



Research article

Plant functional diversity drives carbon storage following vegetation restoration in Loess Plateau, China

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ABSTRACT

Ongoing climatic changes induced by human activities increases in atmospheric carbon dioxide (CO₂), which have considerable effects on the structure and function of ecosystems, including carbon (C) storage, plant functional traits and therefore on a wide set of ecosystem services. Plant functional diversity is benefit to improve plant photosynthesis and enhance C efficiency and therefore decrease CO₂. Here, the focus of this article is on integrating of plant functional diversity and C storage, which aims to contribute to C sequestration for climate change mitigation following vegetation restoration in Loess Plateau, China. Firstly, the CWM (plant community-weighted mean) traits of the most abundant plant species can account for C storage in AGBC (above-ground biomass C), ALC (above-ground litter C), STC (soil total carbon) and TEC (total ecosystem carbon). Secondly, the CWM of plant height and LCC (leaf carbon concentration) had a positive effect C storage in different part (AGBC, ALC, STC and TEC), while the CWM of LNC (leaf nitrogen concentration) and SLA (specific leaf area) had a negative effect on C storage in different part. Further, the CWM of plant height, LCC, SLA and plant functional dispersion (FDis) can be used to predict C storage by multiple linear regression analysis. Finally, the positive association between FDis and C storage was found in SEM, shedding light on the key role of plant functional diversity driving C storage following vegetation restoration. The findings presented here highlight the importance of both plant traits of dominant species and plant functional diversity in regulating C storage, and show that favorable climate conditions, particularly vegetation restoration, tend to increase C storage and plant functional diversity, which have important implications for improving global C cycling and ecosystem services.

1. Introduction

Ongoing climatic changes induced by large-scale human activities increases in atmospheric CO₂ since the early 19th century and represents one of the biggest scientific and political challenges of the 21st century (Nolan et al., 2018; De Nijs et al., 2019). At present, China has the largest annual CO₂ emissions in the world, and reducing CO₂ emissions to mitigate regional and global climate change is one of the most challenging issues facing humanity (Fang et al., 2018; Chen et al., 2019). As a consequence, increasing in atmospheric CO₂ have considerable effects on the structure and function of ecosystems, including C storage, plant functional traits and therefore on a wide set of ecosystem services (Chen et al., 2018; Liu et al., 2018). So plant functional traits are benefit to improve plant photosynthesis and enhance C efficiency and therefore mitigate the increasing in atmospheric CO₂.

Currently, we know little about how plant functional traits drive C

storage (plant C, soil C, and the whole ecosystem C storage) (Kunstler et al., 2015; Anne et al., 2018). Growing evidence have shown that plant functional traits strongly affected plant growth, species richness, biomass and C storage (Pietsch et al., 2014; Moreau et al., 2015; Fang et al., 2018), and there was the evolutionary trade-offs between C acquisition and decomposition (Gardarin et al., 2014; Moreau et al., 2015). For example, acquisitive resource use syndromes are characterized by the combination of attributes such as high SLA (specific leaf area), high LNC (leaf nitrogen concentration), and low LDMC (leaf dry matter content) (Ruiz-Benito et al., 2014; Moreau et al., 2015; Chen et al., 2018). They are consistently associated with high C input through photosynthesis and also high C losses through decomposition (Díaz and Cabido, 2001; Elmqvist et al., 2003; Lu et al., 2018; Wang et al., 2018). On the other hand, plants traits associated with the large plant biomass, plant height and LDMC, are therefore expected to directly influence C storage in above-ground and below-ground (Mokany et al., 2008;

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Nomenclature			
Af	artificial forest	D	soil thickness
Al	abandoned land	Ag	artificial grassland
Ns	natural shrub	Ng	natural grassland
FDis	functional dispersion	FDvar	functional trait dispersion index
AGBC	above-ground biomass carbon	CWM	plant community-weighted mean
STC	soil total carbon	ALC	above-ground litter carbon
SLA	specific leaf area	TEC	total ecosystem carbon
LCC	leaf carbon content	LDMC	leaf dry matter content
AGB	above-ground biomass	LNC	leaf nitrogen content
BA	basal area	DBH	diameter at breast height
SOC	soil organic carbon	CA	crown area
		BD	soil bulk density
		H	height

Schmidt et al., 2011; Zuppinger-Dingley et al., 2014). Plant functional diversity, the extent of functional differences among plant species, is one of the most important plant trait that closely linked to C cycling (Tilman et al., 1997; Petchey and Gaston, 2002; He et al., 2017; Xu et al., 2018). Large numbers of evidence conformed that plant functional diversity can be regarded as the main indicator for forecasting C storage (Chen et al., 2014; Handa et al., 2014; Smiseth et al., 2014). In this case, the abundant plant CWMs (community weighted mean) primarily supported to the biomass ratio hypothesis (Grime, 1998), which proposed that ecosystem function and C storage were mainly driven by

the abundant of plant CWMs (Cong et al., 2015; Fatichi et al., 2014; Wang et al., 2015; Latz et al., 2016). Thus, the abundant of plant CWMs have been proven to be the dominant factors in determining ecosystem function and C storage. Meanwhile, multi-traits of functional dispersion (FDis), weighted by plant relative abundances, could also enhance ecosystem function and C storage (Zuo et al., 2016a; Zuo et al., 2016b; Fang et al., 2018). Previous studies have reported that FDis had a positive effect on ecosystem function and C storage in order to get the more resource niches, supporting the niche-complementarity hypothesis (Flynn et al., 2011; Gardarin et al., 2014; Harrison et al., 2018). For

