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Plant functional composition and species diversity affect soil C, N, and P during secondary succession of abandoned farmland on the Loess Plateau

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The relationships among soil C, N, and P, aboveground plants, and belowground organisms are well-known; however, the impact of the aboveground dynamics of plant communities and their ensuing effects on soil C, N, and P, particularly during secondary succession need clarification. This study explored the effects of plant functional composition and diversity on soil C, N, and P at different soil depths. Soil samples were collected at soil depths ranging from 0 to 60 cm from three grassland sites abandoned for 5, 17, and 30 years in the Yang Qing Chuan catchment. Soil properties and fine root biomass were determined for different soil depths, and the plant community characters at each site were also evaluated. The results revealed that the plant community transitioned from dominance by annual herb to dominance by perennial species during the succession, and the percentage of Leguminosae plants, plant diversity, and species richness increased with succession time. The soil water content, organic carbon, total nitrogen, total phosphorous, C:P ratio, and N:P ratio increased significantly with successional time and decreased significantly with soil depth. In contrast, the soil bulk density and pH decreased significantly with successional time and increased significantly with soil depth. Furthermore, the plant functional group composition and diversity significantly affected soil C, N, and P contents and ratios, but was sensitive to the vertical stratification of soil. Plant functional group composition had a stronger correlation to soil C, N, and P contents and ratios at soil depths of 0–20 cm than that of the 20–60 cm depth primarily due to the fact that the nutrients returned are mostly concentrated on the topsoil and seldom deposited in the deeper soils. However, plant diversity had a stronger impact on soil C, N, and P contents and ratios at soil depths of 20–60 cm than at 0–20 cm depth, because plant diversity exacerbates interspecific competition and forces the roots to grow deeper, which alters nutrients in the deep soil. In addition, the percentage of legumes can be used as a practical indicator of soil quality in the 0–20 cm layer during natural succession of abandoned farmlands. This study provides evidence that plant communities have a strong influence on soil C, N, and P, but that the pathways and degree of influence differ across vertically stratified soil.

1. Introduction

Succession, the non-seasonal and continuous process of colonization and extinction of populations in a specific area (Zhang, 2005), is a matter of joint and synchronous evolution of aboveground phytocoenosium and belowground soil (Zhang et al., 2016). As a typical example of succession, the secondary succession on abandoned farmland without human interference is an effective measure of promoting the restoration of degraded ecosystems with extremely poor environmental conditions (Walker et al., 2010; Wang et al., 2009; Zhao et al., 2015b). During the process of secondary succession, both the aboveground and belowground ecosystems change significantly, with multiple loops of

Abbreviations: SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; LPC, Loess Plateau of China; GTGP, Grain to Green Project; SBD, soil bulk density; SWC, Soil water content; IV, The Importance Value; M, Margalef richness index; H, Shannon–Wiener diversity index; E, Pielou evenness index; RDA, redundancy analysis; RG-5a, RG-17a, and RG-30a, grasslands that had been restored for 5 years, 17 years, and 30 years

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interaction and complex relationships (Zhang and Dong, 2010). However, the potential interactions between soil and vegetation during the secondary succession remain unclear, which greatly limit our understanding of the cooperative restoration process of vegetation and soil. Therefore, investigating the relationship between plant and soil variables is essential for the natural restoration of degraded ecosystems sustainably.

Previous studies have confirmed that both soil properties and vegetation characteristics are altered during the process of vegetation restoration. For instance, as succession progressed, the structure and composition of plant communities became more complex, and the species richness and heterogeneity increased significantly (Zhang et al., 2016; Zhang, 2005). Jiao et al. (2011) and Li et al. (2016) showed that re-vegetating eroded soils can increase soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP). Recently, many studies have analyzed the interaction between vegetation and soil during the process of vegetation restoration. De Long et al. (2016) found that understory plant functional groups and litter species identity were strong drivers of litter decomposition rates, which affects the ecosystem C storage and nutrient cycling. As different plant functional groups have different C, N, and P contents, it leads to uneven return of soil nutrients (Zhang et al., 2018a), and this difference is the most obvious in the surface soil (Li et al., 2016). Meanwhile, the plant functional composition has been proven to be a major factor determining rooting patterns in grasslands restoration that respond to resource availability (Siebenkas and Roscher, 2016), which alters the soil chemical and physical properties. Moreover, Dawud et al. (2016) concluded that more diverse forests had higher C stocks and C:N ratios in the 20–40 cm soil layer, whereas species identity increased the C stocks and C:N ratios on the forest floors. In addition, a biodiversity experiment demonstrated that increased species diversity helps plant roots grow deeper (Mommer et al., 2010), and this will inevitably lead to changes in nutrients in the deep soil (Hu et al., 2016b). In brief, both plant functional composition and species diversity effect soil nutrients, but it is still unclear whether their influences on soil is different, particularly on soil vertical stratification. The C, N, and P ratios are good indicators of soil nutrient status that is tightly linked to the aboveground and belowground components of the ecosystem, whose interactions greatly affect the ecosystem dynamics and functioning (Greig-Smith, 1983; Zhao et al., 2015b). For instance, Fan et al. (2015) revealed that under nutrient limitation in subtropical forests, soil C, N, and P ratios were strongly related to tree growth. Zhao et al. (2015b) showed that changes in plant community composition and diversity after restoration were correlated with changes in soil C, N, and P ratios. Conversely, soil mineral element contents and ratios may reflect the conditions of plant growth and alter soil seed bank diversity, which further influence the plant community composition and diversity (Jiao et al., 2011; Zhang et al., 2014). Therefore, understanding the relationship between plant communities (plant functional composition and species diversity) and soil C, N, and P is critical to understanding the recovery process of fragile ecosystems. In particular, this information helps us to clarify the differences in the effects of species diversity and plant functional composition on soil nutrients, especially at different soil depths.

