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Responses of soil enzyme activity and soil organic carbon stability over time after cropland abandonment in different vegetation zones of the Loess Plateau of China

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ABSTRACT

The effects of cropland abandonment on soil enzyme activity and soil organic carbon (SOC) stability, along with the driving factors, are poorly understood. Here, we aimed to systematically and comprehensively evaluate soil enzyme activity, SOC stability, and the associated driving factors in different vegetation zones after cropland abandonment on the Loess Plateau, China. We selected grasslands with different recovery times along a rainfall gradient encompassing the steppe zone (SZ), forest-steppe zone (FSZ), and forest zone (FZ). We measured and compared the changes in soil enzyme activity (saccharase, polyphenol oxidase, urease, phosphatase, and catalase) and SOC stability as a function of recovery time; we also evaluated the relationships between these two parameters. In SZ and FSZ, soil enzyme activity, fractions of oxidizable carbon (including very labile [C1], labile [C2], and less labile [C3]), and the carbon management index (CMI) increased with recovery time, whereas the SOC stability index (SI) decreased. Conversely, in FZ, polyphenol oxidase activity increased linearly, urease and catalase activities decreased linearly, and the change in saccharase activity was represented by a cubic equation regression. SI showed no obvious changes with recovery time, whereas C1, C2, and C3 initially decreased and then increased. Redundancy analysis showed that, in FSZ and FZ, soil enzyme activity, C1, C2, C3, and SI were influenced by vegetation diversity, coverage, and soil nutrient levels. In comparison, in SZ, these parameters were mainly influenced by soil nutrient levels. Soil enzyme activity was strongly correlated with C1 and C3 in SZ and FSZ, but not in FZ. Overall, in SZ and FSZ, soil enzyme activity increased with recovery time, whereas SOC stability decreased. In contrast, both parameters were relatively stable in FZ, which had higher mean annual precipitation and mean annual temperature.

1. Introduction

Cropland abandonment is considered an effective measure for controlling soil erosion and improving vegetation coverage and soil quality (Good et al., 2013; Wertebach et al., 2017); however, that synergistic complex process between the soil and plants is time consuming (Korb et al., 2010). The soil provides the necessary water and nutrients for plant growth, while plants cycle the nutrients in the soil and enhance its quality by contributing organic matter (Korb et al., 2010). This dynamic interaction leads to the formation of grasslands during the recovery of land abandoned after use for crops. This process effectively improves soil conditions and restores degraded environments; thus, it has been subject to increasing focus in the field of ecology (Xiao et al., 2020).

Soil enzymes are derived from root exudates, litter, and microbial activity (Pausch and Kuzyakov, 2018). They are active components in various biochemical processes and nutrient cycles (Li et al., 2014), providing early warning of biological changes in the soil (Bandick and Dick, 1999). Furthermore, soil enzymes are good indicators of soil quality (Bastida et al., 2006); and are highly sensitive to environmental and anthropogenic stimuli (Rutigliano et al., 2009). Consequently, soil enzyme activity has been extensively investigated to objectively

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evaluate fertility and biological activity (Roldan et al., 2005).

Vegetation coverage, biomass, and plant diversity have important effects on soil enzyme activity (Bandick and Dick, 1999; Ren et al., 2018). Furthermore, water availability is the main factors limiting soil enzyme activity as it affects biological activity and metabolism (Collins et al., 2008). This is especially true in the arid and semi-arid region of the Loess Plateau in China (Cui et al., 2019). Changes in the pattern of precipitation could greatly alter the wetting–drying cycle of the soil, improving the utilization of soil nutrients (Denef et al., 2001), which might further influence soil enzyme activity (Ren et al., 2017). In addition, different types of soil enzymes contribute to the transformation and cycling of different soil nutrients. For instance, soil saccharase, urease, and polyphenol oxidase are important hydrolytic enzymes that are involved in the transformation and cycling of soil carbon, nitrogen, and phosphorus, respectively. Therefore, the activity of different soil enzymes might vary largely and significantly in response to different environmental factors (Ren et al., 2017; Xu et al., 2020b).

The stability of soil organic carbon (SOC) is vital to the soil carbon cycle (Lal, 2003; Xu et al., 2020a). SOC reflects the ability of the soil to resist external disturbance as well as restore and maintain homeostasis (Jastrow et al., 2007). Not surprisingly, the decomposition and transformation of various carbon compounds directly influence SOC stability. Active carbon fractions (very labile [C1] and labile [C2]) of soil oxidizable carbon are important components of SOC that are readily decomposed and oxidized. These components accurately reflect the changes in soil quality and nutrient cycling (Chang et al., 2018). Furthermore, these components provide readily available energy sources that stimulate microbial activity (Phillips et al., 2011). In contrast, passive carbon fractions (less labile [C3] and non-labile [C4]) of soil oxidizable carbon have stable molecular structures, persisting in the soil for a long time by combining with minerals (Kiem and Kögel-Knabner, 2003). Changes in the fractions of active carbon and passive carbon reflect SOC stability (Chan et al., 2001). SOC stability affects the decomposition and storage of soil carbon, substantially impacting soil quality and nutrient cycling, which could potentially mitigate global climate change (Lal, 2003). Conversely, SOC instability hinders plant growth, aggravates soil degradation, and contributes to climate change, blocking sustainable development (Lal, 2004). Therefore, the sequestration and stability of SOC should be systematically and comprehensively evaluated following cropland abandonment in the various vegetation zones of the Loess Hilly Region. This process could provide a solid theoretical foundation for the successful restoration of vegetation in this area.

Soil enzyme activity increases with vegetation restoration (Xiao et al., 2020). Indeed, the conversion of carbon and nitrogen in the soil mainly depends on soil enzyme systems. Consequently, soil chemical properties are likely closely related to soil enzyme activity (Cui et al., 2019). However, previous studies have not associated soil enzyme activity with soil properties or plant diversity (de Vries et al., 2012; Lauber et al., 2008). Moreover, the effects of cropland abandonment on SOC stability, as well as the relationships between soil enzyme activity and SOC stability, in the Loess Plateau remain largely unknown.

Here, we aimed to systematically and comprehensively evaluate soil enzyme activity, SOC stability, and the associated driving factors in different vegetation zones after cropland abandonment on the Loess Plateau, China. The key objectives included elucidating: (1) the changes in soil enzyme activity and SOC stability in different vegetation zones after cropland abandonment; (2) the factors driving the changes in soil enzyme activity and SOC stability; and (3) the relationship between soil enzyme activity and SOC stability. We hypothesized that (1) the active carbon fractions (C1 and C2) would be more sensitive than the passive carbon fractions (C3 and C4) to recovery time, thus reducing SOC stability after cropland abandonment; (2) the changes in soil enzyme activity following cropland abandonment would be positively correlated with rainfall gradients; and (3) the changes in soil enzyme activity and SOC stability would be mainly affected by plant diversity and soil nutrients, whereas SOC stability would be negatively correlated with soil enzyme activity, in the three vegetation zones. The results of this study are expected to help formulate effective guidelines for vegetation restoration in this region and similar regions globally.

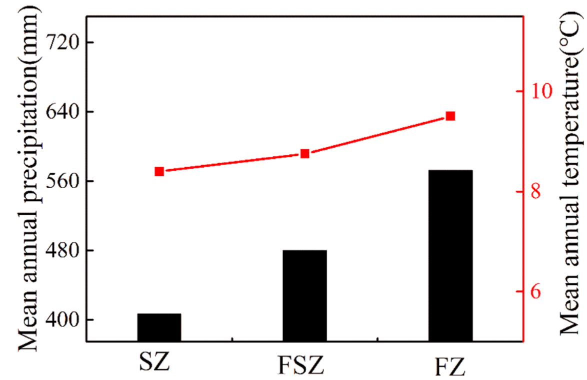

Fig. 1. Mean annual precipitation (MAP) and mean annual temperature (MAT) of the study site on the Loess Plateau of China. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

2. Materials and methods

2.1. Study area

The study site included the steppe zone (SZ), forest-steppe zone (FSZ), and forest zone (FZ) located on the north to south (N-S) latitude belt of the Loess Plateau of China, extending from 37.01° to 40.41° N and 09.626° to 111.78° E. Mean annual precipitation (MAP), mean annual temperature (MAT), and vegetation type show pronounced gradient characteristics from south to north. MAP ranges between 405.4 and 600.6 mm, while MAT ranges between 8.4 and 9.8 °C (Fig. 1). The terrain in this area is broken, with vertical and horizontal gullies. There is major soil and water loss throughout the area, which belongs to a typical ecologically fragile area. The soil is mainly loess, sandy loam, and aeolian sand. These soil types have weak cohesion, poor corrosion resistance, and are susceptible to soil erosion. Before the 1950s, extreme weather (such as droughts, heavy rain, and strong winds) occurred frequently, along with unregulated human activity (such as grazing and farming); consequently, the ecological environment in this area was severely damaged, soil erosion was severe, and soil quality and vegetation coverage were reduced. In 1999, the government began to implement the "Grain-for-Green" project in this region. As a result, vegetation coverage has increased significantly, and soil erosion has been effectively controlled. Thus, overall, soil and environmental quality has improved. Grassland ecosystems cover ~80% of the Loess Plateau and are dominated by *Bothriochloa ischaemum* (L.), *Stipa bungeana* Trin, *Heteropappus altaicus*, *Lespedeza bicolor* Turcz, and *Stipa grandis* (Cui et al., 2019).