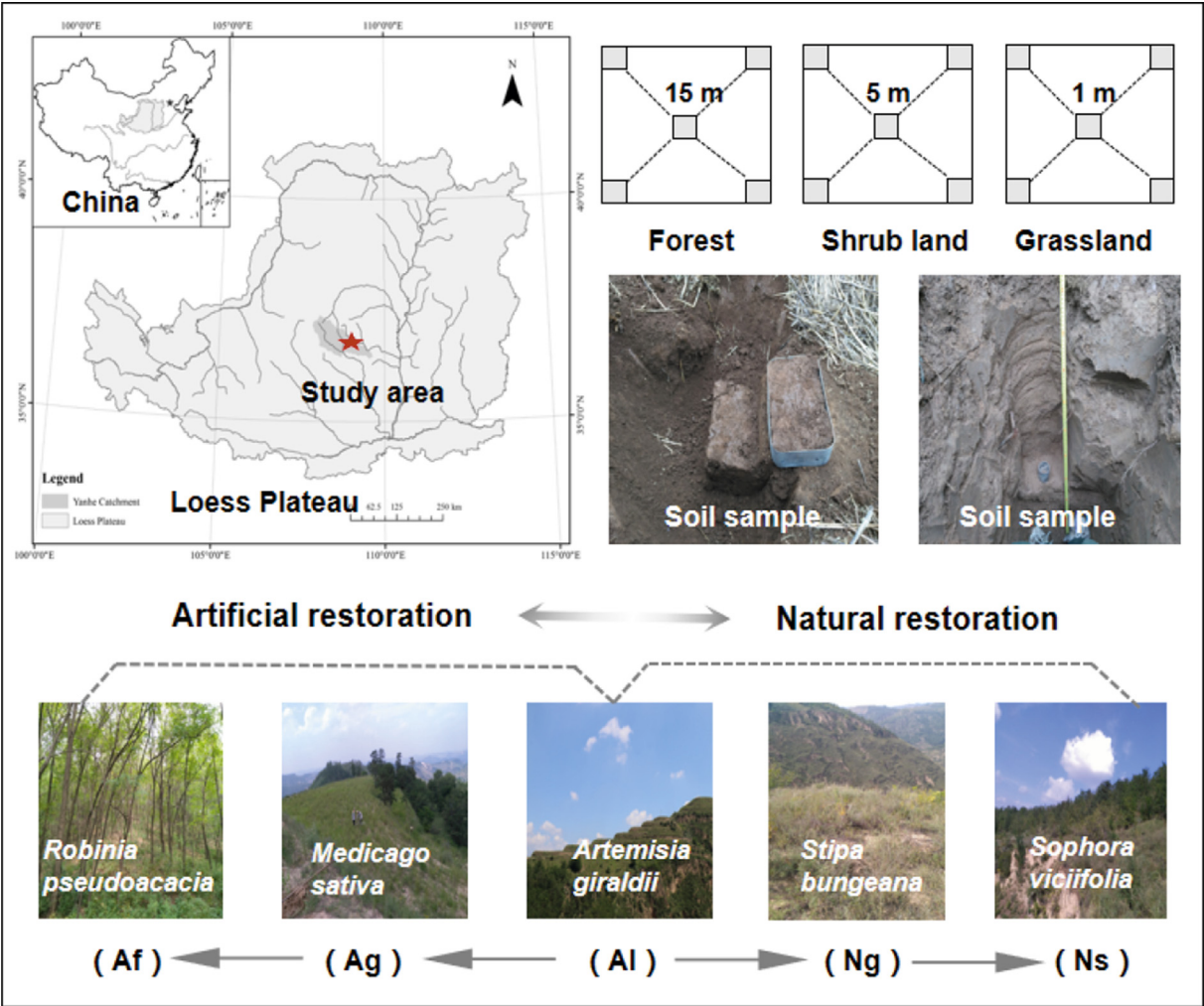


Fig. 1. Location of the study area and layout of the plot, and the picture of the main type of vegetation restoration. The pictures were phoned by Yanxing Dou in July 2016, and generated by ArcMap Version 10.2 (<http://www.esri.com/>).

example, the higher FDis with the diverging values of resource niches, would lead to an increase in niche-complementarity, and then resulting in the higher biomass and C storage. As expected, more evidence demonstrated that niche-complementarity hypotheses and biomass ratio co-regulated ecosystem function and C storage, while they are not necessarily mutually exclusive (Conti and Díaz, 2013; Bragina et al., 2013; Wu et al., 2016).

The Loess Plateau of China is one of the most eroded areas and deepest loess deposits in the world (Fu et al., 2017). To reduce soil water and C loss, soil erosion, the Chinese Government launched a series of remarkable programs in the 1980s (Chen et al., 2015; Feng et al., 2016). Thereafter, the Grain-for-Green program largely contribute to maintaining soil conservation, improving C sequestration since 1999 (Fu et al., 2011). Indeed, a large area of abandoned farmland has been converted to a natural grass-land/shrub-land (natural restoration) or artificial forest (artificial restoration). Subsequently, natural restoration and artificial restoration became the two most successful ecological restoration methods (Li et al., 2017; Tong et al., 2018). In fact, artificial restoration has been regarded as an effective measure for promoting ecosystem restoration by mitigating CO₂ concentrations in the atmosphere (Li et al., 2017; Nave et al., 2018), accelerating soil C sequestration and leading to the increase of soil C storage (Li et al., 2012; Lange et al., 2015; Lal, 2018). In contrast to artificial restoration, natural restoration promotes the ecosystem biogeochemical cycles (particularly soil microbial community activity) by a natural enclosure process (Li et al., 2017; Tong et al., 2018). Most importantly, both of artificial restoration and natural restoration can increase C storage by present studies. For instance, Yang et al. (2018) declared that soil C storage had a strong increase due to vegetation restoration. Similarly, soil nutrients (Zhang et al., 2016) or the other environmental variables make a large contribution to C storage (Karhu et al., 2014; Laforestlapointe et al., 2017; Geml and Wagner, 2018; Tripathi et al., 2018). Whereas, how plant functional diversity changed following vegetation restoration, and the relative contribution of plant functional diversity to C storage still largely unknown in this region.

Plant functional diversity is benefit to improve plant photosynthesis and enhance C efficiency and therefore decrease CO₂. Estimates plant functional diversity following vegetation restoration are critical to predicting future ecosystem C sequestration under global change. Here, the focus of this article is on integrating of plant functional diversity and C storage, which aims to contribute to C sequestration for climate change mitigation following vegetation restoration in the Loess Plateau, China. Thus, we quantified FDis and CWMs and sought to disentangle how plant functional diversity drives C storage (i.e., STC, the soil total carbon; AGBC, the above-ground biomass carbon; ALC, the above-litter carbon; TEC, the total ecosystem carbon) following vegetation restoration in the Loess Plateau. Three questions addressed: (1) How do dominant abundant plant species, plant functional diversity and C storage change following vegetation restoration? and (2) How do plant functional diversity drive C storage following vegetation restoration? If it doing so, we hypothesized that (i) Plant functional diversity affects C storage through the dominant plant functional traits; (ii) C storage in different part could be predicted by FDis or CWMs, based on biomass ratio hypothesis; (iii) C storage in different part are positively associated with FDis, according to niche-complementarity hypothesis.

