

Review of the ecohydrological processes and feedback mechanisms controlling sand-binding vegetation systems in sandy desert regions of China

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Soil water is the key abiotic limiting factor in desert areas and hydrological processes determine the vegetation composition, patterns and processes in desert regions. The hydrological processes can be altered by vegetation succession. In this paper, we review the major advances in ecohydrological research and their potential impact on plant-water relations in revegetated desert communities. The major advances in ecohydrological research over the past 50 years in desert areas were analyzed using a case study that investigated the long-term ecosystem effects of sand-binding vegetation in the Tengger Desert. Key challenges and opportunities for ecohydrology research in the future are also discussed in the context of the major scientific issues affecting sand binding vegetation.

sand binding vegetation pattern and process, water balance, hydrological processes in desert areas, biological soil crusts, stability of artificial vegetation

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The wind-blown sand disaster areas in China are mainly restricted to a well-defined region (longitude 75°–125° and latitude 35°–50°) and include extreme drought, arid, semi-arid and sub-humid areas in various bio-climatic zones. The sandlands and the farming-pastoral ecotone in eastern China, where annual precipitation is more than 250 mm and the desert oasis, desert and desert steppe transition regions to the west of the Helan Mountain, where annual precipitation is less than 200 mm, are the regions most seriously affected by desertification and sand hazards [1]. They were also the key areas for non-irrigated vegetation construction and for ecological barrier building in China [2].

In order to effectively control sand storms and soil erosion and prevent further expansion of desertified land, the government has launched a number of major ecological construction projects, such as the Green Wall Shelterbelt

Forest Program, Returning Farmland to Forest and the Tianjin-Beijing Sandstorm Source Control Program [3]. Artificial vegetation construction has made remarkable progress over the last 50 years and has effectively prevented further desertification and promoted local habitat restoration. However, there were a number of problems in practice, both in the eastern sandlands, with their large precipitation rates, and in the desert areas to the west of the Helan Mountain where precipitation rates are lower. For example, in the desert area, the groundwater was declining and the sand-binding vegetation had died in some regions, which directly influenced the sustainability of the ecological restoration that had taken place and the sand-binding efficiency of the vegetation.

Previous studies showed that soil water was the major driving force in shaping the vegetation patterns and processes in desert areas [4,5] and other ecological process, such as plant growth, vegetation succession and the land-

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scape variability, were also determined by hydrological processes. Land desertification and soil erosion have also been shown to be regulated by sand-binding vegetation. Eco-hydrological processes and their feedback mechanisms were identified as the main problems affecting the restoration and reconstruction of some ecological engineering projects in arid regions [6,7]. Since the 1950s, as soon as the vegetation protective system was established along the Baotou-Lanzhou railway in the sand dune area, Chinese researchers began to study the water cycle and water balance of this sand-binding vegetation system [8] and met with considerable success [9,10]. This long-term positioning research provided valuable information about the eco-hydrological processes controlling the plant-soil system, the feedback mechanisms and vegetation stability in desert areas and has contributed to the strategy used to construct the sand-binding vegetation system over 50 years and will do so in the future. In this paper, based on over 50 years of long-term monitoring and study at the Shapotou Desert Research and Experimental Station on the southeast edge of the Tengger Desert, the authors analyzed and reviewed the major advances in a number of areas of eco-hydrological research and their impacts on the strategies used to restore sand-binding vegetation communities. This paper also proposes new areas of research for ecohydrological studies in the future. They aim to promote the theoretical studies of ecology and hydrology in arid zones and to meet the practical needs of ecological construction and sand hazard mitigation in desert regions.

1 Hydrological processes affecting the vegetation-soil system in desert areas

1.1 Rainfall interception and redistribution by sand-binding shrubs

Precipitation, as the sole source of water replenishment in the Tengger Desert, plays an important role in sustaining the desert ecosystem, and determines the mass transfer process in the soil-vegetation-atmosphere transfer (SVAT). Canopy interception directly affects the hydrological processes in the vegetation-soil system and is one of the key hydrological factors that determine water balance. Long-term continuous monitoring revealed that the interception loss by different types of shrub canopies varied between 0.7 and 1.1 mm, and the relationship between canopy interception, precipitation and precipitation intensity could be described by exponential equations. However, when the rainfall intensity increased to 40 mm d^{-1} , interception losses were nearly constant and the thresholds for the interception rate were about 0.2–0.3 [11,12]. Interception losses were also significantly affected by the canopy structure, canopy size and leaf area index of the different types of shrubs and losses became greater as you moved nearer to the trunk. The interception to precipitation ratio for *Caragana korshinskii*

showed a significant positive correlation with the canopy volume and leaf area index, but this was not the case for *Artemisia ordosica*. The minimum, the optimum and the maximum canopy water storage values and the throughfall coefficient for *C. korshinskii* were 0.46 mm, 0.68 mm, 4.94 mm and 0.47 respectively, while values for *A. ordosica* were 0.38 mm, 0.52 mm, 1.01 mm and 0.62, respectively. The interception losses by *A. ordosica* and *C. korshinskii* accounted for 15% and 27% of the precipitation on a crown area basis and 6% and 11% of the precipitation on a ground area basis [12,13]. The interception losses were less than those in the Chihuahuah and Negev deserts, where the interception loss accounted for 10%–60% of the rainfall [14–18], mainly due to the sparse shrub canopy structure and lower leaf area index. Therefore, with regards to rainfall interception, species with relatively sparse stems and branches should be selected as potential sand-binding species [12,13].