2.2. Selection of study site

To determine the dynamics of soil enzyme activity and soil organic carbon (SOC) stability after cropland abandonment in different vegetation zones, we used the "space for time" method. A total of 19 sites, representing three vegetation zones, were selected depending on the recovery period since abandonment. There were eight groups of SZ that had been abandoned for 1, 5, 6, 8, 10, 15, 25, and 30 years; five groups of FSZ that had been abandoned for 7, 17, 20, 25, and 30 years, and three groups of FZ that had been abandoned for 9, 21, and 30 years. Three 10 m × 10 m plots were marked at each site in each vegetation zones, to produce a total of 57 plots, including 30, 18, and nine plots in the three vegetation zones, respectively. Adjacent plots were located at least 50 m apart. All selected plots had similar elevation, slope, slope

Table 1
The details of the sample sites selected for the study.

Vegetation zones	Sampling site	Recovery years (yr)	Altitude (m)	Geographic coordinates	Slope (°)	Dominant community species
SZ	S1	0	1203	40.41°N, 110.53°E	18	*Setaria italica*
	S2	1	1202	40.40°N, 110.41°E	20	*Artemisia scoparia, xeris denticulata*
	S3	5	1214	40.41°N, 110.58°E	18	*Stipa bungeana, Lespedeza bicolor, Artemisia scoparia*
	S4	6	1239	40°35′N, 110.38°E	15	*Stipa bungeana, Lespedeza bicolor, Artemisia capillaris*
	S5	8	1139	40°25′N, 111.08°E	15	*Stipa bungeana, Lespedeza bicolor, xeris denticulata*
	S6	10	1214	40.38°N, 110.67°E	20	*Artemisia capillaris, Stipa bungeana, Medicago*
	S7	15	1227	39.83°N, 111.64°E	18	*Stipa bungeana, Lespedeza bicolor, Artemisia capillaris*
	S8	25	1235	40.04°N, 111.61°E	17	*Bothriochloa ischaemum, Stipa bungeana,*
	S9	30	1135	40.34°N, 110.62°E	16	*Stipa bungeana、Lespedeza bicolor、Artemisia capillaris*
FSZ	S10	0	1045	37.54°N, 110.31°E	23.5	*Ricinus communis*
	S11	7	1303	37.15°N, 111.09°E	32	*Stipa bungeana, Potentilla bifurca, Lespedeza bicolor*
	S12	17	1303	37.15°N, 111.09°E	31	*Stipa bungeana, Lespedeza bicolor, Potentilla bifurca*
	S13	20	1136	38.49°N, 111.06°E	31	*Artemisia leucophylla, Artemisia sacrorum, Lespedeza bicolor, Stipa bungeana*
	S14	25	1221	37.23°N, 109.26°E	27	*Artemisia sacrorum, Stipa bungeana, Lespedeza bicolor*
	S15	30	1108	38.36°N, 111.13°E	32	*Artemisia sacrorum, Stipa bungeana, Lespedeza bicolor*
FZ	S16	0	1040	37.01°N, 111.57°E	12	*Setaria italica*
	S17	9	1139	37.57°N, 111.27°E	26.5	*Stipa bungeana, Lespedeza bicolor, Artemisia capillaris*
	S18	21	1034	38.03°N, 111.78°E	24	*Artemisia sacrorum, Stipa bungeana, Cleistogenes squarrosajiaohao*
	S19	30	1048	38.03°N, 110.16°E	24	*Artemisia sacrorum, Stipa bungeana, Cleistogenes squarrosa, Artemisia leucophylla*

Note: SZ, steppe zone; FSZ, forest-steppe zone; SZ, forest zone.

aspects, and slope gradient. In addition, we selected two slope-cropland plots in SZ and three slope-cropland plots in FSZ and FZ, respectively, to represent 0-year controls, as grasslands in this region have evolved from slope croplands after abandonment. Details of the sampling sites are shown in Table 1.

2.3. Investigation of plants and soil sampling

Three 1 m × 1 m quadrats were selected per plot. Slopes, plant types, coverage, height, and number of plants in each quadrat were surveyed. Ten soil core samples were collected from the topsoil layer (0–0.2 m) per plot using a soil drilling sampler (0.04 m inner diameter) after removing the litter layer and mixing the cores to form a composite sample. Soil samples were brought to the laboratory, to remove all traces of roots, stones, and visible fauna. Samples were then separated into two portions. One portion was air-dried and sieved (0.25 mm) to determine soil chemical properties including SOC, soil total nitrogen (TN), soil total phosphorus (TP), soil available nitrogen (AN), soil available phosphorus (AP), soil available potassium (AK), soil oxidizable carbon fractions, soil pH, and soil particles. The remaining portion was stored at −4 °C to determine soil enzyme activity, including saccharase activity, polyphenol oxidase activity, urease activity, phosphatase activity, and catalase activity.

2.4. Laboratory analyses

SOC and TN were determined by the Walkley and Black (Nelson and Sommers, 1982) and Kjeldahl (Bremner, 1982) methods, respectively. TP and AP were measured colorimetrically by the ammonium molybdate (Schade et al., 2003) and Olsen (Olsen and Sommers, 1982) methods, respectively. AN was determined by the alkaline $KMnO_4$ method (Subbiah and Asija, 1956). In turn, AK was measured in 1 M NH_4OAc soil extracts by flame photometry (Knudsen et al., 1982). Soil oxidizable carbon fractions were determined by the Walkley and Black method (Chan et al., 2001; Xu et al., 2020a). Briefly, 0.5 g of soil was added to a 500 mL Erlenmeyer flask, followed by the addition of 10 mL (0.167 mol L^{-1}) of $K_2Cr_2O_7$ (0.167 mol L^{-1}). Then, 5, 10, and 20 mL of concentrated H_2SO_4 (18 mol L^{-1}) were added (corresponding to concentrations of 6, 9, and 12 mol L^{-1}), followed by titration with $FeSO_4$ (1 mol L^{-1}). The measured organic carbon was recorded as Cfrac1, Cfrac2, and Cfrac3. C1 is the content of Cfrac1, C2 is the difference between Cfrac2 and Cfrac1, C3 is the difference between Cfrac3 and Cfrac2, and C4 is the difference between SOC content and Cfrac (Cfrac1 and Cfrac2 and Cfrac3). Soil particles were analyzed by the method described by Xiao et al (2014). Soil pH was estimated for a 1:2.5 soil/water mixture using an electronic pH meter fitted with a glass electrode (WTW pH 330, WTW, Weilheim, Germany). Soil enzyme activity was determined using the assays modified from Guan (1986) and described by Xue et al (2017). In brief, saccharase activity was determined by 3, 5-dinitro salicylic acid colorimetry using sucrose as the substrate and expressed as μmol glucose g^{-1} dry sample. Urease activity was determined by indophenol colorimetry using urea as the substrate and expressed as μmol ammonium g^{-1} dry sample. Phosphatase activity was determined by disodium phenyl phosphate colorimetry and expressed as μmol phenol g^{-1} dry sample. Catalase activity was titrated over 20 min using 0.1 mol·L^{-1} $KMnO_4$ and expressed as μmol $KMnO_4$ g^{-1} dry sample. Polyphenol oxidase activity was determined using iodine titrimetric method and expressed as μmol I_2 g^{-1} dry sample.