2. Methods

2.1. Sampling areas

This study was carried out in northern of Shannxi province of the Loess Plateau, located in Zhifanggou (Fig. 1). The studied area has a semi-arid climate, and hills with steep slopes (more than 40%) and cliffs cover 90% of the region with a heavy periodic flooding and seasonal rainfall with the loessal soil. The rainy season is from June to September, while August occupied more than 20% of the total rainfall. The

average annual temperature is from 5 to 9 °C, and the average annual rainfall was approximately 497 mm during two decades.

2.2. Experimental design

Five vegetation types were investigated: Af (artificial forest, *Robinia pseudoacacia*), Ag (artificial grassland, *Sophora viciifolia*), Ng (natural grassland, *Stipa bungeana*), Ns (natural shrub, *Sophora davidii*), Al (abandoned land, *Medicago sativa*). These vegetation types changed by different land-use regimes, including different intensities of extensive grazing and excess reclamation. Despite differences in the historic disturbance regime, currently there was the same soil type among these land use types. We set three replicate plots for each land use type (100 × 100 m) for a total of 45 plots. Each plots were at a distance of 1 km apart, and three replicate sub-plots of 15 × 15 m, 5 × 5 m, and 1 × 1 m were selected for forestland, shrub land, grassland in Sep. 2016. We established five replicate sub-plots in the forest to quantify C in woody, litter and soil at a depth of 100 cm (0–20, 20–40, 40–60, 60–80, 80–100 cm). Specifically, we measured more than 580 trees across the site, and we calculated diameter at breast height (DBH, > 5 cm diameter) and plant height, then estimated above-ground dry biomass by the allometric model in the following formula (Walker et al., 1999):

$$AGB = \exp [-0.548 + \lg(BA)]. \quad (1)$$

BA means the basal area (cm²), which was calculated by $\pi \times (DBH/2)^2$, DBH means the diameter at the breast height (cm).

We established five replicate plots (5 × 5 m) to estimate the shrub biomass. more than 870 shrubs were measured across the site, and then calculated the individual shrub above-ground dry biomass (AGB) according to a general model as following (Jackson et al., 2002):

$$AGB = 1.23 \times \exp (-8.37 + \ln(CA)). \quad (2)$$

CA means the crown area (cm²), defined as the circle, and calculated by the projection diameter. We converted AGB to above-ground biomass C (AGBC) by multiplying 0.5, since C always represents approximately 50% of the dry biomass.

In addition, we harvested all above-ground biomass and litters from five plots (1 × 1 m) to obtain the dry biomass, which was collected from the ground surface. The above-ground biomass and litters were oven-dried at 80 °C until the constant weight (about 36 h) and then weighed. Besides, the dead above-ground biomass were also sampled but not considered in the final calculations. Calculations indicated that the dead biomass represented only 0.1% of the total biomass, which was unlikely to affect the results. In addition, we investigated plant coverage, plant height and the number of species in each site, and the vegetation characteristics, the land-use regimes following vegetation restoration are summarized in Supplementary Table 1.

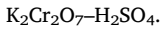
2.3. C storage

The total herbaceous and woody vegetation represented the above-ground biomass C (AGBC, g·m⁻²). The total litter (i.e., the leaf litter and woody debris) represented the above-ground litter C (ALC, g·m⁻²), and we measured the C content of each plant species. The total soil C storage (divided into five depths, 0–20, 20–40, 40–60, 60–80 and 80–100 cm) was quantified by collecting soil from 0 to 100 cm (STC, g·m⁻²). STC was calculated (Deng et al., 2014):

$$STC = SOC \times BD \times D/10 \quad (3)$$

SOC means soil organic carbon (g·kg⁻¹), BD means soil bulk density (g·cm⁻³), D means soil thickness (cm).

Soil samples were collected along an S-shaped curve by a soil corer 10 cm in diameter in each site, air-dried for 20 d, and sieved through a 0.15-mm mesh. SOC was measured by the oxidation method in



$$\text{TEC} = \text{ALC} + \text{AGBC} + \text{STC} \quad (4)$$

TEC means the total ecosystem C.

Meanwhile, latitude, longitude and altitude was determined using Global Position System (GPS).

2.4. Plant functional traits and diversity

To calculate plant trait values across all plots, 42 types of dominant species (a total of 57 species) were collected, since they could account for more than 90% of the total biomass and at least 75% of the total plant coverage. All the plant samples was conducted between 7:30–9:30 a.m. to reduce relative error. Because of variation due to different positions, the leaves were collected from different azimuths without the petiole, and at least six replicates with different maturity and healthy individuals were collected in each plot. The plant functional traits of these dominant plant species presented in [Supplementary Table 2](#).

Generally, LCC, LNC and SLA, are the key traits in the ‘leaf economics spectrum’. LDMC and plant height are trade-off to plant life history strategy and strong related to plant growth. Thus, we selected five key functional traits (i.e., plant height, the LCC, LNC, SLA and LDMC) that are known or expected to affect the C dynamics and storage ([Shipley et al., 2006](#); [Santiago, 2007](#)). The measurements of plant functional traits with the standard method in [Supplementary Table 3](#).

We calculated the dominant trait values by using by the average trait value, and then get the community weighted mean (CWM) ([Villéger et al., 2008](#)). The variety of an individual trait value represents the variance of a trait value, and FDvar (functional trait dispersion index) weighted by each plant species' abundance ([Mason et al., 2003](#)):

$$\text{CWM}(\text{trait}_x) = \sum p_i \cdot x_i. \quad \text{CWM}(\text{trait}_x) = \sum p_i \cdot x_i. \quad (5)$$

$$\text{FDvar} = 2/\pi \arctan(5V), \quad (6)$$

$$V = \sum p_i (\ln x_i - \ln x)^2. \quad (7)$$

CWM (trait_x) refers to the community weighted mean for *x* trait, *p_i* refers to the relative richness of species *i*, and *x_i* refers to the trait value for the species *i*, *V* is plant volume of the species *i*.

