Leguminous plants play a key role in influencing soil physicochemical and biological properties during grassland succession following farmland abandonment in the Loess Plateau, China [Postprint]

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Abstract

Leguminosae are an important part of terrestrial ecosystems and play a key role in promoting soil nutrient cycling and improving soil properties. However, plant composition and species diversity change rapidly during the process of succession, the effect of leguminosae on soil physical-chemical and biological properties is still unclear. This study investigated the changes in the composition of plant community, vegetation characteristics, soil physical-chemical properties, and soil biological properties on five former farmlands in China, which had been abandoned for 0, 5, 10, 18, and 30 a. Results showed that, with successional time, plant community developed from annual plants to perennial plants, the importance of Leguminosae and Asteraceae significantly increased and decreased, respectively, and the importance of grass increased and then decreased, having a maximum value after 5 a of abandonment. Plant diversity indices increased with successional time, and vegetation coverage and above- and below-ground biomass increased significantly with successional time after 5 a of abandonment. Compared with farmland, 30 a of abandonment significantly increased soil nutrient content, but total and available phosphorus decreased with successional time. Changes in plant community composition and vegetation characteristics not only change soil properties and improve soil physical-chemical properties, but also regulate soil biological activity, thus affecting soil nutrient cycling. Among these, Leguminosae have the greatest influence on soil properties, and their importance values and community composition are significantly correlated with soil properties. Therefore, this research provides more scientific guidance for selecting plant species to stabilize soil ecosystem of farmland to grassland in the Loess Plateau, China.

Full Text

Preamble

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Leguminosae plants play a key role in affecting soil physical-chemical and biological properties during grassland succession after farmland abandonment in the Loess Plateau, China

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Abstract: Leguminosae are an important component of terrestrial ecosystems and play a key role in promoting soil nutrient cycling and improving soil properties. However, plant composition and species diversity change rapidly during succession, and the effect of Leguminosae on soil physical-chemical and biological properties remains unclear. This study investigated changes in plant community composition, vegetation characteristics, soil physical-chemical properties, and soil biological properties on five former farmlands in China that had been abandoned for 0, 5, 10, 18, and 30 years. Results showed that with increasing successional time, the plant community developed from annual to perennial species. The importance of Leguminosae and Asteraceae significantly increased and decreased, respectively, while the importance of grasses increased initially and then decreased, reaching a maximum after 5 years of abandonment. Plant diversity indices increased with successional time, and vegetation coverage and above- and below-ground biomass increased significantly after 5 years of abandonment. Compared with farmland, 30 years of abandonment significantly increased soil nutrient content, though total and available phosphorus decreased with successional time. Changes in plant community composition and vegetation characteristics not only altered soil properties and improved soil physical-chemical conditions but also regulated soil biological activity, thereby affecting soil nutrient cycling. Among these, Leguminosae had the greatest influence on soil properties, and their importance values and community composition were significantly correlated with soil properties. Therefore, this research provides scientific guidance for selecting plant species to stabilize soil ecosystems during farmland-to-grassland conversion in the Loess Plateau, China.

Keywords: secondary succession; leguminosae; plant diversity; plant community composition; soil physical-chemical properties; soil biological properties

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Introduction

Secondary succession is a key measure for restoring degraded ecosystems and plays an important role in increasing soil nutrient content and plant diversity (Zeng et al., 2017). During secondary succession, plant productivity and community composition are directly affected (Li et al., 2019; Liu et al., 2019). Previous studies have shown that plant characteristics such as biomass, coverage, evenness, and diversity increase after secondary succession (Fan et al., 2015; Tessema and Belay, 2017), and soil properties may improve with succession due to increased plant biomass (Wang et al., 2009; Zhao et al., 2019). Natural regeneration through secondary succession can restore degraded soil properties and maintain soil fertility (Li et al., 2019, 2022; Zou et al., 2022; Li et al., 2023). Soil physical-chemical properties are influenced by decomposition of plant root exudates and litter (Zhao et al., 2015). In addition to soil microbial biomass, ecological enzyme activity is sensitive to changes in soil and vegetation. Therefore, secondary succession affects soil physical-chemical properties, enzyme activity, and microbial biomass (Zhu et al., 2012).