2.5. Calculation of relationships among parameters

Margalef richness (R), Shannon-Weiner diversity (H′), and Pielou evenness (E) were selected as indices to study the response of vegetation diversity to the number of years of recovery. These indices were calculated as (Beijing, 1995):

$$R = (S-1)/\lg N \tag{1}$$

$$H' = -\sum p_i \ln p_i \tag{2}$$

$$E = H'/\lg S \tag{3}$$

where, S is the number of species in the plot. N is the total number of species. p_i is the relative importance of species i.

The very labile (C1) and labile (C2) fractions of oxidizable carbon represent the active carbon pool (C_{active}). The less labile (C3) and non-labile (C4) fractions of oxidizable carbon represent the passive carbon pool ($C_{passive}$) (Chan et al., 2001). The SOC stability index (SI) was selected to study the response of SOC stability to vegetation restoration and was calculated as:

$$\text{SOC stability index (SI)} = C_{passive}/C_{active} = (C3 + C4) / (C1 + C2) \tag{4}$$

The C1 was considered labile carbon (C_L). Non-labile carbon (C_{NL})

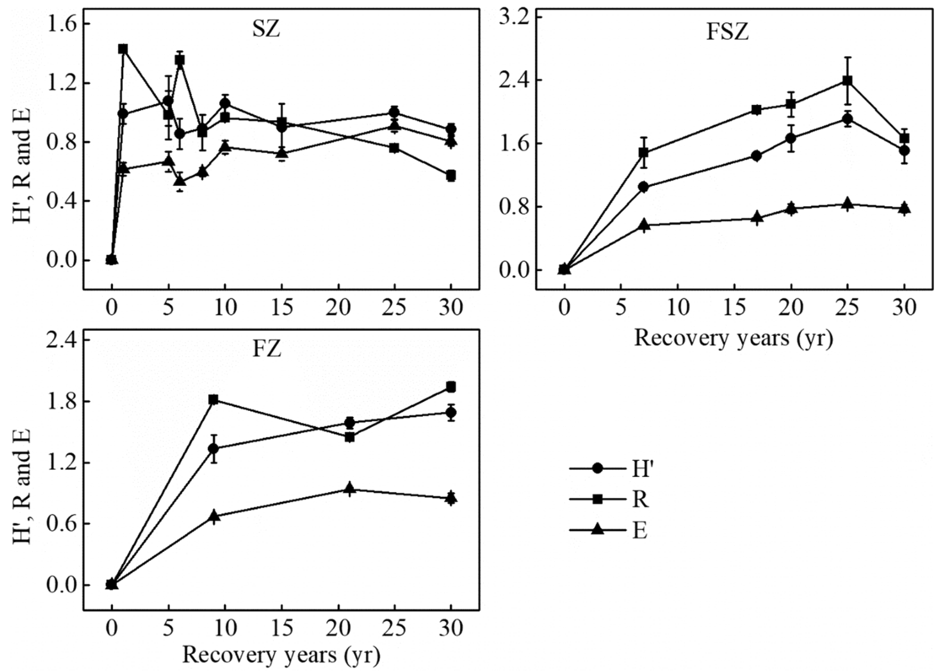

Fig. 2. Changes in the Margalef richness (R), Shannon-Weiner diversity (H′), and Pielou evenness (E) indices of the vegetation zones across the chronosequence. Note: Values on vertical bars are means ± standard error (SE); SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

was calculated as $C_{NL} = SOC - C_L$ (Maia et al., 2007). Other related indices were obtained by the following equations (Blair et al., 1995):

$$\text{Carbon preference index (CPI)} = SOC_{grassland}/SOC_{cropland} \quad (5)$$

$$\text{Lability} = C_L/C_{NL} \quad (6)$$

$$\text{Lability Index (LI)} = \text{Lability}_{grassland}/\ \text{Lability}_{cropland} \quad (7)$$

$$\text{Carbon Management Index (CMI)} = \text{CPI} \times \text{LI} \times 100 \quad (8)$$

The rate of change (K) in soil enzyme activity, oxidizable carbon fractions, CMI, and SI were determined by the linear regression or cubic equation regression analysis of soil enzyme activity, oxidizable carbon fraction content, CMI, SI, and number of years of recovery.

$$f(\mathrm{x}) = y_0 + K_1 \times \mathrm{x} \quad (9)$$

$$K_1 = f'(x) = df(\mathrm{x})/dx \quad (10)$$

$$F(\mathrm{x}) = y_0 + \mathrm{a} \times x^3 + b \times x^2 + c \times x \quad (11)$$

$$K_2 = F'(x) = dF(x)/dx \quad (12)$$

where, $f(x)$ represents liner equation regression model. K_1 indicates the rate of change of different parameters determined by the linear equation regression model. x is the interval of years of recovery. $F(\mathrm{x})$ represents cubic equation regression model. K_2 indicates the rate of change of different parameters determined by the cubic equation regression model. a, b, c are the model parameters of cubic equation regression model.

2.6. Statistical analysis

One-way ANOVA was used to analyze the effects of years of recovery on plant diversity, soil chemical properties, soil enzymatic activity, soil oxidizable carbon fraction content, CMI, and SI. Means were compared by Duncan's post hoc test ($P < 0.05$). The S-W test was used to check the distribution of variations; all data followed a normal distribution. Pearson's correlation analysis was applied to determine correlations among soil enzymatic activity, soil oxidizable carbon fraction content, and SI. All statistical analyses were performed in SPSS v. 21.0 (IBM Corp., Armonk, NY, USA). Figures were drawn using Origin v. 9.0 (OriginLab Corp., Northampton, MA, USA).

Redundancy analysis (RDA) was used to determine the relationships among environmental variables (plant diversity and soil chemical properties) and species variables (soil enzymatic activity, soil oxidizable carbon fraction content, and SI) in the three vegetation zones. Before RDA, gradient lengths were measured by Detrended Correspondence Analysis (DCA). The first gradient lengths of the three vegetation zones were < 3 (0.66, 0.54, and 0.34), thus a linear method was applied. The red arrows represent the environmental variables, and the black arrows represent the species variables. Acute, obtuse, and right angles between arrows indicate positive, negative, and no correlations, respectively. Factors influencing soil enzyme activity, soil oxidizable carbon fraction content, and SOC stability in the vegetation zones were identified. The first gradient length in the DCA was < 3 (0.04); therefore, RDA was performed using Canoco v. 5.0. to determine the relationships among environmental variables (MAP, MAT, plant diversity, and soil chemical properties) and species variables (soil enzymatic activity, soil oxidizable carbon fraction content, and SI).

3. Results

3.1. Changes in the Margalef richness (R), Shannon-Weiner diversity (H′), and Pielou evenness (E) indices of the vegetation zones after cropland abandonment

H′ and E of steppe zone (SZ) initially increased for 0 to 5 years after cropland abandonment, and proceeded to stabilize thereafter. In contrast, R did not change significantly. R for forest-steppe zone (FSZ) had the same characteristics as H′ during recovery. R initially increased, peaked after 25 years, and decreased in subsequent years. E gradually increased over the recovery period. H′, R, and E of forest zone (FZ) initially increased from year 0 to 9 after cropland abandonment, and stabilized thereafter (Fig. 2).