Part of the plant canopy interception-water and some nutrients could also be transported via stem flow directly to the roots. Research has shown that 5%–10% of the precipitation could be collected by stemflow and stemflow by desert shrubs may have distributed the precipitation to the deep soil layers by preferential flow along root channels, which may have stopped a decline in the soil water levels [19]. Stemflow by *C. korshinskii* accounted for 69% of the annual rainfall volume, Around 2.2 mm precipitation was necessary to generate stemflow in the shrub stand which meant that stemflow occurred in 34% of the rain events that happened over the year. Stemflow accounted for 8% of gross precipitation and the average funneling ratio was as high as 90 [20].

1.2 Influences of BSC on various hydrological processes

As plant succession proceeded in the sand-binding vegetation-soil system, a succession of biological soil crusts (BSCs) formed on the surface of the sand dunes, changing from cyanobacteria crusts to mixed (green algae and diatoms) algal crusts, to lichen crusts and finally to moss crusts as time progressed. However, the ecological and hydrological functions of the crusts differed at different successional stages, and these were related to their different hydrological and physical properties of the different crusts [12,21–23]. As the BSC developed, the BSC and the underlying soil layers thickened, the soil bulk density decreased and the soil water-holding capacity increased. Therefore, the water-holding capacity of soils with different types of crusts was expected to increase in the following order: moss crusts > lichen crusts > algae crusts > cyanobacteria crusts [24]. The formation and development of BSCs also correlated with topography as the water holding capacity of the moss crusts that dominated the windward and hollow areas was significantly higher than that of the algae crusts, which mainly covered the leeward and crest areas [7,21–23,25–27].

Moreover, the surface soil hydraulic conductivity was also affected by the different soil crusts. The saturated hydraulic conductivity rate and the unsaturated hydraulic conductivity rate near saturation (soil water potential >-0.01 MPa) of the surface soils covered by BSCs were a magnitude lower than the values for moving sand and moss crusts, which, in turn, were greater than algae crust values. However in dry conditions, the unsaturated hydraulic conductivity (soil water potential <-0.01 MPa) rose as the number of sand-fixed years increased [28,29]. The special hydrological and physical characteristics of BSC improved and promoted the soil microhabitats in desert areas and increased water holding capacity. The higher unsaturated hydraulic conductivity under low soil matric potential conditions could improve soil water availability in the shallow layers, which would improve the survival rates of some shallow rooted shrubs and herbs and small soil animals in the sand-binding vegetation communities [20,30–32]. It may even lead to an increase in population size.

BSCs may significantly alter rainfall infiltration and soil water redistribution because they intercept precipitation and, under certain conditions, could further decrease water replenishment of the deeper soil layers [10,28,31]. Specifically, the reduction in infiltration in response to BSCs occurred in the following order: moss crust $>$ lichen crust $>$ algae crust. There were no significant differences among crusts when rainfall was less than 5 mm or greater than 10 mm. Moreover, the topsoil water contents were highly correlated with infiltration depth. The presence of BSCs significantly increased topsoil water content when the one-off rainfall exceeded 5 mm, especially when the topsoil was covered by moss crust. However, there were no significant increases in topsoil water content with increasing rainfall [7]. Li et al. [33] used the Limburg Soil Erosion Model to analyze topographic effects on BSCs in the sand-binding dunes. They showed that runoff was greater on leeward slopes and these were covered mainly by algal crusts, whereas drier windward slopes were covered with moss crusts. The results of experiments and simulations undertaken by Li et al. [25,33] and Wang et al. [29] suggested that the influence of BSCs on rainfall infiltration depended primarily on the intensity of the rainfall, regional rainfall levels, the physical and chemical properties of the soil matrix under the crust and cryptogam composition. This comprehensive assessment resolved an international debate that had been ongoing between scientists.