Long-term vegetation succession is a key driver of ecosystem recovery in restored areas (van der Heijden et al., 2008; Lucas-Borja et al., 2019; Hao and Chu, 2021), and vegetation changes inevitably affect soil nutrients (Reich, 2005; Peichl et al., 2012). Fast-growing vegetation can influence soil nutrient storage through litter decomposition and root exudates (Berg, 2014; Lozano et al., 2014). Van der Putten et al. (2013) found that plants could influence soil microbial communities and drive changes in soil physical-chemical properties. Additionally, plants can improve microclimate conditions and increase soil microbial activity, thereby promoting soil nutrient cycling and accumulation (Wickander et al., 2021; Bao et al., 2022). In contrast, soil extracellular enzymes are rate-limiting steps in microbial metabolism, affecting microbial decomposition of carbon and nutrients, and their activity is positively correlated with organic carbon content, influencing soil chemical properties (Chabrerie et al., 2003). However, the pattern of enzyme activity change during long-term natural secondary succession remains unclear. Different plant species have varying effects on soil because each possesses unique biological characteristics that may affect nutrient return and organic carbon decomposition differently (Fanin and Bertrand, 2016). For example, Leguminosae typically contain high nitrogen levels, while C4 plants contain high carbon levels and can significantly increase soil nitrogen and carbon contents (Sivaram et al., 2018; Yao et al., 2021). Rapid decomposition of nitrogen-rich plant litter can increase soil nutrient content (Horodecki and Jagodzinski, 2017). Beyond interspecific differences, effects of the same plant functional group on soil properties vary depending on successional stage (Hu et al., 2016). Thus, the effects of vegetation changes on soil properties are variable and uncertain during secondary succession (Zhang et al., 2016; Zhang et al., 2022).

Fewer studies have examined the effects of Leguminosae on soil properties (Fterich et al., 2014), and the potential mechanisms of plant community effects on soil properties need to be determined to help evaluate soil nutrient balance and predict restoration sustainability (Song et al., 2022; Liao et al., 2023). The Loess Plateau of China, covering approximately 64$×10^{4}$ km^2, is characterized by severe soil erosion and excessive desertification (Zheng, 2006; Zhang et al., 2018a). The Chinese government has undertaken ecological restoration projects such as returning farmland to forest and grassland (Fu et al., 2000), which are important measures for increasing vegetation coverage and preventing ecosystem fragmentation and degradation (Lozano et al., 2014; Zhang et al., 2016). After farmland conversion to forest and grassland, secondary succession without human disturbance has significantly improved biodiversity and soil ecosystem functions. Meanwhile, soil physical-chemical properties (Qiu et al., 2022), microbial community dynamics (Liu et al., 2022), soil enzyme activities (Chen et al., 2022), plant community composition (Zhu et al., 2021a), and plant diversity (Zhang, 2005) have changed significantly. However, few studies have examined the variability of Leguminosae effects on soil physical-chemical and biological properties. In this study, we investigated dynamic changes in plant community composition, plant diversity, soil physical-chemical properties, and soil biological properties using different years of secondary successional abandoned cropland and farmland as subjects. We hypothesized that plant community composition and diversity would affect soil physical-chemical and biological properties to different degrees with successional time. Additionally, we hypothesized that Leguminosae are dominant species in the plant community and have greater influence on soil properties during secondary succession. Therefore, we focused on: (1) effects of successional time on plant community composition, species diversity, soil physical-chemical properties, and soil biological properties; (2) effects of plant community characteristics and composition on soil properties; and (3) effects of Leguminosae on soil properties.

2.1 Study Area

A field experiment was conducted in the Zhifanggou watershed of Ansai District (36°42 -36°47 N, 109°13 -109°16 E), Shaanxi Province, northwestern China, located in the center of the Loess Plateau. The soil in this area is classified by the Food and Agriculture Organization (FAO) as extremely erodible Calcaric Cambisol developed from wind-blown loess deposits. Due to long-term wind deposition and soil erosion, the catchment (8.73 km^2) exhibits typical loess hilly and gully landforms with slope gradients varying from 0° to 65° and altitudes ranging from 1000 to 1300 m a.s.l. (Wang et al., 2009). The climate is classified as temperate with an average annual precipitation of 510 mm, approximately 70% of which falls between June and September (Zhang et al., 2016). The average frost-free period exceeds 150 days, and the annual average temperature is 8.8°C, with maximum temperatures of 36.8°C in August and minimum temperatures of -23.6°C in January. The Zhifanggou watershed serves as a model for soil erosion remediation and ecological restoration. In 1973, the Chinese government began integrated soil and water conservation management and vegetation restoration. One of the most widely used methods to prevent soil nutrient loss is converting former farmlands to abandoned grassland for natural recovery without anthropogenic interference (Zhang et al., 2016). After decades of this artificial restoration, vegetation coverage increased significantly, and large-scale herbaceous communities formed, including species such as *Artemisia sacrorum* Ledeb., *Lespedeza dahurica* Schindler, *Artemisia scoparia* Waldst. et Kit., and *Heteropappus altaicus* (Willd.) Novopokr. Additionally, a handful of farmlands remain in gentle slope zones where maize, potatoes, and foxtail millet are cultivated.

2.2 Experimental Design

This study used the space-for-time substitution method, which has been applied in numerous field studies (Walker et al., 2010; Williams et al., 2013; Zhang et al., 2016; Zhang et al., 2018b) and a meta-analysis (Zhou et al., 2017) to investigate effects of natural succession on above- and below-ground ecosystems. Through a comprehensive field survey of the Zhifanggou watershed in Ansai District, four plots were selected. Farmlands abandoned for 5, 10, 18, and 30 years were randomly chosen from areas with similar gradients, slopes, and altitudes. Active farmland served as the control (CK). Detailed information about each successional sequence and reference farmland is presented in Table S1. All selected sample plots had been plowed every spring before abandonment and were planted mainly with maize and cereals, with minimal fertilizer application and irrigation relying primarily on rainfall. No human disturbance occurred during the abandonment period, and vegetation colonized and grew naturally.

