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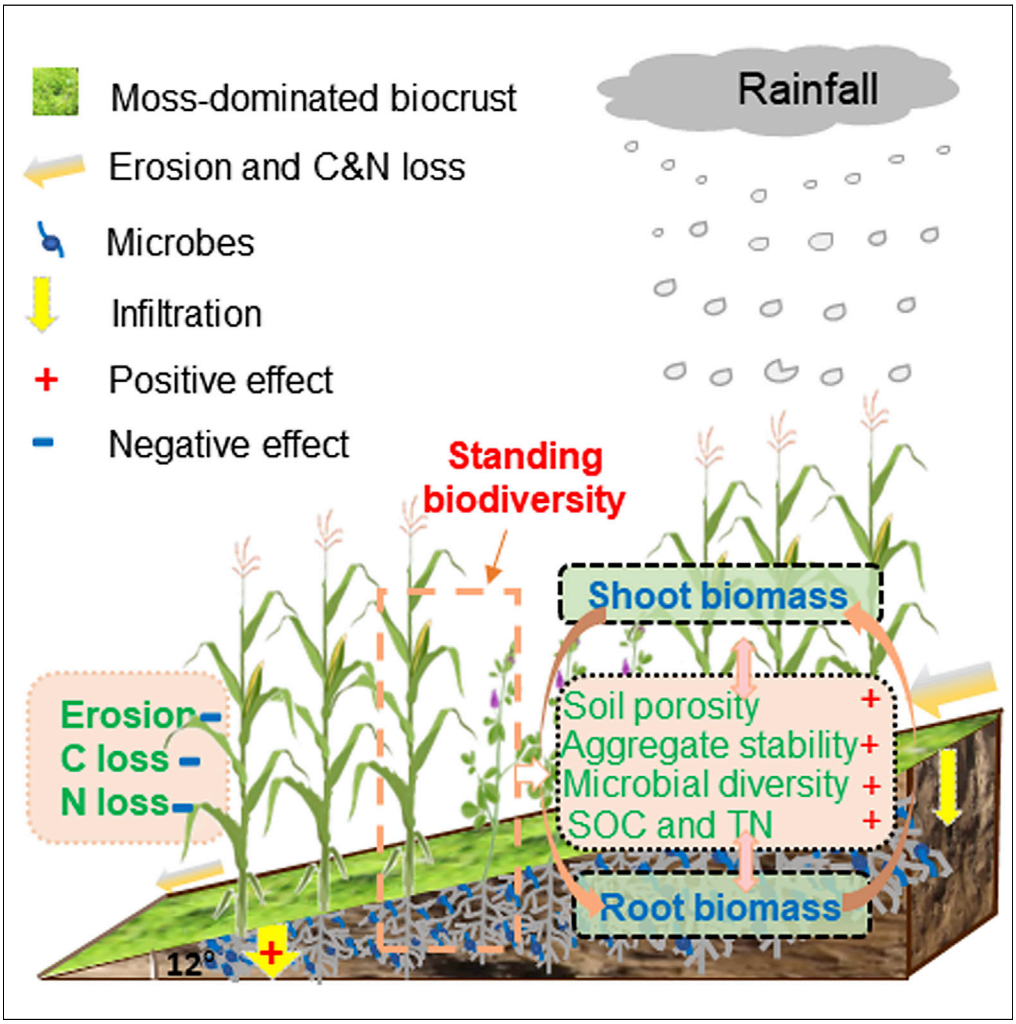

Wei Wang, Meng-Ying Li, Rui Zhou, ..., Wen-Li Wang, Ze-Ying Zhao, You-Cai Xiong

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Highlights

Moss biocrust + intercropping acted as nature-based solution (NbS) in eroded soil

This NbS elevated water interception and lowered surface soil C and N loss ($p < 0.05$)

It also enhanced fungal community abundance via inputting more organic into soils

Moss-led NbS optimized plant-soil-fungi interactions for higher C sequestration

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Moss-dominated biocrust-based biodiversity enhances carbon sequestration via water interception and plant-soil-microbe interactions

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SUMMARY

We investigated a nature-based solution (NbS) via incorporating biocrust into alfalfa-maize intercropping system to test carbon sequestration in seriously eroded agricultural soils. Field investigation showed that the NbS (moss-dominated biocrust + intercropping) massively lowered surface soil erosion by 94.5% and soil carbon (C) and nitrogen (N) loss by 94.7 and 96.8% respectively, while promoting rainwater interception by 82.2% relative to bare land (CK). There generally existed positive interactions between biocrust and cropping in the integrated standing biodiversity system. Enhanced plant biomass input into soils substantially promoted soil fungal community diversity and abundance under NbS ($p < 0.05$). This enabled NbS to evidently improve soil macroaggregate proportion and mean weight diameter. Critically, topsoil carbon storage was increased by 2.5 and 10.7%, compared with CK and pure intercropping ($p < 0.05$). Conclusively, the standing diversity under such NbS fostered soil C sequestration via water interception and plant-soil-microbe interactions in degraded agricultural soils.

INTRODUCTION

Soil erosion is a critical environmental challenge threatening agricultural development globally.[1] Surface runoff and human disturbances are among the main causes of this issue.[2] In the semiarid rainfed agricultural regions, water-driven soil erosion is frequently accompanied by the massive loss of soil carbon (C) and nitrogen (N). This in turn can lead to decreases in land productivity and environmental sustainability.[3] Currently, approximately 1.09 billion hm^2 of global land has been impacted by water-driven soil erosion.[4] The proportion of land degradation caused by erosion has reached up to 84%. More than 201×10^3 km^2 of land worldwide is faced with increasing erosion.[5] To overcome the erosion-led land degradation, some engineering measures, such as terraced field establishment and no-tillage, have been employed in many areas.[6] In this regard, intercropping systems have been widely applied to enhance field productivity and soil quality in dryland agriculture.[7] Intercropping is a typical planting pattern with diversified crop species used on the same farmland. This approach can help establish niche complementarity for better water and nutrient uptake and utilization.[8] In particular, the positive interactions between below- and above-ground parts can result in better canopy cover, which in turn reduces evaporation and soil erosion.[9]

Over last two decades, the nature-based solutions (NbS) have been widely accepted to restore degraded ecosystems. The NbS approach was originally proposed in the early 2000s.[10] It aimed to promote natural resource conservation using a sustainable way.[11,12] It can enhance ecosystem resilience and coordinate environmental and economic developments.[13,14] However, the unreasonable economic growth and extreme climate have caused increasing degradation in natural ecosystems over the last decades, seriously threatening sustainable development.[15] Hence, the introduction of NbS into natural ecosystem management is much needed for better conservation and rehabilitation.[16,17]

Among the applications of NbS, biological soil crust (BSC) inoculation is viewed as a promising strategy to restore degraded soils and ecosystem functions. In general, the biocrust is composed of eukaryotic microalgae, cyanobacteria, bacteria, lichens, fungi, and mosses. It can aggregate on soil surface up to a height of a few centimeters in arid and semiarid areas.[18] Globally, natural BSCs cover up to almost 12% of the earth's terrestrial surface and can enhance soil microbial diversity and protect bare soil surfaces.[19] They can

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increase C and N concentrations via photosynthesis and N fixation.[20] During the process of BSC growth and development, they can produce plant growth-promoting hormones and growth-regulating substances such as vitamins, amino acids and sugars, which can turn to improve plant growth and development.[21]

Therefore, BSCs are endowed with outstanding ecological functions to stabilize soil structure and alleviate soil erosion. The colonization of BSC can enhance the physical protection of surface soil, particularly under increasing biomass.[22] BSCs reshape soil structure and morphology via filaments and exopolysaccharide secretion to bind fine particles and soil organic matter into macroaggregates.[23] A previous study showed that BSC inoculation promoted soil ability to resist erosion by 135%, relative to bare land.[24] In short, BSC inoculation is a crucial NbS to realize the sustainable development of terrestrial ecosystems, because it can generate positive effects on soil microbial diversity and soil quality. It has displayed huge potential in restoring degraded soils as well as against soil erosion.[25] However, previous studies were mostly focused on natural ecosystems, particularly regarding specific traits or functions of BSC from a certain single perspective. Few studies were aimed to explore the effects of BSC inoculation on soil and water conservation and carbon sequestration connecting above- and underground biodiversity in agricultural soils.

In the semiarid rainfed agricultural region, such as the Loess Plateau of China, there exists severe surface soil erosions because of intensive rainfall, slope steeps, erodible loess, vegetation deterioration and unreasonable agricultural activities.[26] In terms of the degraded soil restoration, the moss-dominated biocrust has attracted increasing attention owing to its greater biomass, larger thickness and ecological adaptation relative to other forms of biocrusts.[27,28] On the other hand, the standing biodiversity connecting below- and above-ground organisms is also a feasible and promising approach. Yet, it is so far little reported in this aspect. For this reason, we hypothesized that BSC inoculation might be able to be incorporated into an intercropping system and would act as a deep form of ecosystem (the nature-based performative solutions) to conserve water and soil resources, and enhance carbon sequestration. Specifically, we established the runoff observation ground with and without the inoculation by moss-dominated biocrust (MdB) in monocropped alfalfa (*Medicago sativa* L.), monocropped maize (*Zea mays* L.) and alfalfa-maize intercropped fields. The objectives of this study were designed as follows: (1) To evaluate the effects of the NbS (MdB + intercropping) on water and soil erosion at the field scale; (2) to elucidate the dynamics of soil C and N loss and water interception under the NbS; (3) to reveal the mechanisms how soil structure and soil fungal diversity affect soil C and N storage under the NbS; and (4) to establish a full picture of the interactions between MdB-based standing biodiversity and soil C sequestration in seriously eroded soils.

