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Desertification Reversal Promotes the Complexity of Plant Community by Increasing Plant Species Diversity of Each Plant Functional Type

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Abstract: Desertification reversal is globally significant for the sustainable development of land resources. However, the mechanisms of desertification reversal at the level of plant community are still unclear. We hypothesized that desertification reversal has clear effects on plant community composition, plant functional types (PFTs), and other vegetation characteristics, including plant diversity and biomass, and their changes in the early stages of reversal are more dramatic than in later stages. We investigated the vegetation of four to five different stages of desertification reversal at each of seven large study sites in southwestern Mu Us Sandy Land, China. The results show that the dominant species in very severe desertification areas were replaced by perennial grasses in potential desertification areas. The importance values of annual forbs and perennial sub-shrubs decreased dramatically (from 42.59 and 32.98 to 22.13 and 5.54, respectively), whereas those of perennial grasses and perennial forbs increased prominently (from 13.26 and 2.71 to 53.94 and 11.79, respectively) with the reversal of desertification. Desertification reversal increased the complexity of plant community composition by increasing plant species in each PFT, and C_3 plants replaced C_4 plants to become the dominant PFT with reversal. Plant species richness and species diversity rose overall, and aboveground plant biomass significantly ($p < 0.05$) increased with the reversal of desertification. Most vegetation characteristics changed more strikingly in the early stages of desertification reversal than in later stages. Our results indicate that the type and composition of the plant community were dramatically affected by desertification reversal. Anthropogenic measures are more applicable to being employed in early stages than in later stages, and Amaranthaceae C_4 plants are suggested to be planted in mobile dunes for the acceleration of desertification reversal. This study is useful for designing strategies of land management and ecological restoration in arid and semiarid regions.

Keywords: C_4 plant; ecosystem restoration; plant functional type; restoration strategy; species importance value; species diversity

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1. Introduction

Desertification is a global phenomenon that affects a vast area and a substantial proportion of the earth's population [1–3], causing many problems such as land degradation and the reduction of ecosystem services [4]. Desertification is becoming a serious social–economic and environmental issue worldwide [5,6]. Desertification is, therefore, a matter that needs a global attention and is an important topic for intensive research. On the other hand, because of the reduction in anthropogenic pressure and the improvement in land use and management techniques, desertification in some regions is becoming actively or passively reversed. Desertification reversal is becoming an important field of sustainable development. The science of desertification reversal, especially the process and mechanism of the reversal, is helpful for ecological restoration in arid and semiarid regions. As one of the most prominent elements in terrestrial ecosystems, vegetation plays an important role in the process of desertification reversal. We selected the following variables as vegetation characteristics in the present study: plant community composition, plant functional types, plant biomass, plant species richness, and diversity.

Plant community composition plays a critical role in ecosystem functioning [7,8]. A plant functional type (PFT) is a group of plants that show similar responses to environmental circumstances and exert similar influence on the main ecosystem processes [9–11]. Revealing the changes in PFT is thus beneficial for understanding the process of desertification reversal and understanding useful implications for land management. Plant biomass is the best index to indicate the magnitude of the productivity in a grassland ecosystem and directly shows the quality of the structure and the function of the ecosystem. Biodiversity is another essential characteristic of vegetation. Plant species richness and diversity are indices for plant biodiversity. Previous studies have proposed that desertification contributes significantly to biodiversity loss [3,12], which is alleviated by combating desertification. Plant community composition, PFT, plant biomass, and biodiversity are consequently the prominent indices for the description of an ecosystem undergoing the reversal of desertification. Past studies have shown a close link between desertification reversal and plant responses. A large number of studies have documented that vegetation restoration can effectively promote the reversal process of desertification. In semi-arid regions, the involvement of shrubs increased plant richness, the biomass of fungi, actinomycetes, and other bacteria, and improved soil fertility and the N mineralization rate [13]. Shrubs promote biological soil crusts and have a positive impact on soil quality [14]. Plants can also improve soil properties and promote soil bacterial diversity by changing the soil microbial community structure [15,16]. Another study showed that plant cover in desert ecosystems can be significantly affected by environmental factors like soil nutrients [17]. However, there is relatively less research on plant community responses to desertification reversal at the level of plant functional type and plant diversity and their ecological implications. A study on this topic can contribute to understanding the process and management of ecosystem restoration in desertified grassland.

Plant community structure can be significantly changed by changes in environmental factors [17]. The measurement of changes in plant community composition serves as a good chance to monitor the land degradation [18]. Plant species have different responses to changes in the habitat as a result of plant community succession, and this leads to changes in plant species diversity and community composition [19,20]. But little attention has been paid to plant community succession during the reversal of sandy desertification. [21] found that plant species richness increased significantly under the effect of the hydraulic redistribution of *Populus euphratica*. But how plant diversity changes in a broader ecological context of desertification reversal is still not clear. Plant species diversity may develop more quickly in earlier stages during vegetation restoration [22]. How the magnitude of vegetation development differentiates between different restoration stages is still poorly understood. On the other hand, to expose the differences in the magnitude of vegetation restoration between different stages is useful for understanding the pattern and regularity of ecological restoration and is helpful for grasping and controlling vegetation succession in the process of restoration, which can in further serve land management in degenerated ecosystems.

To solve the problems mentioned above and better understand the process and mechanisms of the reversal of sandy desertification at the plant community level, we hypothesized a clear effect of desertification reversal on plant community composition, functional types, and other vegetation characteristics, including plant diversity and biomass; we also hypothesized that these vegetation characteristics develop more dramatically in the earlier stages of reversal than in the later stages. We carried out this study in different locations in Yanchi County, southern Mu Us Sandy Land, which is one of the largest anthropogenic deserts in China. The desertification reversal in the present study is a process of natural restoration without seedlings due to human measures such as livestock removal. This study will provide a scientific basis for vegetation development and land management in the process of desertification reversal.