Each successional sequence of abandoned farmland was represented by three independent replicates, with sufficient spacing between sites to exclude spatial dependence (<14 m) for the vast majority of soil and plant variables (Marriott et al., 1997). Three replicated plots (30 m × 30 m; Fig. 1 [Figure 1: see original paper]) were randomly established in each site for subsequent investigation and sampling. For each variable, the average value of the three replicates in the same plot constituted observations. Thus, a total of 15 observations were established (5 successional sequences × 3 replicates) for each variable.

2.3 Vegetation Investigation and Soil Sampling

Vegetation investigation and soil sampling were conducted in August 2022. Nine replicated sample points were selected along an "S" shape in each plot for soil sampling (Fig. 1). After removing litter horizons and biological crusts, nine soil samples of 0–10 cm depth were collected from each point using a 5-cm diameter stainless steel auger, then fully homogenized to provide one composite sample per plot. These soil samples were immediately sieved through <2 mm mesh to remove visible litter, animal residue, roots, stones, and debris. Part of each soil sample was immediately transported to the laboratory and stored at 4°C for biological characteristics analysis, while other subsamples were airdried and stored at room temperature for physical-chemical analysis. Soil water content (SWC) and bulk density (BD) were obtained randomly from six points per plot using a 5-cm diameter steel core sampler (Fig. 1), then dried at 105°C to constant weight.

Vegetation characteristics were investigated in situ, and 10 quadrats of 1 m^2 were randomly arranged in each plot to record the name, height, coverage, frequency, and density of each species. Plant coverage was estimated at each plot. Both above- and below-ground parts of all plants in each 1 m × 1 m quadrat were collected by clipping and digging, respectively. After washing roots with tap water, both above- and below-ground parts were dried at 75°C to constant weight to calculate above-ground biomass (AB) and below-ground biomass (BB). The species importance value (IV), Margalef richness index (M), Shannon-Wiener diversity index (H), and Pielou evenness index (E) were calculated (Zhang, 2005; Zhang et al., 2016):

IV = (relative density + relative frequency + relative coverage + relative height)/4 × 100%, where relative density (%), relative frequency (%), relative coverage (%), and relative height (%) are defined as the percentages of density, frequency, coverage, and height of a single species to the total density, frequency, coverage, and height of all species per plot, respectively.

2.4 Soil Physical-Chemical Properties Analysis

Soil organic carbon (SOC) concentration was measured using the $K_2Cr_2O_7$ oxidation method (Bao, 2000). Soil total nitrogen (TN) concentration was determined using a continuous flow analyzer (AA3, Bran+Luebbe, Norderstedt, Germany) after micro-Kjeldahl digestion (Zhang et al., 2016). Concentrations of ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were determined using a continuous flow analyzer (AA3, Bran+Luebbe, Norderstedt, Germany) after extraction of fresh soil with 2 M KCl for 18 h (Zhang et al., 2016). Soil total phosphorus (TP) concentration was analyzed using the Mo-Sb anti-spectrophotography method (Bao, 2000), and soil available phosphorus (AP) was determined by the Olsen method (Olsen et al., 1982). Soil alkaline phosphatase (ALP), urease (URE), catalase (CAT), and saccharase (SAC) activities were determined using methods described in a previous study (Zhang et al., 2018b), shown in Table S2. Soil microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) were estimated from fresh soil samples using a chloroform fumigation-extraction method (Bao, 2000; Ren et al., 2016a). SWC was determined by oven-drying samples at 105°C to constant weight (Bao, 2000). Soil pH was measured using a pH meter (Sartorius PB-10, Goettingen, Germany) after vibrating soil-water (1:5) suspension for 30 min (Ren et al., 2017; Zhang et al., 2018b). Soil BD was determined using the soil core method by calculating the ratio of soil mass to total volume after oven-drying at 105°C to constant weight (Ren et al., 2016b). Soil temperature was measured using a right-angle geothermometer. Soil clay content was determined by a laser particle size analyzer.

2.5 Soil Microbial Respiration and Metabolic Quotient Measurement

Soil microbial respiration was determined using the alkali (NaOH) absorption method as described by Hu et al. (1997) and Liu et al. (2010). Briefly, 25 g of fresh soil from each plot was placed evenly in a 500-mL glass flask. Blank treatments (without soil) served as controls. A 25-mL flask containing 10 mL of 0.5 mol/L NaOH solution was placed inside the 500-mL glass flask to capture CO_2 evolved from the soil. These apparatuses were incubated at 25°C in darkness for two weeks, with flask covers opened for half an hour once daily during the first week and once every two days during the second week. Soil microbial metabolic quotient (qCO_2) was calculated as MR/MBC (where MR is microbial respiration) (Wardle and Ghani, 1995).