In addition, we calculated FDis (the functional dispersion) according to multiple traits, which reflects species divergence in distance, weighted by the multi-trait functional space. In this way, FDis should be closely related to complementarity effects range between 0 and 1.

2.5. Data analysis

All the data analyses were done in Excel 2010 and SAS 9.4 software for windows (SAS Inc., Chicago, IL). Before parametric tests, we tested for the homogeneity of variance. An analysis of variance (ANOVA) and multiple comparisons were used to determine the least significant difference by Tukey's test. For all data tests, statistically significant differences were assigned at *p* < 0.05 or *p* < 0.01. The statistical package FDI-iversity v. 2011 was used to calculate all the functional diversity indices.

Firstly, we used the linear regression analysis to disentangle association between C storage and plant functional diversity. Given the strong correlations between several driving factors, we conducted a principal component analysis (PCA) of the standardized values of those parameters to identify the primary axes of covariation among the driving factors. Then, we used a Monte Carlo permutation test to determine the significance of PCA effects. Secondly, we selected the best

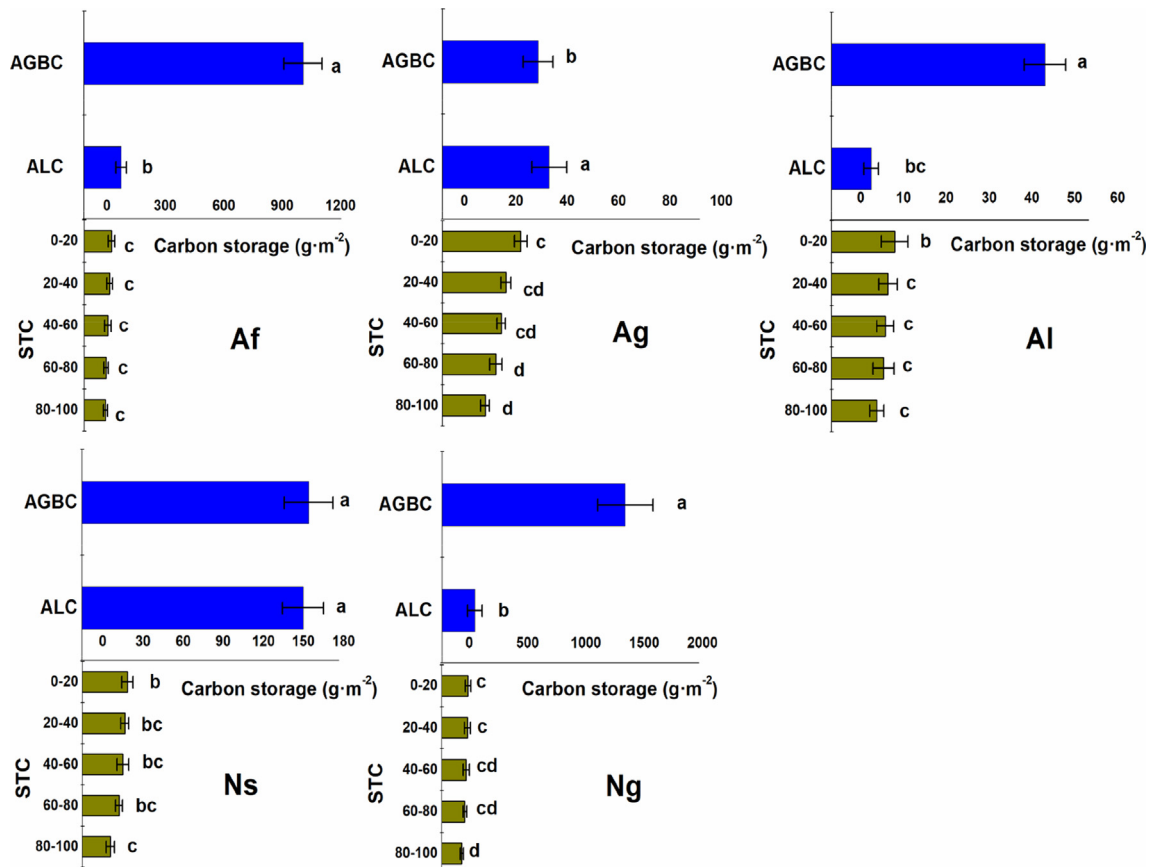


Fig. 2. C storage in different components following vegetation restoration. Different lower-case letters indicate significant differences at *p* < 0.05. artificial forest, Af; natural shrub, Ns; artificial grassland, Ag; natural grassland, Ng; abandoned land, Al.

predictors for explaining C storage in different part by the stepwise regression. Finally, structural equation modeling (SEM) was constructed, and the path coefficients were calculated after 999 bootstraps in AMOS (version 20.0). In SEM, we selected the specific variables that depend on the root mean square error of approximation (RMSEA, $p < 0.05$) and Akaike information criterion (AIC); then, we obtained the indirect and direct effects from the interaction pathways. Finally, we assessed the fitting goodness using the chi-squared tests (χ^2).

3. Results

3.1. C storage and plant function diversity following vegetation restoration

In this study, C storage in artificial forest (Af) and natural shrubs (Ns) followed the order $TEC > AGBC > STC > ALC$, with the lowest C storage in litter, whereas C storage in artificial grassland (Ag) followed the order $TEC > STC > ALC > AGBC$ (Fig. 2). Compared with abandoned land (Al), the average total ecosystem C storage of Af, Ns, Ag and Ng increased 16.79, 11.54, 1.20, and 3.86 times, respectively. Moreover, C storage in litter was higher than in aboveground biomass in Ag (as shown in Fig. 2), litter C in Ng was substantially higher than other land use types. These findings suggested that vegetation restoration (artificial and natural vegetation restoration) could increase C storage in different ecosystem components. In addition, the mainly C storage in

Af, Ng, Ns stored in above ground, whereas the mainly C storage in Ag stored in litter. Besides, soil C storage in Al was $14.2\text{--}15.3\text{ g m}^{-2}$ at $0\text{--}20\text{ cm}$ and $10.4\text{--}10.7\text{ g m}^{-2}$ at $80\text{--}100\text{ cm}$, and no significant difference in Al and Ag ($p > 0.05$). Soil C storage in Ng and Ns were approximately $105.4\text{--}143.0\text{ g m}^{-1}$ at $0\text{--}100\text{ cm}$, and higher than the other vegetation types ($p > 0.05$). As for AGBC, Ns was higher among land use types. TEC in Af, Ns, Ag and Ng were higher than Al and followed $Af > Ns > Ng > Ag > Al$. TEC in Ng was roughly half as much for the other land use types. These results provided a comprehensive comparison for C storage. Besides, a similar vertical distribution of STC (gradually deceased with soil depth) was found following vegetation restoration.