2. Materials and Methods

2.1. Study Area

The study was conducted in Yanchi County (106°30′–107°47′ E, 37°04′–38°10′ N) in Ningxia Autonomous Region in northern China. Yanchi County is located in the southwestern part of Mu Us Sandy Land. The natural environment in this area is unfavorable, with strong wind, much sand, and a drought climate. The climate in this area belongs to the mid-temperate continental climate [23] and is profoundly influenced by dry and cold air from Mongolia and Siberia in the wintertime. The annual mean temperature is 8.1 °C [24]. The average temperature of the hottest month (July) is 22.3 °C and that of the coldest month (January) is −8.9 °C. The highest temperature measured was 38.1 °C and the lowest was −29.6 °C. The multi-year average frostless period is 165 days [24] and the annual precipitation is 296.4 mm, which falls mainly between July and October. The vegetation types in Yanchi County include shrubland, grassland, meadow, sandy land (dune), and desert vegetation [25]. The main types are typical steppe and desert steppe [26]. Vegetation in the typical steppe is composed mainly of xerophytic and mid-xerophytic plant species, such as *Agropyron cristatum*, *Stipa grandis*, *Stipa bungeana*, and *Thymus serpyllum* var. *mongolicus* [25]. Desert steppe includes species like *Oxytropis aciphylla*, *Agriophyllum squarrosum*, and *Salsola beticolor*. The main soil types in this area are sierozem and eolian sandy soil [24,27].

Desertification and its reversal have simultaneously taken place in different areas in Yanchi County during the past 50 years [24,28] because of the natural conditions and anthropogenic effects. This region underwent serious desertification between 1961 and 1989. Human activities, including overgrazing, over-cropping, deforestation, and over-excavation of medicinal plants, have played an important role in the progression of desertification in Yanchi County [29]. The desertification in this region started to reverse after 1989 [28] and especially after 2003 due to grazing prohibition [28]. On the basis of the local policy of the prohibition of grazing in the entire region and the national policy of the Grain for Green Project, the vegetation in this area began to recover naturally. Recent studies show that the policy of grazing prohibition played an important role in the reversal of desertification [30].

This region has been undergoing a marvelous desertification reversal in recent decades due to the application of a series of management measures. As these measures may also be significant for land management in other regions, especially for arid regions that are susceptible to land degradation, we summarize the management measures utilized in this region as follows. Firstly, several ecological projects have been implemented in Yanchi County, including the Three North-Shelter Forest Program, the Grain for Green Project, the Grazing Prohibition Program, and the Project for the Amelioration of Degraded Grassland by Re-seeding. These four projects were implemented in this region in 1979, 2001, 2002, and 2003, respectively, and have been significantly contributing to desertification reversal. For example, from 1979 to 2016, this region underwent five phases of the Three North-Shelter Forest Program. During this period, a large number of drought-tolerant shrubs, such as *Caragana korshinskii* and *Corethrodendron scoparium*, were planted on dunes to fix the mobile sand via other management measures such as setting a straw checkerboard barrier to prevent sand movement.

Secondly, the People’s Congress of Ningxia has legislated several regulations, such as the grassland management regulations of Ningxia Autonomous Region and the grazing prohibition regulations of Ningxia Autonomous Region. The regulations provide a basis for land management during desertification reversal. Thirdly, the government of Yanchi County has launched many publicity campaigns to increase people’s understanding of the significance of grazing prohibition for the restoration of this ecologically vulnerable area. Fourthly, livestock such as cattle and sheep are raised at farmers’ homes during the period of grazing prohibition. Large quantities of grasses are planted in specific rangelands to provide plenty of forage for livestock bred at home. Fifthly, people in this region receive extra money from the government each year as compensation for the grazing prohibition. Sixthly, many rangelands are enclosed with a wire fence, especially in severely desertified areas. Seventhly, several penalty measures are employed when the regulations are violated, e.g., anyone who allows grazing during the period of grazing prohibition will have to pay a fine as a penalty.

Lastly, a series of management measures are applied to supervise the implementation of grazing prohibition. Each level of the government, including the village, the town, and the county, are designated relevant responsibilities for management. The government of the county establishes special police and executive teams to patrol the fields regularly for violation of the regulations. People are also encouraged to report to the police when they see an offense, and they will receive money as a reward if the violation is determined to be true. Additionally, the media are invited to participate in the supervision and expose violations.

2.2. Field Design and Laboratory Analyses

Based on a detailed survey of the whole Yanchi County, we selected seven large study sites located in Southern Mu Us Sandy Land. All selected study sites are located in the former typical desertification areas and are in the middle and northern parts of Yanchi County. At each study site, we used the method of space for time and randomly (in the locations) selected four to five sub-sites with different stages of desertification reversal based on a comprehensive criteria, mainly according to the proportion of bare (mobile) sand area to total ground area (SAND, %) and to vegetation cover (COV, %) [24,26,31,32]. SAND is a critical criterion because it relates to several indices, such as wind erosion intensity and aeolian activity. Due to the drought climate and strong wind, the desertification in this region has mainly been caused by wind erosion from the pressure of human activities. Therefore, we took SAND and COV as the main criteria for the classification of reversal stages. Areas with SAND and COV accounting for (1) more than 50% and less than 10%, (2) 30–50% and 10–30%, (3) 10–30% and 30–40%, (4) less than 10% and 40–50%, and (5) 0% and more than 50% of the total ground area, respectively, were classified as reversal stages of (1) very severe desertification (VSD), (2) severe desertification (SD), (3) moderate desertification (MD), (4) light desertification (LD), and (5) potential desertification (PD), respectively [24,32–35]. In addition to SAND and COV, we also took the intensity of wind erosion and aeolian activity [33,36] into account as subsidiary indices for the classification of stages of desertification reversal. There were only four study sites that had potential desertification areas. These sub-sites were undergoing different stages of desertification reversal due to the differences in factors such as restoration measures, micro-topography, and geographic location (whether directly against the prevailing wind direction).

The vegetation investigation was carried out in July and August during the optimal period for plant growth. Three plots were randomly established in each sub-site. At the center of each plot, we set a quadrat of 1 m × 1 m. Around each quadrat, in the range of 5 m × 5 m, we threw an iron circle with a diameter of 0.5 m ten times, and all the plant names enclosed within the circle were recorded each time. The total number of times that one species was enclosed in the circle was taken as the frequency [37]. For each quadrat, the abundance, height, and cover of each plant species was carefully investigated and recorded. The abundance was counted one by one. The height was measured using the highest plant of each species in the quadrat. The cover of each species was measured via the needling method, with 100 points homogeneously distributed in the quadrat [38]. The aboveground parts of all plants in the quadrat were then cut, collected, and weighed immediately.