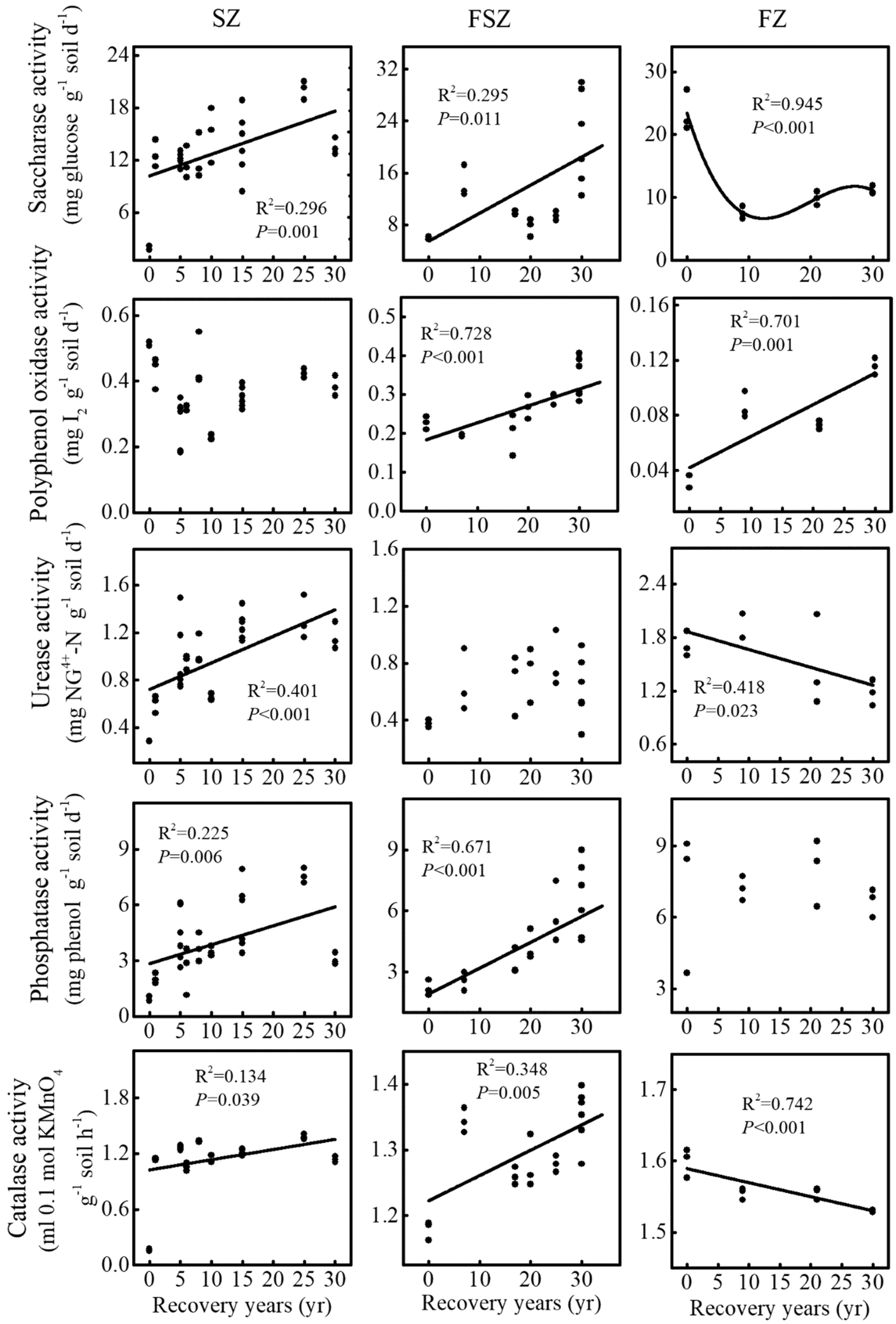

Fig. 3. Changes in the soil enzyme activity of the vegetation zones across the chronosequence. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

3.2. Soil enzyme activity dynamics in the vegetation zones after cropland abandonment

The activity of soil enzymes linearly increased with recovery years after cropland abandonment in SZ (saccharase, urease, phosphatase, and catalase activity), FSZ (saccharase, polyphenol oxidase, phosphatase, and catalase activity), and FZ (polyphenol oxidase activity). Polyphenol oxidase activity did not change significantly in SZ but varied to a greater extent during the early period of recovery than during the late period of recovery. Urease activity increased marginally in FSZ over the recovery period, showing lower variation during the early recovery period than during the late recovery period. The change in saccharase activity was represented by a cubic equation regression with time, which initially decreased from year 0 to 9 after cropland abandonment in FZ, but increased thereafter. Phosphatase activity decreased marginally after cropland abandonment in FZ, whereas urease and catalase activity decreased distinctly over time (Fig. 3). The rates of change in saccharase, phosphatase, and polyphenol oxidase activities were overall higher after cropland abandonment for FSZ (0.356, 0.157, and 0.005, respectively) than for SZ (0.248, 0.102, and 0, respectively) and FZ (-, -, and 0.002, respectively) (except for saccharase, 21 year). Similarly, the rates of change in urease and catalase activity were

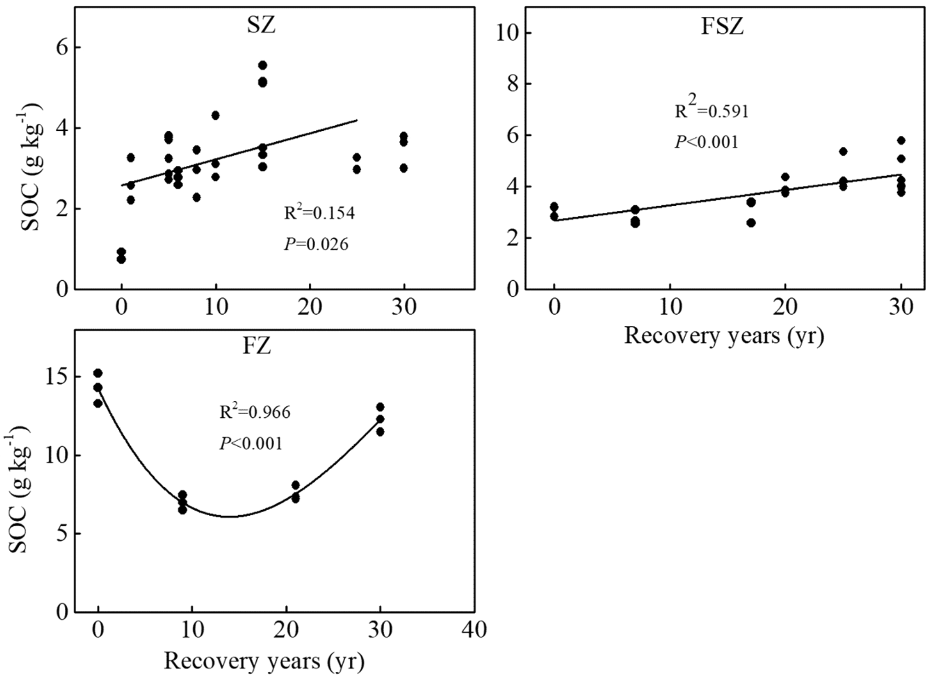

Fig. 4. Changes in the soil organic carbon (SOC) content of the vegetation zones across the chronosequence. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

higher after cropland abandonment for SZ (0.022 and 0.011, respectively) than for FSZ (0 and 0.004, respectively) and FZ (0.020 and 0.002, respectively) (Fig. 3; Tables S1, S2).

3.3. Changes in soil organic carbon (SOC) in the vegetation zones after cropland abandonment

In SZ and FSZ, SOC linearly increased with the number of years of recovery. SOC initially decreased during year 0 to 9 after cropland abandonment in FZ, but increased thereafter (Fig. 4). The rate of change in SOC was lower after cropland abandonment for SZ (0.042) than for FSZ (0.060) (Fig. 4; Table S1).

3.4. Dynamics in the soil oxidizable carbon fraction of the vegetation zones after cropland abandonment

Very labile (C1), labile (C2) and less labile (C3) of soil oxidizable carbon fractions in SZ and C1, C2, C3, and non-labile (C4) of soil oxidizable carbon fraction in FSZ linearly increased with the number of years of recovery after cropland abandonment. C1, C2, and C3 initially decreased in FZ during years 0 to 9 after cropland abandonment, but increased thereafter. In contrast, C4 did not significantly change after cropland abandonment (Fig. 5). The rates of change after cropland abandonment in C1, C2, and C3 for SZ (0.014, 0.010, and 0.007, respectively) were higher than those for FSZ (0.011, 0.008, and 0, respectively) (Fig. 5; Table S1).

3.5. Changes in carbon management index (CMI) in the vegetation zones after cropland abandonment

In SZ and FZ, CMI linearly increased with the number of years of recovery after cropland abandonment. However, CMI in FSZ did not change significantly (Fig. 6). The rate of change after cropland abandonment in CMI was higher for SZ (1.478) than for FZ (1.239) (Fig. 6; Table S1).

3.6. Changes in SOC stability index (SI) in the vegetation zones after cropland abandonment

In SZ and FSZ, SI linearly decreased with the number of years of recovery after cropland abandonment. In contrast, SI did not change significantly after cropland abandonment in FZ (Fig. 7). The rate of change in SI after cropland abandonment was higher for FSZ (0.016) than for SZ (0.010) (Fig. 7; Table S1).