As a component of plant diversity, FDis provides an effective method to study plant species distribution in niche space and resources, which has attracted a great deal of attention. We found that C storage is closely related to vegetation restoration (Fig. 3). Compared to Al, there was an increase in plant height regardless of vegetation types (Table 1). Both of LDMC and SLA in Ag were lower, and LCC in Af and Ns were higher among land use types. LNC in Ns and Ag were higher than Af, Ng and Al. FDis of SLA and LNC showed no significant differences among vegetation types ($p > 0.05$). FDis of LDMC in Ag and Al were significantly lower, and FDis of LCC in Ns was significantly higher among vegetation types ($p < 0.05$). Besides, FDis in Al was significantly lower among vegetation types ($p < 0.05$).



Fig. 3. Correlation of C storage following vegetation restoration. * and ** indicates that the C storage were significantly following vegetation restoration at 0.05 and 0.01 level as detected by analysis of similarities (ANOSIM). The R values of ANOSIM results, which were calculated based on 999 permutations, can be observed under the dissimilarity value.

Table 1
Changes in functional diversity components following vegetation restoration (Mean \pm SE). Means followed by the same letter do not differ significantly at $p \leq 0.05$ by Duncan's multiple range test.

Item	Artificial restoration		Abandoned land (Al)	Natural restoration		F	p
	Artificial forest (Af)	Artificial grassland (Ag)		Natural grassland (Ng)	Natural shrub (Ns)		
Community weighted mean (CWM)							
Height (cm)	620.3 \pm 23.5 ^a	30.3 \pm 6.9 ^d	26.9 \pm 3.6 ^d	81.6 \pm 9.8 ^c	196.8 \pm 18.4 ^b	56.32	< 0.001
SLA (m ² kg ⁻¹)	21.8 \pm 3.2 ^a	13.3 \pm 1.3 ^c	15.7 \pm 2.8 ^b	14.5 \pm 2.1 ^{bc}	19.6 \pm 1.8 ^a	9.28	< 0.01
LDMC (g kg ⁻¹)	215.0 \pm 23.6 ^a	120.5 \pm 15.3 ^d	136.8 \pm 15.9 ^d	174.2 \pm 16.2 ^c	192.3 \pm 19.8 ^b	42.01	< 0.001
LCC (%)	45.7 \pm 6.9 ^a	34.5 \pm 4.2 ^c	35.1 \pm 5.1 ^c	39.9 \pm 6.1 ^b	43.0 \pm 5.8 ^a	32.17	< 0.001
LNC (%)	2.98 \pm 0.56 ^b	3.26 \pm 0.69 ^a	2.54 \pm 0.61 ^b	2.85 \pm 0.23 ^b	3.03 \pm 0.41 ^{ab}	13.25	< 0.05
FDIs	0.09 \pm 0.02 ^c	0.09 \pm 0.01 ^c	0.005 \pm 0.01 ^d	0.25 \pm 0.05 ^a	0.19 \pm 0.03 ^b	5.98	< 0.05

Height, plant height; SLA, specific leaf area; LDMC, leaf dry matter content, LCC, leaf carbon content, LNC, leaf nitrogen content. Different lower-case letters indicate significant differences at $p < 0.05$.

3.2. Correlation analysis between C storage and functional diversity

We examined the correlation between functional diversity and C storage in different ecosystem compartments. Not unexpectedly, functional diversity was significantly related to C storage in different part (Supplementary Table 4). Specifically, the CWM of LCC and plant

height were positively related to AGBC, ALC, STC and TEC ($p < 0.01$), while the CWM of LNC was negatively related to AGBC, ALC, STC and TEC ($p < 0.01$). The CWM of SLA and LDMC were positively related to TEC ($p < 0.01$). Besides, FDis was positively related to AGBC, ALC, STC and TEC ($p < 0.01$). Not unexpectedly, plant functional diversity was positively related to C storage in different part. As a consequence,