The influence of different types of BSCs on surface evaporation also varied. Laboratory simulations revealed that fully saturated soil samples with well-developed crusts had a higher evaporation rates compared to samples without crusts. There were significant differences between the evaporation process occurring in the soil samples with a crust and in the control samples, which did not have a BSC. The evaporation rate was relatively stable during the early stages of evaporation (the stable evaporation rate stage),

meaning that the presence of BSCs improved effective evaporation. During the later stages, however, the evaporation rate declined, indicating that BSCs eventually restricted evaporation [23,34,35]. Field experiments showed that the presence of BSCs reduced evaporation in topsoil after small rainfall events (when the precipitation volumes were <7.5 mm and < 5 mm for moss and algal crusts, respectively). However, during large precipitation events (>10 mm), the situation was reversed. As 60% of the precipitation events produce less than 5 mm of rain in the Shapotou region, it is possible to conclude that the formation of BSCs in the sand-binding dunes actually reduces soil evaporation [36,37]. The presence of BSCs prolonged the residence time of water in the shallow soil layer. This was particularly important during drought stress because any increase in the soil water levels will facilitate plant germination, establishment and survival in the shallow soil layers [11,26,38–43]. This means that soil water levels are an important factor driving the biogeochemical cycles in the soil-vegetation system [27].

Dew deposition has also been found to be an important factor linking the crusts to hydrological processes [36,44, 45]. In the desert, dew serves as a precious water resource for cryptogams in the crusts as well as for other small animals. The presence of dew can activate the cryptogams, which starts a short period of photosynthesis and initiates nitrogen-fixation processes in organisms such as cyanobacteria and a number of lichen species. The amount of dew trapped by surfaces with crusts increased as the BSC development stages progressed. Due to the presence of a large amount of organic material in BSCs, dew depositions on moss crusts and algae crusts were greater than that found on physical crusts. The amounts deposited averaged about 0.15 mm d^{-1} and reached a maximum of nearly 0.5 mm d^{-1} . Long-term monitoring revealed dew formed on 74% of the total observation days. The dew on the sand, the physical crusts and the BSC surfaces amounted to 15.9%, 22.9% and 37.9%, respectively of the total precipitation over a given period [45]. BSCs in arid zones, especially those zones with annual precipitation of less than 200 mm, had an important ecohydrological influence on the shallow soil water content and led to profound changes in the original water balance in the desert area [46].

In general, the formation of BSCs after the establishment of sand-binding vegetation profoundly changed hydrological processes, such as precipitation infiltration, soil evaporation, dew deposition and the water balance of the original soil-vegetation system because the hydro-physical characteristics of stable soils are different from moving sand. The changes to the composition, structure and function of the sand-binding vegetation explained the decline in the sand-binding vegetation and also revealed the basic law of sand-binding vegetation evolution in China, namely that zonal vegetation succession is specific to individual bioclimates [10].

1.3 Evapotranspiration and water balance for sand-binding vegetation at different spatial scales

The transpiration rate and water use efficiency of *A. ordosica* leaves were significantly higher than those of *C. korshinskii* when they were grown in a monoculture. The transpiration rates for both species were lower when the plants were grown in a mixed plantation, being around 80% and 60% of the rates recorded in the monocultures stand for *C. korshinskii* and *A. ordosica*, respectively [47,48]. When drought stress occurred, *A. ordosica* showed a greater drop in transpiration rate than *C. korshinskii* because *C. korshinskii* adapted to water stress mainly by osmotic adjustment whereas the response by *A. ordosica* was characterized by the need to maintain turgor. The water adjustment capacity of *A. ordosica* was higher than that of *C. korshinskii*, which meant that the stomatal adjustment capacity of *A. ordosica* was higher than that of *C. korshinskii* [47–50].

At the individual level, *C. korshinskii* had a fast sap flow velocity because its crown size and leaf area index were higher than those of *A. ordosica*. In the growing season, the sap flow velocity of *C. korshinskii* was determined by solar radiation and relative humidity, but the sap flow velocity of *A. ordosica* was driven by solar radiation, soil temperature and moisture. The transpiration rate of *A. ordosica* was vulnerable to soil hydro-thermal factors, partly because the root system distribution of *A. ordosica* was shallower than that of *C. korshinskii*. Furthermore, the sap flow velocities of *C. korshinskii* and *A. ordosica* had a significant linear relationship with the crop reference evapotranspiration volume. Moreover, the initial and the maximum stem sap flow velocities of these two plants occurred much earlier than the leaf transpiration rate and this was probably due to the plants' buffer response to soil drought [51,52]. A study by Wang et al. [53] on soil water dynamics at a revegetated *C. korshinskii* stand showed that the soil water contents of root dense layers generally decreased, but had a diurnal trend of falling in the daytime and rising at night. Psammophyte also had a maximum leaf water potential just before dawn and then decreased during the daytime before rising again at dusk [54,55], which verified the interactive relationship between the water-absorption and soil water dynamics in plants.