3.7. Influence of soil factors, R, E, and H′ on soil enzyme activity and SOC stability

The RDA analysis showed certain differences in the relationships among soil enzyme activity, soil oxidizable carbon fractions, SI, and environmental factors for the three vegetation types (Fig. 8a, b, c). For SZ, vegetation diversity and soil chemical factors explained 71.3% of the variation in soil enzyme activity, soil oxidizable carbon fraction content, and SI. The first two axes explained 56.4% and 19.6% of the variation, respectively. Simple term effects showed that E explained 48.1% of the variation, whereas total carbon (TN), H′, SOC, and coverage explained 18.1%, 4.3%, 3.8%, and 3.8% of the variation, respectively. SOC, TN, available potassium (AK), available nitrogen (AN), available phosphorus (AP), E, and H′ were positively correlated with C1, C2, C3, urease activity, phosphatase activity, and catalase activity but were negatively correlated with C4 and SI. R, clay, silt, and coverage were positively correlated with C4 and SI but were negatively correlated with C1, C2, C3, urease activity, phosphatase activity, and catalase activity (Fig. 8a).

For FSZ, vegetation diversity and soil chemical factors explained 72.6% of the variation in soil enzyme activity, soil oxidizable carbon fraction content, and SI. The first two axes explained 80.2% and 5.5% of the variation, respectively. Simple term effects showed that TN explained 35.1% of the variation, whereas E, sand, AK, and SOC explained 18.8%, 9.8%, 5.8%, and 4.8% of the variation, respectively. SOC, TN, AK, AN, coverage, R, E, and H′ were positively correlated with C1, C2, C3, total phosphorus (TP), urease activity, phosphatase activity, polyphenol oxidase activity, saccharase activity, and catalase activity but were negatively correlated with SI (Fig. 8b).

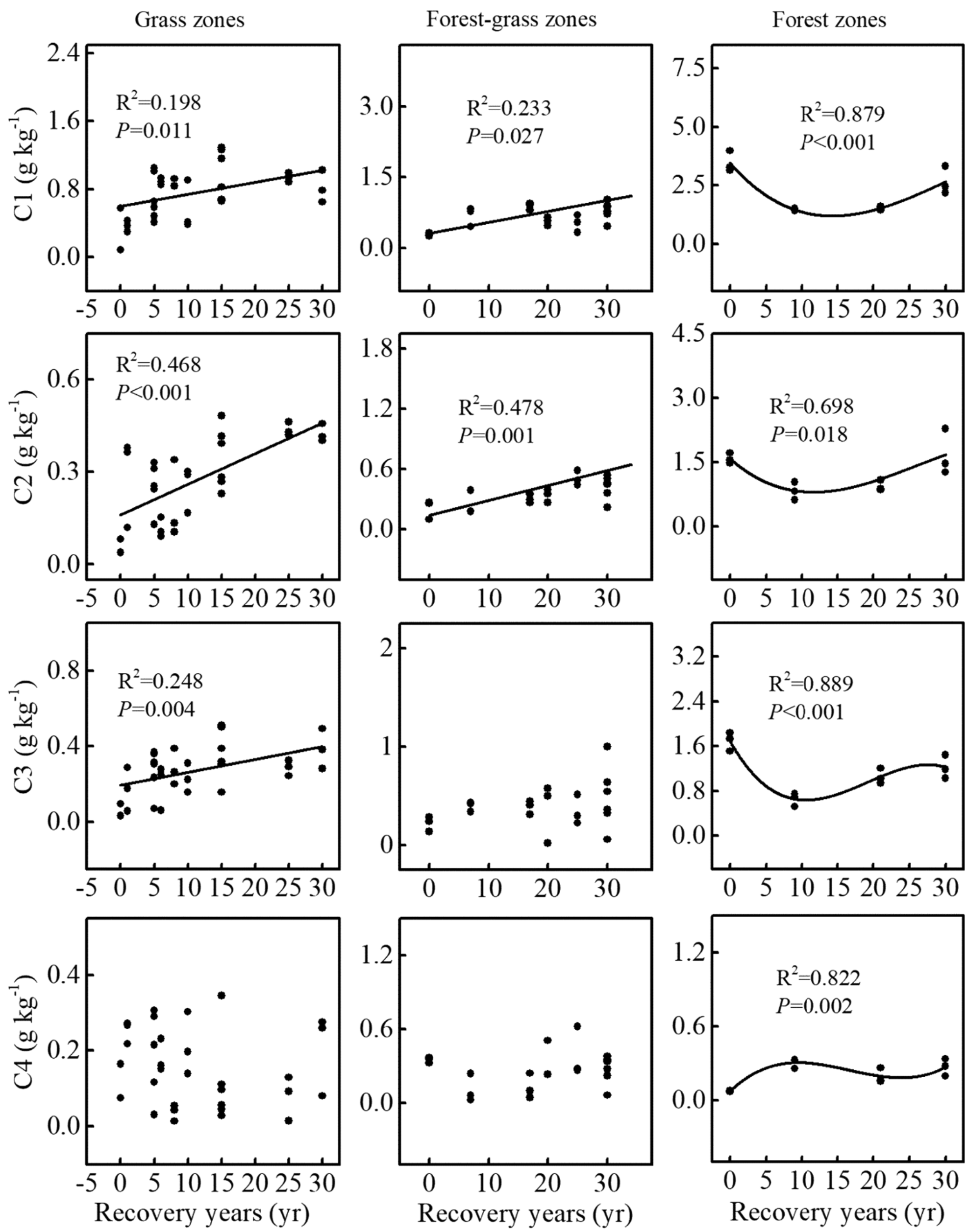

Fig. 5. Changes in the very labile soil oxidizable carbon fraction (C1), labile soil oxidizable carbon fraction (C2), less labile soil oxidizable carbon fraction (C3), and nonlabile soil oxidizable carbon fraction (C4) of the vegetation zones across the chronosequence. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

For FZ, vegetation diversity and soil chemical factors explained 95.0% of the variation in soil enzyme activity, soil oxidizable carbon fraction content, and SI. The first two axes explained 93.9% and 4.4% of the variation, respectively. Simple term effects showed that R explained 79.2% of the variation, whereas TN, AK, AN, and sand explained 10.0%, 3.1%, 2.5%, and 1.7% of the variation, respectively. SOC, TN, AN, AP, and sand were positively correlated with C1, C2, C3, urease activity, saccharase activity, and catalase activity but were negatively correlated with C4, polyphenol oxidase activity, and SI. R, E, H′, TP, and pH were significantly and positively correlated with C4, polyphenol oxidase activity, and SI but were negatively correlated with C1, C2, C3, urease activity, saccharase activity, and catalase activity (Fig. 8c).

4. Discussion

4.1. Effect of time of recovery and vegetation zone on soil enzyme activity

Our results showed that overall soil enzyme activity increased after cropland abandonment in steppe zone (SZ) and forest-steppe zone (FSZ). This observation is consistent with previous studies (An et al., 2009; Xiao et al., 2020; Xu et al., 2020b). Soil enzymes are mainly derived from root exudates, litter, and microorganisms (Pausch and Kuzyakov, 2018). Vegetation restoration has positive effects on the end root system (Han et al., 2012), litter biomass (Chang et al., 2017), and soil microbial activity (Xu et al., 2020b), which, in turn, increase soil