RESULTS

The variations in soil and water erosion as affected by NbS

Among the planting modes, the MdB inoculation significantly decreased surface erosion, while improving rainwater interception and infiltration ($p < 0.05$). There were no significant differences between MdB inoculation and planting modes (Figure 1, Tables S1 and S2). Compared with CK (bare land), the sand content, total sediment, erosion and runoff in the treatments without MdB inoculation tended to significantly decrease ($p < 0.05$) by 47.1–75.0%, 77.0–91.6%, 77.0–91.6% and 47.5–82.8% respectively. Similarly, the above erosion-related parameters under MdB inoculation were observed to decline by a greater margin, i.e. by 62.6–81.3%, 90.2–94.5%, 90.2–94.5% and 62.4–81.0% respectively, relative to CK. In all seven observational groups, the highest values were recorded in CK, including those of the sand content (26.7 g L^{-1}), total sediment (290 g $plot^{-1}$), erosion (80.7 kg ha^{-1}) and runoff (4.06 m^3 ha^{-1}), respectively. And the lowest values were observed in the MdB treatments, including the sand content (0.33 g L^{-1}), total sediment (0.84 g $plot^{-1}$), erosion (0.23 kg ha^{-1}) and runoff (0.04 m^3 ha^{-1}), respectively. Furthermore, the one-way repeated-measures ANOVA analysis showed that the MdB inoculation resulted in significant declined affects in sand contents, erosion and runoff ($p < 0.05$), relative to the control, whereas only exerted slight effects compared with the no-MdB treatments (excepting for the runoff).

Carbon and nitrogen loss with runoff under the NbS

Across two growing seasons, MdB inoculation substantially restricted C and N loss with runoff. Yet, there were no obvious interactive effects in the MdB ×planting model (Figure 2, Tables S3 and S4). Among all the treatments, the C content of sediment presented less change, and did not show significant differences. However, the N content of sediment, and its C and N losses were significantly higher in CK than those of in the six treatments ($p < 0.05$). Furthermore, under the condition without MdB inoculation, the N content

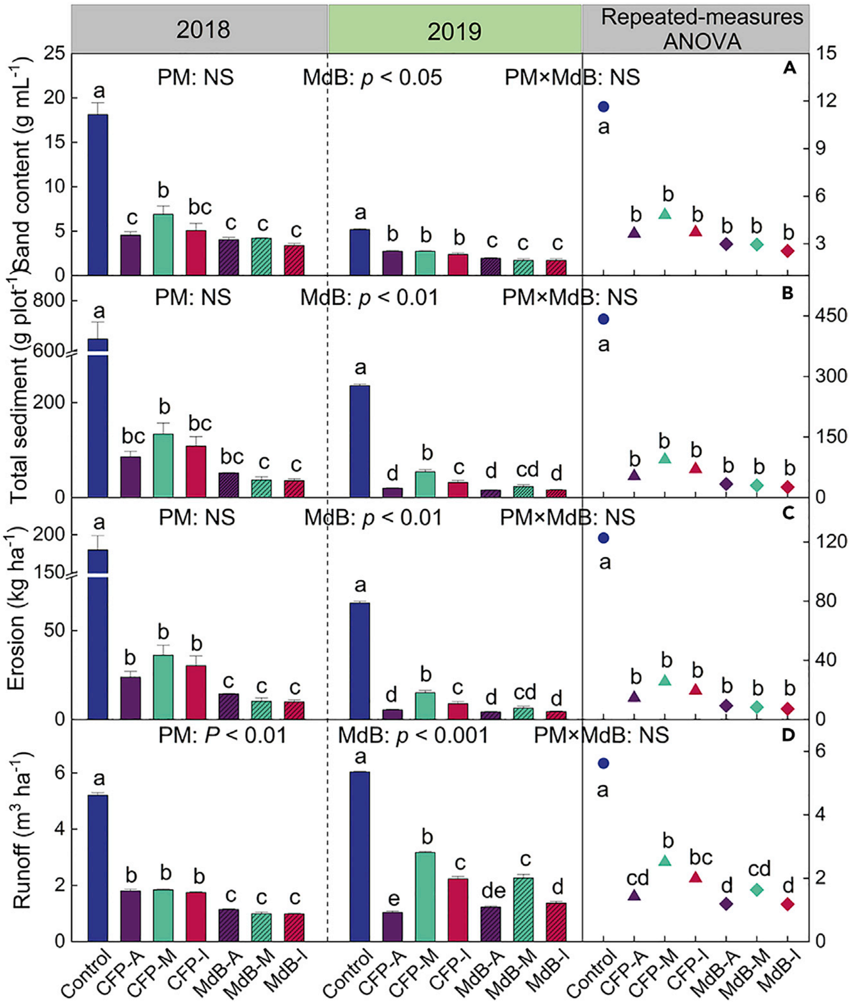

Figure 1. The variations of soil erosion parameters and runoff amount in response to the standing biodiversity system across two years (2018–2019)

Notes: (1) (A) sand content of erosion; (B) total sediment; (C) soil erosion; (D) runoff. (2) CFP-A, conventional flat planting (i.e., no-MdB treatment) for monoculture alfalfa; CFP-M, conventional flat planting for monoculture maize; CFP-I, conventional flat planting for the alfalfa-maize intercropping. (3) MdB, moss-dominated biocrust; MdB-A, MdB for monoculture alfalfa; MdB-M, MdB for monoculture maize; MdB-I, MdB for the alfalfa-maize intercropping. (4) PM, planting model (monoculture and intercropping). (5) Different letters indicate significant differences among planting treatments at the 0.05 level (the same in the below).

of sediment, and its C and N losses were observed to significantly decline by 22.1–45.4%, 77.2–92.0% and 84.0–94.4% respectively, relative to those of CK ($p < 0.05$). In contrast, under the MdB inoculation, the N content of sediment, and the C and N losses showed dramatic declines, i.e., lower by 23.0–41.2%, 90.7–94.7%, and 93.8–96.8% respectively, compared to CK ($p < 0.05$). To sum up, the losses of soil C & N with surface erosion in the MdB + intercropping treatment were significantly lower than those in the other treatments. In general, one-way repeated-measures ANOVA analysis demonstrated that the MdB inoculation significantly lowered C and N loss ($p < 0.05$), compared with the control level, but showed slight change in compared with the no-MdB treatments.

Responses of soil physical properties to the NbS

In general, the MdB inoculation generated significant effects on the size distribution of soil particles and the porosity of soil across all the planting modes. It massively enhanced soil stability and reduced the K value of soil erodibility (Table 1). Compared with CK, the levels of soil clay, sand and STP were increased by 1.42–2.85%, 0.10–3.17% and 1.46–13.0% respectively, under the no-MdB inoculation. In contrast, the silt

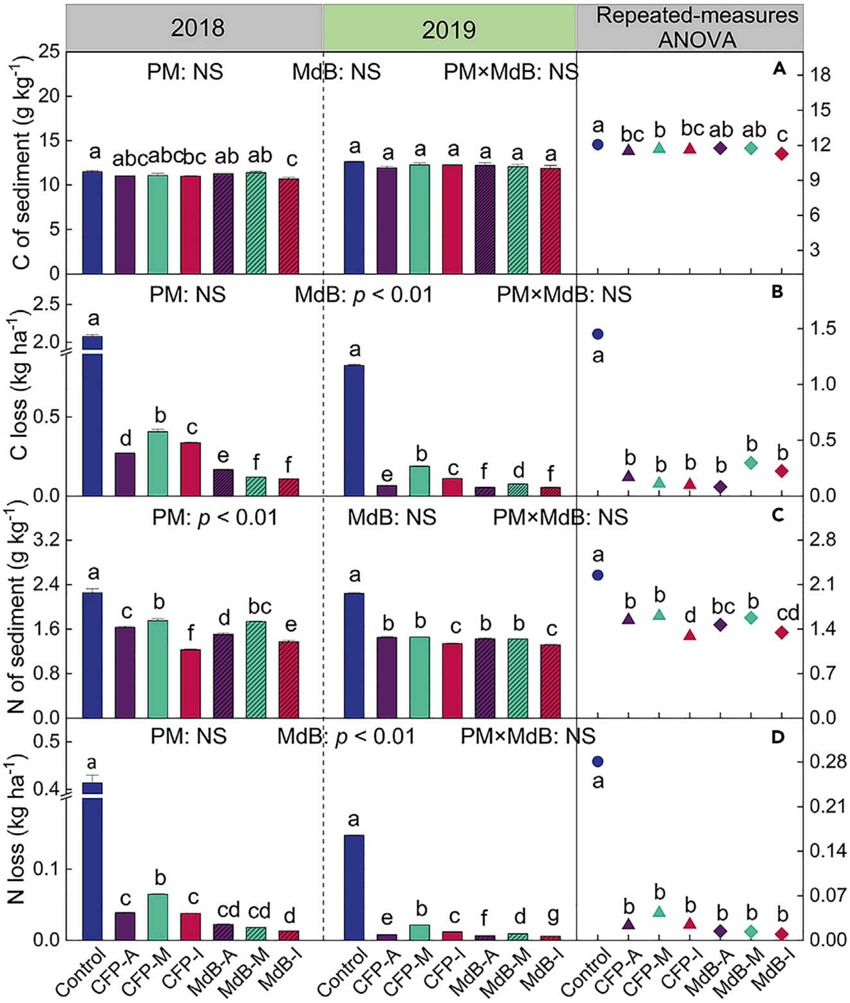

Figure 2. The variations of sediment C & N levels and their losses in response to the standing biodiversity system across two years (2018–2019)

Notes: (A) SOC content of sediment; (B) total SOC loss; (C) TN content of sediment; (D) total TN loss.

proportion, soil bulk density (SBD), and erodibility K values were lowered by 2.19–10.4%, 0.22–14.7%, and 1.93–3.88% respectively. Similarly, the levels of soil clay, sand, and soil total porosity (STP) in the MdB inoculated groups showed obvious increasing trends ($p < 0.05$), up to 4.63%, 14.4%, and 12.7%, respectively, much higher than those of the no-inoculated groups. In addition, the levels of soil silt, SBD, and erodibility K value also presented significant downward trends ($p < 0.05$), with the decreasing rates of 49.2%, 15.6 and 20.7% respectively. In general, the intercropping system combined with MdB inoculation showed positive interactive effects on soil physical properties.