At the community level, due to water utilization by sand-binding vegetation and the formation of BSCs on dune surfaces, the water balance pattern of the original sparsely covered natural vegetation-soil system eventually changed [9,10]. Using a large weight lysimeter and after more than 10 years' observations, the results showed that evapotranspiration (ET) in the sand-binding vegetation area amounted to 90% of the precipitation and there was no water recharge of the soil below 2.2 m. However, evaporation in the bare sand amounted to 70.5% of the total precipitation and water recharge in the deep layers amounted to 12.6% of the total precipitation. During the growing season, in a rainy year,

daily ET rates for *A. ordosica* and *C. korshinskii* were the same, i.e. 0.86 and 0.87 mm d⁻¹, respectively. In a dry year, the daily ET rate of *A. ordosica* decreased to 0.68 mm d⁻¹, but that of *C. korshinskii* remained at around 0.80 mm d⁻¹. Comparing the monthly ETs of *A. ordosica* and *C. korshinskii* showed that *C. korshinskii* had a high ET in a month with high precipitation during a dry year. This suggested that the *C. korshinskii* stand may have had a larger soil water storage capacity than the *A. ordosica* stand, which had a low monthly ET. These results indicated that different plant species have different water utilizing mechanisms, that ET varies with annual precipitation and that there are significant differences between species. The daily average and maximum evaporation rates in bare sand were almost half the rates found in the sand-binding plantation areas [56]. Over 30 continuous non-rain days, the volumetric soil water content (SWC) in the *C. korshinskii* stand decreased from 1.8% to 0.5% or less and the average ET rate came down from a previous 2.2 to 0.6 mm d⁻¹. The volumetric SWC in the *A. ordosica* stand varied by about 1% and the average ET rate fell from 1.8 to 0.9 mm d⁻¹, which were smaller decreases than were recorded in the *C. korshinskii* stand. The SWC in bare sand remained above 2%, the average ET rate decreased from 1.1 to 0.4 mm d⁻¹, which was about 60% of the levels seen in the shrub stands. The deep drainage from the bare sand was 113.4 mm per year and accounted for 40.5% of precipitation and the drainage rate averaged 0.63 mm d⁻¹ [54]. All these observations revealed why the sand dune covered with sparse natural vegetation has a water storage capability and why small areas of desert wetland landscape appear in hollows. Sand-binding vegetation could utilize this water by infiltration, change the water into biomass and decrease percolation losses in the deep soil layer [9,10]. However, from another perspective, revegetation influenced the original water cycle and weakened the linkage between dunes and other ecosystems, such as low wetland and grassland. Very large plantations could even lead to the degradation of low wetland and grassland in the vicinity, which is an important conclusion we made after reviewing more than 50 years of research on ecohydrological processes in the Shapotou region.

Observations on the water balance components in the sand-binding area, namely plant transpiration, soil evaporation, canopy interception, deep percolation and soil water storage in a wet year, a normal year and a dry year showed that decreased precipitation during the growing season also led to reductions in canopy interception, transpiration, evaporation and ET. Canopy interception and transpiration were higher in the mixed plantations compared to the monoculture stand, but evaporation and ET showed no significant differences. Even in a wet year, *C. korshinskii* in the monoculture stand and the mixed plantation showed an over consumption of soil water. But *A. ordosica* showed a water deficit in normal and dry years. In comparison with the bare sand, no percolation occurred in the revegetated areas. The

ratio of transpiration to ET decreased as annual precipitation declined, while the ratio of evaporation to ET increased. Drought stress decreased transpiration and ET and increased precipitation loss due to evaporation, which, in turn, led to a large decrease in available water for plant growth [46]. After the re-establishment of vegetation in the desert, the soil water was used by plant growth and so no water percolation occurred [53], which meant that the original water balance in the dune was replaced by a new water balance [10,11,26,27,57,58]. The change in water balance directly influenced the composition, coverage and biomass of the vegetation and thus drove vegetation succession [9,10]. These results may help improve the establishment of sand-binding plantations and subsequent ecological management.

1.4 Temporal-spatial pattern of soil water content in sand-binding dunes

Long-term monitoring and research on the desertification of grassland that receives less than 200 mm of annual precipitation showed that after the re-establishment of vegetation, SWC in the 0–3.0 m layer decreased from 3.0%–3.5% at the beginning to about 1.5% after 10 years and reached 1.2% after 40 years. Average monthly soil water storage values for many years was 67.9 mm, which was nearly half that of the moving sand (136.6 mm). In the early stages, precipitation influenced SWC both in the shallow soil layer (0–0.4 m) and in the deep layer (0.4–3.0 cm). However, 10 years after revegetation, with the shallow soil water-holding capacity increasing to 80% and soil water availability increasing, SWC in the shallow layer was, instead, significantly related to the temporal distribution of precipitation. However, the SWC in the deep layer decreased from 4%–5% to 1% and had no significant relationship with the temporal distribution of precipitation [10,59]. The SWC below 60 cm soil depth was higher in the summer and lower in the winter, which was the opposite trend to precipitation. This indicated that plant water consumption by ET was higher than the precipitation recharge volume during the growing season [60].

