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Disentangling the direct and indirect effects of cropland abandonment on soil microbial activity in grassland soil at different depths

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ABSTRACT

Cropland abandonment strongly affects plant-soil interactions. However, knowledge remains limited about how the production and diversity of plants and soil physicochemical parameters drive changes in soil microbial activity (such as microbial biomass, respiration, and enzyme activity) after cropland abandonment. Here, we investigated a grassland restoration chronosequence (0–30 years) to determine the dynamics of soil microbial biomass, respiration, and enzyme activity in the Loess Hilly, Region (China). Overall, cropland abandonment caused an increase in soil microbial activity primarily in the 0–20 cm soil layers. The metabolic quotient in the 0–10 cm layer decreased linearly with time since abandonment (recovery years). Structural equation models showed that recovery years directly and indirectly affected changes to soil microbial activity. Plant species richness, aboveground biomass, and soil organic carbon explained a large proportion of the variability in soil microbial activity in the 0–20 cm layer. However, the variability in soil microbial activity was mostly explained by plant species richness, belowground biomass, and soil total nitrogen in the 20–50 cm layers. Our results indicate that during recovery after cropland abandonment, changes in soil microbial activity are driven by plant characteristics and soil physicochemical parameters, with different drivers at different soil depths.

1. Introduction

Cropland abandonment is an effective way to improve soil quality (Chang et al., 2017). However, cropland abandonment directly and negatively affects the quality and quantity cultivated land, subsequently impacting national food security and social stability (Raj and Watanabe, 2006). The process of cropland abandonment could help to improve the productivity of land, along with slowing soil and water loss, which could have important practical significance for improving the ecology of the natural environment (Raj and Watanabe, 2006). However, such improvement highly depends on well programmed and managed cropland abandonment strategies for some years, such as soil and water conservation techniques to avoid land degradation (Shi and Shao, 2000).

Soil microbial biomass refers to the total amount of living microorganisms living in the soil (Jenkinson et al., 2004). It is highly dynamic and is related to soil carbon, nitrogen, and phosphorus cycling (Jenkinson et al., 2004; Yevdokimov et al., 2016). Soil enzymes are mainly derived from root exudates, litter, and microorganisms (Nannipieri et al., 2018; Pausch and Kuzyakov, 2018). Soil respiration regulates the key processes that facilitate ecosystem functioning (Singh et al., 2010). Soil microorganisms play a functional role in the cycling of nutrients in ecosystems (Geisseler and Scow, 2014). Soil microbial activity is an important indicator of soil fertility and quality (Geisseler and Scow, 2014; Kristiina et al., 2014; Yevdokimov et al., 2016). Soil respiration is closely related to microbial activity and reflects the functional characteristics of soil microbial communities. Therefore, it has been widely used in the evaluation of soil ecosystems and soil quality (Singh et al., 2010). Nutrient cycling by soil microorganisms, for example, the decomposition of plant litter into soil nutrients, is

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Table 1
Detailed information on the sample sites selected for the study.

Treatments	Vegetation age (a)	Numbers of sites	Slop (°)	Vegetation coverage(%)	Main vegetations
Slop cropland	0	3	19–24.5	–	*Setaria italic, Glycine* max
Grassland	2	3	13–27	12.1–19.8	*Geranium wilfordii, Artemisia capillaris, Euphorbia humifusa,Setaria viridis*
	5	3	17.3–19	30.7–57.3	*Artemisia leucophylla, Artemisia capillaris, Sonchus oleraceus,Lespedeza bicolo, Heteropappus altaicus*
	8	8	12–40	18–60.4	*Lespedeza bicolo, Artemisia capillaris, Potentilla bifurca, Bothriochloa ischaemum, Stipa bungeana*
	11	3	23–37	24–76.3	*Tripolium vulgare, Lespedeza bicolo, Stipa bungeana, Cleistogenes squarrosa, Artemisia capillaris, Heteropappus altaicus*
	15	3	14–19	39.8–76	*Tripolium vulgare, Lespedeza bicolo, Stipa bungeana, Cleistogenes squarrosa, Stipa grandis, Heteropappus altaicus*
	18	3	22–30	16–49	*Bothriochloa ischaemum, Artemisia leucophylla,Tripolium vulgare, Lespedeza bicolo, Stipa bungeana, Cleistogenes squarrosa, Stipa grandis*
	26	4	22–28	21.8–68.9	*Bothriochloa ischaemum, Artemisia leucophylla, Tripolium vulgare, Lespedeza bicolo, Stipa bungeana, Cleistogenes squarrosa*
	30	7	14–29	33–79.7	*Bothriochloa ischaemum, Artemisia leucophylla, Tripolium vulgare, Lespedeza bicolo, Stipa bungeana, Cleistogenes squarrosa, Stipa grandis*
Natural grassland	> 50	4	12–31	34–89.2	*Bothriochloa ischaemum, Artemisia leucophylla, Tripolium vulgare,Lespedeza bicolo, Cleistogenes squarrosa, Stipa grandis*

important for vegetation growth (Liang et al., 2017; Spohn et al., 2016). Soil enzymes play an important role in this process (Mooshammer et al., 2014). Therefore, the study of soil microbial activity can be used to explore and analyze the structure and function of soil ecosystems, crop yield, and sustainable use of soil.

Soil microbial activity is strongly affected by vegetation restoration and has been found to gradually improve along a revegetation chronosequence (Zhang et al., 2019; Zhu et al., 2019; Xiao et al., 2020; Xu et al., 2020a). Meanwhile, many studies have shown that precipitation (Na et al., 2019), vegetation type (Sinha et al., 2009), soil type (Cui et al., 2018), and soil depth (de Medeiros et al., 2017) strongly influence soil microbial activity.

However, the mechanisms driving changes to soil microbial activity in response to cropland abandonment remain poorly understood. Various studies have demonstrated that the plant biomass, plant diversity, and soil nutrient concentrations in grasslands significantly increase after abandonment (Cui et al., 2019; Liu et al., 2017). Through a *meta*-analysis, Chen et al. (2019) showed that plant diversity is positively correlated with soil microbial biomass. Another study showed that the species richness and biomass of plants significantly affect soil microbial composition, enzyme activity, and respiration (Zhu et al., 2019). However, knowledge remains limited on how soil microbial activity changes in relation to soil and plant community characteristics at different soil depths.

