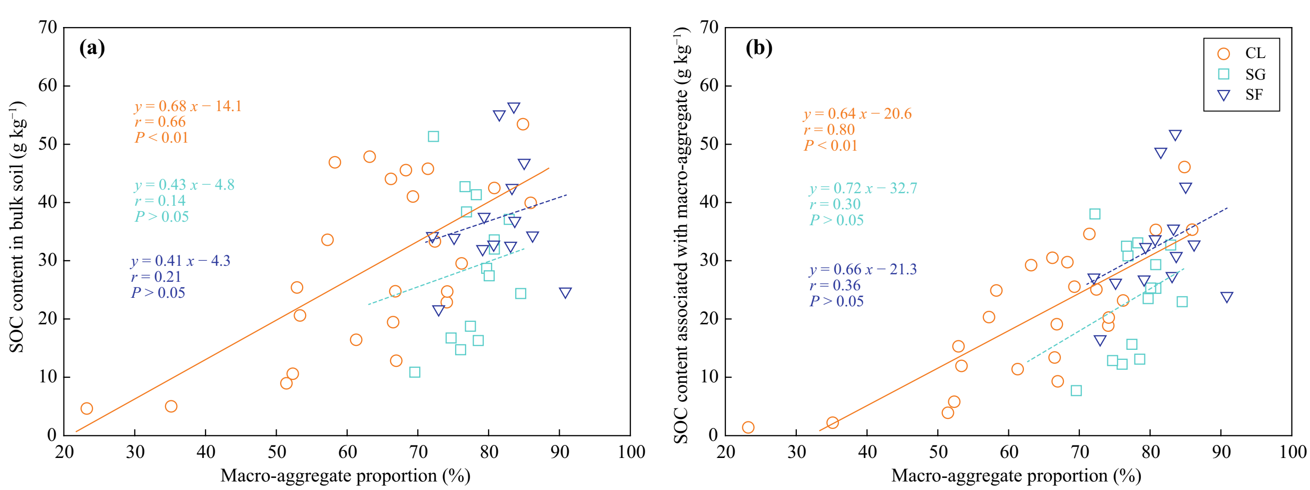

Fig. 2 Relationships of macro-aggregate proportions with SOC contents in bulk soils (**a**) and SOC contents associated with macro-aggregates (**b**) under different land-use types. Their linear relationships in the soils under different land-use types were determined by the linear regression analysis. *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