In the laboratory, the aboveground parts of the plants were dried in an oven at 105 °C for 30 min and then at 80 °C for 24 h until the weight of the plants stopped changing. All of these dried plants were then weighed again after cooling to room temperature. The dried weight was taken as the aboveground plant biomass (hereafter, "plant biomass"). The plants were identified to be C_3 and C_4 species by observing their leaves and by compiling data from 23 published works [39–61]. The C_3 and C_4 plants were identified by measuring the stable carbon isotope ratio ($\delta^{13}C$) of plant tissues in the cited studies [45,60].

2.3. Statistical Analyses

The data were processed with Excel 2021 and SPSS 13.0. The importance value (IV) of a given plant species was calculated with the following formula [21] (Equation (1)):

$$\mathrm{IV} = (\mathrm{RA} + \mathrm{RH} + \mathrm{RC} + \mathrm{RF})/4 \times 100 \tag{1}$$

where RA, RH, RC, and RF represent the relative abundance, relative height, relative cover, and relative frequency, respectively. RA is the proportion of the number of individuals of this species to the sum of the individuals of all species in the same quadrat. RH, RC, and RF were calculated in the same way [62]. The formula was developed from the following equation [63] (Equation (2)):

$$\mathrm{DV} = (\mathrm{RA} + \mathrm{RH} + \mathrm{RC})/3 \times 100 \tag{2}$$

where DV is the dominance value; RA, RH, and RC represent the same meanings as above.

The number of plant species in a quadrat was taken as the species richness. Species diversity was calculated with the Shannon–Wiener index [64–67] (Equation (3)):

$$\mathrm{H}' = -\sum_{\mathrm{i}=1}^{\mathrm{S}} \mathrm{P_i} \ln \mathrm{P_i} \tag{3}$$

where H' is the Shannon–Wiener index, S is the number of plant species, and $\mathrm{P_i}$ is the proportion of the number of individuals of species i to the total number of individuals of all plant species (Equation (4)):

$$\mathrm{P_i} = \mathrm{n_i}/\mathrm{N} \tag{4}$$

where $\mathrm{n_i}$ is the number of individuals of species i, and N is the total number of individuals of all plant species.

The Kolmogorov–Smirnov test (K-S test) for normality was implemented for each group of data. For data whose distributions were not normal, a logarithmic transformation of the data was conducted and then they were tested again with the K-S test. Variance analyses between different desertification reversal stages were conducted with SPSS 13.0 [68].

3. Results

3.1. Changes in Vegetation Conditions and Quantitative Plant Characteristics

Plant species importance values (IVs) changed dramatically with the reversal of sandy desertification (Table 1). In the very severe desertification (VSD) areas and severe desertification (SD) areas, *Artemisia ordosica* and *Agriophyllum squarrosum* were the dominant species of the plant communities. The total IVs of these two species accounted for 62.2% and 28.6% in VSD and SD areas, respectively. The IV of *A. ordosica* decreased gradually from VSD areas via the middle desertification (MD) areas to potential desertification (PD) areas. *A. squarrosum* disappeared in the MD and PD areas and almost in the light desertification (LD) areas. *A. ordosica* and *A. squarrosum* are pioneer plants for sand fixation in sandy desertification areas.

The IVs of perennial grass species, including *Leymus secalinus*, *Pennisetum flaccidum*, *Cleistogenes squarrosa*, *Agropyron mongolicum*, and *Stipa bungeana*, increased in general with the reversal of desertification (Table 1). The IV of *Artemisia scoparia* increased substantially from 0.41% in VSD to 15.80% in PD. However, the IVs of some other annual species, such as *Salsola beticolor* and *Setaria viridis*, decreased in general with the desertification reversal. It was more common for the IVs to change much more significantly in the early stages (from VSD to MD) of desertification reversal than in the later stages (from MD to PD) (Table 1).

Table 1. Effects of the reversal of sandy desertification on plant species importance values (IVs) in Southern Mu Us Sandy Land, China *.

		Desertification Reversal Stage				
Species	**Life Form**	**VSD**	**SD**	**MD**	**LD**	**PD**
Artemisia ordosica Krasch.	PS	32.89	12.25	14.72	10.54	4.31
Agriophyllum squarrosum (L.) Moq.	AF	29.27	16.35		0.47	
Leymus secalinus (Georgi) Tzvel.	PG	9.52	21.30	4.96	11.85	26.46
Salsola beticolor Iljin	AF	9.42	5.99	1.46	4.30	2.26
Setaria viridis (L.) Beauv.	AG	8.46	5.38	1.26	5.88	2.85
Pennisetum flaccidum Griseb.	PG	3.74	0.69	12.58	4.34	9.26
Bassia scoparia (L.) A.J.Scott	AF	2.85	3.43	0.81	2.29	
Ixeris chinensis subsp. *versicolor* (Fisch. ex Link) Kitam.	PF	2.18	3.68	6.62	9.94	4.11
Panzerina lanata var. *alaschanica* (Kuprian.) H. W. Li	PF	0.53	0.09	0.09		
Artemisia scoparia Waldst. et Kit.	AF	0.41	1.01	19.42	18.98	15.80
Euphorbia humifusa Willd.	AF	0.30	1.32	0.75	0.18	0.82
Chenopodium acuminatum Willd.	AF	0.16		5.21	1.84	0.34
Tribulus terrestris L.	AF	0.11	0.60			
Lespedeza potaninii Vass.	PS	0.09	1.81	1.37	2.32	0.10
Grubovia dasyphylla (Fisch. & C. A. Mey.) Freitag & G. Kadereit	AF	0.07	2.06	0.48	0.46	0.88
Oxytropis racemosa Turcz.	PL		8.06	0.25	0.31	
Sophora alopecuroides L.	PS		6.77	1.65	1.19	1.04
Cleistogenes squarrosa (Trin.) Keng	PG		1.89	5.20	2.13	7.09
Astragalus melilotoides Pall.	PL		1.85	0.98	2.82	0.58
Salix psammophila C.Wang et Ch.Y. Yang	SH		0.96			
Corethrodendron fruticosum var. *mongolicum* (Turczaninow) Turczaninow ex Kitagawa	PS		0.74			
Agropyron mongolicum Keng	PG		1.03	0.66	2.91	8.44
Oxytropis aciphylla Ledeb.	PS		0.69			
Cynanchum thesioides (Freyn) K. Schum	PF		0.54	0.13		
Gueldenstaedtia stenophylla Bge.	PL		0.53	0.72	0.19	
Inula salsoloides (Turcz.) Ostenf.	PF		0.32			
Vincetoxicum mongolicum Maxim.	PF		0.24	0.27		0.34
Olgaea leucophylla (Turcz.) Iljin	PF		0.13			
Euphorbia esula L.	PF		0.13	0.81	0.09	
Polygala tenuifolia Willd.	PF		0.09			
Echinops gmelinii Turcz.	AF		0.06	0.32	0.29	0.59
Chenopodium album L.	AF			4.13	1.14	0.94
Stipa breviflora Griseb.	PG			3.62	4.46	0.98
Thermopsis lanceolata R. Br.	PL			3.57	1.79	0.20
Aster altaicus Willd.	PF			2.25	1.88	4.66
Setaria arenaria Kitag.	AG			1.46	0.08	1.13
Cuscuta chinensis Lam.	AF			1.36		
Glycyrrhiza uralensis Fisch.	PL			1.14	1.74	1.93
Equisetum ramosissimum Desf.	PF			0.94		
Polygonum aviculare L.	AF			0.40		
Stipa bungeana Trin.	PG			0.16		1.71
Plantago asiatica L.	PF			0.12		0.11
Incarvillea sinensis Lam.	AF			0.11	0.19	
Kalidium foliatum (Pall.) Moq.	SH				1.27	
Artemisia sacrorum Ledeb.	PF				1.24	
Limonium aureum (L.) Hill. ex Kuntze	PF				1.00	
Peganum nigellastrum Bge.	PF				0.91	
Typha minima Funk.	PF				0.54	0.88
Sonchus arvensis L.	PF				0.34	
Lactuca tatarica (L.) C. A. Mey.	PF				0.09	
Artemisia dubia Wall. ex Bess. var. *subdigitata* (Mattf.) Y. R. Ling	PF					1.37
Artemisia mongolica Fisch. ex Bess.	PF					0.32
Silene conoidea L.	AF					0.27
Oxybasis glauca (L.) S. Fuentes, Uotila & Borsch	AF					0.23