Since the beginning of the 20th century, the natural environment of the Loess Plateau has been subjected to increasing degradation due to increasing human population and unregulated development and utilization of land resources. These activities have reduced vegetation coverage and caused major soil erosion. To reduce soil erosion, and improve vegetation coverage, soil quality, vegetation productivity, and soil sustainability, China began implementing the “Grain for Green” project in 1999. Cropland abandonment is one of the main measures that has been implemented to restore vegetation in this region.

Existing research and theories have demonstrated that cropland abandonment enhances soil microbial activity in grasslands (Cui et al., 2019; Xiao et al., 2020); however, knowledge remains limited on how these effects are indirectly mediated by the productivity and diversity of plants and soil physicochemical parameters. Therefore, our aim is to address the following questions: (1) how the productivity and diversity of plants and soil physicochemical parameters drive changes of soil microbial activity along a grassland restoration chronosequence, and (2) whether these changes vary with soil depth. We hypothesized that: (1) the number of years since abandonment (recovery years) had direct and indirect effects on soil microbial activity changes; (2) the indirect effect of recovery years is mainly through changes in plant characteristics and soil physicochemical parameters; and (3) both direct and indirect effects decrease with increasing soil depth, owing to a decrease in influencing factors with depth.

2. Materials and methods

2.1. Study site

This study was conducted at the Zhifanggou watershed on the central Loess Plateau, China (36°51′ N, 109°19′ E; 1010–1400 m above sea level [a.s.l.]). This region covers 8.27 km^2 and is a national demonstration area for China’s “Grain for Green” program. This area has a warm temperate and semi-arid climate. The annual average precipitation is 483 mm, and the annual average temperature is 8.8 °C. The watershed is characterized by vertical and horizontal gullies, broken terrain, and sparse vegetation. The soil type is mainly loess soil, which has a porous texture, and poor retention of water and fertilizer. The grass communities are dominated by *Bothriochloa ischae*, *Stipa bungeana, Artemisia giraldii*, and *Artemisia gmelinii*, depending on the stage of succession.

2.2. Study site selection

To determine the dynamics of soil microbial activity after cropland abandonment, we adopted the "space for time" method in this study. Thirty-four grassland sites were selected, with eight age classes of abandonment (2, 5, 8, 11, 15, 18, 26, and 30 years since abandonment) (Table 1), for which detailed records had been collected by the local experimental station. In addition, three sloped cropland sites and four natural grassland (NG) sites (grassland for over 50 years) were selected to represent cropland before abandonment (age = 0 years) and to assess the stage of recovery, respectively.

2.3. Biomass sample collection

First, three 2 m × 2 m plots were randomly selected at each site. Sampling surveys were conducted to determine the direction of slope, along with information on the plant species present and their height and abundance. Aboveground biomass (AGB) and litter biomass (LB) were determined using the full access method at each plot. Belowground biomass (BGB) was determined by excavating roots from the 0–50 cm soil layer. Next, the samples were transferred to the laboratory. Roots were rinsed to remove attached soil particles. Then, all biomass samples were placed in an oven at 105 ℃ for 5 min and further dried at 65 ℃ until a constant weight was attained.

2.4. Soil sample collection

Soil bulk density was obtained using the ring knife method. In short, we use a ring knife to take soil samples from four soil depths (0–10 cm, 10–20 cm, 20–30 cm, and 30–50 cm) of two soil profiles (to 50 cm depth) in each plot. A soil drilling sampler (4-cm inner diameter) was used to sample soils from four depths in each plot. A random sampling method was adopted in this process. Fifteen samples were collected at each depth. Soil samples from the same plot and depth were mixed to form composite samples, and were transferred to the laboratory. Roots, stones, and visible animals were removed, and the soil samples were separated into two portions. One of the portions was used for the determination of soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP). The other portion was kept at 4 ℃ and used to determine soil microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), basal respiration (BR), saccharase activity (SA), urease activity (UA), phosphatase activity (PA), and catalase activity (CA).

2.5. Laboratory analysis

SOC and TN were measured using the Walkley and Black method and Kjeldahl method (Nelson and Sommers, 1982; Bremner et al., 1982), respectively. TP was measured using the ammonium molybdate method (Schade et al., 2003). Soil microbial biomass was measured using the fumigation extraction method (Vance et al., 1987). SA, UA, PA, and CA were determined using an assay modified from Guan (1986) as described by Wang et al. (2012) and Xue et al. (2017). BR was measured using the method described by Xue et al. (2017).

2.6. Data analysis

Following the description by Beijing (1995), plant diversity indexes were calculated as follows:

$$\text{Shannon} - \text{Weinerdiversityindex}(H') = -\sum p_i \ln p_i \quad (1)$$

Pielou evenness index (E)=H′/lgS (2)

Margalef richness index (R) = (S − 1)/lgN (3)where: p_i is the relative importance of species i; N is the total number of species; and S is the number of species.

The metabolic quotient (qCO_2) (d^{-1}) was calculated as described by (Powlson and Jenkinson, 1976):

$$qCO_2 = \frac{BR}{MBC} \quad (4)$$

where: BR is the basal respiration (mg kg^{-1} d^{-1}) and MBC is the soil microbial biomass carbon (mg kg^{-1}).

2.7. Statistical analysis

To test whether MBC, MBN, BR, qCO_2, SA, UA, PA, and CA differed statistically with years after abandonment (recovery years), one-way ANOVAs were used ($P < 0.05$). The distribution of all variables was assessed before the ANOVAs using the S-W test.

To further link soil microbial activity with plant productivity (AGB, BGB, and LB, of which BGB was the total biomass in the 0–50 cm soil layers), and plant diversity (R, E and H'), and soil physicochemical properties (bulk density, SOC, TN, and TP of each soil depth), structural equation models (SEMs) were used. SEMs is a data analysis method where the model can be summarized using latent variables, with linear relationships existing between latent variables (Bollen, 1998). The latent variable of activity included MBC, MBN, BR, qCO_2, SA, UA, PA, and CA. All sites were used in the SEMs except for the NG sites, as we cannot ensure the specific recovery year for these sites. Maximum likelihood (ML) was used to calculate the path coefficients between different variables.

Based on the SEMs, redundancy analysis (RDA) was selected to evaluate the associations between plant characteristics and soil physicochemical parameters, and species variables (MBC, MBN, soil BR, qCO_2, SA, UA, PA and CA) at the four soil depths. Before conducting the RDA, the gradient length was tested using detrended correspondence analysis (DCA). Detrended correspondence analysis and RDA were performed using CANOCO 5.0.