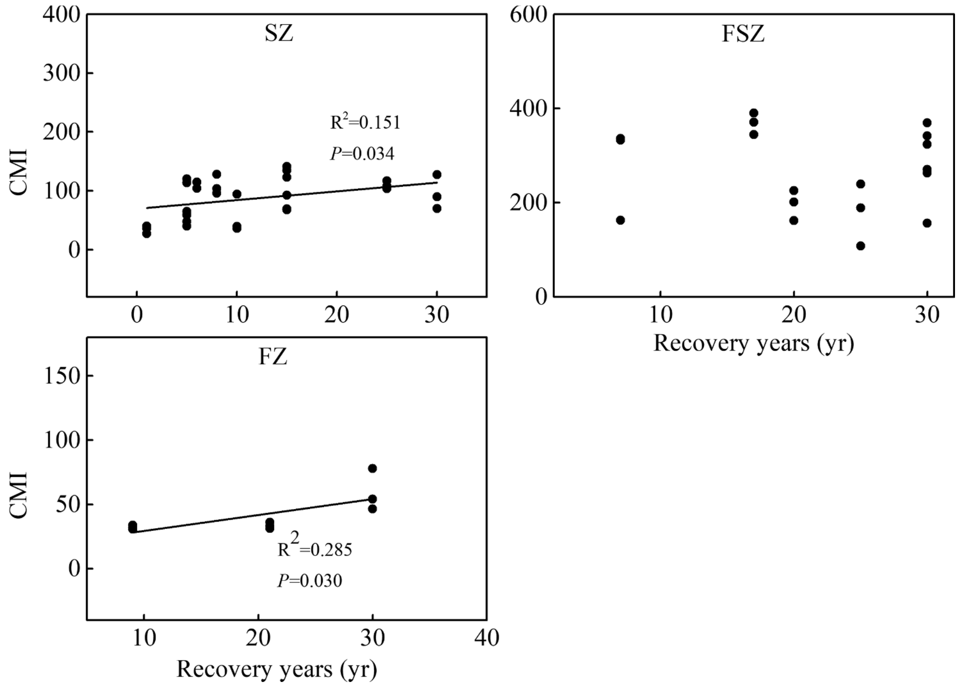

Fig. 6. Changes in the soil organic carbon management index (CMI) of the vegetation zones across the chronosequence. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

enzyme activity. In parallel, soil enzyme activity is strongly influenced by substrate supply (Yin et al., 2019). After the vegetation cover has recovered, plant litter accumulates on the soil surface, increasing soil nutrients (Xu et al., 2019). In turn, the amounts of carbon and nitrogen available to soil microorganisms also increase (Bowles et al., 2014). Similarly, vegetation stimulates soil enzyme activity, contributing to the development of a conducive soil environment and nutrient accumulation and cycling (Ren et al., 2017). Simultaneously, the accumulation of organic carbon significantly improves the biological and chemical properties of soil, increasing the number and diversity of microorganisms as well as the number of enzymes secreted (An et al., 2009). After cropland abandonment, plants grow profuse root systems in the soil. As these systems develop, the energy requirements of the plant for growth increase. Root growth and metabolism reportedly alter microbial communities and populations (Jones et al., 2009). Roots secrete numerous enzymes (Han et al., 2012) and enhance soil enzyme activity. After cropland abandonment, soil water retention and fertility are augmented (Liu et al., 2018). These responses increased the migration of soil material, along with soil water, promoting enzyme movement and activity. The current study demonstrated that soil

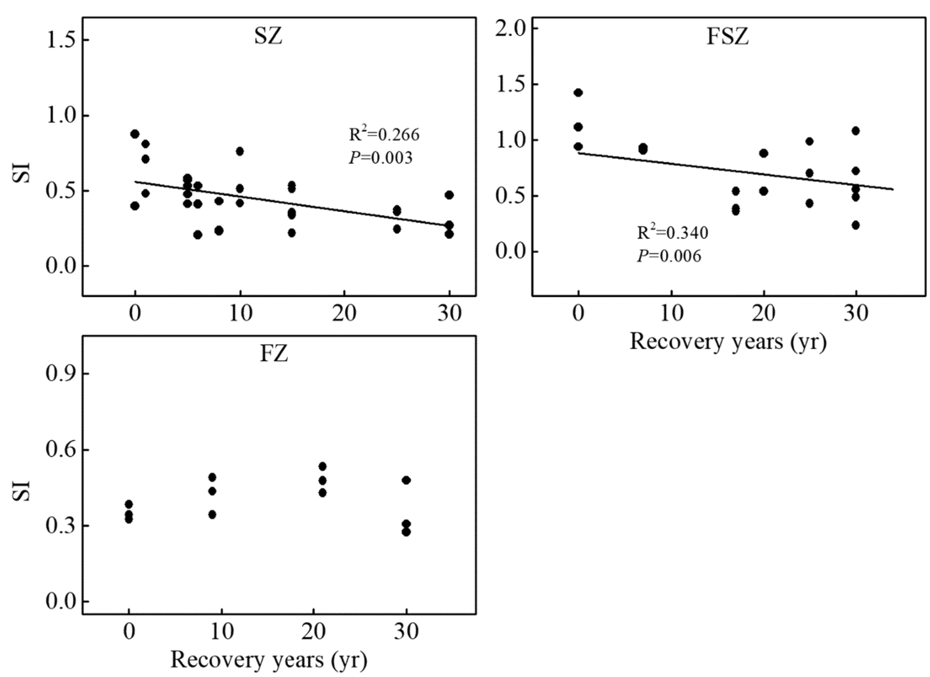

Fig. 7. Changes in the soil organic carbon stability index (SI) of the vegetation zones across the chronosequence. Notes: SZ, steppe zone; FSZ, forest-steppe zone; FZ, forest zone.