Responses of soil water-stable aggregates to the NbS

In general, the composition of soil macroaggregates were evidently promoted as a result of MdB inoculation in all observational groups. The MdB inoculation displayed positive effects on soil structure stability and was thus beneficial to prevent soil erosion (Table 2). First, the pure planting without MdB inoculation evidently improved the percentages of >2.0 mm, 1.0–2.0 mm and 0.5–1.0 mm soil aggregates by 621%, 230 and 89.8% respectively, relative to CK. Accordingly, the proportion of 0.25–0.5 mm and <0.25 mm aggregates turned to decline by 41.5 and 37.9% respectively. When inoculated with MdB, the proportions of soil aggregates of >2.0 mm, 1.0–2.0 mm and 0.5–1.0 mm were elevated by 641%, 217%, and 98.6% respectively, in comparison with those of CK. Correspondingly, the proportions of 0.25–0.5 mm and <0.25 mm particles

Table 1. Variations of soil physical properties and its erodibility K factor in response to the standing biodiversity system in two growing seasons

	Soil particle size distribution (%)			SBD (g cm^{-3})		STP (%)		Soil erodibility K factor (Mg h MJ^{-1} mm^{-1})
Treatments	Clay	Silt	Sand	2018	2019	2018	2019	
Control	28.1 ± 0.03days	18.3 ± 0.21a	53.6 ± 0.19cd	1.13 ± 0.03a	1.28 ± 0.00a	55.8 ± 0.80c	51.6 ± 0.02days	0.093 ± 0.0003a
CFP-A	28.5 ± 0.06c	16.4 ± 0.03b	55.1 ± 0.03b	1.10 ± 0.02 ab	1.23 ± 0.01b	57.5 ± 0.70bc	53.5 ± 0.48c	0.089 ± 0.0001b
CFP-M	28.7 ± 0.07bc	16.5 ± 0.12b	54.8 ± 0.18bc	1.06 ± 0.02b	1.13 ± 0.01c	58.9 ± 0.70b	58.4 ± 0.47a	0.089 ± 0.0001b
CFP-I	28.9 ± 0.03b	17.9 ± 0.26 ab	53.2 ± 0.30days	1.13 ± 0.01a	1.09 ± 0.01cd	56.6 ± 0.39c	57.9 ± 0.36 ab	0.091 ± 0.0003 ab
MdB-A	29.4 ± 0.09a	9.80 ± 0.15c	60.8 ± 0.06a	1.08 ± 0.02 ab	1.10 ± 0.01cd	58.4 ± 0.50b	57.6 ± 0.48 ab	0.074 ± 0.0004c
MdB-M	29.4 ± 0.03a	9.80 ± 0.50c	60.8 ± 0.48a	1.06 ± 0.01b	1.08 ± 0.01day	58.9 ± 0.22b	56.5 ± 0.24b	0.075 ± 0.0013c
MdB-I	29.4 ± 0.06a	9.30 ± 0.51c	61.3 ± 0.46a	1.00 ± 0.01c	1.08 ± 0.02days	61.0 ± 0.24a	58.2 ± 0.81a	0.074 ± 0.0014c
PM	NS	NS	NS	NS		NS		NS
MdB	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.05$		$p < 0.05$		$p < 0.001$
PM×MdB	$p < 0.001$	$p < 0.05$	$p < 0.01$	NS		NS		NS

Notes: 1) Clay, silt and sand represent the soil particles with the size of <0.002, 0.002–0.02 and 0.02–2 mm, respectively. 2) SBD, soil bulk density; STP, soil total porosity. 3) Control, bare land without planting; CFP-A, conventional flat planting for monoculture alfalfa; CFP-M, conventional flat planting for monoculture maize; CFP-I, conventional flat planting for the alfalfa-maize intercropping. 4) MdB, moss-dominated biocrust; MdB-A, MdB inoculation for monoculture alfalfa; MdB-M, MdB inoculation for monoculture maize; MdB-I, MdB inoculation for the alfalfa-maize intercropping. 5) Different small letters indicate significant differences among planting treatment at the 0.05 level. The values are mean +SE (error bar). NS indicate no significant different. 6) PM, planting model (monoculture and intercropping) (the same in the below).

Table 2. Variations of soil water-stable aggregate composition in response to the standing biodiversity system

	Composition of soil aggregate (%)						
Treatments	>2 mm	2–1 mm	1–0.5 mm	0.5–0.25 mm	<0.25 mm	$R_{0.25}$ (%)	MWD (mm)
Control	4.19 ± 0.91c	2.07 ± 0.57b	4.24 ± 0.15b	17.6 ± 0.89a	71.9 ± 0.42a	28.1 ± 0.42c	0.30 ± 0.01c
CFP-A	18.0 ± 3.41 ab	5.80 ± 1.02 ab	7.60 ± 0.57 ab	11.9 ± 1.74b	56.7 ± 1.08b	43.3 ± 1.08b	0.62 ± 0.04b
CFP-M	16.4 ± 1.10b	5.75 ± 0.88 ab	6.15 ± 1.08 ab	11.8 ± 1.37b	59.9 ± 2.82b	40.1 ± 2.82b	0.58 ± 0.03b
CFP-I	21.7 ± 3.7 ab	5.79 ± 1.4 ab	7.41 ± 1.3 ab	10.4 ± 2.1b	54.7 ± 7.4b	45.3 ± 7.4b	0.68 ± 0.08b
MdB-A	31.0 ± 2.52a	6.50 ± 0.84a	7.40 ± 0.40 ab	10.2 ± 0.26b	44.9 ± 3.15c	55.1 ± 3.15a	0.87 ± 0.06a
MdB-M	26.2 ± 4.05 ab	6.40 ± 0.30a	8.40 ± 0.66a	10.2 ± 1.42b	48.8 ± 3.28c	51.2 ± 3.28a	0.78 ± 0.07a
MdB-I	30.2 ± 2.92a	6.75 ± 0.68a	8.05 ± 1.42 ab	10.3 ± 1.04b	44.7 ± 1.03c	55.3 ± 1.03a	0.86 ± 0.05a
PM	$p < 0.05$	NS	NS	NS	$p < 0.05$	$p < 0.05$	$p < 0.05$
MdB	$p < 0.05$	NS	NS	NS	$p < 0.05$	$p < 0.05$	$p < 0.05$
PM×MdB	NS	NS	NS	NS	NS	NS	NS

Notes: $R_{0.25}$, aggregates of diameter >0.25 mm. MWD, mean weight diameter.

were significantly lowered by 42.1 and 37.7%, respectively ($p < 0.05$). Finally, the mean weight diameter (MWD) reached the highest value as a result of MdB inoculation, as high as 0.87 mm. Yet, the interaction between MdB and cropping did not reach a significant level.

Dynamics of soil nutrients under the NbS

As indicated in Figures 3 and S5, the addition of MdB into mono- and intercropping systems broadly improved soil labile C content, and microbial biomass, and C & N accumulation in the surface soils. When it came to the non-MdB treatment groups, the levels of soil easily oxidized organic carbon (EOC), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), soil organic carbon (SOC), total nitrogen (TN), EOC/SOC and MBC/SOC tended to increase relative to the CK levels, in which the variations in EOC, MBC and MBN, EOC/SOC and MBC/SOC reached significant levels ($p < 0.05$). On the other hand, the MdB treatment resulted in markedly higher EOC, MBC, MBN, SOC, TN, EOC/SOC and MBC/SOC than CK. The percentage of increase was up to 54.7–335.4%, 43.2–155.0%, 25.5–100.7%, 1.54–27.1%, 25.5–67.5%, 43.2–258.9% and 18.0–132.7% respectively ($p < 0.05$), except for the ratio of SOC-TN. The MdB × planting model interaction did not reach a significant level in terms of the above indicators (except MBC). Finally, one-way repeated-measures ANOVA analysis showed that the MdB inoculation significantly affected EOC, MBC, MBN, SOC and TN content ($p < 0.05$), relative to the control and no- MdB inoculation levels.

Changes in soil microbial community characteristics under the NbS

Overall, soil microbial community (i.e.. fungi, the same in the below) diversity was significantly affected by MdB inoculation (Figures 4 and S2). The observed species, Chao 1, Shannon and Simpson indexes of microorganisms in soils were higher under intercropping treatments than those in the single-species planting and control groups, whereas those under MdB inoculation were dramatically higher than those without MdB treatment ($p < 0.05$). In addition, the non-metric multidimensional scaling (NMDS) analyses showed that there were evident differences in operational taxonomic unit (OTU) among those treatments. To say, the non-inoculated MdB groups and the MdB inoculation groups were sorted in different areas. This showed that the inoculation of MdB into intercropping had a significant impact on soil fungal community.