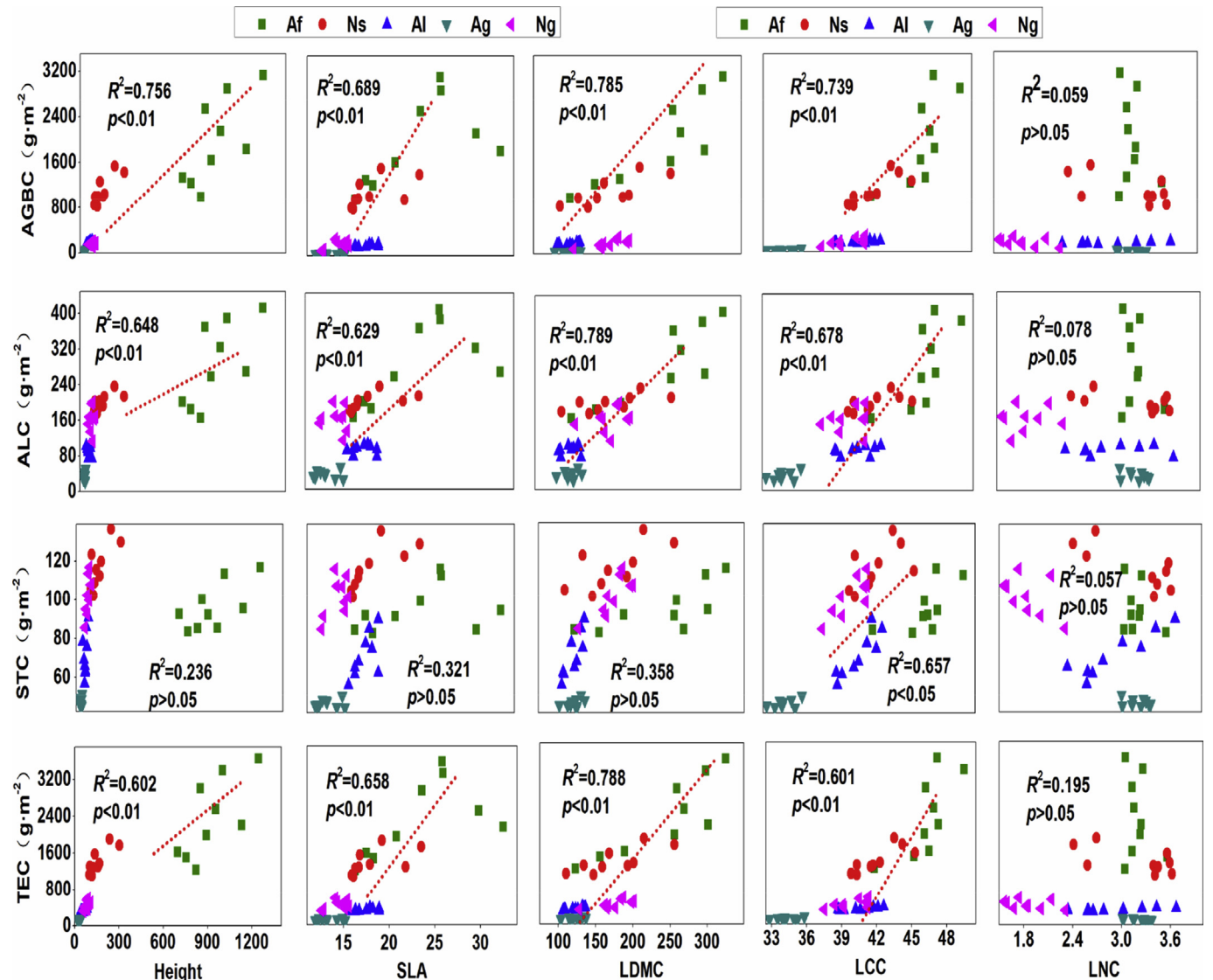


Fig. 4. Simple linear regression analyses between the magnitude of C storage and functional diversity components following vegetation restoration. Only variables included in the multiple linear regression analysis are shown ($n = 45$).

individual plant traits would be more appropriate to explain C storage according to linear regression models (Fig. 4). Among these plant functional traits, the CWM of plant height, SLA, LCC, LNC, and LDMC explained more variation for C storage in different part. Specifically, the CWM of plant height could positively predict C storage except for STC. The CWM of SLA and LDMC positively predicted C storage in AGBC, ALC and TEC but not well explained C storage in STC. In addition, the CWM of LCC positively predicted C storage in different part, and the CWM of LNC had no significant relationship with C storage ($p > 0.05$).

In total, all the plant functional diversity could explain C storage well in the different part, only the single-trait indices explained C storage well in the final models (Table 3). Specifically, AGBC was positively predicted by the CWM of plant height and LCC. ALC was best predicted by FDis and the CWM of plant height. STC was positively predicted by the CWM of SLA and plant height. Finally, TEC was negatively predicted by FDis and the CWM of LDMC and plant height.

3.3. Plant functional diversity drives C storage following vegetation restoration

A principal component analysis (PCA) of plant functional traits were used to identify the correlations between C storage and functional diversity components (Fig. 5A). PCA axis 1 primarily reflected plant height, LDMC, LCC, which accounted for 49.13% of the overall variance; axis 2 mainly reflected SLA, explaining 34.78% of the standardized variance, suggesting that plant height, LDMC, LCC were positively correlated with C storage, while LNC and SLA had no significant difference ($p > 0.05$). In addition, Partial correlations between the magnitude of C storage and functional diversity components was also similar to PCA analysis (Table 2).

Based on these above analyses, structural equation models (SEM) was built to summarize the pathways of the interactions between plant functional diversity and C storage ($F = 236.14$, $p = 0.537$, $df = 27$, $\chi^2 = 6.52$, $GFI = 0.953$, $AIC = 156.31$, $RSMEA = 0.001$) (Fig. 5B, Supplementary Table 5), and we tested for the possible influence in a priori structural equation model (Supplementary Fig. 1). The variation of all of the explanatory factors was 75.04%, indicating that this model could explain C storage well ($p < 0.01$). In the final SEM, FDis was negatively related to the CWM of LNC and SLA, however, the CWM of SLA and LNC was negatively related to AGBC, ALC and TEC with the higher standard coefficient. Similarly, the CWM of plant height and LCC, which showed a positive association with FDis, were regarded as the main predictors for C storage, suggesting that both the mass ratio hypothesis and the niche complementarity hypothesis were not mutually exclusive, they explain C storage in the ecosystem compartments together, which were agreement with the results from linear regression analyses. Further, SEM would provide a new insight to the underlying ecological relationships between FDis and C storage in the ecosystem compartments, such as, FDis increased with the increased species richness following vegetation restoration, supporting the evidence that

the more rich species in ecosystem had the more C storage. This is related to that the richness species enhanced above-ground biomass, and then resulted in a higher C storage. In total, increased CWMs of plant trait was not associated with species richness but with C storage in different ecosystem compartments.

4. Discussion

4.1. C storage and plant function diversity following vegetation restoration

C sequestration plays an important role in mitigating anthropogenic increases in atmospheric carbon dioxide (CO_2). Compelling evidence indicates that large amounts of C have been lost because of the effects of climate change and human disturbance (Nolan et al., 2018; De Nijs et al., 2019). Specially, previous studies have suggested that the increased C storage in Asian terrestrial ecosystems can primarily be attributed to considerable afforestation and reforestation, especially China's vegetation restoration project (Chen et al., 2015; Feng et al., 2016). Recently, NASA Earth satellites showed that Earth has grown markedly greener since the turn of the millennium, and human activity in China and India dominate the greening of our planet, thanks to forest conservation and tree planting, as well as intense crop cultivation (Chen et al., 2019). Here, this study is focus on integrating the possible mechanisms that plant functional diversity explaining C storage, and also test the links between plant functional diversity and C storage in the Loess Plateau. Here, three aspects of our study distinguished from previous studies. First, unlike few studies of the effect of plant functional diversity on C storage, our study not only clarified the changes of C storage and plant functional diversity in terms of vegetation restoration, but also examined the relationships between plant functional diversity and C storage. Second, our study was conducted in the Loess Plateau, which has the world's highest rate of C erosion and faces severe C loss (Fu et al., 2017). It represents a rare exploration of an ecologically important but vulnerable area in the world, and we focused on deciphering association between C storage and plant functional diversity following vegetation restoration. The third and most important, our study demonstrated the positive association between plant functional diversity and C storage, providing an evidence that there were strong links between plant functional diversity and C storage regardless of vegetation restoration in the Loess Plateau.