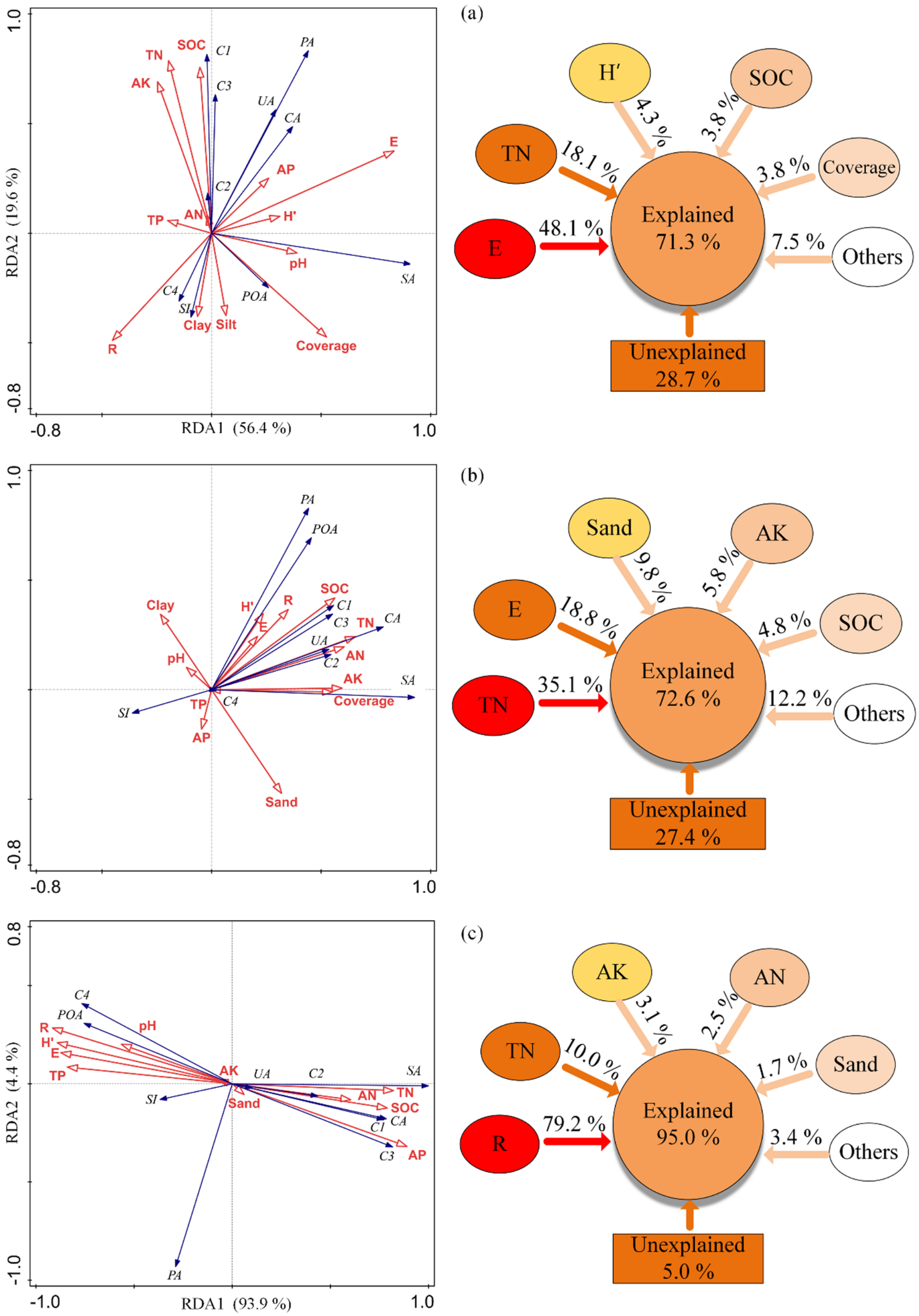

Fig. 8. Relationships among plant diversity, soil physicochemical properties index, soil enzyme activity, soil oxidizable carbon fraction, and soil organic carbon index (SI) according to redundancy analysis (RDA) and % of variance explained by each factor. (a) Analysis of the relationships among plant diversity, soil physicochemical properties index, soil enzyme activity, soil oxidizable carbon fraction, and SI in the steppe zone (SZ). (b) Analysis of the relationships among plant diversity, soil physicochemical properties index, soil enzyme activity, soil oxidizable carbon fraction, and SI in the forest-steppe zone (FSZ). (c) Analysis of the relationships among plant diversity, soil physicochemical properties index, soil enzyme activity, soil oxidizable carbon fraction, and SI in the forest zone (FZ). Notes: R, Margalef richness; H′, Shannon-Weiner diversity; E, Pielou evenness; SA, soil saccharase activity; POA, soil polyphenol oxidase activity; UA, soil urease activity; PA, soil phosphatase activity; CA, soil catalase activity; SOC, soil organic carbon; C1, very labile soil oxidizable carbon fraction; C2, labile soil oxidizable carbon fraction; C3, less labile soil oxidizable carbon fraction; C4, non-labile soil oxidizable carbon fraction; TN, soil total nitrogen; TP, soil total phosphorus; AN, soil available nitrogen; AP, soil available phosphorus; AK, soil available potassium.

enzyme activity sensitively reflects the process of vegetation recovery after cropland abandonment, with increased soil enzyme activity indicating improvements in soil biological properties in response to vegetation restoration.

The current study showed higher rates of change in saccharase activity, phosphatase activity, and polyphenol oxidase activity after cropland abandonment in FSZ than in SZ and in forest zone (FZ). Conversely, higher rates of change were observed in urease activity and catalase activity after cropland abandonment in SZ than in and FZ. Redundancy analysis (RDA) (Fig. 8) showed that Margalef richness (R), Shannon-Weiner diversity (H′), and Pielou evenness (E), and soil organic carbon (SOC) were the dominant factors responsible for the changes in phosphatase activity and polyphenol oxidase activity in FSZ after cropland abandonment. In contrast, vegetation coverage and SOC were the main factors influencing changes in saccharase activity, phosphatase activity, and polyphenol oxidase activity. In turn, saccharase activity was strongly and positively correlated with vegetation coverage. High plant diversity supported higher soil enzyme levels. Increases in plant diversity enhance plant productivity (Chang et al., 2017) and reduce surface transpiration, increasing soil water content and nutrients (Liu et al., 2018). These effects provided more carbon and nitrogen sources for soil enzymes and increased the quantity of enzymes

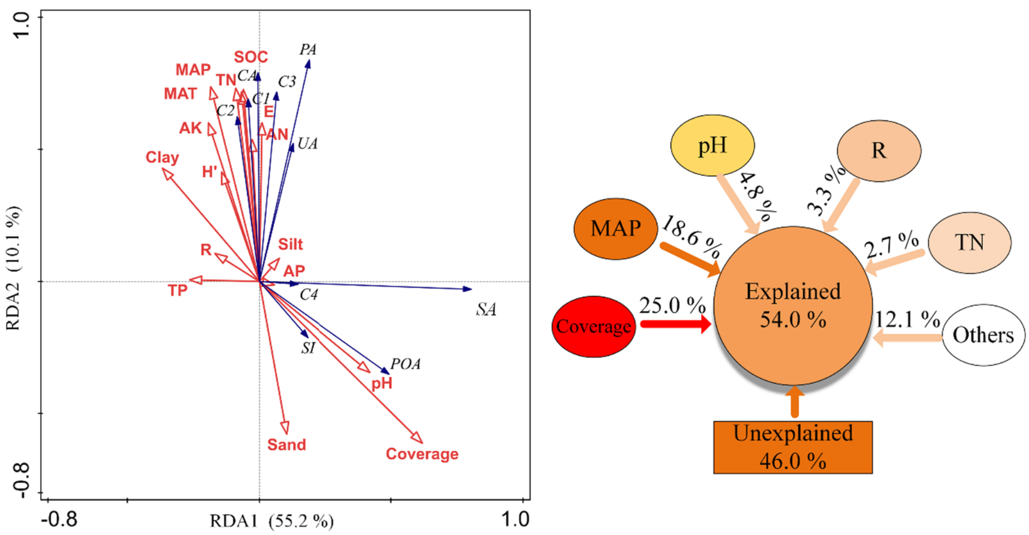

Fig. 9. Relationships among plant diversity, soil physicochemical properties index, mean annual precipitation (MAP), mean annual temperature (MAT), soil enzyme activity, soil oxidizable carbon fraction, and soil organic carbon index (SI) according to redundancy analysis (RDA) and % variance explained by each factor. Notes: R, Margalef richness; H′, Shannon-Weiner diversity; E, Pielou evenness; SA, soil saccharase activity; POA, soil polyphenol oxidase activity; UA, soil urease activity; PA, soil phosphatase activity; CA, soil catalase activity; SOC, soil organic carbon; C1, very labile soil oxidizable carbon fraction; C2, labile soil oxidizable carbon fraction; C3, less labile soil oxidizable carbon fraction; C4, non-labile soil oxidizable carbon fraction; TN, soil total nitrogen; TP, soil total phosphorus; AN, soil available nitrogen; AP, soil available phosphorus; AK, soil available potassium.

secreted. In SZ, however, soil enzyme activity was only slightly affected by plant diversity. In addition, we found that soil enzyme activity in FZ first decreased and then increased (saccharase activity), or decreased (urease activity, catalase activity), which contradicted our second hypothesis. RDA (Fig. 9) showed that the mean annual precipitation (MAT), mean annual temperature (MAP), SOC, total nitrogen (TN), available nitrogen (AN), available potassium (AK), H′, E, and vegetation coverage were the main factors influencing the changes in enzyme activity, except saccharase activity. FZ had relatively higher MAT, MAP (Fig. 1), SOC, TN, AN, and AK (Fig. 4, S1), with soil enzyme activity being positively correlated with soil nutrient content but negatively correlated with plant diversity (Fig. 8c). Thus, FZ had environmental conditions that were conducive to microbial survival and metabolic activity. Rainfall also affected the restoration of primary productivity and soil organic matter at the ecosystem level, which, in turn, influenced substrate availability and microbial nutrient metabolism (Ru et al., 2017). The sloped croplands in FZ had relatively higher soil enzyme levels and activity than SZ and FSZ. A previous study showed that soil microbial activity increased with MAP (Cui et al., 2019). In the present study, plant diversity did not significantly increase in FZ over 9 years. Consequently, enzyme activity in this region increased non-significantly or decreased. Saccharase activity and urease activity are key enzymes for carbon and nitrogen mineralization in the soil, respectively (Li et al., 2003), and are often strongly affected by the supply of substrates (Yin et al., 2019). This observation was confirmed in the current study through the initial decline and subsequent increase in SOC and TN content (Fig. S1). The results showed that MAT, MAP, soil nutrients, and plant diversity were the main factors affecting soil enzyme activity after cropland abandonment, and soil enzyme activity in FZ, which had relatively higher MAT and MAP, showed no significant changes.

4.2. *Effect of recovery time and vegetation zone on SOC stability*

SOC, very labile (C1), labile (C2) and less labile (C3) of soil oxidizable carbon fractions increased linearly in SZ and FSZ, whereas SOC stability decreased linearly after cropland abandonment. Plant litter and root exudates are the main sources of soil carbon (Fontaine et al., 2007). In general, plant biomass, plant coverage, root system development, and number of root systems increase with recovery time (Chang et al., 2017; Han et al., 2012; Xu et al., 2020b). Litter and root exudates are returned to the soil by microorganisms; thus, the soil capacity for carbon also increases with time (Pausch and Kuzyakov, 2018). In parallel, soil erosion and nutrient loss decline over time (Liu et al., 2018). Thus, soil microbial activity increases during the period of recovery, with soil carbon storage and conversion being enhanced (Leon et al., 2016). RDA showed that soil nutrient levels were the dominant factors driving changes in soil oxidizable carbon fractions and SOC stability in the current study. In particular, the soil nutrient content (except for available nutrients) increased with time since cropland abandonment (Fig. S1). Therefore, nutrient levels caused soil oxidizable carbon fractions to increase and SOC stability to decrease. In addition, the rates of increase in the fractions were higher for C1 (0.014 and 0.011) and C2 (0.010 and 0.008) than for C3 (0.007 and 0.006) in SZ and FSZ. This difference explained the decline in SOC stability over time, supporting our first hypothesis. Our study showed that cropland abandonment enhanced the SOC and active carbon fractions; however, SOC under these conditions was unstable.