The BSC and sub-soil layer depths increased as the years following revegetation increased, which led to an improvement in soil water availability in the topsoil [7]. Due to the low water-holding capacity of moving sand dunes, precipitation easily infiltrated into the deep soil layer and led to a higher SWC, which was close to field capacity below 2 m depth. After 16 years of vegetation establishment, the shrub roots had become concentrated in the 1–3 m soil layer where there was aridification due to plant water uptake and no rainwater recharging. However, the 0–1 m soil layer could receive part of precipitation due to thin BSC layer. After 34 years, a dry sand layer occurred below 0.2 m soil depth where SWC was close to the wilting point. After 42 years, the whole layer had almost no available soil water and SWC was highest at 0.1 m depth due to the difference

in soil texture between sand and BSCs [61,62]. The different sand-binding dune locations and the variation in the types of BSC covering them led to variability in SWC in the top soil layers [63]. SWC increased in the hollows and on the leeward slopes and windward slopes but the variability in SWC in the hollows was lower than in the soil on the leeward and windward slopes. Geomorphological features strongly influenced the SWC spatial distribution of the leeward and windward topsoils and subsoils. However, the SWC spatial distribution of windward topsoils was determined mainly by environmental features such as wind [64]. When deep-rooted shrub coverage decreased to <10%, the SWC at the deeper soil depths (1.5–3.0 m) was stable and improved compared to shallower soil depths [7,46].

1.5 Relationship dynamics between hydrological processes, vegetation patterns and precipitation in desert regions

Because of the complex underlying surfaces in arid desert regions and land surface processes, the SPAC water and energy transfer model and parameterization were developed or further improved [65–68]. But the SVAT process was very complex due to the unique, sparse vegetation cover in arid and semiarid zones [69–71]. Compared with the continuous coverage seen in forests and on cropland, the soil heterogeneity and vegetation boundary differences in the desert made the parameters in the SPAC model very large and hard to obtain. In addition, the fluctuation and stochastic features of precipitation led to large fluctuations in the water cycle. Because of these limitations, researchers in China often focused on a single-process in the SPAC system, such as water infiltration in desert regions [72–74].

The relationships between rainfall infiltration, water redistribution and the land surface of the revegetated desert areas were identified. The mathematical models for the rate and the amount of rainfall infiltration and the total amount of infiltration and precipitation were established by Li et al. [10,59]. Based on the macroscopic model, water data from different soil depths and information about different plant root distributions, Huang [75] created root water uptake models for *C. korshinskii* and *A. ordosica*, and then used them to confirm the root water uptake rate and its relationship with a number of influencing factors using numerical simulation. Empirical models of the ET for different vegetation cover with variable precipitation over the same period were established by Wang et al. [59,75].

The transpiration rates of different species of xerophytic shrubs and sand-binding shrubs were measured using the porometer stem heat balance technique and the auto-weighing lysimeter method during various growing seasons. The results were then scaled up from the leaf to the population level based on the effective coverage and the leaf area index. Linear equations for transpiration rate were obtained using the data obtained from the monoculture and mixed

stand observations and then the transpiration results were scaled up from population to community level. These scaled up results were compared with the ETs calculated by the water balance method and soil evaporation by micro-lysimeter and these comparisons confirmed the feasibility of scaling [47,48,51,76].

Highly organized vegetation patterns can be found in arid desert regions. In recent years, a number of authors have investigated the processes underlying vegetation pattern formation, such as the Tiger or Banded vegetation landscapes. This became an important research topic in theoretical ecology and experimental ecology [77,78] and was one of the theoretical bases for vegetation reconstruction in desert regions [79]. The annual precipitation series from 1955 to 2009 for the Shapotou station was analyzed by a multi-time scale using the Morlet wavelet. The results showed that the precipitation changes over 10–12 and 25–27 years were greater in the Shapotou area, which was consistent with vegetation succession and rainfall periodic oscillations. This verified the importance of precipitation on vegetation succession in desert areas [80]. Based on these results, it was possible to create deterministic differential equations that described the vegetation and soil water dynamics. Numerical simulation, based on the multi-year average precipitation conditions ($P = 0.25 \text{ mm d}^{-1}$), revealed that the vegetation pattern would change within a certain rainfall range and showed that vegetation would have a mainly patchy distribution in the Shapotou area rather than a uniform distribution [75].