* Desertification reversal stages: VSD: very severe desertification; SD: severe desertification; MD: moderate desertification; LD: light desertification; PD: potential desertification. Life forms: AF: annual forb (a forb is an herbaceous plant that is not a grass species); AG: annual grass; PF: perennial forb; PG: perennial grass; PL: perennial legume; PS: perennial sub-shrub; SH: shrub. The abbreviations in the following tables have the same meanings.

The number of plant species of annual forbs and perennial grasses increased from SD to MD, and that of perennial forbs and perennial legumes increased abruptly from VSD to SD and then maintained relative stability (Table 2). The IVs of life form groups noticeably changed with the reversal of sandy desertification. The IVs of annual forbs and perennial sub-shrubs decreased dramatically from 42.59% and 32.98% in VSD to 22.13% and 5.54% in PD, respectively. That of perennial grasses and forbs increased prominently from 15.97% in VSD to 65.83% in PD. Perennial grasses became the main life form in PD, with an IV value of 53.94%. In general, the number of plant species and IVs summarized in life forms changed more dramatically in the early stages (from VSD to MD) of desertification reversal than in the later stages (from MD to PD) (Table 2).

Table 2. Effects of the reversal of sandy desertification on plant life forms in Southern Mu Us Sandy Land, China *.

Life Form		Desertification Reversal Stage				
		VSD	**SD**	**MD**	**LD**	**PD**
AF	S	8	8	11	10	9
	IV	42.59	30.82	34.45	30.14	22.13
AG	S	1	1	2	2	2
	IV	8.46	5.38	2.72	5.96	3.98
PF	S	2	8	8	9	7
	IV	2.71	5.22	11.23	16.03	11.79
PG	S	2	4	6	5	6
	IV	13.26	24.91	27.18	25.69	53.94
PL	S	0	3	5	5	3
	IV	0.00	10.44	6.66	6.85	2.71
PS	S	2	5	3	3	3
	IV	32.98	22.26	17.74	14.05	5.54
SH	S	0	1	0	1	0
	IV	0.00	0.96	0.00	1.27	0.00

* S: the number of plant species. The other abbreviations are the same as in Table 1.

3.2. Effects of Desertification Reversal on Plant Functional Types

Six plant functional types were classified, including C_3 and C_4 plants, forbs, grasses, legumes, and sub-/shrubs (Table 3). We identified 35 species of C_3 plants and 17 species of C_4 plants. Amaranthaceae comprised the largest numbers of C_4 species (eight species), followed by Poaceae (with four C_4 species) (Table 3). Desertification reversal had clear effects on the composition of plant functional types (PFTs). In the early stages of reversal, PFTs were mainly forbs and sub-shrubs; in the middle and later stages, other PFTs such as grasses were included (Table 3). In VSD, C_4 plants accounted for 66.67% of the total number of plant species, and their importance value (IV) was much higher than that of C_3 plants (Table 3). Most of the C_4 plants found in VSD were also distributed in other stages, and only 4 of 17 C_4 species occurred just in one reversal stage, such as *Polygala tenuifolia* in SD (Table 3), suggesting an extensive range of adaptation in C_4 plants. The IV of C_3 plants increased steadily from 12.20 to 68.52 in the process of desertification reversal (Table 4). Although the percentages of the number of plant species (S%) in the later stages (from MD to PD) of desertification reversal remained relatively steady for legumes, grasses, and forbs, the IV of legumes decreased from 20.45 to 3.85 from VSD to PD, and that of grasses increased from 21.72 to 57.92 in the whole process of reversal (Table 4). On the other hand, most PFTs changed more dramatically in the early stages (from VSD to MD) in both S% and IVs than in the later stages, except for grasses in S% and IV and forbs in IV (Table 4).

Table 3. Effects of the reversal of sandy desertification on plant composition and the detailed information of plant functional types in Southern Mu Us Sandy Land, China *.