3. Results

3.1. Soil microbial biomass varied in relation to recovery years and soil depths

Overall, soil microbial biomass increased linearly with recovery years in the 0–20 cm layers (Fig. 1a, b). MBC increased from 35.08 to 244.95 mg kg^{-1} soil in the 0–10 cm layer and from 35.91 to 130.36 mg kg^{-1} soil in the 10–20 cm layer. MBN increased from 17.55 to 32.62 mg kg^{-1} soil in the 0–10 cm layer and from 10.84 to 19.84 mg kg^{-1} soil in the 10–20 cm layer. Overall, soil microbial biomass decreased with increasing soil depth under all recovery years (Fig. 1a, b). In the 0–10 cm layer, the MBC and MBN of GL30 were lower than that in NG. Specifically, the MBC of GL30 accounted for 54.87% that of NG, while MBN accounted for 60.11% (Fig. 1c, d).

3.2. BR and qCO_2 varied with recovery years and soil depths

Overall, the BR of the 0–20 cm layers increased linearly over 30 years of abandonment, increasing from 39.36 to 61.48 mg CO_2-C kg^{-1} d^{-1} in the 0–10 cm layer and from 40.86 to 51.55 mg CO_2-C kg^{-1} d^{-1} in the 10–20 cm layer (Fig. 2a). The qCO_2 of grassland soils linearly decreased in the 0–10 cm layer over 30 years of abandonment, decreasing from 1.77 to 0.28 d^{-1} (Fig. 2b). Overall, soil BR decreased with soil depth for all recovery times (Fig. 2a, b). Across all four depths, the BR in the four soil depths of GL30 was significantly lower than that in NG. Specifically, the BR of GL30 accounted for 71.24%, 77.26%, 74.62%, and 86.24% that of NG in the four layers, respectively (Fig. 2c). However, compared with NG, qCO_2 in the four soil depths of GL30 showed no significant difference (Fig. 2d).

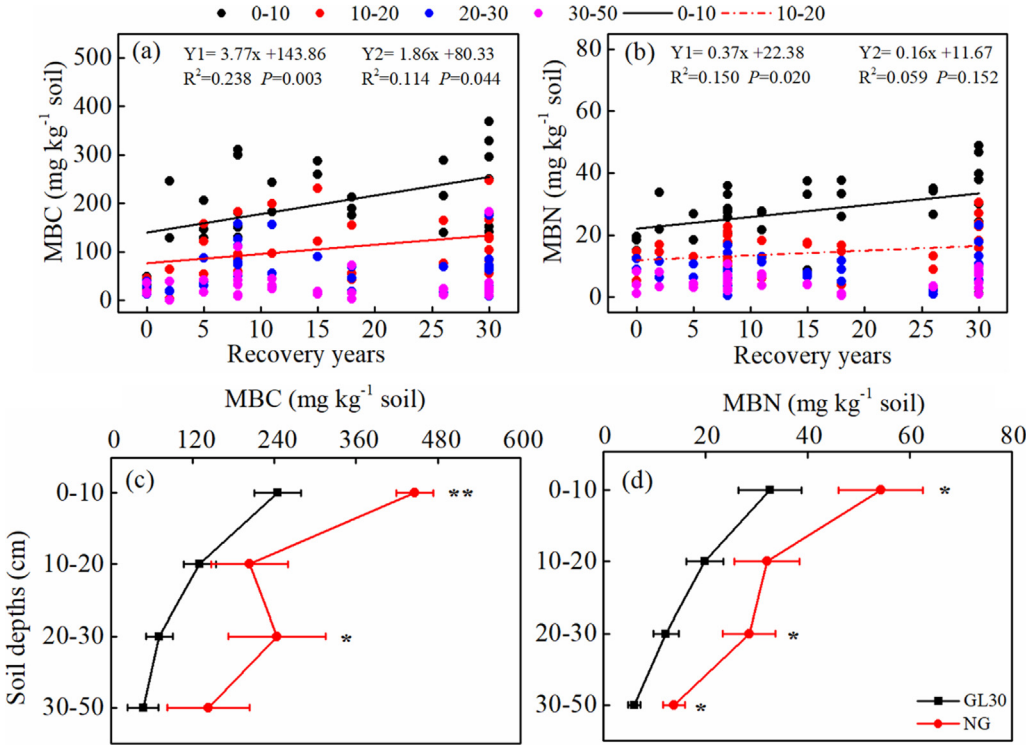

Fig. 1. Changes in (a) soil microbial biomass carbon (MBC) and (b) soil microbial biomass nitrogen (MBN) across the chronosequence; (c) MBC and (d) MBN at different soil depths in a grassland (GL) at 30 years of recovery compared to that in a natural grassland (NG). Note: * denotes significant differences at $P < 0.05$; ** denotes significant differences at $P < 0.01$; Y1 represents the linear regression of the 0–10 cm layer; Y2 represents the linear regression of the 10–20 cm layer; solid lines represent linear regressions that reached a significance level of $P < 0.05$, and the dashed lines represent linear trends that have not reached statistical significance; un-regressed data points indicate that there is no obvious change across the recovery years.

3.3. Soil enzyme activity varied with recovery years and soil depths

SA and PA in the 0–30 cm layers, UA in the 0–20 cm layers, and CA in the 0–10 cm layer linearly increased with recovery years (Fig. 3a, b, c, d). In comparison, overall SA, UA, PA, and CA decreased with soil depth for all recovery times (Fig. 3a, b, c, d). The UA and PA of GL30 were significantly lower than those of NG in the 0–10 cm layer. Specifically, the UA of GL30 accounted for 74.56% of that of NG, while PA accounted for 73.09% (Fig. 4b, c).

3.4. Factor affecting patterns in soil microbial activity

For the 0–10 cm layer, the SEMs explained 69% the variability in soil microbial activity. Recovery years indirectly affected soil microbial activity through R, AGB, LB, and SOC (Fig. 5a). For the 10–20 cm layer, the SEMs explained 53% of the variability in soil microbial activity. Similarly, recovery years indirectly affected soil microbial activity through R, AGB, LB, and SOC (Fig. 5b). In the 20–30 cm layer, the SEMs explained 33% of the variability in soil microbial activity. R, AGB, BGB,