2.6 Statistical Analyses

Distribution of all data was checked using the Shapiro-Wilk test, and all variables were found to follow a normal distribution. One-way analysis of variance (ANOVA) and Duncan' s multiple range test ($P < 0.05$) were used to assess effects of successional stage on plant community composition, plant species diversity, soil physical-chemical properties, and soil biological activity using R v.3.1.3 software (R Core Team, 2015). Correlations between plant characteristics, soil physical-chemical properties, and soil biological activity were identified using redundancy analysis (RDA) and relative interpretation rates of vegetation characteristics on soil properties. Venn diagram analysis of relative interpretation rates of Leguminosae dominant species on soil physical-chemical and biological properties was undertaken. Clustering of different samples along successional stages by soil and plant characteristic variables was revealed through nonmetric multidimensional scaling (NMDS). Both RDA and NMDS were conducted using CANOCO v.5.0 software package (Ter Braak and Smilauer, 2002). Analysis of interpretation rate of Leguminosae dominant species with soil physical-chemical and biological properties used the Venn diagram package in R v.4.2.1.

3.1 Changes in Plant Community Characteristics

Vegetation characteristics changed significantly with successional time (Table 1). Plant community coverage, AB, and BB increased rapidly at the 5-year plot, decreased at the 10-year plot, and increased significantly again from 10 to 30 years (Table 1). Plant community coverage, AB, and BB ranged from 40.44% to 58.94%, 116.12 to 275.06 g/m^2, and 44.58 to 117.54 g/m^2, respectively, with minimum and maximum values occurring at the 10- and 30-year plots, respectively (Table 1). The M, H, and E indices significantly increased with successional time, ranging from 1.62 to 3.51, 1.13 to 3.65, and 0.47 to 0.95, respectively (Table 1).

Plant community composition was considerably affected by successional time (Table 2), and NMDS suggested that sampling plots clearly grouped into four well-differentiated clusters at the plant community level (Fig. S1). The importance value of *Artemisia capillaris* Thunb. significantly decreased with successional time; this species dominated the community at 5- and 10-year plots but became a companion species in plots abandoned for more than 18 years. Although *Heteropappus altaicus* was also dominant at the 5-year plot, its dominance was replaced by *Stipa bungeana* Trin., which appeared at the 10-year plot but was absent at the 30-year plot. The importance value of *Lespedeza dahurica* significantly increased during the first 18 years of abandonment, decreased at the 30-year plot, and dominated the plant community at 18–30 years. Two perennial species, *A. sacrorum* and *Artemisia giraldii* Pamp., appeared during succession at the 10-year plot and became dominant at 18 and 30 years, respectively. Overall, dominant species gradually transitioned from *A. capillaris* and *H. altaicus* to *L. dahurica*, *A. sacrorum*, and *A. giraldii* during 30 years of abandonment. Regarding plant species composition, the importance value of Compositae plants decreased rapidly during the first 18 years of abandonment and then increased at the 30-year plot, with the lowest point at the 18-year plot (31.10%) and peak at the 5-year plot (54.09%). The importance value of Gramineae plants significantly increased and then decreased with successional time, peaking at the 18-year plot (29.43%). The importance value of Leguminosae plants significantly increased with successional time, ranging from 9.86% to 36.49%.

3.2 Changes in Soil Physical-Chemical Properties

NMDS revealed that soil physical-chemical properties significantly changed with successional time (Fig. S2). SOC and soil clay content significantly increased, ranging from 3.53 to 5.70 g/kg and 18.86% to 20.81% for farmland and the 30-year plot, respectively (Fig. 2 [Figure 2: see original paper]; Table 3). Compared with farmland, SWC, TN, NH_4^+-N, and NO_3^--N contents were significantly lower at the 5-year plot but significantly higher with successional time, rising to farmland levels at the 10-year plot (Table 3). SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay contents reached their highest values at the 30-year plot, being 61.47%, 45.51%, 13.11%, 65.32%, 36.23%, and 10.34% higher than farmland, respectively (Table 3). BD, soil temperature, TP, and AP values were higher in farmland than in abandoned plots and decreased significantly with increasing successional time, ranging from 1.15 to 1.29 g/cm^3, 16.44°C to 18.71°C, 0.53 to 0.60 g/kg, and 0.61 to 1.95 mg/kg, respectively (Table 3). Additionally, soil pH was slightly higher at all plots than in farmland, although no statistical differences existed between plots (Table 3).