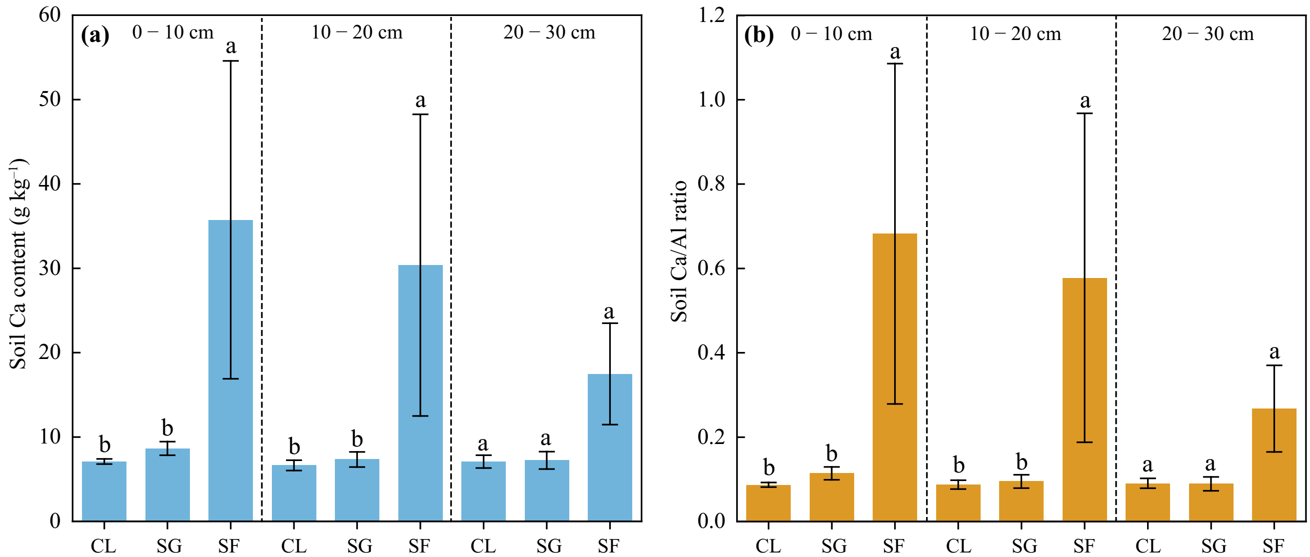

Fig. 3 Soil Ca contents (**a**) and Ca/Al ratios (**b**) in the soils at different depths under different land-use types. The error bar is the standard error (SE). Different lowercase letters indicate significant differences in soil Ca contents and Ca/Al ratios among different land-use types, based on the one-way ANOVA with LSD test at the level of $P < 0.05$. *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

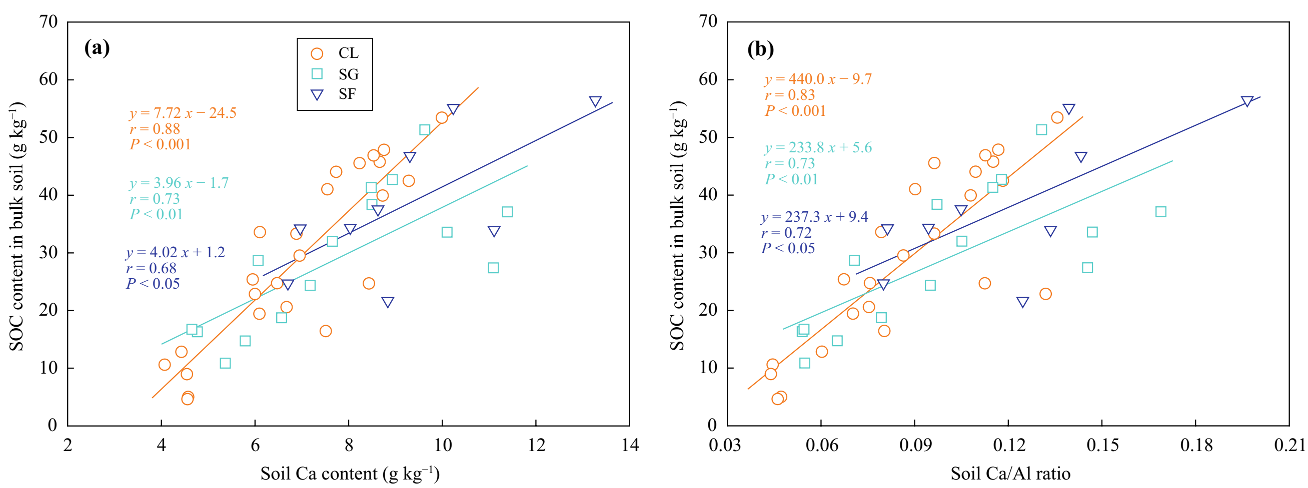

Fig. 4 Relationships of SOC contents in bulk soils with soil Ca contents (**a**) and Ca/Al ratios (**b**) during different land-use types. Their linear relationships in the soils under different land-use types were determined by the linear regression analysis. *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

(Six et al. 2002). Thus, soil aggregation and SOC stabilization in the croplands are generally weaker than those in the secondary forest lands. The SOC contents associated with macro-aggregates significantly increased during the secondary succession of agricultural abandonment, but the SOC contents associated with micro-aggregates and silt + clay sized fractions did not (Fig. 1). Furthermore, the SOC contents associated with macro-aggregates positively correlated with the proportions of macro-aggregates at all stages of agricultural abandonment (Fig. 2). These results indicate a close link between macro-aggregates and SOC sequestration during the secondary succession of agricultural abandonment. Generally, the response of macro-aggregates is more rapid to land-use change or land-use management compared to other smaller-sized aggregates (Franzluebbers and Arshad 1997; Six et al. 2004). Conventional tillage management preferentially destroys macro-aggregates rather than micro-aggregates (Franzluebbers and Arshad 1997), but the restoration of macro-aggregates is also more rapid with the cessation of tillage. Macro-aggregate formation and stabilization are closely linked to SOC dynamic because macro-aggregates provide physical protection for SOC (Liu et al. 2019).