We found that vegetation restoration (artificial and natural restoration) had a significant effect on C storage (Fig. 2). STC was significantly higher in natural restoration (natural grassland, natural shrub) than in artificial restoration (artificial grassland, artificial forest), while AGBC was significantly greater in artificial restoration (artificial forest) than in natural restoration (natural grassland, natural shrub). The findings revealed that STC increased following vegetation restoration. The possible reason maybe that vegetation restoration (*Robinia pseudoacacia* and *Sophora davidii*) were dominated by *Leguminosae* plants in this region, which are beneficial to accumulate more

Table 2

Partial correlations between the magnitude of C storage and functional diversity components. The p values were calculated on the basis of 999 permutations irrespective of plant species.

Item	Total variance explained (84.36%)	AGBC		ALC		STC		TEC	
		Partial correlation coefficient	Sig.	Partial correlation coefficient	Sig.	Partial correlation coefficient	Sig.	Partial correlation coefficient	Sig.
Height	18.36	0.725	< 0.01**	0.716	< 0.01**	0.396	ns	0.658	< 0.01**
SLA	12.05	0.201	ns	0.159	ns	0.251	ns	0.223	ns
LDMC	13.47	0.695	< 0.01**	0.671	< 0.01**	0.303	ns	0.685	< 0.01**
LCC	17.95	0.674	< 0.01**	0.759	< 0.01**	0.517	< 0.05*	0.701	< 0.01**
LNC	0.68	0.196	ns	0.257	ns	0.324	ns	0.216	ns

Note: Values in bold indicate a significant difference. * and ** signify $p < 0.05$ and $p < 0.01$, respectively. ns, not significant. AGBC, Aboveground biomass carbon; ALC, Aboveground litter carbon; STC, The soil total carbon; TEC, Total ecosystem carbon.

Table 3

Final models obtained from multiple linear regression analysis of the magnitude of C storage and functional diversity components following vegetation restoration, using a stepwise ascending procedure. All multiple regression models were statistically significant ($p < 0.05$). R^2 , regression adjusted coefficient for the multiple regression model.

Response variable (y)	Model form	Predictor variables (x)	Slope	p	R^2
Aboveground biomass carbon (AGBC)	AGBC = 38.25 + 2.14 Height-23.45 LCC	Model		< 0.001	0.856
		Height	-	< 0.001	
		LCC	+	0.016	
Aboveground litter carbon (ALC)	ALC = -19.58 + 1.27 Height + 178.23 FDis	Model		< 0.001	0.785
		Height	+	< 0.001	
		FDis	+	0.029	
The soil total carbon (STC)	STC = -985.36 + 22.58 Height + 105.89 SLA	Model		< 0.001	0.813
		Height	+	< 0.001	
		SLA	+	< 0.001	
Total ecosystem carbon (TEC)	TEC = -2154.62 + 54.13 Height + 5231.47 FDis + 11.02 LCC	Model		< 0.001	0.874
		Height	+	< 0.001	
		FDis	+	0.008	
		LCC	+	0.013	

nitrogen (N) by N-fixing microorganisms, and then promote an increase in C storage (An et al., 2013; Deng et al., 2014). In particular, STC was higher in natural restoration (Ns, Ng), and AGBC was more higher compared to abandoned land (Al). Further, there was a large AGBC and TEC due to the large above-ground biomass, leading to more C storage. As for Al, a lower C input and higher C mineralization resulted in less C storage, because conventional tillage was still used in this area, which induced large C losses (Beare et al., 1994; Skjemstad et al., 2008). Overall, the findings confirmed the fact that C storage has been increased due to vegetation restoration in the Loess Plateau.

Moreover, the findings of the higher C storage in the surface soil layer do agree with the results from An (An et al., 2013), Wang (Fu et al., 2011), Deng (Deng et al., 2014), Fang (Fang et al., 2018) and Liu (Liu et al., 2018), because of the higher C input in the surface litters. However, this findings were not in agreement with the study of Fu (Fu et al., 2011) and Liu (Liu et al., 2018), who reported that soil C storage in artificial grassland (Ag) was slightly less than in abandoned land, nor did they agree with the results of Chen (Chen et al., 2015) and Tang (Tang et al., 2018), who reported that soil C storage in artificial grassland was significantly higher in the top soil (0–20 cm). This is related to the management and regimes from government in land use

types. Artificial grassland was mowed several times to feed cattle or sheep in this region, leading to a reduction in C storage, while artificial forest was usually managed with no application of chemical or organic fertilizer, resulting in the large plant biomass and C storage (Wang et al., 2010; Fu et al., 2011; Chen et al., 2015). Overall, conversion of the vegetation types in this region, i.e., vegetation restoration, could increase C storage in different ecosystem compartments. Interestingly, the plant functional traits showed the similar variation trend with the C storage (Table 1), suggesting a strong links between plant functional traits and C storage.

4.2. Plant functional diversity drives C storage following vegetation restoration

The present study had shown how plant functional diversity explained ecosystem C storage in terms of vegetation restoration in the Loess Plateau, which could be extensively discussed in the role of plant functional diversity effects on ecosystem function. Specially, we found that C storage is closely related to vegetation restoration (Fig. 3) and apparently linked to plant functional diversity (Table 2; Fig. 4), supporting our first hypothesis that plant functional diversity affects C