2 Vegetation patterns and processes in the sand-binding areas

2.1 Natural succession in vegetation composition, structure, and function in the sand-binding areas

With more than 50 years of experience in using revegetation to stabilize moving sand dunes in China, a large number of practical lessons have been learned [81]. In the beginning, the main way to stabilize moving sand dunes was to choose relatively few species and plant them at high densities. The application of this method over large areas resulted in the lowering of groundwater levels and degradation of the vegetation, even in the eastern sandlands where precipitation is 300–450 mm [82]. However, better species selection and revegetation configuration could maintain the stable function and structure of the newly planted vegetation in arid desert regions where precipitation was only 100–200 mm [11,25]. The results collected from long-term observation over 56 years of a sand-binding plantation that was planted to protect the Baotou-Lanzhou railway section, showed that plant coverage increased from 10% to 35% 10 years after the re-establishment of vegetation using different types of species and at different densities and that the dune's surface had been stabilized. However, coverage gradually declined

to 10% after 50 years [79] and a stable community of sand-binding vegetation had appeared. This showed that the revegetated areas had gained the ability to self-regulate and the dominant species, such as *C. korshinskii* and *A. ordosica* could form stable populations [83]. What's more, some annual herbs inhabited and reproduced on the dune surface [59]. The coverage and the number of annual species increased from 1%–2% and two species during the initial stage, to 30%–40% and 16 species after 50 years. Some perennial herbs also appeared in the sand-binding dunes. Moreover, cryptogams appeared in the sand-binding dunes and the species number increased from five species of cyanobacteria after 5 years to 24 species of cyanobacteria, five species of lichen and 10 species of moss after 50 years [22,26,27].

The original single shrub synusium structure evolved into a multi-synusium, mixed community [21]. With regards to vegetation functional group composition, the sparsely covered sand-binding shrubs remained but were joined by an increasing number of C_4 plants and cryptogams [63]. C_4 plants diversified the ways that plants used water in the desert and cryptogams became an important resource and provider of soil carbon in the sand-binding areas [84,85]. Carbon sequestration by BSCs meant that nitrogen fixation by cyanobacteria and lichens could take place. This increased the nitrogen content in the sandy soils, which was then available for use by the herbs [86]. BSCs were also able to stabilize the sand surface efficiently and stop dust being blown into the atmosphere above the sand-binding dunes [59].

2.2 Maintenance of diversity and vegetation patterns in desert regions

Understanding the mechanism behind the maintenance of natural vegetation composition diversity in desert areas was important if the construction of sand-binding vegetation was to be sustainable [87]. Shrubs were the dominant plant life forms in arid desert regions in China [88,89] and the existing shrub community was an integral part of the ecological restoration of degraded desert systems [90]. Compared to herbs, shrubs are more tolerant of and adapt better to wind erosion, sand burial and other abiotic factors, such as drought stress and grazing disturbance. Furthermore, they have relatively small soil nutrient requirements [21]. In contrast, herb growth is restricted by overgrazing, sand burial and dry climate conditions. For this reason, during the initial stages of sand-binding vegetation establishment, xerophytic shrubs, not herbs, should be chosen [91].

Shrub species richness patterns not only reflected the effects of climate and environmental factors in arid desert/sandy areas, but also indicated the long-term combined effects of human activities, such as overgrazing, and ecological processes [92]. Studies on desert/sand shrub vegetation diversity and the ways in which it is sustained in the Alashan Desert, to west of the Helan Mountain, showed that

SWC in the deep soil layer (0.4–3 m) played a decisive role in shrub species richness and abundance patterns [92]. The results did not support the hypothesis that soil texture determines woody plant diversity patterns in semiarid areas [93]. The shallow SWC (0–0.4 m) influenced the richness and diversity of herbs, especially annual, ephemeral and semi-ephemeral plants [94].

After recording more than 50 years of succession in the sand-binding vegetation in the Shapotou area, the dominant species gradually evolved from artificial woody plants into herb based natural plant communities. The spatial pattern of the vegetation changed from an artificial homogeneous distribution to a patchy distribution, similar to the vegetation pattern seen in the steppe desert found on the southeastern edge of the Tengger Desert [27,64].

Cryptogams, an important component of the desert ecosystem and sandlands, stabilized the dune surface and created a suitable habitat for lower vascular plants [59]. The BSC development was an important feature of desert/sandy vegetation and distinguished it from other vegetation types. Li et al. [63] discussed how BSC cryptogam diversity was maintained in arid areas and thought that small scale changes in water levels caused by complex micro-geomorphological processes was the key factor behind maintaining diversity and small scale changes in soil physicochemical and biological properties, especially soil texture, determined species diversity and group differences. At a regional scale, precipitation gradients determined BSC species distribution and coverage. For instance, Horqin and Mu's sandlands, with more than 300 mm of annual precipitation were suitable for BSC development that was dominated by moss. In stabilized sand dunes with less than 200 mm of annual precipitation, lichen developed as the dominant crust species and cyanobacteria was the dominant crust species in disturbed desert areas [63].

Soil water was confirmed as the main determining factor for desert vegetation patterns and processes. Other hydrological factors, such as precipitation and groundwater, were only used by vegetation when they were transformed into soil water. Therefore, the quantity and quality of desert soil water are the most important components in desert vegetation construction.