RDA showed that soil physical-chemical properties were significantly correlated with vegetation characteristics and plant community composition (Fig. 3 [Figure 3: see original paper]). For vegetation characteristics, the first two axes significantly explained 96.37% of all considered variables, indicating that M, H, E, AB, BB, Leguminosae, Gramineae, Compositae, and the sum of Leguminosae, Gramineae, and Compositae were positively correlated with SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay, and negatively correlated with TP, AP, BD, and soil temperature (Fig. 3a). Conversely, Compositae plants were negatively correlated with SOC, TN, NH_4^+-N, NO_3^--N, SWC, and clay, and positively correlated with TP, AP, BD, and soil temperature. For plant community composition, the first two axes explained 75.68% of all considered variables, and SWC, AP, NH_4^+-N, and NO_3^--N were the most influential factors causing changes in plant composition, contributing to 48.40%, 47.80%, 46.70%, and 44.20% of total variation, respectively (Fig. 3b).

3.3 Changes in Soil Biological Properties and Responses to Plant Community Characteristics

Four soil enzymatic activities (SAC, URE, ALP, and CAT) responded consistently with successional time (Figs. 4a–d and S3). Notably, activities of all four soil enzymes were significantly higher in abandoned lands than in farmland, with increased rates ranging from 25.46% to 292.19% (SAC), 38.08% to 112.34% (URE), 39.02% to 211.12% (ALP), and 4.23% to 21.37% (CAT), respectively. All four soil enzymatic activities increased significantly with successional time and reached maximum values at the 30-year plot. Similarly, MBC and MBN significantly increased with successional time, with growth rates ranging from 26.33% to 156.55% and from 17.58% to 116.79% for farmland and the 30-year plot, respectively (Fig. 4e [Figure 4: see original paper] and f).

Soil microbial respiration increased and peaked at the 10-year plot, then sharply decreased with successional time (Fig. 4g). Soil respiration in abandoned lands was higher than in farmland (Fig. 4g). The qCO_2 value increased significantly at the 5-year plot compared with farmland, then dramatically decreased with successional time (Fig. 4h). Additionally, qCO_2 values at 18- and 30-year plots were significantly lower than those at farmland, 5-, and 30-year plots.

RDA showed a significant correlation between soil biological properties and plant community characteristics (Fig. 5 [Figure 5: see original paper]). For vegetation characteristics, the first two axes significantly explained 93.37% of all considered variables (Fig. 5a). In particular, Leguminosae plants were the most important factor, contributing 81.60% of total variation. RDA indicated that M, H, E, AB, BB, Leguminosae, Gramineae, and the total of Leguminosae, Gramineae, and Compositae were positively correlated with MBC, MBN, SAC, URE, ALP, and CAT and negatively correlated with qCO_2 (Fig. 5a). Conversely, Compositae plants were negatively correlated with MBC, MBN, SAC, URE, ALP, and CAT, and positively correlated with qCO_2 (Fig. 5a). Additionally, all plant community composition variables significantly explained 78.83% of total soil biological variation (Fig. 5b).

3.4 Effect of Leguminosae on Soil Physical-Chemical Properties and Biological Characteristics

RDA showed that Leguminosae had the greatest influence on soil physical-chemical properties, with a relative explanation percentage of 75.90%, significantly higher than other vegetation characteristics (Table 4). Moreover, RDA showed that Leguminosae had the greatest influence on soil biological properties, with a relative explanation percentage of 81.60%, significantly higher than other vegetation characteristics (Table 5). Among plant community compositions, Leguminosae were the most dominant community, with the most dominant species *Medicago sativa* L. making the greatest relative contribution to soil physical-chemical and biological properties at 10.60% and 36.90%, respectively (Fig. 6 [Figure 6: see original paper]). In summary, Leguminosae plants can be regarded as the most important plant factors associated with soil physical-chemical and biological properties, rather than dominant species or species diversity alone.

4.1 Plant Characteristics Over Successional Time

A. capillaris, an annual species belonging to Compositae, was a pioneer species that first colonized bare farmland and quickly became dominant at the 5-year plot (Table 2). Its strong resource competitiveness and rapid environmental adaptability led to rapid growth and inhibited other species (Zhang et al., 2016), resulting in low H, M, and E at the 5-year plot (Table 1). This study showed that H, M, and E significantly increased with successional time until the 30-year plot (Table 1), with more species appearing in 18- and 30-year plots, such as *S. bungeana*, *A. sacrorum*, and *Astragalus melilotoides* Pall. (Table 2). Similar results were found in previous studies, with high species diversity and richness occurring during middle successional stages of the Chinese Loess Plateau (25 years of abandonment) (Wang et al., 2009; Zhang et al., 2016; Sun et al., 2017). Plant colonization improved soil conditions and provided more living space for additional species during secondary succession (Zhu et al., 2021b; Wang et al., 2022), demonstrated by increased SWC and clay content and decreased BD and pH (Table 3). Meanwhile, many species of different ecotypes interacted to reach a stable state in these improved community environments (Liu et al., 2023; Yang et al., 2023), thereby increasing species diversity and richness (Sun et al., 2022; Gu et al., 2023; Kong et al., 2023). Additionally, results showed that importance values of Leguminosae and Gramineae plants increased with successional time (Table 2), indicating these families are more adaptable to the arid Loess Plateau environment than others (Zhang et al., 2021; Liu et al., 2022). For example, Leguminosae have deeper roots to obtain water and nutrients (Hu et al., 2016). Moreover, M, H, and E were positively correlated with Leguminosae and Gramineae plants (Figs. 3, 5, and S2). The strong C and N fixation capacity of Gramineae and Leguminosae plants can increase soil C and N inputs to improve availability (Hu et al., 2016; Tian et al., 2016), thereby creating suitable conditions for plant colonization that increase species diversity and richness. In contrast, Gramineae and Leguminosae plants can coexist with other species due to complementarity, facilitation, and niche differentiation (HilleRisLambers et al., 2004; Wu et al., 2017), resulting in increased species diversity and richness. However, Compositae plants can inhibit other species' growth due to allelopathic effects (Baličević et al., 2016), leading to negative correlations with M, H, and E