For FZ, SOC, C1, C2, and C3 decreased at the onset of recovery. This phenomenon might be attributed to the relatively low plant growth during the early stages of recovery (Liu et al., 2013). Consequently, very low plant productivity was returned to the soil. Plant growth depends on an increase in the metabolic rate and the consumption of large quantities of soil organic matter (Groenendijk et al., 2002). However, in our study, SOC, C1, and C3 were lower at the later stage of recovery (30 years) than at 0 years. SOC, C1, and C3 are affected by soil nutrients, temperature, and humidity (Ziegler et al., 2013). Relatively high rainfall and temperature influence plant growth and microbial activity by affecting the physical structure and nutrient levels of soil (Smith, 2008). Thus, FZ might have supported comparatively high plant productivity, soil organic matter decomposition rates, root exudate levels, and soil microbial activity at 0 years. Plant biomass and root exudates are returned to the soil as carbon sources via microbial action (Pausch and Kuzyakov, 2018). During the latter stages of recovery from cropland abandonment, plants are restored, but to a level below that in the sloped cropland. In parallel, the soil nutrient content is lower than that of the sloped cropland (Fig. S1). In particular, SOC, C1, C2, and C3 showed no significant change after 0 years. In addition, SOC stability did not significantly change over time. This observation contradicted our second hypothesis. The soil nutrient content after cropland abandonment was either lower than, or not significantly different to, that of sloped cropland (Fig. S1). Initially, C1, C2, and C3 decreased and then increased with the number of years of recovery, thus offsetting the influence of the active carbon fractions on SOC stability. Therefore, SOC

Table 2
Pearson correlations among soil enzyme activity, soil oxidizable carbon fraction, and soil organic carbon index (SI) for the vegetation zones.

Vegetation zones	Soil enzyme activity	C1	C2	C3	C4	SI
	Catalase activity	0.469*	0.416*	0.508**	−0.042	−0.375*
	Polyphenol oxidase activity	−0.239	−0.110	−0.216	−0.275	0.010
SZ	Phosphatase activity	0.716**	0.323	0.663**	−0.288	−0.434*
	Urease activity	0.726**	0.159	0.622**	−0.276	−0.499**
	Saccharase activity	0.159	0.193	0.347	−0.029	−0.132
	Catalase activity	0.679**	0.222	0.520**	−0.274	−0.528**
	Polyphenol oxidase activity	0.535**	0.036	0.422*	−0.148	−0.155
FSZ	Phosphatase activity	0.530**	0.257	0.447*	−0.056	−0.291
	Urease activity	0.778**	0.284	0.612**	0.027	−0.328
	Saccharase activity	0.537**	0.424*	0.382*	−0.037	−0.448*
	Catalase activity	0.494	0.019	0.466	−0.691*	−0.184
	Polyphenol oxidase activity	−0.396	−0.047	−0.544	0.821**	0.019
FZ	Phosphatase activity	−0.037	−0.166	0.079	−0.140	0.236
	Urease activity	−0.184	−0.462	−0.182	−0.001	0.312
	Saccharase activity	0.785**	0.422	0.820**	−0.769**	−0.358

Notes: SZ, steppe zone; FSZ, forest-steppe zone; SZ, forest zone; C1, very labile soil oxidizable carbon fraction; C2, labile soil oxidizable carbon fraction; C3, less labile soil oxidizable carbon fraction; C4, nonlabile soil oxidizable carbon fraction.

* Indicates a significant difference at the level of 0.05.

** Indicates a significant difference at the level of 0.01.

stability did not change significantly.

4.3. Association between soil enzyme activity and SOC stability

The activity of soil enzyme is closely related to C1 and C3 transformation and changes in SOC stability, possibly because of the mutual promotion and synergy among soil enzyme activity, soil oxidizable carbon fraction content, and soil microbial biomass (Cui et al., 2019). Soils with high nutrient levels generally have comparatively higher microbial content and soil enzyme activity, with increased soil enzyme activity accelerating soil carbon decomposition and transformation (Xaio et al., 2020). For FZ, the effects of soil enzyme activity (except for saccharase activity) on C1, C2, C3, and SOC stability index (SI) were not significant (Table 2). Therefore, we believe that changes in soil enzyme activity had no effect on soil oxidizable carbon fractions or SOC stability. However, there were significant correlations among catalase activity, polyphenol oxidase activity, saccharase activity, and non-labile (C4) of soil oxidizable carbon fraction. Soil enzyme activity, soil oxidizable carbon fractions, and changes in SOC stability are associated with soil chemical properties, plant diversity, soil microbial type and quantity, parent material, temperature, moisture, aggregates, and fauna (Sardans and Peñuelas, 2005). These interactions are extremely complex. Future research should focus on elucidating the reasons for the changes in soil enzyme activity and SOC stability in the various vegetation zones. The mechanisms by which soil enzyme activity alters SOC stability must also be investigated.

Overall, this study provided new insights into the manner in which vegetation restoration affects soil enzyme activity and SOC stability in different vegetation zones (SZ, FSZ, and FZ), facilitating the assessment of changes in soil enzymes after vegetation restoration in the arid and semi-arid regions of the Loess Plateau (China) and global climate change assessment. In parallel, we provided direct evidence of the factors that drive the changes in soil enzyme activity and SOC stability in the three vegetation zones. However, the results of the current study contradict the findings of Tang et al. (2010) and Jiang et al. (2018). These previous studies showed that SOC stability enhanced the overall ecological restoration. In our study, SOC stability was enhanced in SZ and FSZ after cropland abandonment, but not in FZ. Soucémarianadin et al. (2018) showed that SOC stability is also affected by soil type and climate. Tang et al. (2010) studied soils in a tropical temperate climate, whereas Jiang et al. (2018) studied red soil in a subtropical climate. In comparison, in our study, we studied loess soils in arid and semi-arid regions. Thus, it was not possible to determine whether these differences were driven by soil type or climate. In addition, SOC stability is influenced by plant lignin and the soil microbial community (Ma et al., 2019), the chemistry of the tissues of different plant and tree species (Angst et al., 2019), plant biomass, and soil depth (Xu et al., 2020a). Thus, future research should focus on evaluating SOC stability under different soil types and climatic conditions. Moreover, additional factors, such as soil microbial community, plant biomass, plant species, and plant functional characteristics, influencing the changes in SOC stability should be evaluated after cropland abandonment.

5. Conclusion

Mean annual precipitation and temperature were the main factors affecting soil enzyme activity, soil oxidizable carbon fractions, and SOC stability. They caused different changes in these parameters over time in different vegetation zones after cropland abandonment. The results showed that active carbon fractions (very labile [C1] and labile [C2]) of soil oxidizable carbon fractions exhibited relatively higher rates of increase than passive carbon fractions (less labile [C3] and non-labile [C4]) of soil oxidizable carbon fraction, resulting in a decrease in SOC stability with the number of years of recovery in steppe zone (SZ) and forest-steppe zone (FSZ). In contrast, the SOC stability of forest zone (FZ) did not significantly change. Contrary to our hypothesis, the changes in soil enzyme activity with time did not positively correlate with rainfall gradients. Briefly, the soil enzyme activity increased linearly with time in SZ and FSZ. In FZ, polyphenol oxidase activity increased linearly, urease and catalase activities decreased linearly, and the change in saccharase activity was represented by a cubic equation regression with time. The rates of change in saccharase, phosphatase, and polyphenol oxidase activities were overall higher in FSZ than in SZ and FZ. Plant diversity and soil nutrient levels were the main factors affecting soil enzyme activity and SOC stability in FSZ and FZ, with catalase, phosphatase, and urease activities being negatively correlated with SOC stability. Soil enzyme activity and SOC stability in SZ were weakly correlated with plant diversity. The findings of this study are expected to help guide the evaluation of soil enzyme activity and the management of SOC and global climate change in various vegetation zones after cropland abandonment on the Loess Plateau of China.

Declaration of Competing Interest

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

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Declaration of Competing Interest

All the authors declare no conflicts of interest.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2020.104812.

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