2.3 Temporal-spatial patterns for sand-binding revegetation

BSC changed the shallow SWC by increasing condensed water capture and by altering evaporation by changing the soil surface structure. These changes affected the sand-binding vegetation responses to water variation at the composition, structure and function levels. Shallow rooted herbs became a larger part of the vegetation composition (recording increases in species richness and abundance, cover and biomass), whereas deep rooted woody plants declined (recording decreases in coverage and biomass). C_4 plants also

increased in number and cover [7].

Long-term ecological studies on sand-binding vegetation-soil systems in the Shapotou area showed that BSCs directly affected the spatial pattern of sand-binding vegetation [21,26,57,59,95]. BSCs, especially complete lichen and moss crusts, reduced the potential for seeds to be washed down into the soil, which decreased the soil seed bank in the areas covered by crusts. Because of wind erosion in the Shapotou area, mature seeds often gathered under the shrub crowns or around the burrows of ants and soil animals [33], so seed germination declined in areas covered by BSCs [38]. Even if seeds on the crust surface did germinate after precipitation events, they often died quickly due to rapid water loss before the roots were able to enter the soil [26]. Therefore, the BSCs ultimately led to the patchy spatial distribution of sand-binding vegetation. It was also one of the most important factors driving the change from a sand-binding vegetation pattern to a natural vegetation pattern, namely a mosaic distribution of vascular plants and BSCs.

2.4 Characteristics and theoretical modeling of vegetation restoration

Sand storms are a very serious hazard in desert steppe regions. Sand burial or local dune activation often means that the native vegetation landscape is replaced by a primary moving sand landscape [83,95]. The re-establishment of vegetation is one of the most effective methods available for ecological restoration [96,97]. Studies have shown that soil property (physical, chemical and biological properties) heterogeneity rose as vegetation degradation increased in desert steppe. When the heterogeneity reached a certain level, it became difficult to restore the soil habitat using natural processes (such as natural recovery by preventing grazing or enclosing land). The re-establishment of vegetation initially increased soil property heterogeneity, but as time progressed, soil property heterogeneity declined. Therefore vegetation tended to be in a dynamic but steady state. These results indicated that soil habitat restoration relied on vegetation system recovery. A decrease in soil property heterogeneity was an indication that the system was recovering, whereas increasing heterogeneity indicated that the system was degenerating [80]. This theoretical model explained the evolutionary mechanism behind the vegetation distribution over nearly 3 million ha desert areas in China and has important implications for vegetation construction and for the ecological management of the existing vegetation in desert regions [6,24].

Li et al. [25] simulated and predicted the recovery process and rate for soil properties in the vegetation-soil system around the southeastern edge of the Tengger Desert. The results showed that after 50 years of sand-binding vegetation establishment in the moving sand dune, most of the topsoil properties (parameters) could be restored to 60% of the natural vegetation area (desert steppe vegetation before

being covered by moving sand dunes). It would require 70–245 years for the clay content, topsoil water content, topsoil crust thickness and soil bulk density to return to the natural vegetation soil property levels. Soil properties, such as the percentage of sand and silt in the soil, CaCO_3 , organic carbon and electrical conductivity, could only return to 20%–40% of the natural vegetation values. During 50 years of recovery, the speed of soil property recovery was faster during the early stages of recovery (1–15 years) and slower during the latter recovery stages (40–50 years). The C/N ratio showed the fastest rate of recovery (reaching 90% of the model curve asymptote value after 18 years) and soil bulk density was the slowest to recover (245 years) [24]. Soil moisture conditions needed at least 120 years to return to the shallow soil moisture conditions seen under natural vegetation. However, following sand burial, vegetation construction promoted the water-holding capacity of the topsoil, but after 50 years it had only recovered to 79% of that seen under the natural vegetation. For some soil properties, such as the percentage content of sand, silt and organic carbon, even if after a much longer period than 50 years, the model showed that they would still not reach the levels seen under the natural vegetation. These projected results indicated that once the soil habitat was destroyed, the ecological restoration of soil properties in arid desert regions was a very long process and very difficult and the decline in some soil properties was irreversible [6, 24].

3 Response of sand-binding vegetation to hydrological processes

3.1 Morphological adjustment and the regulation threshold of vegetation to soil water variation

Morphological adjustment was the primary means by which plants adapted to water change at the individual level. For example, *Tamarix ramosissima* and *Haloxylon persicum* in the Gurbantunggut Desert showed different water use strategies. The root architecture of the former means that its survival depends on groundwater and the root architecture of the latter means that it directly relies on atmospheric precipitation for survival [98]. But when drought occurred, *H. persicum* adjusted its root morphology so that it could use groundwater [99]. Sand-binding shrubs were able to make morphological adjustments at any time in order to adapt to seasonal drought. *C. korshinskii* survived during the dry period mainly by losing its leaves and by entering dormancy and ceasing growth. *A. ordosica* adapted to drought by losing some or all parts of the plant and storing a large number of seeds in the soil seed bank, which would germinate into new plants when conditions improved. Annual plants were the opportunists in the sand-binding dunes. They only germinated during the rainy season and quickly completed their life cycles [14,27,100,101].