Specifically, *Ascomycota*, *Basidiomycota*, *Mortierellomycota* and other unidentified species were the dominant phyla of fungi in the sole and intercropping systems under the no-MdB and MdB inoculation groups (Figures 4F and S3). Moreover, the relative abundances of *Ascomycota*, *Basidiomycota* and *Mortierellomycota* were different, ranging from 63 to 72%, 6–14% and 7–13% respectively. The abundance of *Basidiomycota* increased significantly in the MdB inoculation groups, compared to the CK and no-MdB groups ($p < 0.05$), whereas that of *Ascomycota* and *Mortierellomycota* was significantly lowered ($p < 0.05$). It was noted that 19 fungal genera were identified in soils with the different planting methods, and we chose ten dominant genera to use for variance analyses (Figures 4G and S4). Particularly, the abundances of *Gibberella*, *Holtermanniella*, *Epicoccum*, *Fusarium* and *Podospora* were significantly promoted as a result of inoculation with MdB, compared with those of the CK and no-MdB groups ($p < 0.05$).

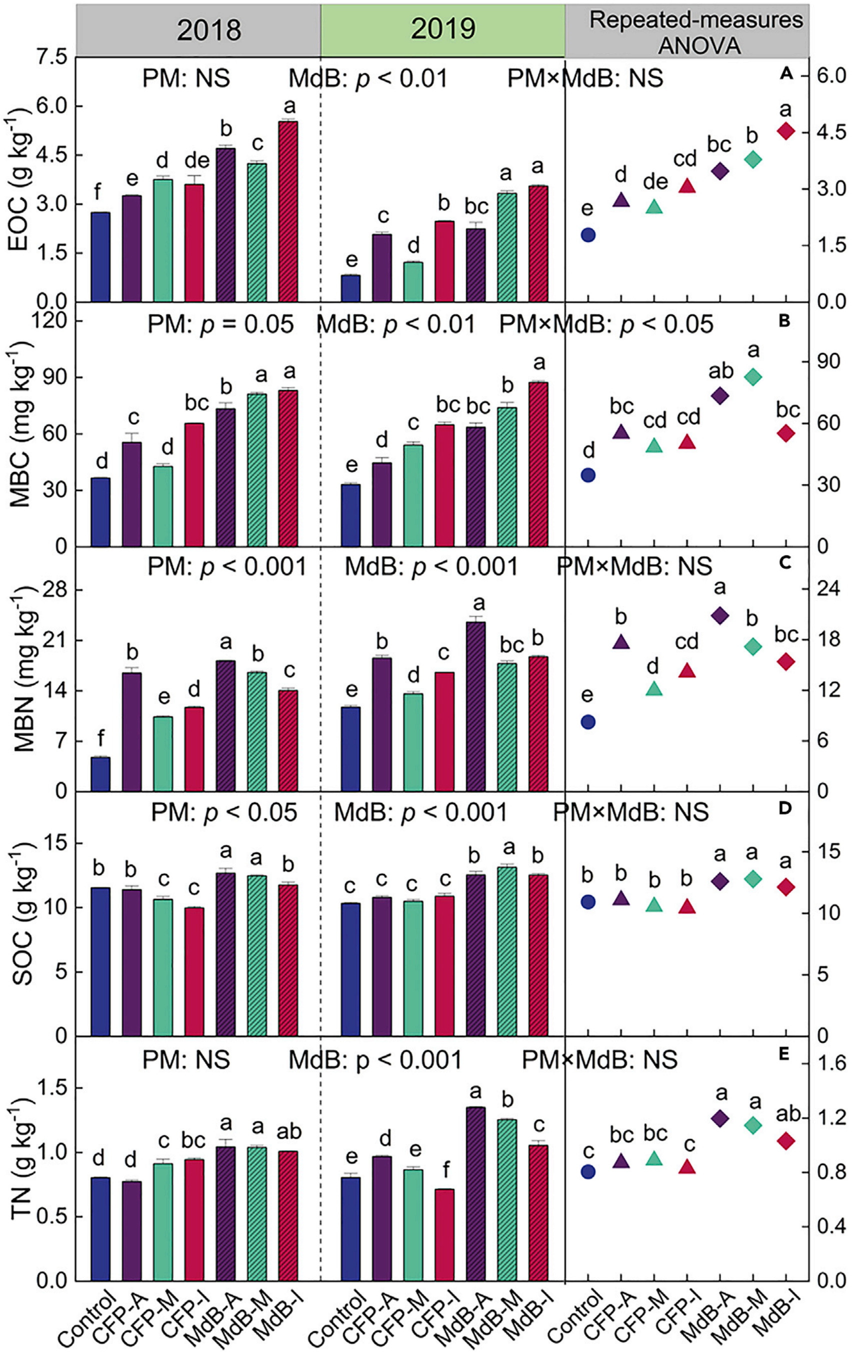

Figure 3. Variations of soil organic C&N levels and microbial biomass C&N levels in response to the standing biodiversity system in two years (A) easily oxidized organic carbon content; (B) microbial biomass carbon content; (C) microbial biomass nitrogen content; (D) the content of soil organic carbon; (E) the content of soil total nitrogen.

Notes:SOC, soil organic carbon; EOC, easily oxidized organic carbon; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; TN, total nitrogen.

Plant biomass and water use efficiency as affected by the NbS

Generally, plant shoot biomass, root biomass and WUE were highly dependent on the planting model and MdB inoculation (Figure 5). Under the no-MdB condition, the aboveground biomass, root biomass, total

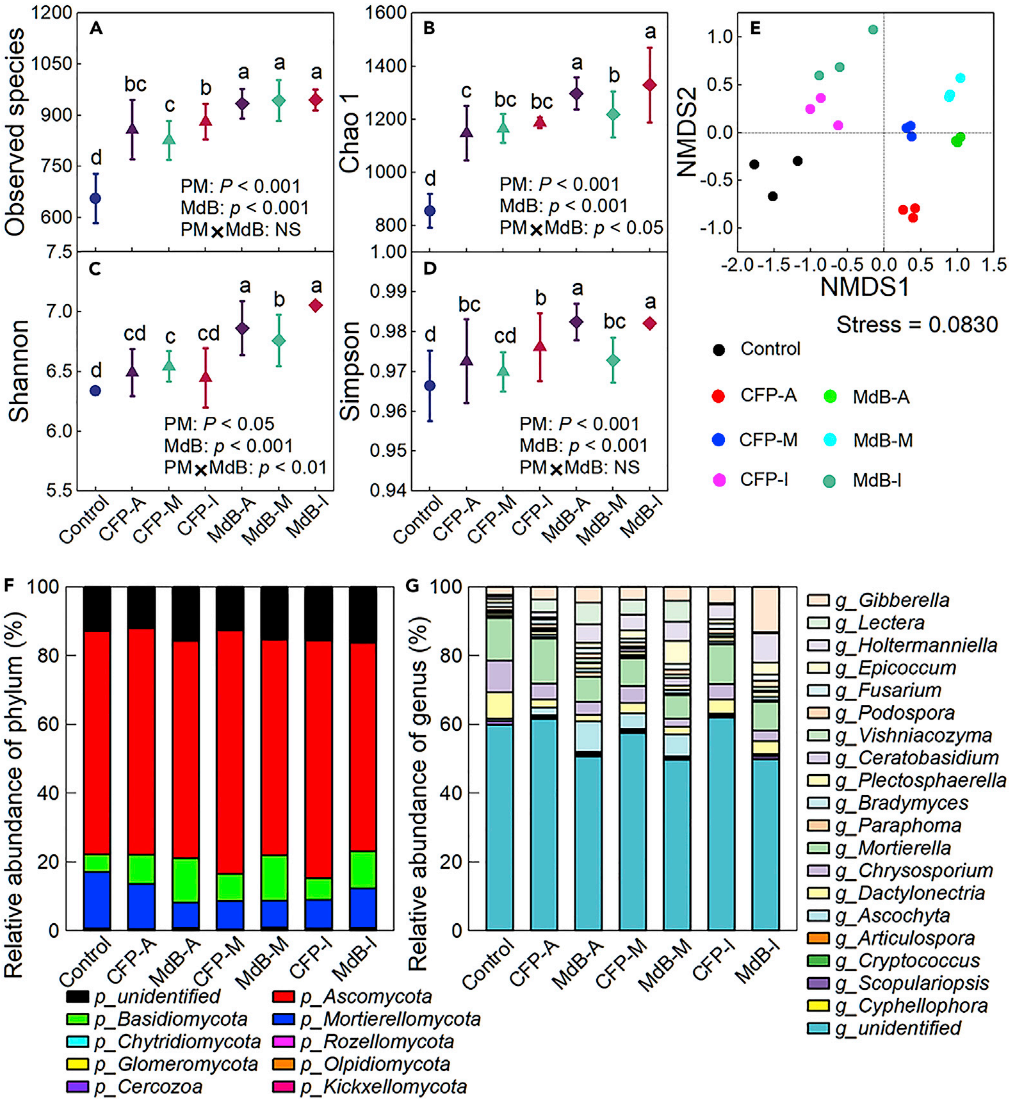

Figure 4. Variations of soil fungal community diversity, composition and abundance in response to the standing biodiversity system following two-year treatments

Notes: (A) is the observed species; (B) is the chao index; (C) is the Shannon index; (D) is the Simpson index. (E) indicates the NMDS of fungi communities based on weighted UniFrac distance metrics; (F) represents the relative abundance of different fungus taxa at the phylum level; (G) shows the relative abundance of different fungus taxa at the genus level.

biomass, and WUE in the intercropping groups were 3.47–14.5%, 9.20–24.4%, 5.52–16.3% and 8.68–42.3% greater than those of monoculture (as described in the above, i.e., flat planting (CFP) treatment) in two growing seasons, respectively ($p < 0.05$). As a result of MdB inoculation, aboveground biomass, root biomass, total biomass and WUE were markedly elevated in monoculture alfalfa and maize, compared with those of no-MdB groups ($p < 0.05$). Critically, the MdB inoculation into intercropping system was observed to further promote shoot biomass, root biomass, total biomass and WUE by 33%, 70.5%, 39.8% and 82.2% respectively, relative to CK ($p < 0.05$), up to the highest levels. In this case, planting mode and MdB inoculation had pronounced interactive effects on biomass and WUE (except for WUE in alfalfa fields). In addition, repeated-measures ANOVA analysis showed that compared with no-MdB treatments, MdB inoculation significantly increased alfalfa's and maize's shoot biomass, root biomass, total biomass and WUE ($p < 0.05$).