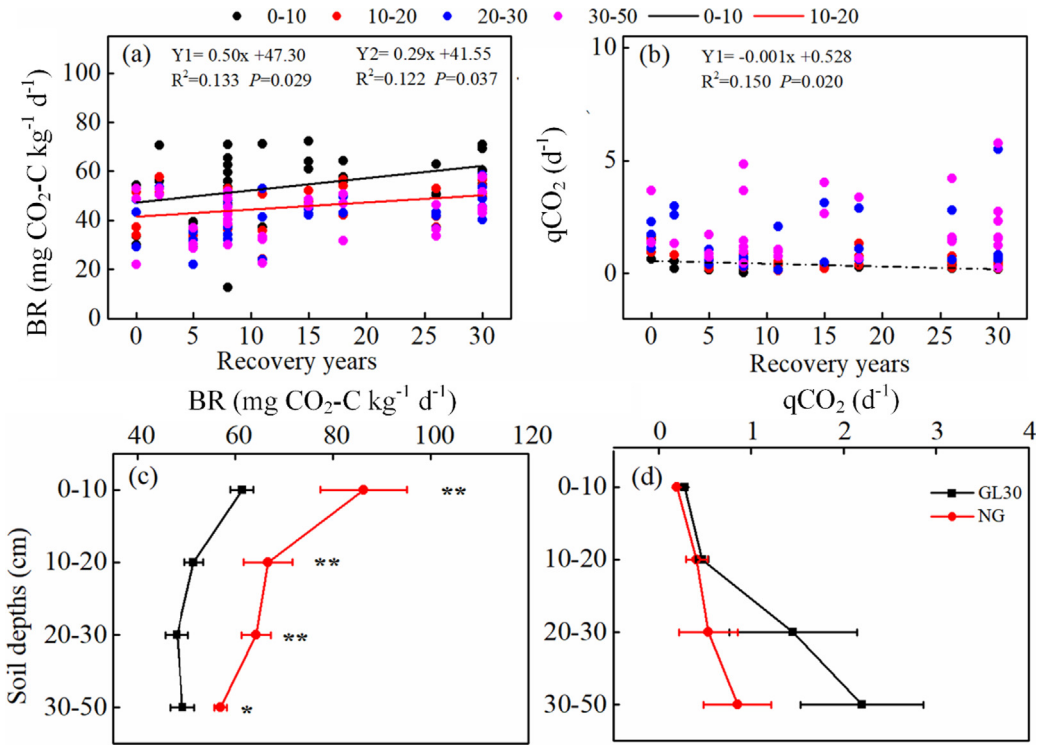

Fig. 2. Changes in (a) soil basal respiration (BR) and (b) metabolic quotient (qCO_2) across the chronosequence; (c) BR and (d) qCO_2 at different soil depths in a grassland (GL) at 30 years of recovery compared to that in a natural grassland (NG). Note: * denotes significant differences at $P < 0.05$; ** denotes significant differences at $P < 0.01$. *** denotes significant differences at $P < 0.001$; Y1 represents a linear regression of the 0–10 cm layer; Y2 represents a linear regression at the 10–20 cm layer; solid lines represent linear regressions at a significant difference level of $P < 0.05$, and the dashed line represent linear trends that have not reached statistical significance; un-regressed points indicate that there is no obvious linear change across the recovery years.

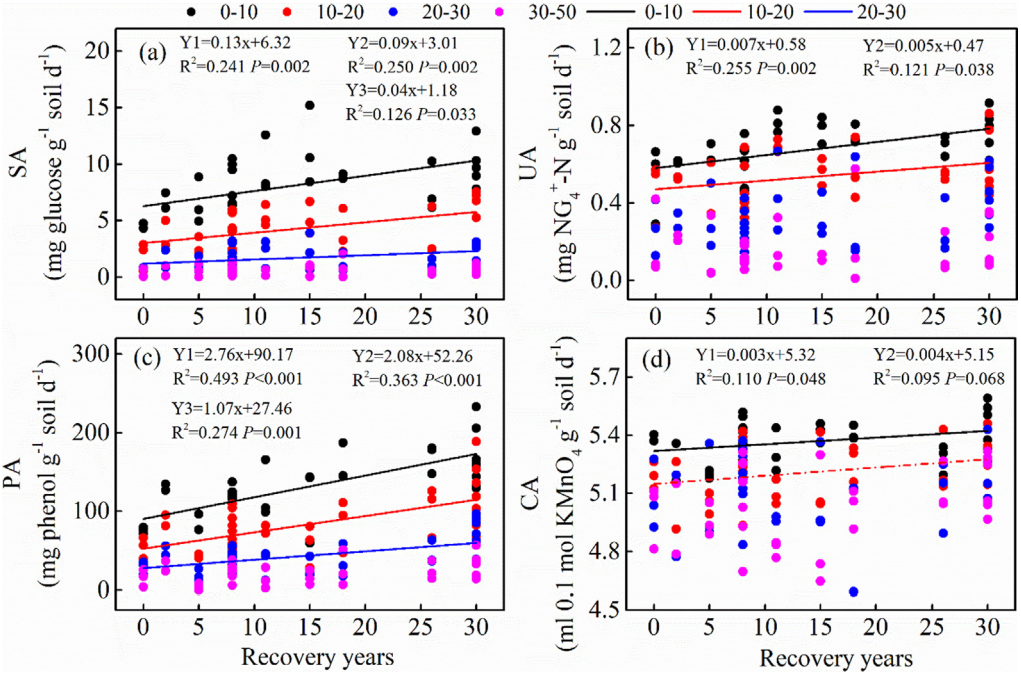

Fig. 3. Changes in (a) soil saccharase activity (SA), (b) soil urease activity (UA), (c) soil phosphatase activity (PA) and (d) soil catalase activity (CA) across the chronosequence. Note: Y1 represents linear regressions of the 0–10 cm layer; Y2 represents linear regressions of the 10–20 cm layer; Y3 represents linear regressions of the 20–30 cm layer; solid lines represent linear regressions that reached a significant difference level of $P < 0.05$, and dashed lines represent trends across the chronosequence that have not reached statistical significance; un-regressed points represent factors that do not show any linear relationship across the recovery years.

and TN directly affected soil microbial activity. Recovery years indirectly affected soil microbial activity through R, AGB, BGB, LB, TN, and SOC (Fig. 5c). The SEMs explained 8% of the variability in soil microbial activity for the 30–50 cm layer. R, BGB, and TN directly affected soil microbial activity. However, recovery years indirectly affected soil microbial activity through R, AGB, BGB, TN, and SOC (Fig. 5d).

4. Discussion

4.1. Dynamics of soil microbial activity among recovery years and soil depths

The current study demonstrated that cropland abandonment mainly increased soil microbial activity in the 0–20 cm layers, supporting the findings from previous studies (Xiao et al., 2020; Xu et al., 2020a). Soil microbial activity is regulated by many factors, including climate, vegetation, and soil (Nannipieri et al., 2018). Vegetation restoration affects the spatiotemporal dynamics of soil microbial activity, influencing the microclimate, plant biomass, above- and below-ground carbon input, and soil physicochemical properties (Caldwell, 2005).