Furthermore, 60–80% of SOC in the soils at the 0–30 cm depth was stored in macro-aggregates (Fig. 1). Thus, the restoration of macro-aggregates plays an important role in enhancing SOC sequestration during the secondary succession of agricultural abandonment. Soil aggregates not only promote SOC accumulation but also enhance its stabilization (Six et al. 1998; Six and Paustian 2014; Zhu et al. 2021). Liu et al. (2020) found that SOC within micro-aggregates is younger than that within macro-aggregates through a comparison between the ^{13}C composition of SOC within different-sized aggregates in the calcareous soils of this study area. According to the aggregate hierarchy model (Six et al. 2000), micro-aggregates occur within macro-aggregates during the formation process. Thus, the SOC contained in micro-aggregates is more stable because of multiple protections from micro-aggregates and macro-aggregates (Beare et al. 1994). During the secondary succession of agricultural abandonment, the restoration of macro-aggregates promotes the formation of interior micro-aggregates (Six et al. 2000), which is conducive to protecting the young SOC within micro-aggregates. More labile SOC is stabilized by micro-aggregates with the increase in macro-aggregates after cropland abandonment, which slows down the turnover rate of the whole SOC pool.

The proportions of macro-aggregates in the croplands were significantly greater than those in the shrub-grass lands, but SOC contents between them were not significantly different. These results indicate that the restoration of macro-aggregates is more rapid than SOC recovery during the secondary succession of agricultural abandonment. The SOC storage (or content) in surface soils depends on the dynamic balance between organic C input rate and decomposition rate (Jobbagy and Jackson 2000). The SOC input and/or decomposition rate varies after a land-use change until reaching a new balance (Chen et al. 2021). In this study, SOC has gradually accumulated after cropland abandonment, which implied a higher SOC input rate compared to its decomposition rate during the secondary succession of agricultural abandonment. The change in SOC input and/or decomposition rate is a long-term process, closely associated with the variations in soil properties, plant structure, and soil microbial community composition (Novara et al. 2014). For example, Li et al. (2018) found that bacterial and fungal residue C stocks in the croplands were significantly lower than those in the secondary forest lands but were not significantly different from those in the shrub-grass lands in this study area (Fig. 5). This indicates that the restoration of soil microbial community composition is also a long-term process during the secondary succession of agricultural abandonment. But the restoration of macro-aggregates is a relatively short-term process because the formation of macro-aggregates is significantly expedited with the cessation of tillage and vegetation recovery after

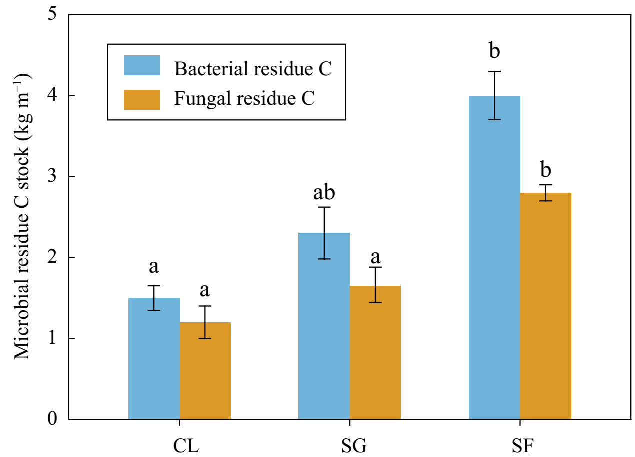

Fig. 5 Microbial residue C stock under different land-use types. The error bar is the standard error (SE). Different lowercase letters indicate significant differences in bacterial or fungal residue C stock under different land-use types, based on the one-way ANOVA with LSD test at the level of $P < 0.05$. The data were quoted from Li et al. (2018). *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