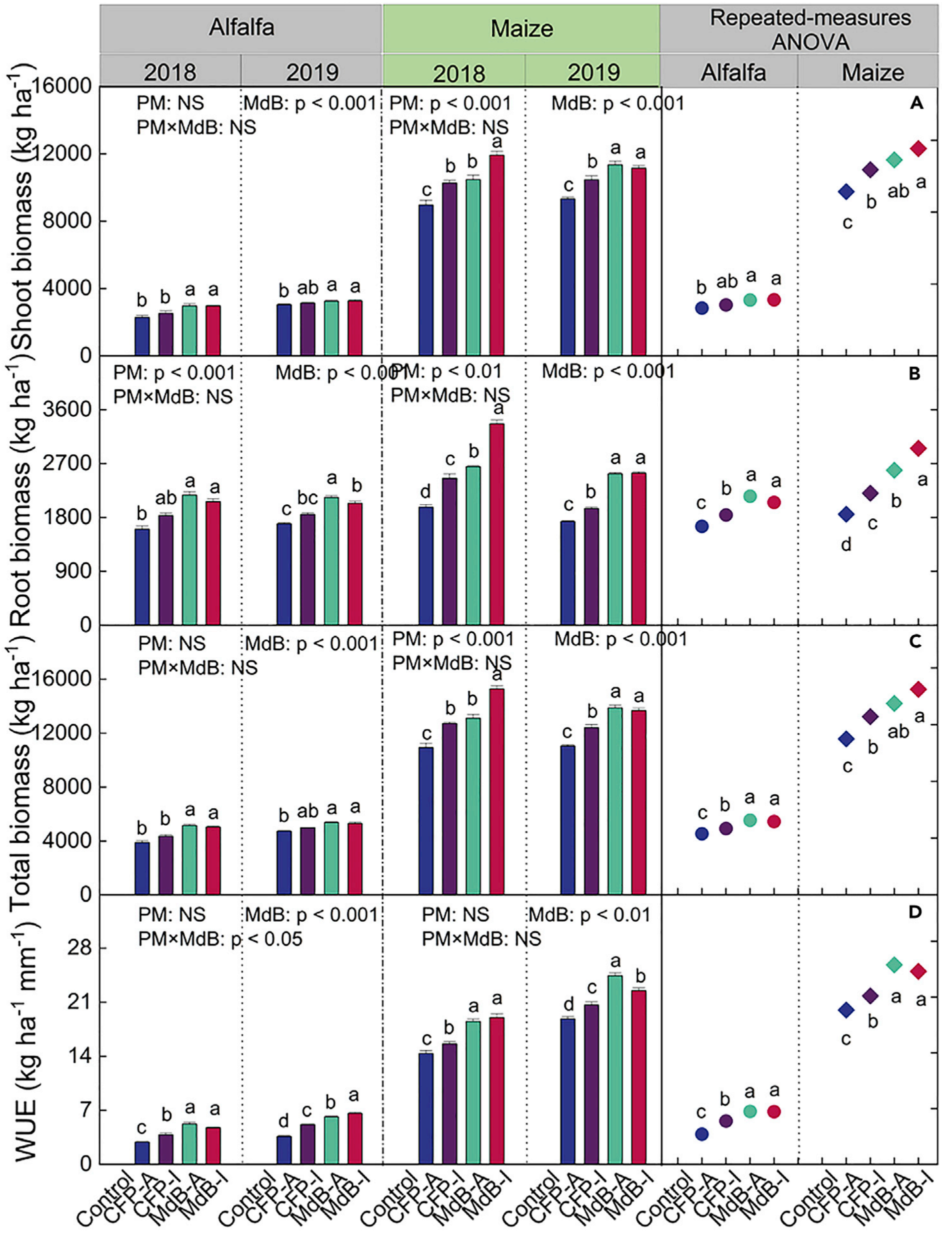

Figure 5. The variations of biomass and water use efficiency in response to the standing biodiversity across two growing seasons.

Note: (A) shoot biomass; (B) root biomass; (C) total biomass; (D) water use efficiency (WUE).

The variations of shoot biomass (A), root biomass (B), total biomass (C), and water use efficiency (WUE) (D) in alfalfa and forage maize in response to the standing biodiversity system in two growing seasons.

Note: Control, bare land without planting (no data shown).

Structural equation model analyses on soil properties, soil erosion and plant biomass accumulation

The correlation analyses showed that microbial diversity was significantly positively correlated with plant biomass, EOC, SOC, MBN and TN levels ($p < 0.05$), and extremely correlated with MWD ($p < 0.01$) (Figure 6). Also, microbial diversity was negatively correlated with SBD, SOC/TN, C&N loss and soil erosion ($p < 0.05$), and with extremely significant correlations with the K values ($p < 0.01$). There existed a dramatically positive correlation between soil erosion and C&N loss ($p < 0.01$), whereas the aggregate MWD was negatively associated with soil erosion and C&N loss ($p < 0.01$).

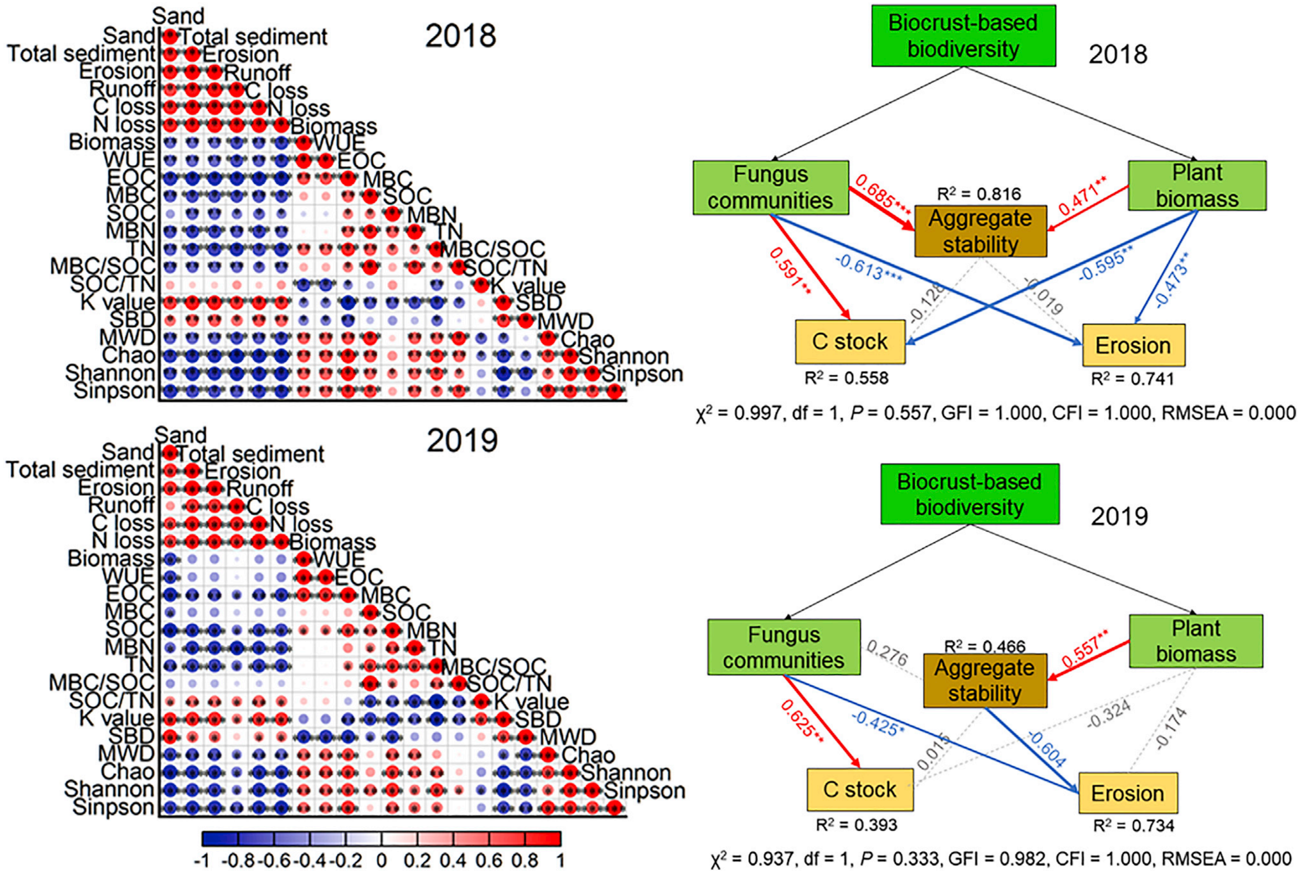

Figure 6. Correlation analyses on the variables in the plant-soil-microbe interactions via the correlation matrix and structural equation models (SEMs) in two growing seasons

Notes: 1) *, ** and *** indicate significant levels of $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. Color and the size of the circles are proportional to the correlation coefficients between the variables (n = 21). 2) Red lines represent positive relationships, blue lines indicate negative relationships, and gray lines indicate no significant relationships respectively; The R^2 represents the proportion of variance explained; 3) Sand refers to sand content of erosion SOC and TN loss means the total loss of SOC and TN with soil erosion. 4) SBD, soil bulk density; MWD, the aggregate mean weight diameter; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; WUE, water use efficiency (with the reference to biomass); TN, total nitrogen; SOC, soil organic carbon; EOC, soil easily oxidizable organic carbon; Biomass, the sum of shoot and root biomass.