The Loess Plateau of China (LPC) is on the boundary of arid and semiarid areas, has an area of 624,000 km^2, and is the most vulnerable ecological region in the world (Shi and Shao, 2000). With an average erosion rate of 150 ton ha^{-1} per year (Fu et al., 2000), LPC was characterized by severe soil erosion and low vegetation coverage before management activities began (Bai and Dent, 2009). To remedy this, the Chinese government has initiated various measures to prevent soil erosion and rehabilitate the vegetation since 1950 (Deng et al., 2016; Zhang, 2005), especially the “Grain to Green Project” (GTGP), which has converted large-scale steep croplands (with slope $> 25°$) into forests (trees and shrubs) or grasslands since 1999 (Deng et al., 2016; Ren et al., 2016c). In this time, more than 9.27 million ha of farmland have been recovered, and the recovery of vegetation has greatly reduced soil erosion and affected soil element circulation apart from improving the soil quality in the LPC (Lu et al., 2012). For forests, afforestation could significantly improve plant community composition and diversity (Zhao et al., 2015b), litter decomposition rate (Zhang et al., 2018a), soil physical-chemical properties (Zhang et al., 2018b), microbial dynamics (Ren et al., 2016c), and enzymatic activities (Ren et al., 2016a). However, different afforestation species have different effects on soil variables. For secondary succession of abandoned farmlands, researchers revealed that plant community composition and life-forms changed significantly (Zhang, 2005), and the richness, species diversity, and heterogeneity increased significantly during succession (Sun et al., 2017; Zhang, 2005). As the succession progressed, the improvement of soil physico-chemical and microbiological properties would be slow and required a considerably long period of time (Wang et al., 2011). By investigating the rhizosphere and bulk soils dynamics, Zhang et al. (2012) showed that trace element accumulation was significantly correlated to SOC and TN content for the later successional species. In addition, Zhu et al. (2018) revealed that a long-term efficient management approach could prevent degradation of grasslands by estimating the effect of grazing on soil nutrient storage and plant diversity. Above all, these studies have described changes in soil and plant variables to a certain degree during secondary succession. Nevertheless, it is unclear whether plant functional composition and diversity are the main influences on soil C, N, and P, or whether these two factors mainly influence topsoil or deeper soil layers, especially during the secondary succession of abandoned farmland as species diversity and composition usually changed rapidly.

In this study, we hypothesized that the plant community characteristics (plant diversity and functional composition) and soil C, N, and P contents and ratios change synchronously during secondary succession of abandoned farmland. We predicted that the influence of plant diversity and functional composition on soil C, N, and P is different in vertically stratified soils. Our objectives were to: (i) show the changes in soil physico-chemical properties, plant diversity, and plant functional composition during time, (ii) analyze the interactions between soil and vegetation, and (iii) determine whether the effects of plant diversity and functional composition on soil C, N, and P are same during natural succession, especially between the topsoil and deeper soil layers.

2. Materials and methods

2.1. Study area

This study was conducted in the Yangqingchuan catchment of Wuqi County, northern Shaanxi, China (36°52′22″–36°52′32″ N, 108°14′17″–108°14′32″ E), which is a typical area in the middle of LPC with many gullies and hills (Fig. S1). The altitude of the study area is between 1233 and 1809 m. This area has a typical semi-arid climate with an average annual precipitation of 466 mm (mainly from July to August) and an annual average temperature of 7.8 °C. The maximum temperature is 37.1 °C during summer and the minimum temperature is −25.1 °C during winter. On an average, the frost-free period is 146 days. The soil, developed from wind-accumulation, is mainly classified as a Loessial soil (Calcaric Cambisols, FAO) and is highly erodible. Total thickness of the loess deposits is close to 200 m. The average thickness of the loess layer in the area ranges from 30 to 80 m (Zhu et al., 1983), and the loess has been deposited on top of a Mesozoic bedrock (sandstone, siltstone) (Hessel and van Asch, 2003).

Before the 1970s, natural vegetation in this area was removed to plant maize (*Zea mays* L.) and foxtail millet (*Setaria italica*), which caused huge water losses and soil erosion. In 1999, with the implementation of the GTGP, many slope croplands were converted to abandoned land, grassland, and reforested land. The sloped farmland was fertilized each year with 50 kg ha^{-1} urea and 25 kg ha^{-1} phosphorus pentoxide (P_2O_5). However, due to severe soil erosion, there is