cropland abandonment (Liu et al. 2019). Additionally, the proportions of different-sized aggregates and SOC contents associated with them were significantly different among the three land-use types in the topsoil (0–20 cm depth), but not in the soil below 20 cm depth (Table 1 and Fig. 1). The effect of agricultural abandonment on the formation and stabilization of soil aggregates and related SOC has weakened in deep soil. This is mainly attributed to microbial processes, which are closely associated with the formation and stabilization of soil aggregates and related SOC (Six and Paustian 2014). For the topsoil, microbial community compositions and activities are mainly affected by the variety and quantity of organic matters (as important material and energy sources) under different land-use types (Zhang et al. 2013). However, microbial quantity and activity will be restricted in deep soil due to the decreases in food sources and oxygen concentration (Luo et al. 2019). Guo et al. (2019) reported that soil microbial enzyme activity decreased with increasing soil depth in this study area.

Reducing soil erosion

Soil erosion is an important force affecting SOC dynamics (Haring et al. 2013). The karst region of southwestern China is a typical soil erosion area (Guo et al. 2017; Wang et al. 2019). Liu and Han (2020) assessed soil erodibility of surface soils under different land-use types by estimating the *K* factor in the Erosion Productivity Impact Calculator (EPIC) model in this study area. The *K* values of the soils at the 0–30 cm depth in the croplands were significantly greater than those in the shrub-grass lands and much greater than those in the secondary forest lands (Fig. 6), demonstrating that soil erodibility significantly decreases during the secondary succession of agricultural abandonment. The *K* factor in the EPIC model is estimated based on the variables related to soil structure, such as SOC content and the proportions of different-sized particles (Sharpley and Williams 1990). Water-stable aggregates also directly affect soil erodibility, because soil aggregates are the base unit of soil structure (Jastrow 1996). Additionally, water-stable aggregates accounted for 77–90% of the total soil mass in this study (Table 1). Thus, the proportion of water-stable aggregates should be considered when estimating soil erodibility. Soils containing many water-stable aggregates have a loose structure with many large-sized soil pores, which enhances soil permeability to resist runoff influences, i.e., reduces soil erodibility (Varela et al. 2010; Ding and Zhang 2016). In contrast, the surface soils with few water-stable aggregates are easily compacted by rainfall to form a soil crust. Soil crusts can enhance surface runoff and reduce water infiltration, which enhances soil erodibility (Goldshleger et al. 2002). Generally, the proportion of water-stable aggregates is negatively correlated with the soil erodibility *K* factor. For example, Ren et al. (2019) reported that the proportions of water-stable macro-aggregates were significantly negatively correlated with the *K* factor in the Universal Soil Loss Equation (USLE) model. Liu and Han (2020) reported that the proportions of water-stable aggregates in the calcareous soils were significantly negatively correlated with the *K* factor in the EPIC model. In the study area, the proportion of water-stable aggregates significantly increased and the *K* factor significantly decreased during the secondary succession of agricultural abandonment (Table 1 and Fig. 6), indicating that soil erosion also significantly decreased. Furthermore, based on field observation, vegetation coverage and canopy thickness increased during the secondary succession of agricultural abandonment, which reduces soil erosion by cushioning the force of rainfall on surface soils (Wang et al. 2016). Reduced soil erosion following ecological restoration has been widely reported in the karst area (Zhu et al. 2018; Liu and Han 2020). Soil erosion can directly reduce SOC content through the loss of POC and DOC (Haring et al. 2013). Moreover, soil erosion can cause soil Ca loss, which indirectly affects SOC content by hindering the formation of OM–Ca^{2+}–mineral complexes and soil aggregates (as discussed in Soil Ca accumulation). Thus, soil erosion is closely linked to SOC dynamics. Liu et al. (2019) reported that SOC contents significantly increased with the increasing proportions of water-stable macro-aggregates and with the decreasing *K* factor values during the secondary succession of agricultural abandonment. The reduced soil erosion after cropland abandonment is conducive to enhancing SOC sequestration.