Moreover, the structural equation modeling (SEM) analyses (n = 21) demonstrated that the biocrust-based biodiversity evidently altered soil microbial community structure, soil aggregate structure, and biomass. This tendency provided critical base for surface runoff prevention and soil C storage (Figure 6). In general, the MdB inoculation and planting mode were mechanically linked with plant biomass and fungus communities, and the latter can exert positive effects on the former. Also, the latter can indirectly mediate soil erosion and carbon storage. According to our observations, soil erosion was strongly affected by fungus communities. Moreover, the variations in fungi communities were highly associated with soil C storage. In short, the changes in biomass played a vital role in the NbS model, that is, different planting systems affected biomass and microbial abundance & diversity, and in turn determined soil water storage, soil conservation and soil nutrient retention.

DISCUSSION

Currently, the NbS have become a priority option to ensure sustainable management of agricultural ecosystems. Also, the MdB inoculation and its establishment can act as a crucial role of ecosystem engineer.[29,30] As such, we speculated that biocrust-standing biodiversity played an engineer role mediating soil and water conservation and soil carbon storage. Although a previous study reported that surface runoff and soil microbial diversity were greatly affected by MdB inoculation,[31] the standing biodiversity linked with soil & water conservation and its related carbon cycle have been rarely investigated in agricultural soils. Based on this, we introduced MdB into the intercropping system in a semiarid rainfed agricultural area. This solution was found to evidently improve soil microbial diversity following a period of cultivation. It was indeed helpful to establish a standing biodiversity system incorporating the aboveground organisms, MdB and belowground microorganisms.

Sensitivity of soil erosion in response to the NbS

Existing knowledge suggests that soil erosion can be minimized by reducing erosivity (capacity of agents causing erosion) and declining soil erodibility (susceptibility of soil to erosion).[6] Previous studies showed that gravel mulching can alleviate the rain-induced soil erosion. The covering gravel could enhance the soil interception of raindrops and reduce kinetic energy, which, in turn, diminished soil erosion.[26] Our results showed that the MdB inoculation in the intercropping system significantly alleviated surface soil erosion and restricted sediment loss (Figure 1), which was derived from increased surface coverage and soil structure stability via standing biodiversity. Simultaneously, rainfall events exerted considerable influences on soil erosivity, and rainfall intensity and duration played a crucial role in the rainfall-erosion relations.[32] Our observations showed that the middle stage (57 days in 2018, and 41 days in 2019) led to the highest total sediment, erosion and runoff across two growing seasons, whereas the above three parameters appeared to be relatively low in the seedling and late growth stages (Tables S1 and S2). This may be associated with the rainfall event and vegetation cover. During the middle period, the maximum precipitation amount within 30 min was up to 7.4 mm in 2018 and 9.0 mm in 2019 respectively, evidently higher than that of the other two stages. Because of the high rainfall in the short term, the infiltration ability of rainwater proved to become weaker and result in increasing slope runoff (Table S5).

On the other hand, soil aggregate composition is an important parameter influencing soil erodibility, because fine particles have the advantage to combine with SOC to form soil aggregates. Specifically, the stability of soil aggregates and the level of SOC are the key determinants affecting the resistance against soil erosion.[22] In the present study, planting alfalfa and forage maize slightly increased the proportion of macroaggregates. Importantly, the MdB inoculation further promoted aggregate stability, and macroaggregate formation. The data showed that the MWD content under the MdB was significantly higher than that in the control and no-MdB groups (Table 2 and Figure 6). It was possible that biological soil crust inoculation can reduce soil water evaporation and the differences in soil temperature between day and night, and ultimately formed a relatively favorable microenvironment. This trend was beneficial to rapid extension of plant root system, and accordingly enhanced the binding capacity of root system with soil particles. It turned to facilitate the formation of soil aggregate structure and promote soil stability and erosion resistance. Moreover, MdB organisms can exude the polysaccharides that boosted the macroaggregate formation and reduced soil erosion.[33] In this study, microbial diversity was negatively correlated with the K factor of soil erodibility (Figure 6). This phenomenon demonstrated that the MdB in combination with the standing biodiversity can strategically alleviate soil erosion through lowering the K value of soil erodibility and improving microbial diversity.

Responses of soil microbial community to the NbS

Frequently, microbial activity can be influenced by soil water, root input, and labile C, because they are the main driving factors affecting C mineralization and plant residue decomposition.[34] In the present study, when covered with MdB in the sole and intercropping systems, soil microbial community diversity (Figure 4) and microbial biomass (Figures 3B and 3C) were significantly elevated. In this respect, the standing biodiversity covering from aboveground organisms to surface MdB and further to belowground microorganisms might act as a deep form of ecosystem. To some extent, it can help form a relatively favorable microenvironment, which can effectively reduce soil water evaporation. As a product of increased input of organic matters into soils, it was likely to promote soil microbial activity.[35] Particularly, higher root biomass inputs can activate microbial community activity and improve its composition in soils.[36]

As mentioned above, higher shoot and root biomass were derived from the inoculation with MdB (Figure 5). In this case, the microbial community diversity (Chao 1, Simpson and Shannon index) was significantly positively associated with biomass accumulation (Figure 6). In addition, fresh organic matter input help stimulate the accumulation of microbial biomass in a short term, i.e., so-called priming effect.[37] In our study, the MdB inoculation successfully induced soil system to generate priming effect regardless of planting pattern, in which MBC and MBN contents were markedly promoted (Figures 3B and 3C). This phenomenon was frequently accompanied with high microbial activity because of the promoted labile C components (soil EOC was evidently improved) (Figure 3A). Under the basis of the standing biodiversity, the MdB can efficiently mediate the microbial activity via intra- and inter-species interactions.[38] In practice, when inoculated with MdB, the -biocrust rhizoids with a certain labile C have been applied to surface soil, which can further enhance soil C mineralization (data not shown). Under such circumstance, microbial community growth was therefore accelerated and its structure was also optimized. This phenomenon has been identified in previous study.[37]

Of interest, we found that the fungal relative abundance under alfalfa-forage maize intercropping was different from that under the sole cropping system (Figure 5). This can be explained by the fact that intercropping with legumes can promote the microbial N fixation in the rhizosphere. Our finding was consistent with that of,[39] who reported that the size of soil fungal community was increased averagely by 115.5% under the intercropping, relative to that of the monoculture. Actually, the observed species under the MdB inoculation was evidently higher than those of the control and no-MdB treatments. It showed that MdB inoculation can change the number of species in the soil fungal community, especially for the relative abundance of *Basidiomycota* species. The higher fungal community abundance and diversity played a critical role in soil nutrient accumulation, whereas these nutrients were generally unavailable to bacteria.[20] Another possible mechanism was the occurrence of the relatively humid microenvironment under MdB inoculation and intercropping, and this enriched the contribution of soil moisture to fungal community development.[40]

The effects of NbS on soil C and N loss

A recent study showed that soil C and N losses were sensitive to many environmental factors, such as rainfall, topography, soil properties, vegetation, and anthropogenic activities.[26] In general, there were two pathways for runoff to cause surface soil nutrient losses. The first one was that surface nutrient can be dissolved into water and then transited into soil sediment. The second one was that the nutrients were transported by water to cause nutrient losses. In this case, precipitation intensity and duration can markedly affect the transfer of surface nutrients from soils to runoff.[41] As presented in the above, the C and N losses were relatively lower at the seedling and later growth stages across all the treatments in 2018 and 2019 (Figure 2). Conversely, the C and N losses were enhanced rapidly during the mid-term growth stage, i.e. on the 57- and 41-day in 2018 and 2019 respectively (Tables S3 and S4). Certainly, this phenomenon was caused by rainfall intensity and duration in the middle term of plant growth, when the rainfall intensity was much higher than that of the other two growth stages, and the rainfall duration was also relatively shorter. This in turn enhanced the carrying capacity of surface runoff. This phenomenon was supported by the observational results by Snyder and Woolhiser,[42] in which the raindrop intensity resulted in nutrient loss with runoff. In the degraded agricultural soils, soil nutrients were mainly concentrated on topsoil, which directly led to C and N losses in sediment through erosion.

In addition, vegetation coverage is also one of the most important determinants affecting soil nutrient losses by runoff.[43] Crop mulching can effectively reduce soil erosion and nutrient loss in sloping and tilled fields.[44] Barger et al.[45] focused on a small runoff plot scale and found that C and N losses were much lower in a developing MdB than a recent or early successional MdB. In our study, the soil C and N losses from MdB inoculation were significantly lowered, in comparison with those from crop mulching and bare land. It can be argued that there existed double protective effects in the MdB + intercropping system. Indeed, the combined coverage with alfalfa and forage maize acted as the first protective wall against soil C and N losses and can enhance the interception of rainfall. This was helpful to weaken the raindrop energy and potential erosion. Furthermore, the MdB establishment can enforce the structure and function of standing biodiversity and act as a second protective pathway, i.e. the hidden deep form of ecosystem. This trend further relieved the raindrop kinetic energy from plant leaves. In this case, the standing biodiversity can in turn retain the sediment C and N, accordingly enhancing soil C sequestration.