(Figs. 3 and 5). Overall, these results validate the hypothesis that plant community composition and species diversity significantly changed with successional time.

4.2 Responses of Soil Physical-Chemical and Biological Properties to Plant Community Characteristics

Soil physical properties are sensitive to alterations in plant characteristics such as population composition, species diversity, and biomass (Ile et al., 2021; Cotrufo et al., 2022). Results indicated that dynamics of plant diversity (M, H, and E) and coverage corresponded to accumulation of above- and below-ground biomass (Table 1), with both being related to SWC, BD, soil temperature, and clay (Fig. 3a). This demonstrated that secondary succession of plant communities can alter soil physical properties (Jiao et al., 2011). First, increased above-ground biomass implies improved vegetation and litter coverage (O' Halloran et al., 2013; DeBerry and Atkinson, 2014), thereby reducing solar radiation on the soil surface (Zhao et al., 2015) and ultimately increasing SWC while decreasing soil temperature with successional time (Table 3). Second, community composition changed from annual herbs to perennial Compositae, Leguminosae, and Gramineae plants (Table 2), and these species can reduce soil moisture loss through evaporation and transpiration due to their coverage degree and drought tolerance (Jiao et al., 2011; Hu et al., 2016). Finally, accumulation of plant biomass provided food sources for soil animals (Table 1), and animal disturbance could decrease BD and increase soil clay content during secondary succession (Háněl, 2003; Jing et al., 2014). Ren et al. (2017) also found that plant diversity (M, H, and E) synchronously increased with soil microbial diversity and biomass during restoration, and that microbial dynamics could alter soil texture (e.g., BD and clay). However, pH changed more slowly with successional time than SWC, BD, soil temperature, and clay (Table 3), consistent with previous studies (An et al., 2008; Zhang et al., 2016). This suggests that secondary succession of abandoned farmlands has little effect on soil pH, since pH results from multiple synergistic interactions between biotic and abiotic factors (Criquet et al., 2000).

Additionally, results showed that soil chemical properties (SOC, TN, TP, NH_4^+-N, NO_3^--N, and AP) were coupled to changes in plant diversity, coverage, AB, and BB (Fig. 3a). Unsurprisingly, plant colonization fixes atmospheric CO_2 through photosynthesis and returns C to soil as litter and rhizodeposition from the initial succession period (Ohtsuka et al., 2010; Xiao et al., 2021), causing SOC to increase significantly with successional time (Fig. 2a). In contrast to SOC, TN, NH_4^+-N, NO_3^--N, TP, and AP decreased significantly at the 5-year plot compared with farmland (Fig. 2b–f), attributable to cessation of fertilizer input and plant absorption (Zhang et al., 2016). As above- and below-ground biomass gradually increased, contents of TN, NH_4^+-N, and NO_3^--N increased significantly with successional time (Fig. 2b, e, and f) due to increased Leguminosae plants with N-fixing capacity, raising N content in the plant-soil system

(O' dea et al., 2015). Phosphorus is a more 'rock-derived' element fixed only slowly from the atmosphere (Huang et al., 2013), and continuous increases in above-ground biomass absorbed large amounts of P from soil (Chen et al., 2000), causing significant decreases in TP and AP contents with successional time (Fig. 2c and d). Although soil nutrients declined somewhat during early succession, they rose to farmland levels at 10- and 18-year plots and exceeded farmland levels at the 30-year plot (Fig. 2), indicating that soil nutrient status can improve with successional time (Wang et al., 2009; Zhang et al., 2016). Enhanced net primary productivity during secondary succession (Table 1) increased plant litter and dead root quantities, ultimately improving soil nutrient levels (Peichl et al., 2012). Simultaneously, improved soil environment accelerated organic matter decomposition and increased soil nutrient accumulation (Zhang et al., 2018b). Additionally, plant growth controlled soil erosion, reducing losses of soil C, N, and P from surface runoff (Zhu et al., 2021a; Luo et al., 2022).