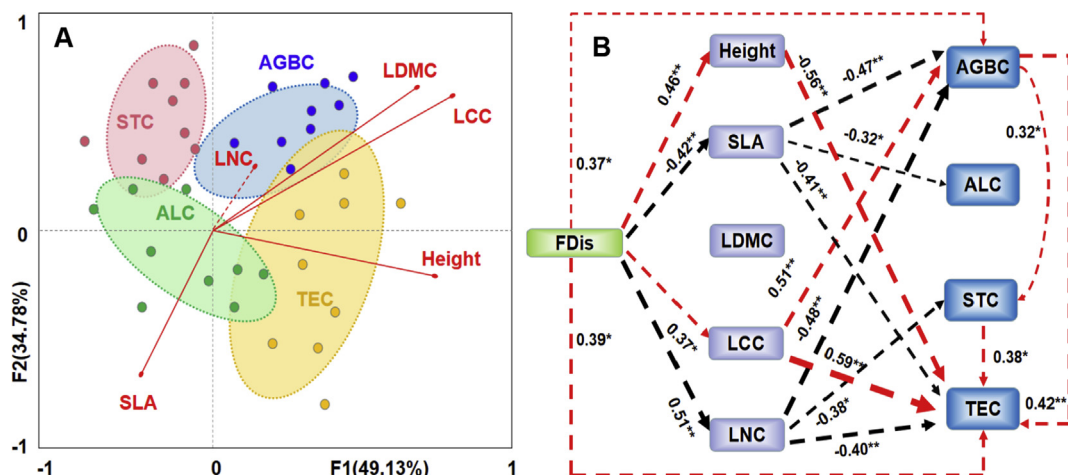


Fig. 5. Principal component analysis of the magnitude of C storage and functional diversity components (A); Each arrow represents the eigenvector corresponding to an individual variable. PC1 accounted for 49.13% of the overall variance, and PC2 accounted for 34.78% of the overall variance. The structural equation model (SEM) of FDis and functional diversity components effects on C storage (B). The structural equation model considered all plausible pathways through which CWM of plant functional traits influence C storage. Red, black arrows represent significant positive and negative pathways, respectively. Bold numbers indicate the standard path coefficients are significant difference. Arrow width is strongly related to the path coefficients. R^2 represent the proportion of variance explained for each dependent variable in SEM. *, and ** indicate statistically significant paths at $p < 0.05$, $p < 0.01$, respectively. ($F=236.14$, $p=0.537$, $df=27$, $\chi^2=6.52$, $GFI=0.953$, $AIC=156.31$, $RSMEA=0.001$, 75.04%). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

storage through the dominant plant functional traits. Further, a strong relationship between C storage and plant functional diversity was found in different ecosystem compartments (Fig. 4). This result indicates that plant functional diversity represents the abiotic variables and independently explains C storage in different ecosystem compartments. Specifically, the CWM of plant height was significantly and positively correlated with ALC, AGBC, STC and TEC ($p < 0.01$), which explained C storage in regression analyses. Not surprisingly, the CWM of plant height was an important factor in explaining C storage. This can be explained by that the higher abundant species can increase plant biomass due to vegetation restoration, thus contributing to the higher C storage, and supporting the first hypotheses that the trait values of the dominant abundant species could predict C storage in different ecosystem compartments (Wright et al., 2006; Weng et al., 2014; Xiao et al., 2014; Kammann et al., 2015; Nie et al., 2015). Besides, the CWM of plant traits (plant height, LCC) were significantly and correlated to C storage in different ecosystem compartments, supporting our second hypothesis that C storage in different ecosystem compartments could be predicted by CWMs in accordance with the biomass ratio hypotheses. Most importantly, the positive association between C storage and plant functional diversity were found, providing an evidence that strong links between C storage and plant functional diversity regardless of vegetation restoration in the Loess Plateau.

In addition, PCA was used to identify the correlations between C storage and plant functional diversity (Fig. 5A), and we found that FDis was positively related to C storage in structural equation model (SEM) (Fig. 5B, Supplementary Table 5). This result partly supported the third hypothesis that a higher FDis was associated with greater C storage, suggesting that FDis has an important role in explaining C storage. This result is also consistent with other findings because different plant species can use C in a complementary manner (Cornelissen and Cornwell, 2014; Prentice et al., 2014). On the one hand, dominant plant species increase the above-ground biomass, which is known as the “selection effect” due to vegetation restoration. On the other hand, this is related to the “niche-complementarity effect”—at a higher diversity, a greater range of plant functional diversity will be represented, providing opportunities for more efficient use of C resources (Fierer et al., 2005; Manzoni et al., 2011; McCormack et al., 2015). Following changes in dominant species and richness in vegetation restoration, C storage were mainly governed by litter quality, and the above- and under-ground biomass (Thakur et al., 2015; Freschet et al., 2015). Therefore, the links between the plant functional diversity and C storage may primarily be explained either by the biomass ratio hypothesis or the niche-complementarity model (Cornelissen and Cornwell, 2014; Prentice et al., 2014). This result supported the findings that the mass ratio and niche-complementarity hypotheses in combination explain C storage. Besides, FDis was negatively related to the CWM of plant traits, and C storage was negatively related to the CWM of SLA and LNC with a higher standard coefficient (Table 3). Similarly, the CWM of plant height and LCC, which showed a positive association with FDis, were regarded as significant predictors for C storage. Giving the reason that plant height and LCC would improve microclimatic factors, such as soil temperature, humidity and natural resources, so plant height largely determines C storage. Therefore, we can get the conclusion that the FDis and CWM traits, together explained C storage, supporting most of previous studies (Walker et al., 1999; Berg and Meentemeyer, 2002; Murphy et al., 1998). These findings supported some previous results that FDis and CWM traits can explain C storage reported by Zuo (Zuo et al., 2016a) in Horqin sandy and Conti and Díaz (2013) in semi-arid forest ecosystems. These findings have important implications for improving global C cycling and ecosystem services. Although our results demonstrated that the major plant functional diversity-dominant trait values are the main drivers for C storage in Loess Plateau, the other environmental drivers (such as the climate factors, land use types, human management, temperature, precipitation and so on) affecting C storage should be considered in further study.

5. Conclusions

In summary, we found the strong positive effect of plant functional diversity on C storage, by increasing plant functional diversity, may enhance C storage, indicating that vegetation restoration contribute to plant functional diversity and C storage in the Loess Plateau, and the prevalence of particular trait combinations may also increase C storage. These results imply that increasing C storage can be better achieved by managing the functional composition of restored communities. So the implementation of vegetation restoration could be a quantitatively important strategy, and thus should be continually paid a great attention.

6. Practical implications

Our study highlights the importance of both plant traits of dominant species and plant functional diversity in regulating C storage in the Loess Plateau. The current vegetation restoration can be greatly improved by incorporating plant functional diversity into C storage in the future, providing some guidance for management for C storage in terms of vegetation restoration. Thus, maintaining high levels of plant functional diversity can help sustain the benefits of C storage and ecosystem services in the Loess Plateau.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2019.06.054>.

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