Mechanisms of carbon sequestration as affected by the NbS

Another common phenomenon is that biodiversity has the potential to influence soil C sequestration by modifying C input and loss processes. High levels of biodiversity can contribute to soil C sequestration and productivity.[31] Actually, above- and belowground biodiversity played a role of ecosystem engineer in mediating soil microbial community and soil C storage. Conversely, high levels of C storage were in turn to generate a positive feedback toward species diversity and plant productivity by enhancing soil water-holding capacity and sustaining necessary fertility.[46] On the other hand, the increased WUE (with the reference of biomass) and soil water storage were observed in the MdB inoculation treatments, which accordingly accelerated the growth and development of soil microbial community and forage biomass (Figure 6). In this respect, biomass accumulation played an important role in soil organic matter input (Figure 6). Thereafter, the MdB can be incorporated into the standing biodiversity system for better soil water-holding capacity (Wang et al., 2022). Actually, the dynamics of soil C storage is highly dependent on the balance between C inputs, such as plant leaf and root detritus, and C outputs through microbial community decomposition.[47,48] In the present study, the standing biodiversity was endowed with active structural and functional forms of ecosystem, which therefore can promote soil properties, microbial diversity and soil C sequestration. Taken together, it displayed great potential to determine aboveground production and ecosystem functions.

Critically, both biodiversity and belowground biomass can exert positive effects on soil C storage. Recent studies revealed that enhancing plant diversity can increase rhizosphere soil C inputs, promote the activity and diversity of soil microbes, and therefore suppress carbon losses via restraining soil microbial decomposition.[35] Tilman et al.[49] proposed that the interactions between soil C stock and belowground biomass played a vital role in regulating the relationships between biodiversity and C cycle. Chen et al.[31] also reported the positive effects of biodiversity and belowground biomass on C sequestration, as a result of high C storage and cycling. Particularly, Dumig et al.[50] found that biological soil crust can form a medium to connect soil and air, to capture atmospheric dust and particles because of its rugosity. This process ultimately can enhance carbon fixation through increased photosynthetic capacity. The evidences from this study showed that soil microbial diversity, microbial biomass, and above- and belowground biomass were markedly promoted under the MdB inoculation across the sole and intercropping systems (Figure 6). This implied that the standing biodiversity dominated by MdB significantly promoted the aboveground and belowground biomass accumulation, and accordingly enhanced the belowground C inputs. Also, because of the labile C source input from MdB, soil microbial activity and diversity were evidently promoted. The above two aspects were the determinants improving microbial contribution to soil C storage. To sum up, the inoculation of MdB directly improved surface soil roughness, and was conducive to capture more surface litter and microbial residues for higher input of carbon source in soils. Thus, the MdB combining with standing biodiversity can act as a deep form of ecosystem in preventing soil and water conservation for better carbon sequestration.

The reconstruction of biological soil crusts is the key to ecological restoration. Previous studies have reported the cultivation of biological soil crusts, and artificially cultivated biological soil crusts have been applied to desertification control.[51–53] In our experiment, the inoculated biological soil crusts belong to moss-biological crusts, which are widely distributed in semiarid areas of China[28] and are relatively easy to obtain. Meanwhile, the moss-biological soil crusts belong to spore propagation, which has been sold in China. In addition, for agricultural practitioners, the simplest and most affordable method is to collect local natural crusts for crushing and use as inoculum materials. At the same time, to ensure rapid colonization of biological soil crusts, soil within 2 cm of the crusts can be collected as inoculum materials.

Conclusions

The MdB establishment can act as a crucial NbS to enhance soil carbon sequestration, which provided a novel insight into soil conservation and surface runoff alleviation in the seriously eroded agricultural soils. The data showed that the MdB -based strategy can connect below- and above-ground organisms, enhance soil carbon storage and diminish water & soil erosion. It was first reported that the standing biodiversity formed by MdB + intercropping can play a critical role in preventing surface runoff, and lowering C and N losses. Soil microbial diversity, especially that of *Basidiomycota* was significantly improved by the MdB, and the latter enabled more plant organic matter to input into soils. In this way, the diversity and abundance of soil microbial community were enriched, and in turn intensified the feedback effects on plant growth and biomass accumulation. Simultaneously, soil water, C and N absorption and utilization were accordingly enhanced in plant system. Certainly, more root system exudates and root biomass as organic matters were transited into soils. This feedback loop can drive to establish the positive interactions in plant-soil-microbe system for stronger carbon sequestration. Finally, structural equation model further confirmed that soil biocrusts, as ecosystem engineer, can induce the priming effects on soil cycling and storage. Therefore, the biocrust-based biodiversity proved to be a feasible solution to improve soil structure stability, increase soil microbial diversity, alleviate soil and water erosion, and ultimately reduce soil C and N losses. In conclusion, compared with simple biodiversity investigation as reported previously, the biocrust-based biodiversity acted as a hidden deep form of ecosystem to enhance rainwater interception for greater soil carbon sequestration.

Limitations of the study

In the present study, the biological soil crusts material we collected was moss, and further investigations will be needed in terms of different biological soil crusts developing stages (such as lichen and algae) to explore the inoculating effects. Also, further studies should pay attention to the developmental characteristics of biological soil crusts under inoculated in the fields. In addition, this study was only conducted in the semiarid rainfed agricultural land of the Loess Plateau; it is needed to investigate the ecological and productive effects of biological soil crusts in a similar climate zone in the world.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare that they have no conflict of interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Barbula constricta	This paper	N/A
Chemicals, peptides, and recombinant proteins		
PremiSTAR HS	TaKaRa	R040Q
Puc-T TA cloning kit	Cowin Bio.	Cw2591s
Sensory cells, DH5α	Cowin Bio.	Cw0808s
SYBR® Premix Ex Taq™ II (Tli RNaseH Plus), ROXplus	TaKaRa	RR82LR
DL2,000 DNA Marker	TaKaRa	3427Q
Primer synthesis	Invitrogen	N/A
Oligonucleotides		
5′-CTTGGTCATTTAGAGGAAGTAA-3′	Allwegene Tech.	N/A
5′- TGCGTTCTTCATCGATGC-3′	Allwegene Tech.	N/A
Software and algorithms		
IBM SPSS Statistics 22	IBM	https://www.ibm.com/
IBM SPSS Amos Graphics v22.0	IBM	https://www.ibm.com/
Origin 2021	OriginLab	https://www.originlab.com/
GenStat 14th	England & Wales	https://www.genstat.co.uk/
Mothur	The Patrick Laboratory	mothur.github.io
Excel	Microsoft	N/A
Other		
Spectrophotometer	Therno scientific	NANODROP 2000
Centrifuge	Eppendorf	Centrifuge 5415D
Gel imaging system	Tanon Technology	Tanon 1600
Quantitative fluorescence PCR instrument	Applied Biosystems	ABI7500
Elemental vario TOC cube	Elementar	Elementar vario TOC
Aggregate fraction Analyzer	This paper	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, You-Cai Xiong (xiongyc@lzu.edu.cn).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All original code is available from the lead contact upon request.
- This study did not generate original code.
- Any additional information required to reanalyze the data reported in this work is available from the lead contact upon reasonable request.

METHOD DETAILS

Experimental site

The location observations were performed at the Agricultural Ecological Scientific Observation Station, Gansu Province, China (36°02′N, 104°25′E) at 2400 m above mean sea level. This study area is characterized by a semiarid medium-temperate climate. The local annual mean temperature was 5.4°C in 2018 and 5.6°C in 2019 respectively, while the monthly average maximum temperature was 16.5°C in 2018 and 16.3°C in 2019 respectively. the average minimum temperature was −9.0°C in 2018 and -7.6°C in 2019, and the annual precipitation was 459.8 mm and 422.5 mm in 2018 and 2019 respectively. The basic physical and chemical properties of soils in the 0–20 cm soil layers were as follows: the SOC content was 12.3 g kg^{-1}, the TN content was 1.25 g kg^{-1}, and the pH value was 8.15.

Experimental design

The experiment was arranged in randomized blocks with two main treatments: 1) no BSC inoculation (CFP) and moss-dominated biocrust inoculation (MdB), and 2) three planting modes including sole alfalfa (A), sole forage maize (M) and alfalfa-forage maize intercropping (I). A total of seven groups consisted of: 1) control, bare land without planting; 2) CFP-A, conventional flat planting of sole alfalfa; 3) CFP-M, conventional flat planting of sole forage maize; 4) CFP-I, conventional flat planting of 3-row alfalfa intercropped with 3-row forage maize; 5) MdB-A, flat planting with MdB inoculation of sole alfalfa; 6) MdB-M, flat planting with MdB inoculation of sole forage maize; and 7) MdB-I, flat planting with MdB inoculation of 3-row alfalfa intercropped with 3-row forage maize. Both mono- and intercropped forage maize and alfalfa had 50 cm and 30 cm row spacing, respectively. The intercrop planting distance between forage maize and alfalfa was 40 cm. Each plot was 6 × 2 m = 12 m^2 in area and was surrounded by ridges. The interval of each plot is 100 cm between left and right, and the upper and lower interval 170 cm. Besides, before our experiment, the slope field was planted *Avena sativa* L. and the straws were cleaned by hand before the sowing of 2018 growing season (Figure S1).

Experimental materials and arrangements

Local widely planted alfalfa (*Algonquin*) and forage maize (*Jinsui 3*) varieties were chosen as the testing materials. The treatments were established in a slope (12° ± 1°) field across two years from 2018 to 2019. According to the local planting conventions, alfalfa seeds (net seed weight) were planted with 40 g (intercropped plot was 20 g) in each plot at a depth of 2 cm. Forage maize seeds were sown at a depth of 5 cm using a hole-driller. The sowing dates were May 10, 2018 and May 1, 2019, respectively. Seedlings emerged 7 days later, and the plants grew to about 5 cm in 15 days.