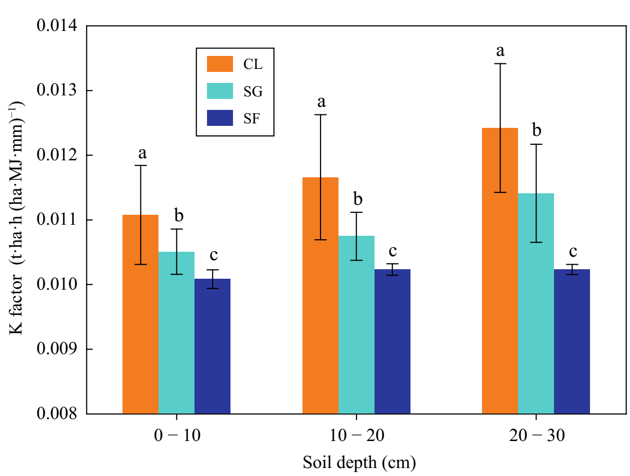

Fig. 6 The *K* factor of EPIC model in the soils under different land-use types. The error bar is the standard error (SE). Different lowercase letters indicate significant differences in the *K* factor among different land-use types, based on the one-way ANOVA with LSD test at the level of $P < 0.05$. The data were quoted from Liu and Han (2020). *CL* cropland, *SG* shrub-grass land, *SF* secondary forest land

Soil Ca accumulation

In the karst region, the weathering of limestones (mainly consisting of calcites) provides abundant Ca^{2+} into the calcareous soil (Li et al. 2017). Soil Ca in the croplands was depleted compared to that in the secondary forest lands (Fig. 3), mainly resulting from leaching loss and harvesting (Guo et al. 2010). The soil Ca/Al ratios in croplands were slightly (not significantly) greater than those in the shrub-grass lands and significantly greater than those in the secondary forest lands (Fig. 3), indicating near-surface soil Ca accumulation during secondary succession of agricultural abandonment. As the soil Ca content is constant at the stage of cropland, the Ca output flux by Ca^{2+} leaching must be equal to its input flux by limestone weathering. After cropland abandonment, Ca influx does not vary because the limestone weathering rate is constant. However, increased SOM promotes the formation of stable OM–Ca^{2+}–mineral complexes against Ca^{2+} leaching (Kaiser et al. 2011). Additionally, reduced soil erosion restricts soil Ca^{2+} leaching loss (Liu and Han 2020). These factors lead to a decrease in Ca output flux and an accumulation of soil Ca. Soil Ca has depleted during long-term cultivation, but it can be replenished during the secondary succession of agricultural abandonment. At the bottom of the soil layer, limestone weathering produces dissolved Ca^{2+}. Generally, dissolved Ca^{2+} rises into upper soil by capillary movement or is absorbed by the plant and then returns to surface soil through litter and root exudates (Burt et al. 2010).

Soil Ca contents and Ca/Al ratios were significantly positively correlated with SOC contents under the three land-use

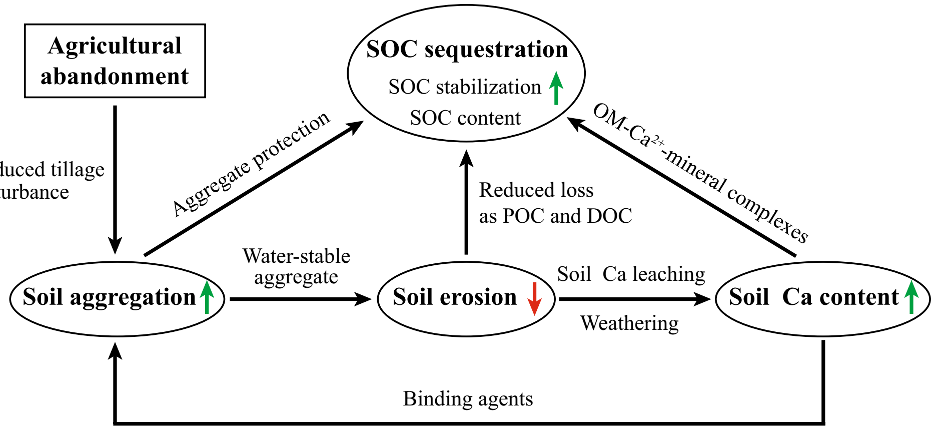

Fig. 7 A conceptual model for SOC sequestration during the secondary succession of agricultural abandonment in the karst ecosystem. *OM* organic matter, *POC* particulate organic carbon, *DOC* dissolved organic carbon. The green arrows indicate the positive processes and the red arrows indicate the negative processes