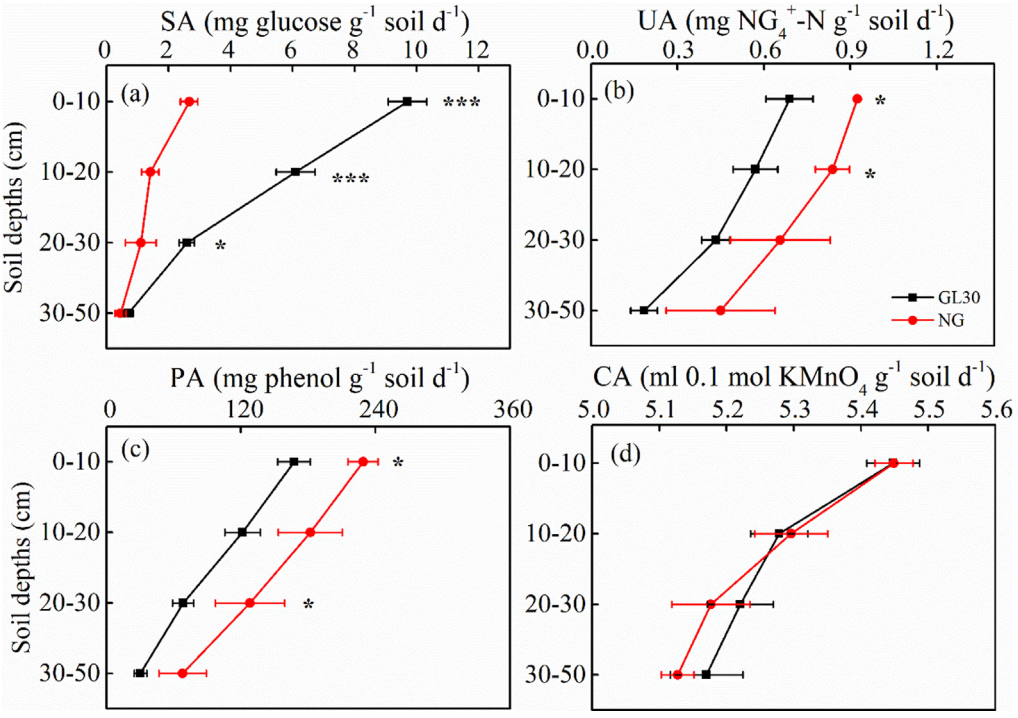

Fig. 4. Soil enzyme activity ((a) soil saccharase activity (SA), (b) soil urease activity (UA), (c) soil phosphatase activity (PA) and (d) soil catalase activity (CA)) at different soil depths in a grassland (GL) at 30 years of recovery compared to that in a natural grassland (NG). Note: * denotes significant difference at $P < 0.05$; *** denotes significant differences at $P < 0.001$.

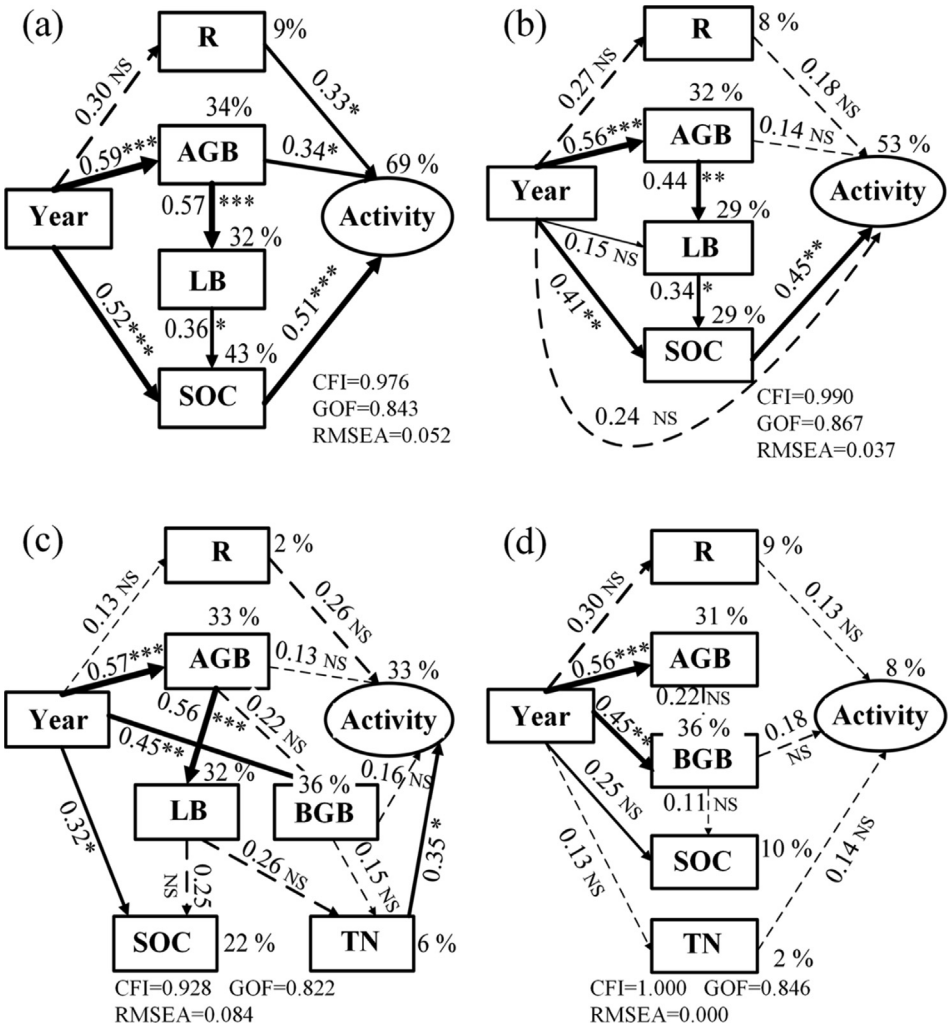

Fig. 5. Structural equation models (SEMs) demonstrating the direct and indirect effects of recovery years on soil microbial activity at: (a) 0–10 cm soil depth; (b) 10–20 cm soil depth; (c) 20–30 cm soil depth; and (d) 30–50 cm soil depth. Note: CFI, comparative fit index; GOF, goodness of fit; RMSEA, root mean square error of approximation; Solid arrows indicate significant relationships ($p > 0.05$); dashed arrows indicate insignificant path coefficients; numbers above arrows indicate standardized path coefficients. Values associated with arrows indicate standardized path coefficients (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, insignificant difference); R, Margalef richness index; AGB, aboveground biomass; BGB, belowground biomass; LB, litter biomass; SOC, soil organic carbon; TN, soil total nitrogen.