Development of plant coverage and biomass forms the foundation of soil restoration (Ren et al., 2017) and strongly affects soil biological property dynamics (Ren et al., 2016a). Results showed that soil enzymatic activities (SAC, URE, ALP, and CAT) and microbial biomasses (MBC and MBN) significantly increased with successional time (Figs. 4 and S3), and these alterations were coupled to shifts in plant biomass and soil physical-chemical properties (Figs. 5 and 6). This indicated that secondary succession improves plant residues and soil microenvironment, ultimately promoting soil biological activities. For example, increased plant residues during secondary succession contain abundant substrates that stimulate microbial growth and enzyme synthesis (Lucas-Borja et al., 2016). Improved soil environment (SWC, BD, and clay; Table 3) during secondary succession can promote microorganism growth and contribute further to microbial biomass and enzymatic activities (Yang et al., 2020; Guan et al., 2022). Additionally, development of below-ground biomass accelerates soil ventilation, promoting release of exogenous enzymes by increasing rhizosphere exudates and ultimately altering microbial biomass and enzymatic activities (Zhang et al., 2011; Zhang et al., 2018a). In contrast to microbial biomass and enzymatic activities, microbial respiration and qCO_2 increased significantly at 5- and 10-year plots compared with farmland but then decreased dramatically with successional time (Fig. 4g and h). As qCO_2 indicates maintenance energy requirements of microbial communities and substrate utilization efficiency, it is a sensitive index reflecting environmental influences on microbial activity (Liu et al., 2010). At early succession stages, fast-growing vegetation requires large quantities of nutrients, so microorganisms must accelerate nutrient fixation to meet vegetation needs (Zhang et al., 2016). Results showed that qCO_2 and microbial respiration increased when microbial turnover rates and energy consumption increased (Plaza et al., 2004; Zhang et al., 2011). As succession progressed, reduced environmental stress (lower BD and higher SWC) increased microbial efficiency and decreased qCO_2 because microorganisms required less energy for maintenance (Ren et al., 2018; Zhao et al., 2018). This allowed soil to retain sufficient active organic matter to maintain good properties and sustainable utilization potential (Liu et al., 2010; Ren et al., 2018).

4.3 Effects of Plant Community Composition, Species Diversity, and Dominant Species on Soil Properties

Plant community composition can reflect varying quality and quantity of plant residues (litter and rhizodeposition) provided to decomposers (Yahdjian et al., 2017) and may create diverse micro-environmental conditions (Kardol and Wardle, 2010). These resultant shifts relate to sources and turnover of soil nutrients and ultimately alter soil physical-chemical and biological properties (Xiao et al., 2017). Results showed that plant community composition was more closely related to soil physical-chemical and biological properties than species diversity and dominant species (Figs. 3 and 5), indicating that plant functional groups better reflect soil properties. Li et al. (2018) found that plant functional groups represent classes of species with similar physiological and biochemical characteristics (N fixation and C fixation), which are more capable of dominating nutrient feedback and ecosystem circulation than single species (Wu et al., 2017; Chou et al., 2018). Previous research has also shown that plant functional group composition can affect soil environmental conditions and nutrient supply to determine species diversity (Chen et al., 2021; Sidlauskaite et al., 2022); therefore, it can better reflect interactive relationships between vegetation and soil than species diversity alone. Additionally, results showed that Leguminosae plants were the most important plant community factor associated with soil physical-chemical and biological properties (Fig. 6). Leguminosae plants play important roles in promoting soil C and N accumulation and mineralization due to their capacity for N_2-fixation by symbiotic root bacteria (Wu et al., 2017). Furthermore, Leguminosae plants contribute a net increase in litter N concentration due to strong N fixation ability and low N retranslocation from old to new leaves (Li et al., 2012; Li et al., 2015). Additionally, litter with higher N content contains more unstable complexes that are easily decomposed by microorganisms (Fanin and Bertrand, 2016; Zhang et al., 2018a; Zheng et al., 2021). Therefore, Leguminosae plants promote nutrient transfer between plants and soil by accelerating litter decomposition and increase functional diversity and activity of soil microbial communities by enhancing substrate inputs (Li et al., 2012; Hu et al., 2016). Increasing MBC and MBN and decreasing qCO_2 and microbial respiration over successional time confirmed this deduction (Fig. 4). Fterich et al. (2014) also found that Leguminosae plants could increase soil organic matter and positively affect soil enzyme activity as well as C and N use efficiency of microorganisms. These variations in soil biological variables were significantly correlated with soil physical-chemical properties (Fig. 6), indicating that Leguminosae plants can change soil nutrients and environmental conditions by affecting soil microbial and enzyme activities. In contrast, co-improvement of soil physical-chemical and biological properties caused by legume species stimulates mycorrhizal fungi development, which strengthens plant nutrient absorption (Zhang et al., 2011) and leads to shifts in species diversity and plant community composition (Tables 1 and 2). Overall, plant functional composition can better reflect soil physical-chemical and biological properties than species diversity and dominant species, with Leguminosae plants in particular serving as indicators for observing vegetation and soil restoration status during secondary succession.