Desertification Reversal Stage		Species	Family	C_3/C_4	PFTs
VSD and SD	Early stages	*Tribulus terrestris* L.	Zygophyllaceae	C_4	Forb
SD		*Salix psammophila* C.Wang et Ch.Y. Yang	Salicaceae	C_3	Shrub
SD		*Corethrodendron fruticosum* var. *mongolicum* (Turczaninow) Turczaninow ex Kitagawa	Fabaceae	C_3	Legume/ sub-shrub
SD		*Oxytropis aciphylla* Ledeb.	Fabaceae	C_3	Legume/ sub-shrub
SD		*Inula salsoloides* (Turcz.) Ostenf.	Asteraceae	C_3	Forb
SD		*Olgaea leucophylla* (Turcz.) Iljin	Asteraceae	C_3	Forb
SD		*Polygala tenuifolia* Willd.	Polygalaceae	C_4	Forb
SD MD		*Cynanchum thesioides* (Freyn) K. Schum	Asclepiadaceae	C_3	Forb
VSD SD MD		*Panzerina lanata* var. *alaschanica* (Kuprian.) H. W. Li	Labiatae	C_3	Forb
VSD SD LD		*Agriophyllum squarrosum* (L.) Moq.	Amaranthaceae	C_4	Forb
MD	Middle stages	*Cuscuta chinensis* Lam.	Convolvulaceae	C_4	Forb
MD		*Equisetum ramosissimum* Desf.	Equisetaceae	C_3	Forb
MD		*Polygonum aviculare* L.	Polygonaceae	C_3	Forb
SD MD LD		*Oxytropis racemosa* Turcz.	Fabaceae	C_3	Legume
SD MD LD		*Gueldenstaedtia stenophylla* Bge.	Fabaceae	C_3	Legume
SD MD LD		*Euphorbia esula* L.	Euphorbiaceae	C_3	Forb
MD LD	Later stages	*Incarvillea sinensis* Lam.	Bignoniaceae	C_3	Forb
LD		*Kalidium foliatum* (Pall.) Moq.	Amaranthaceae	C_4	Shrub
LD		*Artemisia sacrorum* Ledeb.	Asteraceae	C_3	Forb
LD		*Limonium aureum* (L.) Hill. ex Kuntze	Plumbaginaceae	C_3	Forb
LD		*Peganum nigellastrum* Bge.	Zygophyllaceae	C_3	Forb
LD		*Sonchus arvensis* L.	Asteraceae	C_3	Forb
LD		*Lactuca tatarica* (L.) C. A. Mey.	Asteraceae	C_3	Forb
LD PD		*Typha minima* Funk.	Typhaceae	C_3	Forb
PD		*Artemisia dubia* Wall. ex Bess. var. *subdigitata* (Mattf.) Y. R. Ling	Asteraceae	—	Forb
PD		*Artemisia mongolica* Fisch. ex Bess.	Asteraceae	C_3	Forb
PD		*Silene conoidea* L.	Caryophyllaceae	C_3	Forb
PD		*Oxybasis glauca* (L.) S. Fuentes, Uotila & Borsch	Amaranthaceae	C_4	Forb
SD MD PD		*Vincetoxicum mongolicum* Maxim.	Asclepiadaceae	C_3	Forb
MD PD		*Stipa bungeana* Trin.	Poaceae	C_3	Grass
MD PD		*Plantago asiatica* L.	Plantaginaceae	C_3	Forb
MD LD PD		*Chenopodium album* L.	Amaranthaceae	C_4	Forb
MD LD PD		*Stipa breviflora* Griseb.	Poaceae	C_3	Grass
MD LD PD		*Thermopsis lanceolata* R. Br.	Fabaceae	C_3	Legume
MD LD PD		*Aster altaicus* Willd.	Asteraceae	C_3	Forb
MD LD PD		*Setaria arenaria* Kitag.	Poaceae	C_4	Grass
MD LD PD		*Glycyrrhiza uralensis* Fisch.	Fabaceae	C_3	Legume
VSD SD MD LD	Common stages	*Bassia scoparia* (L.) A.J.Scott	Amaranthaceae	C_4	Forb
SD MD LD PD		*Sophora alopecuroides* L.	Fabaceae	C_3	Legume/ Sub-shrub
SD MD LD PD		*Cleistogenes squarrosa* (Trin.) Keng	Poaceae	C_4	Grass
SD MD LD PD		*Astragalus melilotoides* Pall.	Fabaceae	C_3	Legume
SD MD LD PD		*Agropyron mongolicum* Keng	Poaceae	C_3	Grass
SD MD LD PD		*Echinops gmelinii* Turcz.	Asteraceae	C_3	Forb
VSD MD LD PD		*Chenopodium acuminatum* Willd.	Amaranthaceae	C_4	Forb
VSD SD MD LD PD		*Artemisia ordosica* Krasch.	Asteraceae	C_4	Sub-shrub
VSD SD MD LD PD		*Leymus secalinus* (Georgi) Tzvel.	Poaceae	C_3	Grass
VSD SD MD LD PD		*Salsola beticolor* Iljin	Amaranthaceae	C_4	Forb
VSD SD MD LD PD		*Setaria viridis* (L.) Beauv.	Poaceae	C_4	Grass
VSD SD MD LD PD		*Pennisetum flaccidum* Griseb.	Poaceae	C_4	Grass
VSD SD MD LD PD		*Ixeris chinensis* subsp. *versicolor* (Fisch. ex Link) Kitam.	Asteraceae	C_3	Forb
VSD SD MD LD PD		*Artemisia scoparia* Waldst. et Kit.	Asteraceae	C_3	Forb
VSD SD MD LD PD		*Euphorbia humifusa* Willd.	Euphorbiaceae	C_4	Forb
VSD SD MD LD PD		*Lespedeza potaninii* Vass.	Fabaceae	C_3	Legume/ sub-shrub
VSD SD MD LD PD		*Grubovia dasyphylla* (Fisch. & C. A. Mey.) Freitag & G. Kadereit	Amaranthaceae	C_4	Forb

* PTF: plant functional types. The other abbreviations are the same as in Table 1.

Table 4. Effects of the reversal of sandy desertification on plant species richness and importance values summarized in plant functional types in Southern Mu Us Sandy Land, China *.