First, after cropland abandonment, reduced nutrient loss and large inputs of organic matter result in more nutrients for microbial growth. This can explain the substantial increase in microbial biomass (Burns et al., 2013; Pausch and Kuzyakov, 2018). After cropland is abandoned, vegetation gradually recovers, with an overall increase in the amount of litter (Fig. S1 a), root residue, and secretions being returned to the soil (Xu et al., 2020b). These parameters provide more substrate for microorganisms, which produce more soil enzymes in response (Kurganova et al., 2020; Pausch and Kuzyakov, 2018). Second, compared with croplands, grasslands have more developed ventilation tissues (roots). These tissues excrete more microorganisms, thus changing microbial activity (Caldwell, 2005). Third, soil structure and quality are improved, resulting in a significant increase in the metabolism of microorganisms (Cui et al., 2019; Kalinina et al., 2019).

The current study also showed that soil microbial activity (except SA and PA) changes were poor in the 20–50 cm soil layers. According to the resource allocation theory, soil microbial activity is positively correlated with nutrient availability (Xu et al., 2017). Topsoil directly receives soil nutrients from the litter and root exudates. Overall soil microbial activity decreased with soil depth for all years in our study, corroborating the results of previous studies (Könönen et al., 2018). This may be because of favorable soil ventilation conditions, as well as more litter and humus in the topsoil, which enhance the survival and reproduction of microorganisms (Sinha et al., 2009). With increasing soil depth, SOC content and root biomass decrease (Berger et al., 2002; Xu et al., 2019), ultimately causing soil microbial activity to decline.

In contrast, in the upper soil layer, secretions from plants, animals, and microorganisms accumulate, with strong physiological activity enhancing the secretion of enzymes (Sinha et al., 2009; Yi et al., 2010). qCO_2 is often used as a sensitive indicator of carbon use efficiency by soil microbes (Dilly and Munch, 1996). Thus, a decrease in qCO_2 after cropland abandonment enhances the carbon use efficiency of soil microbes, soil microbial biomass, and humus (Dilly and Munch, 1996). In parallel, when a low qCO_2 indicates that microorganisms are more stable and mature (Huang et al., 2009). The current study showed that soil biological functions gradually recover over time, with damage to soil microbial diversity gradually decreasing after several years of vegetation restoration. In addition, qCO_2 did not change significantly with recovery years in the 10–50 cm layers. Previous studies showed that qCO_2 is significantly affected by soil organic matter (Huang et al., 2009). Thus, qCO_2 might not be sensitive in the 10–50 cm layers because changes to SOC sensitivity in this layer were lower than those in the 0–10 cm layer (Fig. S1 c).

Previous studies showed that soil nutrients fail to reach NG levels after cropland abandonment (Xu et al., 2020c). More importantly, the current study showed that soil microbial activity (except SA and CA) was lower in GL30 compared to NG in the 0–10 cm layer. This result might be attributed to the lower plant biomass, coverage, and plant diversity under GL30 compared to NG (Chang et al., 2017). These disparities lead to lower litter and energy availability for soil microorganisms in grassland, due to more decaying roots (Bastida et al., 2008). In parallel, differences to vegetation biomass can alter the organic matter input to the soil, with soil nutrients failing to reach the levels documented in NG (Fig. S2). In addition, a previous study showed

that the composition of soil microorganisms in abandoned cropland is simpler than that in NG (Thoms et al., 2010). Therefore, the restoration of soil microbial activity might be limited by soil nutrient content during cropland abandonment. Thus, the recovery of soil microorganisms is possible; however, the complete recovery of soil microbial activity was not detected in our chronosequence. Therefore, a number of years are required for the complete recovery of microbial activity after cropland abandonment in this semi-arid environment.

4.2. Factors driving soil microbial activity along the grassland restoration chronosequence at different soil depths

Our results support the general theoretical predictions and empirical findings that soil microbial activity is regulated by recovery time (Chen et al., 2019). Our study showed that plant characteristics and soil physicochemical parameters contribute towards predicting soil microbial activity after cropland abandonment. In particular, R, AGB, LB, and SOC were the major predictors of changes in soil microbial activity in the 0–20 cm soil layers. R, AGB, LB, BGB, TN, and SOC were the major predictors of change in soil microbial activity in the 30–50 cm soil layers, based on the best-fitting models.

Our study demonstrated that changes in R, AGB, and SOC explained a large proportion of the variability in soil microbial activity in the 0–20 cm layers. This coincided with patterns in plant, soil, and soil microorganism relationships in the grassland community (Chen et al., 2019). As the number of years of recovery increased, plant diversity and abundance at the plant community level also increased. Higher diversity and abundance cause vegetation productivity and topsoil SOC content to increase (Kurganova et al., 2020). The plant biomass (Fig. S1 a), plant species diversity (Fig. S1 b), and soil nutrients (0–20 cm layers) (Fig. S1 c) overall increased with recovery years (Xu et al., 2020b). These positive interactions caused soil microbial activity to increase (Chen et al., 2019). Higher levels of carbon input and better microclimate conditions associated with plant diversity generate more active and diverse microbes and higher enzyme activities (Lange et al., 2015; Kurganova et al., 2018). This high abundance and biomass subsequently reduces evaporation of topsoil moisture, which, in turn, promotes higher soil microbial activity (Lange et al., 2014). Furthermore, high organic carbon content promotes the respiration of soil microbes, which increases the absorption of nutrients (Thomas et al., 2005) and, hence, soil microbial activity. We showed that AGB had a direct and significantly positive effect on LB, with this effect being enhanced by LB. An RDA showed that AGB, R, and SOC were positively correlated with MBC, MBN, BR, SA, UA, PA, and CA. Thus, plant and soil characteristics influence soil microbial activity, which changed along the grassland restoration chronosequence (Fig. 6a, b and Table S1). The biomass and respiration of microbes, along with enzyme activity, responded to SOC in the soil, corroborating R and AGB; however, these responses were higher for SOC when compared with plant characteristics (Fig. 7).