5 Conclusions

Plant communities transitioned from annual herbs to perennial species during 30 years of secondary succession. The importance values of Leguminosae and Gramineae significantly increased with successional time, whereas that of Compositae significantly decreased. Moreover, plant community coverage, AB, and BB decreased at the 10-year plot and then increased between 10 and 30 years, while species diversity significantly increased during the first 18 years of secondary succession and then decreased at the 30-year plot. Soil physical-chemical and biological properties (except TP and AP) significantly improved during secondary succession, even though some variables (e.g., TN, NH_4^+-N, NO_3^--N, and SWC) degraded at early stages compared with farmland. Changes in plant community composition had greater effects on soil physical-chemical and biological properties than species diversity and dominant species. Particularly, Leguminosae plants were the most important factor affecting soil physical-chemical and biological properties and can therefore serve as indicators for observing vegetation and soil restoration status during secondary succession. This study provides guidance for selecting suitable planting species for better vegetation restoration during secondary succession in the Chinese Loess Plateau.

Conflict of 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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Appendix

Table S1 Geographical features and dominant species at different plots

Plot	Slope degree (°)	Aspect (°)	Elevation (m)	Location	Dominant species
Farmland	-	North by east 45	36°46 N, 109°15 E	-	-
5-year	40	North by west	36°45 N, 109°15 E	*A. capillaris*, *H. altaicus*	
10-year	55	North by east	36°44 N, 109°16 E	*S. bungeana*, *A. capillaris*	
18-year	38	North by west	36°45 N, 109°16 E	*L. dahurica*, *A. sacrorum*	

Plot	Slope degree (°)	Aspect (°)	Elevation (m)	Location	Dominant species
30-year	42	North by east	36°44 N, 109°16 E	*A. giraldii*, *L. dahurica*, *B. ischaemum*	

Note: *A. capillaris*, *Artemisia capillaris* Thunb.; *H. altaicus*, *Heteropappus altaicus* (Willd.) Novopokr; *S. bungeana*, *Stipa bungeana* Trin.; *L. dahurica*, *Lespedeza dahurica* Schindler; *A. sacrorum*, *Artemisia sacrorum* Ledeb.; *A. giraldii*, *Artemisia giraldii* Pamp.; *B. ischaemum*, *Bothriochloa ischaemum* (Linnaeus) Keng. "-" indicates no dominant species.

Table S2 Methods for determination of soil enzymatic activities

Type of enzyme	Detailed measurement method
Soil catalase activity	Determined by addition of 40 mL distilled water and 5 mL 0.3% H_2O_2 to 2 g fresh soil. The mixture was shaken for 20 min (at 150 r/m) and filtered (Whatman 2V) immediately. The filtrate was titrated with 0.1 mol/L $KMnO_4$ under sulfuric acid conditions. Results expressed as 0.1 mol $KMnO_4/(g \cdot 20\ min)$.
Soil saccharase activity	Determined using 8% glucose solution as substrate. Approximately 5 g fresh soil was incubated with 15 mL substrate, 5 mL 0.2 M phosphate buffer (pH 5.5), and 5 drops toluene for 24 h at 37.8°C. After incubation, the mixture was filtered (Whatman 2V) immediately and 1-mL aliquot reacted with 3 mL 3,5-dinitrylsalicylate in a volumetric flask, then heated for 5 min. Soil solution was quantified in an ultraviolet spectrometer subsystem (UVS) at 508 nm at room temperature. Results expressed as mg glucose/$(g \cdot 24\ h)$.

Type of enzyme	Detailed measurement method
Soil urease activity	Determined using 10% urea solution as substrate. Approximately 5 g fresh soil was incubated for 24 h at 37.8°C with 5 mL citrate solution at pH 6.7 and 5 mL substrate. The reaction mixture was diluted to 50 mL with distilled water. After incubation, the mixture was immediately filtered and 1 mL supernatant treated with 4 mL sodium phenol solution and 3 mL 0.9% sodium hypochlorite solution. Ammonium released from urea hydrolysis was quantified in UVS at 578 nm. Results expressed as mg $NH_4{}^+$-N/(g · 24 h).
Soil alkaline phosphatase activity	Determined by addition of 10 g fresh soil, 2 mL toluene, 10 mL disodium phenyl phosphate solution, and 10 mL 0.05 M borate buffer. The reaction mixture was incubated for 2 h at 37.8°C. After incubation, the mixture was immediately filtered, then the filtrate was treated with 0.5 mL of 2% 4-aminoantipyrine and 8% potassium ferrocyanide; phenol released was determined in UVS at 510 nm. Results expressed as mg phenol/(g · 24 h).

Fig. S1 Nonmetric multidimensional scaling (NMDS) analysis of plant community composition over successional time

Fig. S2 Nonmetric multidimensional scaling (NMDS) analysis of soil physical-chemical properties over successional time

Fig. S3 Nonmetric multidimensional scaling (NMDS) analysis of soil biological properties over successional time

Note: Figure translations are in progress. See original paper for figures.

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