Plant Functional Type		Desertification Reversal Stage				
		VSD	SD	MD	LD	PD
C_3 plant	S	4	18	22	22	18
	S%	26.67	60.00	62.86	62.86	60.00
	IV	12.20	49.85	50.47	65.07	68.52
C_4 plant	S	10	11	12	13	11
	S%	66.67	36.67	34.29	37.14	36.67
	IV	87.27	50.05	49.42	34.92	30.11
Legume ^{a}	S	1	7	7	7	5
	S%	6.67	23.33	20.00	20.00	16.67
	IV	0.09	20.45	9.68	10.36	3.85
Grass	S	3	5	8	7	8
	S%	20.00	16.67	22.86	20.00	26.67
	IV	21.72	30.29	29.90	31.65	57.92
Forb	S	10	16	19	19	16
	S%	66.67	53.33	54.29	54.29	53.33
	IV	45.30	36.04	45.68	46.17	33.92
Sub-shrub	S	2	6	3	5	3
	S%	13.33	20.00	8.57	14.29	10.00
	IV	32.98	23.22	17.74	16.51	5.45

* Legumes, including sub-shrubs, that also belong to *Fabaceae*. The included legume sub-shrubs were also included in the plant functional type of sub-shrub.

3.3. Responses of Plant Diversity and Biomass to the Reversal of Sandy Desertification

Species richness varied between 1.0 and 11.3; species diversity changed from 0.0 to 2.01 (Table 5). For each study site, species richness and diversity generally increased with the reversal of sandy desertification. There were significant differences ($p < 0.05$) in variables of species richness and diversity between different desertification reversal stages. In most study sites, plant species richness changed more dramatically in the early stages (from VSD to MD) than in the later stages (from MD to PD) of desertification reversal, whereas plant species diversity changed more obviously in the early stages in around half of all study sites, whereas in other study sites it changed more clearly in the later stages (Table 5). Taking all study sites as a whole, the trends in summary statistics of vegetation characteristics were clearer than those for single study sites. Mean species richness and diversity increased from 3.0 and 0.57 in VSD to 9.0 and 1.22 in PD, respectively, for the whole data set for all study sites.

Table 5. Effects of the reversal of sandy desertification on plant diversity in Southern Mu Us Sandy Land, China *.

Study Site	Reversal Stage	Species Richness	Species Diversity
NHZ	1	2.3 ± 0.6^{a}	0.67 ± 0.04^{a}
	2	7.0 ± 2.0^{b}	1.08 ± 0.51^{ab}
	3	9.3 ± 0.6^{b}	1.05 ± 0.16^{ab}
	4	8.0 ± 2.6^{b}	1.51 ± 0.13^{b}
HB	1	2.3 ± 0.6^{a}	0.56 ± 0.26^{a}
	2	4.0 ± 1.0^{b}	1.02 ± 0.19^{ab}
	3	7.7 ± 1.2^{c}	1.02 ± 0.59^{ab}
	4	7.7 ± 1.5^{c}	1.19 ± 0.21^{b}
	5	8.7 ± 2.9^{c}	1.01 ± 0.31^{ab}
HBN	1	2.7 ± 0.6^{a}	0.92 ± 0.25^{ab}
	2	4.3 ± 2.5^{ac}	0.82 ± 0.81^{a}
	3	9.7 ± 1.5^{bd}	2.01 ± 0.10^{b}
	4	5.7 ± 1.5^{c}	1.13 ± 0.28^{ab}
	5	11.3 ± 1.2^{d}	1.62 ± 0.66^{ab}
YZZ	1	6.3 ± 1.2^{a}	0.88 ± 0.25^{a}
	2	8.0 ± 1.0^{a}	0.50 ± 0.10^{a}
	3	7.7 ± 1.5^{a}	0.65 ± 0.33^{a}
	4	10.3 ± 1.2^{b}	1.66 ± 0.13^{b}

Table 5. *Cont.*

Study Site	Reversal Stage	Species Richness	Species Diversity
MC	1	4.3 ± 1.5 ^{a}	0.90 ± 0.23 ^{a}
	2	6.0 ± 1.0 ^{ac}	1.13 ± 0.29 ^{a}
	3	10.3 ± 1.2 ^{b}	1.28 ± 0.06 ^{a}
	4	7.3 ± 1.5 ^{c}	0.90 ± 0.33 ^{a}
WZZ	1	1.0 ± 0.0 ^{a}	0.00 ± 0.00 ^{a}
	2	5.7 ± 2.1 ^{b}	0.89 ± 0.37 ^{b}
	4	5.7 ± 2.1 ^{b}	0.71 ± 0.13 ^{b}
	5	9.0 ± 1.0 ^{c}	1.47 ± 0.30 ^{c}
LJHZ	1	2.3 ± 1.2 ^{a}	0.07 ± 0.07 ^{a}
	2	5.0 ± 1.0 ^{bc}	0.68 ± 0.24 ^{b}
	3	3.7 ± 1.5 ^{ab}	0.22 ± 0.26 ^{ac}
	4	5.3 ± 0.6 ^{bc}	1.42 ± 0.14 ^{bd}
	5	7.0 ± 1.7 ^{c}	0.80 ± 0.52 ^{bd}
All study sites	1	3.0 ± 1.8 ^{a}	0.57 ± 0.40 ^{a}
	2	5.7 ± 1.9 ^{b}	0.87 ± 0.41 ^{b}
	3	8.1 ± 2.5 ^{cd}	1.04 ± 0.62 ^{bc}
	4	7.1 ± 2.2 ^{c}	1.22 ± 0.37 ^{c}
	5	9.0 ± 2.3 ^{d}	1.22 ± 0.53 ^{c}

* Desertification reversal stages: (1) very severe desertification (VSD); (2) severe desertification (SD); (3) moderate desertification (MD); (4) light desertification (LD); (5) potential desertification (PD). All study sites: taking the data set for all study sites as a whole. Values are shown as mean ± standard deviation. Different letters within the same study site and variable indicate significant differences between the different desertification reversal stages at the $p < 0.05$ level.

The value of plant biomass was very small in very severe desertification areas and increased gradually with the reversal of desertification at each study site (Figure 1). There were significant differences between different reversal stages. However, there were also some exceptions. At the study site of HBN, the plant biomass in LD was greater than in PD; at the study site of YZZ and LJHZ, the plant biomass in MD was higher than in LD. In general, changes in plant biomass were larger in the early stages of desertification reversal than in the later stages (Figure 1).