R, AGB, BGB, and TN explained a unique proportion of soil microbial activity in the 20–30 cm layer. In comparison, the direct effects of R, AGB, and SOC gradually weakened in the model. AGB becomes increasingly concentrated in the soil surface through the formation of litter (Chen et al., 2019); consequently, the effect of microbial activity decline. However, AGB indirectly affected soil microbial activity through its effect on BGB. Previous studies showed that the properties of the topsoil mainly depend on AGB, whereas the properties of deeper layers mainly depend on the roots of vegetation (Vesterdal et al., 2002). The RDA showed that AGB, BGB, LB, and SOC were positively correlated with MBC, BR, SA, UA, and PA (Fig. 6c and Table S1). Thus, AGB, BGB, LB, and SOC could be used to indicate changes in soil microbial activity in the 20–30 cm layer. R, BGB, and TN weakly affected soil microbial activity, while the direct effects of AGB and SOC disappeared in the 30–50 cm layer. Our study showed that AGB and SOC did not drive variation in soil microbial activity at soil depths > 30 cm. Furthermore, previous studies have shown that roots are mainly distributed in the 0–30 cm layers (Ugawa et al., 2010). Consequently, R, BGB, and TN only had minor effects on soil microbial activity.

Our study showed that R affected soil microbial activity at all soil depths; however, the overall influence of R on microbial activity gradually declined with increasing soil depth (Fig. 7). During the process of cropland abandonment, plant species richness represents a major factor regulating changes in soil microbial activity at different soil depths. Specifically, high plant species richness enhances soil microbial activity (Fornara and Tilman, 2010). Guenay et al. (2013) demonstrated that plant species richness has a greater effect on microbial activity in deeper soil. In comparison, other studies showed that this effect is stronger in the topsoil and weaker in deeper soil (Steinbeiss et al., 2010). This difference might be influenced by vegetation richness increasing with recovery time. Higher productivity might enhance soil carbon and nutrient input to the soil, with the nutrient content of soil microorganisms gradually increasing (Lange et al., 2015; Ma and Chen, 2018); however, nutrient input decreases with increasing soil depth (Fornara and Tilman, 2010). Therefore, when assessing changes in soil microbial activity, the relationship between soil microbial activity, plants, and soil at greater soil depths must be clarified. Our study showed that the overall effect of recovery time on soil microbial activity gradually decreased with increasing soil depth (< 0.2 in the 30–50 cm soil layer) (Fig. 6b). Thus, vegetation restoration has little effect on microbial activity in deep soil layer, directly or indirectly. This phenomenon was confirmed in our study, showing that the soil microbial activity changes was poor in the 30–50 cm layer, even after 30 years.

4.3. Limitations and uncertainties

Our research identified the factors driving changes in soil microbial activity at different soil depths after cropland abandonment on the Loess Plateau. However, Kim et al. (2019) reported that soil moisture has significant effects on soil microbial biomass and enzyme activities, which might be related to the soil microclimate. After cropland abandonment, the growth of vegetation led to an increase in vegetation coverage (Xu et al., 2020b). Some studies found that vegetation growth will increase shade and reduce water evaporation, thereby creating a warm and humid environment for soil microorganisms, which is conducive to the growth and activity of microorganisms (Settineri et al., 2018). Meanwhile, soil temperature is also an important factor affecting soil microbial activity (Yang et al., 2017), as warm conditions can promote microbial metabolism (Alvarez et al., 1995). Additionally, pH can also affect soil microbial biomass and general microbiological rates (Hinojosa et al., 2004; Speir et al., 1999). Therefore, in our study, it is not clear whether the increase in soil microbial activity after the cropland abandonment is affected by soil moisture, temperature, and pH. Further research on soil microbial activity should be conducted to investigate these variables. Furthermore, we only assessed the impact of recovery of grassland on soil microbial activity, without considering the type of cropland, shrubland and forestland after vegetation restoration, which may lead to uncertainty in our results. Thus, future studies should consider different ecosystems. Additionally, altered precipitation regimes have a marked impact on global climate change (precipitation and temperature), thus having a significant effect on soil microbial activity. For example, in a *meta*-analysis of 70 published articles, Ren et al. (2017) found that higher precipitation results in significantly higher soil microbial activity. However, our understanding of the factors driving these changes in soil microbial activity under different rainfall conditions in still insufficient. Therefore, there is an urgent need to conduct more field experiments on a larger spatial scale (such as the global scale) to determine the drivers of soil microbial activity under different environmental conditions (e.g., rainfall).