types (Fig. 4), indicating a close link between soil Ca and SOC content at all stages of cropland abandonment. The bivalent Ca^{2+} can easily combine with OM and clay minerals to form stable OM–Ca^{2+}–mineral complexes, which can enhance SOC content and stabilization (Kaiser et al. 2011). Moreover, soil Ca^{2+} is an important binding agent promoting aggregate formation, which indirectly affects SOC sequestration. Li et al. (2017) suggested that soil exchange Ca^{2+} is the major factor that affects SOC storage after cropland abandonment. Moreover, the ratio of exchange Ca^{2+} to SOC can be used as an index to assess the capacity of SOM accumulation (Li et al. 2017). Thus, soil Ca replenishment plays an important role in enhancing SOC sequestration during the secondary succession of agricultural abandonment.

Conceptual model

According to the effects of soil aggregates, soil erosion, and soil Ca on SOC dynamics, we propose a conceptual model for enhancing SOC sequestration during the secondary succession of agricultural abandonment in the karst region (Fig. 7). The cessation of agricultural activities after cropland abandonment is conducive to the formation and stabilization of soil aggregates. Soil aggregates provide physical protection for SOC to enhance its content and stabilization. Soil erodibility *K* factor significantly decreases during this process, indicating reduced soil erosion. Decreasing soil erosion restricts the loss of DOC and POC, which is conducive to SOC accumulation. Soil Ca contents and Ca/Al ratios significantly increased during this process, indicating soil Ca replenishment. Soil Ca accumulation promotes the formation of OM–Ca^{2+}–mineral complexes to enhance SOC content and stabilization. Additionally, there are interactive relationships between soil aggregation, soil erosion, and soil Ca content. For example, water-stable aggregates can improve soil structure to reduce soil erosion. Reduced soil erosion restricts the leaching loss of soil Ca^{2+}. Soil Ca^{2+} accumulation is beneficial for soil aggregation due to its role as a binding agent during aggregate formation. Thus, the enhanced SOC sequestration during the secondary succession of agricultural abandonment in the karst region is mainly attributed to the protection of SOC by soil aggregates and OM–Ca^{2+}–mineral complexes and reduced soil erosion. This conceptual model suggests that there are positive effects of secondary succession on the abandoned croplands under the GGP program in enhancing SOC sequestration and soil quality improvement. These have important implications for global climate change and regional ecological restoration.

Conclusions

Under the GGP program, the mechanisms of enhanced SOC sequestration during the secondary succession of agricultural abandonment were identified in the karst region of southwest China. The proportions of macro-aggregates and water-stable aggregates, SOC contents, soil Ca contents, and Ca/Al ratios significantly increased after cropland abandonment, and the soil erodibility *K* factor decreased. The SOC contents were significantly positively correlated with macro-aggregate proportions and soil Ca contents. A conceptual model for enhancing SOC sequestration during the secondary succession of agricultural abandonment was proposed in the karst region. The enhanced SOC sequestration during this process is mainly attributed to the protection of SOC by soil aggregates and OM–Ca^{2+}–mineral complexes and reduced soil erosion. This conceptual model reflects the positive effects of the secondary succession of agricultural abandonment under the GGP program on SOC sequestration and ecological restoration.

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Author contributions Conceptualization: ML and GH; Methodology: ML and GH; Formal analysis and investigation: ML and QZ; Visualization: ML and QZ; Writing—original draft preparation: ML and GH; Writing—review and editing: ML, GH, and QZ; Funding acquisition: GH; Resources: GH; Supervision: GH.

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Availability of data and materials The data that support the findings of this study are available on request from the corresponding author.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Research involving human participants and/or animals This article does not contain any studies with human participants performed by any of the authors.

Informed consent Informed consent was obtained from all individual participants included in the study.

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