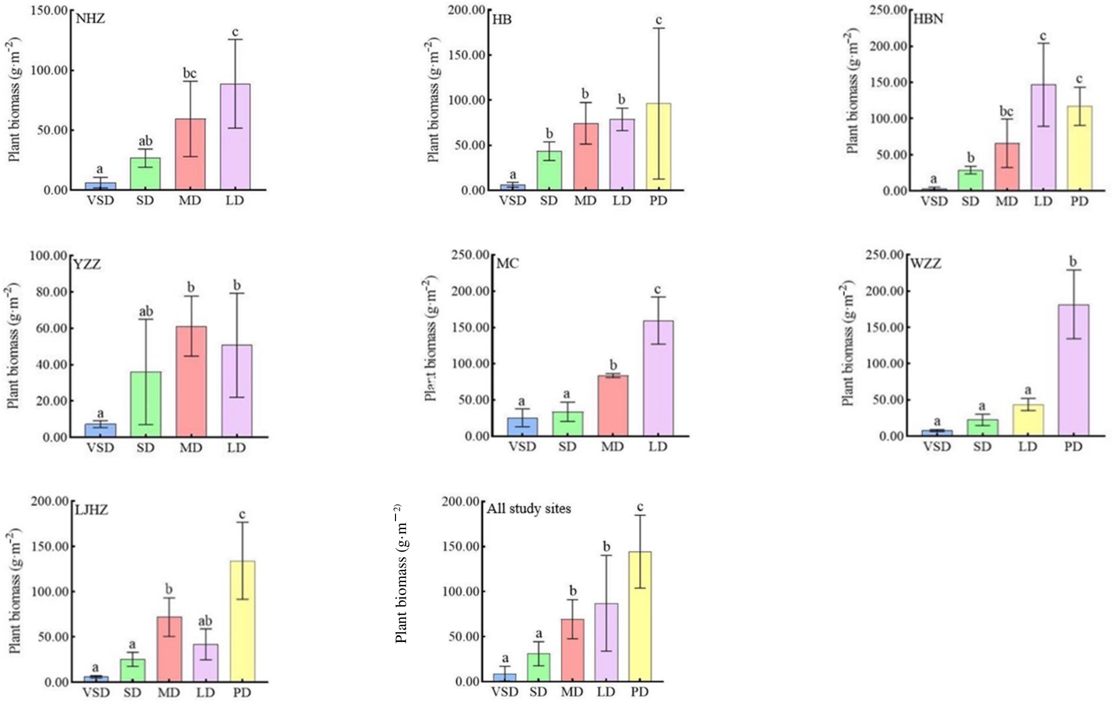

Figure 1. Effects of the reversal of sandy desertification on plant biomass in Southern Mu Us Sandy Land, China. Different letters within the same study site indicate significant differences between the different stages of desertification reversal at the $p < 0.05$ level. The length of the column is the mean value of plant biomass; the length of the bar on each column is the value of the standard deviation.

4. Discussion

4.1. Changes in Vegetation Conditions and Plant Community Characteristics with Desertification Reversal

Our hypotheses were supported by the results. For the first hypothesis, the species importance values (IVs) of both pioneer plant species (*Artemisia ordosica* and *Agriophyllum squarrosum*) for sand fixation decreased dramatically along the desertification reversal sequence, indicating a reversal process of sandy desertification. This result is consistent with the desertification classification in this study based on bare (mobile) sand area proportion, vegetation cover, the intensity of wind erosion, and aeolian activity. This agreement shows that plant community composition could also be an index for desertification reversal.

Changes in IVs of *A. squarrosum* and *Artemisia scoparia* occurred in opposite directions. *A. squarrosum* disappeared suddenly in moderate desertification (MD) areas, where its IV was 0, whereas the IV of *A. scoparia* increased abruptly in MD areas. These two plant species are both annual forbs. The reason for the observed change may be competition between plant species with the same life form. The environment in MD areas was not suitable for *A. squarrosum* anymore, and it was replaced by *A. scoparia* and some other plant species. *A. scoparia* is a species that does not survive well in an extremely harsh environment like the VSD areas, and [69] showed that the growth of *A. scoparia* significantly benefited from higher nitrogen concentrations.

Our results also show that sub-shrubs, together with shrubs, accounted for a significant IV in very severe desertification (VSD) areas, severe desertification (SD) areas, and MD areas, indicating the importance of the existence of sub-shrubs and shrubs in the process of desertification reversal. In accord with this study, ref. [13] showed that the establishment of shrubs was an important step for desertification reversal, and the number of vascular plant species increased due to shrub establishment.

This may be attributed to the positive effects of organic matter provided by perennial shrubs on microbial activity [70] and the effects of shrub rhizosphere components on microbial diversity [71], which both contribute to ameliorating soil conditions and may be beneficial to the re-establishment of perennial grasses. The establishment of shrubs also leads to substantial changes in plant community composition [13], as was also shown by this study. One related mechanism that changes plant species diversity and community composition may be the inhabitation of seed-spreading birds on shrubs; other comprehensive factors may include mycorrhizas and symbionts [13]. Moreover, ref. [72] showed that soil properties in shifting dunes were improved by shrub establishment and sand immobilization; this process facilitated the establishment of herbaceous plant species in the ecosystem [73,74]. Consequently, the growth of shrubs and sub-shrubs in severely desertified grasslands may be an advantage for the initiation of the reversal of sandy desertification, although shrubs and sub-shrubs will be replaced gradually by perennial grasses and other herbaceous taxa during the process of desertification reversal.

The changes in IVs of *L. secalinus*, *P. flaccidum*, *C. squarrosa*, *A. mongolicum*, and *S. bungeana* in our study suggest that the importance of perennial grasses as a plant group gradually increased in communities with the reversal of sandy desertification. This plant group may play an important role in communities, especially in potential desertification (PD) areas. The changes in perennial grasses, perennial forbs, sub-shrubs, and annual forbs indicate that plant communities developed gradually from sub-shrub- and annual forb-dominated communities to perennial grass-dominated communities. Previous studies also suggested the re-establishment of perennial grasses as a consequence of desertification reversal [2], which is consistent with our results.

Perennial grasses are re-established with the reversal of desertification, which is probably affected by the interactions between three factors, including soil nutrients, compaction, and infiltration [2]. Soil compaction is a decrease in soil porosity or an increase in soil bulk density caused by internal or external loads [75]. Water infiltration is the capability of soil to absorb irrigation or rainfall. The accumulation of soil nutrients is affected by changes in soil infiltration and compaction [2]. Previous studies have suggested that increased infiltration is significantly related to decreased soil compaction [76]. An increase in infiltration and a decrease in soil compaction were reported as a consequence of long-term livestock removal [77], which supported the accumulation of soil nutrients over time [2]. This result will further affect the re-establishment of perennial grasses, which will provide a favorable environment for the further reversal of sandy desertification.