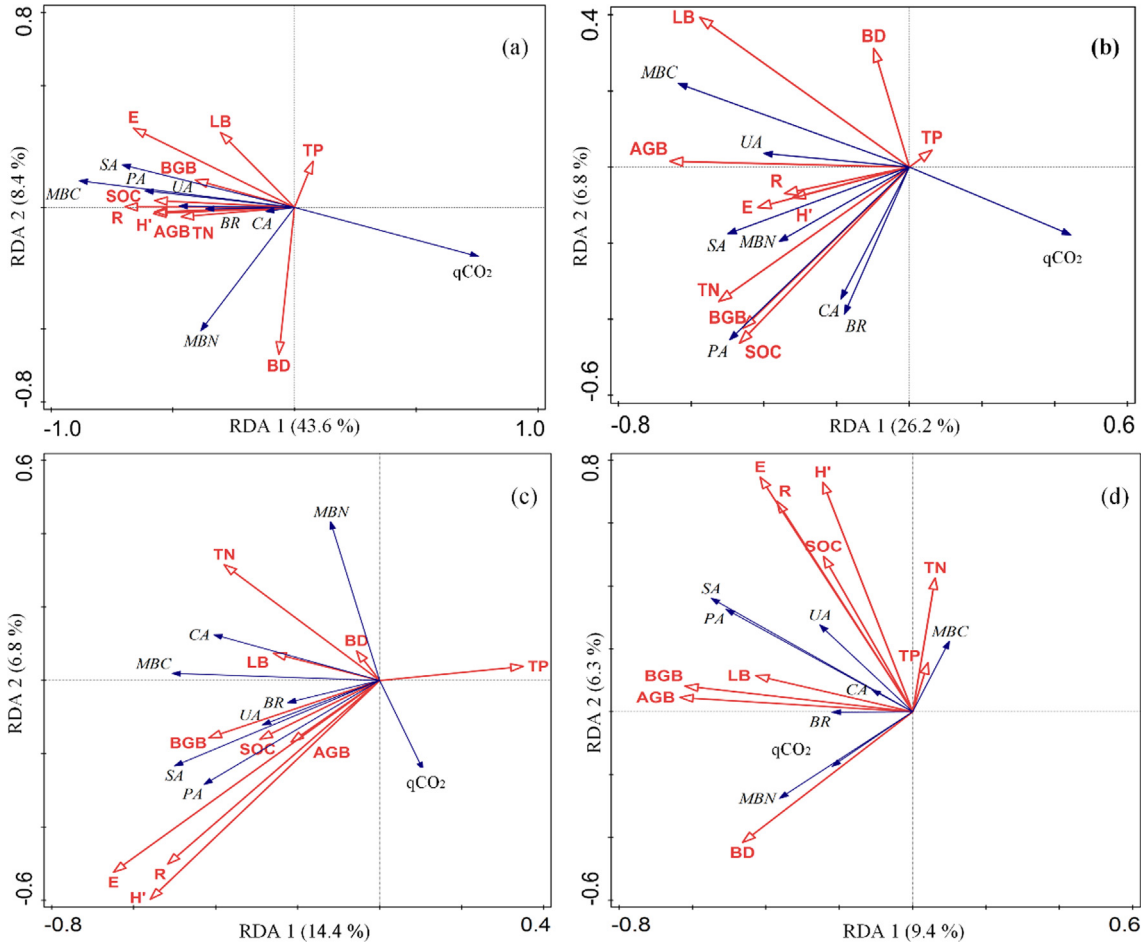

Fig. 6. Relationships among soil microbial biomass, respiration, and enzyme activity (blue arrows), soil properties (red arrows), and plant biomass and plant diversity (red arrows) of 0–10 cm (a), 10–20 cm (b), 20–30 cm (c), and 30–50 cm (d) soil layers based on redundancy analysis (RDA). Notes: H', Shannon-Weiner diversity index; E, Pielou evenness index; R, Margalef richness index; AGB, aboveground biomass; BGB, belowground biomass; LB, litter biomass; BD, soil bulk density; SOC, soil organic carbon; TN, soil total nitrogen; TP, soil total phosphorus; SA, soil saccharase activity; UA, soil urease activity; PA, soil phosphatase activity; CA, soil catalase activity; qCO_2, metabolic quotient. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

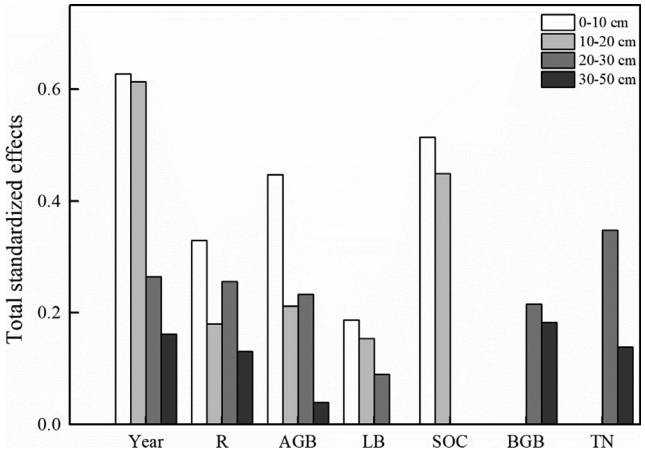

Fig. 7. Total standardized effects for the indexes at different soil depths from structural equation models (SEMs). Note: R, Margalef richness index; AGB, aboveground biomass; BGB, belowground biomass; LB, litter biomass; SOC, soil organic carbon; TN, soil total nitrogen.

4.4. Implications of our studies

Our research showed that overall soil microbial activity in the 0–20 cm soil layers increased after cropland abandonment and identified the effects of plant characteristics and soil physicochemical parameters on soil microbial activity at different soil depths. Previous studies reported that plant diversity, plant biomass, and soil nutrients are important factors affecting soil microbial biomass, enzyme activity, and respiration (Chen et al., 2019; Lange et al., 2015; Na et al., 2019), without considering the effect of soil depth. However, we found that soil depth is important for determining the drivers of soil microbial activity. In our study, soil microbial activity in the 0–20 cm layers was affected by plant species richness, aboveground biomass, and SOC. However, as soil depth increased, plant species richness, belowground biomass, and soil total nitrogen became the main factors influencing soil microbial activity. As our study was based on a relatively longer recovery sequence (2, 5, 8, 11, 15, 18, 26, and 30 years) of grassland after cropland abandonment, it can be used as a reference for the driving factors of soil microbial activity after cropland abandonment in arid and semi-arid areas (Loess Plateau of China). We found that plant characteristics and soil physicochemical parameters provide sufficient information for assessing changes in soil microbial activity with soil depth. Therefore, we propose that plant species richness, aboveground biomass, and soil organic carbon should be used to evaluate changes in soil microbial activity in the 0–20 cm layers, whereas plant species

richness, belowground biomass, and soil total nitrogen should be used to evaluate changes in soil microbial activity in the 20–50 cm layers. This could be widely applied to the grassland restoration process in arid and semi-arid areas.

5. Conclusion

Our study provided direct evidence that cropland abandonment promoted soil microbial biomass, enzyme activity, and respiration in the surface soil (0–20 cm soil layers), with these microbial properties increasing linearly with time since abandonment. We also showed that soil microbial biomass, enzyme activity (except SA and PA), and respiration changes were poor in the 20–50 cm soil layers with time since abandonment. This indicates that cropland abandonment has a greater effect on the surface soil microbial environment, and therefore, it could have a large impact on nutrient cycling in the surface soil. The growth of grass is strongly influenced by the surface soil environmental condition; thus, the increase in microbial activity in the surface soil could play a vital role in improving vegetation productivity. Recovery years affected changes in soil microbial activity in different soil layers, either directly or indirectly, based on plant characteristics and soil physicochemical parameters. Plant species richness, aboveground biomass, and soil organic carbon represented key drivers of variation in soil microbial activity in the 0–20 cm soil layer. As soil depth increased, plant species richness, belowground biomass, and soil total nitrogen became the main factors influencing these changes. In addition, the overall effect of recovery years on soil microbial activity gradually decreased with soil depth, explaining 69%, 53%, 33%, and 8% in the four soil layers, respectively. In conclusion, we identified the drivers of changes in soil microbial activity after cropland abandonment. This study highlights the importance of plant production and diversity, as well as soil physicochemical parameters, in driving changes in soil microbial activity at different soil depths. Further studies are needed to assess the role of soil moisture, temperature, and pH in driving the observed changes in soil microbial activity. Additionally, there is an urgent need to perform more field experiments in different ecosystems, such as croplands, grasslands, and forests, and at larger spatial scales to identify the factors driving changes in soil microbial activity under different ecosystems and environmental conditions.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2020.104774.

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