Moss (*Barbula constricta*) was chosen for the MdB, and was locally collected from the topsoil layer within the scope of the experimental station (nearby the experimental field) during early spring. The SOC, TN, and pH values of the MdB soil were 18.4 g kg^{-1}, 1.25 g kg^{-1} and 7.96, respectively. Two months before sowing, approximately 2 cm thick biological crusts were collected by a small shovel (containing rhizosphere soil) and then sieved (2 mm) to remove small weed root fragments. Subsequently, the MdB samples were mixed and dried in the shade for later application. After sowing (seedings reach to 5 cm) and rainfall, the MdB were then evenly distributed on soil surface by hand both 2018 and 2019. The inoculating amount of MdB was 12 kg $plot^{-1}$ (Figure S1).

One day before sowing, the urea and diammonium phosphate fertilizers of 300 and 250 kg ha^{-1} were applied to each plot directly by hand respectively. The BSCs were evenly spread (applied by 1 kg in each plot) by hand on the plot ground surface, when alfalfa and forage maize grew up to almost 5 cm high. In addition, the weeding and other field management practices were kept uniform.

Sampling methods

Soil sampling

At early October of 2018 and 2019, soil samples were taken according to conventional agronomic methods. The soil particle size distribution and soil water-stable aggregate composition were collected in the October of 2019. Specifically, all soil samples were taken from the 0–20 cm soil layer. Within each plot, three soil cores (5 cm in diameter, 20 cm deep) were collected from randomly selected locations and homogenized together after removing surface litter, and then passed through a 2 mm sieve to remove small fine root fragments. Each soil sample was divided into two parts. One was air-dried to determine the soil physical and chemical properties, and the other was stored at −80°C for microbial diversity determination. Soil bulk density (SBD) was determined using a soil auger, and soil total porosity (STP) were calculated using the method described by Zhou et al.[29] Soil organic carbon (SOC) was determined by the potassium dichromate-concentrated sulfuric acid external heating oxidation method.[54] Soil total nitrogen (TN) were determined by the Kjeldahl method with an -automatic nitrogen analyzer.[54] Soil texture was analyzed by the Bouyoucos Hydrometer method.[55] Easily oxidized organic carbon (EOC) was performed by the $KMnO_4$ oxidation method.[56] Soil microbial biomass carbon and nitrogen (MBC and MBN) contents were determined by the chloroform fumigation-K_2SO_4 extraction method.[57] The soil aggregate fraction was measured by the wet-sieving method, and separated into five size fractionations of >2.0, 1.0–2.0, 0.5–1.0, 0.25-0.5 and < 0.25 mm.[58]

High throughput sequencing (HTS) and data processing

DNA extraction

According to previously published protocols, total genomic DNA was extracted from 5 g of each homogenized soil sample,[59] and purified using the Powersoil DNA Isolation Kit (MoBio, Carlsbad, CA, USA) (as instructed in the manual). The DNA concentration was then quantified via a NanoDrop spectrophotometer (Thermo Scientific).

PCR amplification

The fungal ITS region was amplified on an Eppendorf Mastercycler Gradient Thermocycler (Germany), with the primers ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′- TGCGTTCTTCATCGATGC-3′).[60] The 5′ ends of both primers were tagged. The ultra-PAGE purified primers were ordered from Invitrogen, China. The PCR mixtures were made as follows: 12.5 μL KAPA 2g Robust Hot Start Ready Mix, 1 μL Forward Primer (5 μM), 1 μL Reverse Primer (5 μM), 5 μL DNA (total template quantity was 30 ng), and 5.5 μL H_2O. The thermocycling consisted of an initial denaturation at 95°C for 5 min, followed by 28 cycles of 95°C for 45 s, 55°C for 50 s, and 72°C for 45 s and a final extension of 72°C for 10 min. Three separate reactions were conducted to account for potentially heterogeneous amplification from the environmental template for each sample. Finally, the PCR products were purified using an AXYGEN Gel Extraction Kit (QIAGEN) and quantified using QPCR.

Data analysis

The MEGAN program was used to assign BLAST hits to taxa of the NCBI taxonomy. After removing non-fungal sequence reads, the fungal sequences were clustered into operational taxonomic units (OTUs) at a 97% similarity level using Uclust. Since, low-abundance OTUs (fewer than 2 reads, including singletons) might influence richness and diversity estimates. They were therefore excluded from the subsequent analyses.[61] For each sample, the rarefaction, richness estimators (Chao 1) and diversity indices (Shannon and Simpson) were calculated using the software Mothur. Visualization of beta-diversity information was achieved via ordination plotting with Nonmetric Multidimensional Scaling (NMDS).

Biomass and water use efficiency

Shoot and root biomass (30 cm deep) was measured by clipping plants from a 1 m × 1 m quadrat in each plot of October between 2018 and 2019. The harvested biomass was naturally dried until its water content was less than 15% to measure the total biomass (kg ha^{-1}). In addition, water use efficiency (WUE) was calculated accordingly by the method of Gu et al.[62]

Runoff collection and carbon & nitrogen loss

A PVC drainage channel with a diameter of 10 cm was set to collect the runoff from each plot. The capacity of the collection device was 30 L to accommodate surface runoff. Each runoff event was recorded from the beginning to end of the rainfall date across each growing season from 2018 to 2019. In the present study, runoff generation was recorded at 9 days, 57 days and 102 days after BSC inoculation in 2018, and at 10 days, 41 days and 120 days after BSC inoculation in 2019 respectively (Table S1). Each rainfall event was automatically recorded by nearby a weather station. The amount and duration of precipitation and its maximum intensity are shown in Table S3.

To determine the amount of sediment lost to erosion, runoff water was collected and then thoroughly stirred. Three 500-mL plastic bottles were used to collect sediment samples from each reservoir to determine the amount of sediment accumulated. The suspensions were placed in the oven and dried at 105°C and weighed. The soil loss of each rainfall plot was obtained by calculating the sediment. The dried-soil method was employed to determine the SOC and TN concentrations. The sand content (Sc), total sediment (Ts), erosion (Er), runoff (Ro) and carbon and nitrogen losses were calculated by the Equations 1, 2, 3, 4 and 5 respectively.[6,63]

$$\mathrm{Sc} = (Gt - Gh) \times 1000/500 \qquad \text{(Equation 1)}$$

$$\mathrm{Ts} = \mathrm{W} \times Sc \qquad \text{(Equation 2)}$$

$$\mathrm{Er} = (W \times Sc) \times 10^{-3}/36 \times 10^{-4} \qquad \text{(Equation 3)}$$

$$\mathrm{Ro} = [(W - Er)\,/\,2.24] \times 10^{-6}\,/\,36 \times 10^{-4} \qquad \text{(Equation 4)}$$

$$\mathrm{C}(N)\mathrm{loss} = \sum \left[Ro \times \mathrm{C}(\mathrm{N})/_{S} \times 0.01 \right] \qquad \text{(Equation 5)}$$

where Sc is sediment content (g L^{-1}), Gt is the wet weight of soil in 500 mL (g), GH is the dry weight of soil in 500 mL (g), Ts is the total amount of sediment (g plot^{-1}), W is the volume of suspension water after each runoff event (mL), Er is the amount of erosion caused by each runoff event (kg ha^{-1}), Ro is the runoff generated by each rainfall (m^3 ha^{-1}), and C (N) loss is organic carbon and total nitrogen loss (g ha^{-1}). In this formula, C and N represents the soil organic carbon and total nitrogen of eroded sediment (g kg^{-1}). S is the area of each plot (m^2).

Soil erodibility of the K factor

To assess the soil erodibility of the K factor, the erosion productivity impact calculator (EPIC) model was used to estimator by following Equation 6'[64]:

$$K = -0.01383 + 0.51575 \times Kepic \qquad \text{(Equation 6)}$$

$$\begin{aligned} Kepic = {} & \{0.2 + 0.3\exp[-0.0256Ca \times (1 - Cb/100)]\} \times [Cb/(Cb + Cc)]^{0.3} \\ & \times \{1.0 - 0.25SOC/[SOC + \exp(3.72 - 2.95SOC)]\} \\ & \times \{1.0 - 0.7Cn/[Cn + \exp(-5.51 + 22.9Cn)]\} \end{aligned}$$

where Kepic is the erosion productivity impact calculator (EPIC) model value, Ca is the sand content (%), Cb is the silt content (%), Cc is the clay content (%), SOC is the soil organic carbon, and Cn = 1-Ca/100.

QUANTIFICATION AND STATISTICAL ANALYSIS

Two-way analysis of variance (ANOVA) was used to test differences in biomass, soil parameters and soil erosion among the treatments. Mean comparisons were carried out using Tukey-HSD at the 0.05 level of significance. The interactive effects were estimated across the two growing seasons. One-way repeated-measures ANOVA analysis of Tukey-HSD was used GenStat 14th software to checking the significant different among the treatments at 0.05 level. The correlation coefficients were obtained by performing Pearson correlation analyses based on the original data. To reveal the direct and indirect relationships among soil physicochemical parameters, soil microbes, soil erosion and biomass among the treatments, we used a structural equation model (SEM) (n = 21) for quantitative evaluation in Amos Graphics v22.0. The $\chi 2/\mathrm{df} < 3$, goodness-of-fit index (GFI) > 0.90, relative-of-fit index (GFI) > 0.90, and root mean square error of approximation (RMSEA) < 0.08 were adopted to fit the SEM. Data analyses were conducted by SPSS 22.0 software, and the figures were drawn by Origin 2021 software.