4.2. Relationships between Vegetation Characteristics and Desertification Reversal

In contrast to widely accepted knowledge, *Amaranthaceae*, rather than *Poaceae*, is the family that included the largest number of C_4 species in our study, suggesting a more complex situation of plant composition in desertified areas than in areas with normal conditions. This is mainly due to the fact that plant species of Amaranthaceae are more adaptive to the xerophytic environment in desert ecosystems. This result is in accordance with [78]. Our study found that C_4 plants accounted for the largest number of plant species and importance values in VSD areas, indicating that C_4 plants are more adaptive to the first stage of desertification reversal than C_3 plants. This further indicates that C_4 species may be considered for planting in mobile dunes as an anthropogenic measure to promote desertification reversal. We also found that C_4 plants could adapt well to habitats of different stages of desertification reversal. On the other hand, few C_3 plants were found in the early stages (Table 4), indicating the relatively narrow adaptation of C_3 plants. Our results are supported by another study that held that C_4 plants should be a useful measure for combating desertification [79]. All of these findings indicate that an application of selected Amaranthaceae C_4 plants in mobile dunes would be more efficient and practical than an application of C_3 or other C_4 plants and may also be beneficial for the maintenance of vegetation in later stages of desertification reversal.

Our study shows that species richness and diversity generally increased with the reversal of sandy desertification. Plant species diversity was found to be strongly related to soil chemical and physical properties, which resulted in different habitats [80]. The ameliorated soil conditions in less desertified grasslands can lead to higher species diversity due to the relatively adequate soil fertility [22] and other improved soil properties [65]. Plant diversity improved by shrub encroachment was also shown to be associated with higher soil fertility [13].

Plant species diversity increases not only in the natural process of desertification reversal described in our study but also during ecological restoration management by planting artificial shrubs in mobile dunes [72]. On the other hand, changes in plant species diversity also influence the reversal of sandy desertification. Higher plant species diversity yields more differences in litter components in both physical and chemical aspects, which is beneficial to soil formation and nutrient cycling [3]. Soils in areas with desertification reversal, therefore, have better conditions and higher rates of nutrient cycling due to higher species diversity. This, in turn, promotes the further reversal of sandy desertification. Moreover, ref. [81] showed that soil microbial communities responded rapidly to changes in plant species diversity in grassland ecosystems, and higher plant diversity resulted in higher bacterial activity and diversity, which is important for litter decomposition and other biogeochemical processes. In addition to plant species diversity, plant biomass also increased significantly with the reversal of sandy desertification in our study. Plant biomass is an important vegetation characteristic reflecting plant growth status. Plants grew better in the reversed grasslands than in the desertified grasslands, which might have been due to the improved soil conditions in the former. Increments in plant biomass, in turn, contribute to the further reversal of sandy desertification. Plant cover is of key importance for the accumulation of organic matter and fine particles in the soil, providing a physical barrier [70] that will prevent aeolian soil erosion. Both the organic matter accumulation and physical barrier function caused by plant cover will promote the continued process of desertification reversal.

4.3. Differences in Changes in Vegetation Characteristics between Early and Later Stages of Desertification Reversal

Our results also supported our second hypothesis. Most vegetation characteristics changed more dramatically in the early stages of desertification than in the later stages. These results indicate that applying engineering measures in the early stages is more practical than in the later stages, when these measures are considered. Engineering measures such as using straw checkerboards to arrest the sand and establishing sand barriers have been demonstrated to be successful methods in practice [72,82]. These methods are particularly suitable for vegetation restoration and dune stabilization [82] in the first two stages of sandy desertification reversal. Some other measures, such as leveling the ground of dunes [83], are advantageous for the reversal of very severe desertification areas. Additionally, to plant pioneer plant species in areas of the first two stages is helpful for vegetation recovery, especially Amaranthaceae C_4 plants in mobile dunes. It is particularly useful to protect the native perennial grasses that occur in the early stages, which will facilitate the community succession to the later stages of desertification reversal. On the other hand, engineering measures would help vegetation restoration by providing better physical conditions. But engineering measures need a significant input of energy and resources, and the physical conditions in later stages are normally much better than in early stages. Engineering measures in later stages may thus not generate as many effects as in early stages. Nevertheless, some basic human measures such as enclosure [84] are still necessary for the later stages of desertification reversal. In a word, anthropogenic and natural restoration should be combined, and the early stages, rather than the later stages, should apply appropriate anthropogenic measures when they are under consideration.

5. Conclusions and Implications

The plant community composition, functional types, and other vegetation characteristics (plant diversity, biomass, etc.) of different sites in different desertification reversal stages were analyzed. The natural dominant species in the sites evolved from annual forbs and sub-shrubs to perennial grasses and forbs. In the later stage of restoration, relatively stable near-natural sand-fixing vegetation was formed, showing a trend of succession to desertification grassland. Our results show that plant community composition, species importance value, and plant functional types changed significantly during the process of desertification reversal, and most of the vegetation characteristics changed more in the early stages of desertification reversal than in the later stages. In the early stages, the importance value of C_4 plants was higher than that of C_3 plants. With the reversal process, C_3 plants gradually replaced C_4 plants as the dominant species, indicating that C_4 plants have stronger adaptability than C_3 plants and can survive in harsher environments. Therefore, in the process of artificial sand fixation, C_4 plants or sub-shrubs should be considered for application to mobile sand dunes to change the soil quality and accelerate the reversal of desertification. Collectively, desertification reversal promotes the complexity of the plant community by increasing the plant species diversity of each plant functional type, especially in the early stages of desertification reversal.

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Abbreviations

COV	Vegetation cover
IV	Importance value
DV	Dominance value
LD	Light desertification
MD	Moderate desertification
PD	Potential desertification
PFT	Plant functional type
RA	Relative abundance
RC	Relative cover
RF	Relative frequency
RH	Relative height
S%	Percentages of the number of plant species
SAND	Proportion of the bare (mobile) sand area to the total ground area
SD	Severe desertification
VSD	Very severe desertification

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