The morphological adjustments to plant roots took two

forms: changes in vertical distribution and changes in seasonal dynamics. Compared to *A. ordosica*, *C. korshinskii* had a deeper root distribution and could use deep soil water through the dry periods when precipitation did not supply the deep soil. *A. ordosica* had a greater proportion of its root distribution in the shallow soil layers and was therefore limited to using precipitation [13,29,102]. The seasonal dynamics of fine roots were significantly influenced by SWC. SWC in the 0–1 m soil layer had two peaks every year, which coincided with two rapid sand-binding plant root growth periods. But the root peaks would lag behind those of SWC by about one month and the maximum soil water consumption periods corresponded to the maximum root growth periods. If SWC in the stand was less than 2.75% (*A. ordosica*) or 2.60% (*C. korshinskii*), then the root growth peaks would appear one month later, but if SWC was higher, then there were no root growth peaks. This indicated that a certain SWC value may be a threshold value for fine root growth and may determine the ecological strategies followed by plants. If SWC is higher than the threshold, the plants do not need a huge root system to meet its water demand and guarantee its aboveground biomass production, so the root-shoot ratio will be smaller. When SWC is lower than this threshold, the plants are water stressed and need a large root system so that they can obtain sufficient water to maintain normal physiological activities. This study revealed the response of the desert plant roots to water variation and the ecological countermeasures taken by them [29,102]. The ecological mechanism adapted by many desert plants seemed to be to produce large root systems [6].

3.2 Population survival strategies used by sand-binding dominant plants

Population survival strategy is an important theoretical issue in modern ecology. The harsh desert habitat has forced plants to adapt [103]. The growth pattern and dynamics of *A. ordosica* in the sand-binding areas were a consequence of long-term adaptation to the lack of soil water. Research on the static life table of *A. ordosica* populations in two sample plots (plots revegetated in 1981 and 1964) located on the southeast edge of the Tengger Desert showed that the survival curves of the *A. ordosica* population in the 1981 revegetated plot was a Deevey II type, namely showing population growth, while the *A. ordosica* population changes in the 1964 revegetated plot was unclear. The survival curves indicated that the populations were either stable, growing or declining depending on the total number of plants, the reproduction rate and the survival rate, respectively [104,105]. They indicated that as the stabilization time in the sand-binding area increased, the evolutionary trend of the population showed a trend from fast growing to slow growing and then decline, leading finally to a smaller population than had existed previously. This pattern could be mainly attributed to changes in total biomass, reproductive biomass,

capitula number and reproductive rates. The capitula allocation showed a decreasing trend due to the deterioration in the soil water conditions [106].

During sand-binding vegetation succession, annuals might replace shrubs, such as *A. ordosica* and *C. korshinski*, and become the dominant species [104,107]. As the length of time that the sand had been fixed for increased and with the improvement in habitat conditions, annuals were able to use more resources and energy for reproduction, leading to an increase in population size. Whereas in the dunes, where the sand stabilization period was relatively short, more resources and energy were used for vegetative growth by annuals so that they could withstand adverse soil water conditions [108]. For example, *Eragrostis poaeoides* was the dominant species in the sand-binding herb synusium. The main adaption strategy to the desert environment was seed dormancy. In the growing season, only part of the seed bank germinated and the rest of the seed was saved for the next growing season or longer. When comparing sand-binding dunes of different ages, individual size, propagule size and sexual reproduction allocation were significantly different, while ground vegetative biomass, stem weight, leaf number and leaf weight were not significantly different [109]. Over a short time scale, the dynamics of the herb synusium correlated closely with precipitation. After large precipitation events, many annual seeds germinated. However, when drought conditions occurred again, the annual plant populations began to decrease, with sharp decreases recorded for *E. poaeoides* and *Chloris virgata* populations, but only slight reductions recorded for the *Setaria viridis*, *Bassia dasyphylla* and *Corispermum declinatum* populations. However, because precipitation increased during the later stages of the growing season, each species in the synusium could complete its life cycle [110].

3.3 Soil-plant system evolution

After stabilization of the mobile dunes using sand-fixing plants, a stable sediment environment formed on the dune surfaces. Around 350–440 kg hm⁻² a⁻¹ of deadwood and defoliation material and 4866 kg hm⁻² a⁻¹ of dustfall entered the BSC layer. The thickness of the BSC layer varied from 3 to 15 cm on the dunes that had been stabilized for 20 years due to different sediment environments. The soil profile changed from simple soil aeolian sand deposition to the dualistic profile structure of a BSC layer underlain by aeolian sand. The re-establishment of vegetation on dune surfaces meant that *Ari-Sandic Entisols* (aeolian sand soil) developed into *Hap-Orthic Aridisols* (a zonal soil) and calcium carbonate sediments formed on leeward slopes with deep, crusted layers [62]. The soil profile differences, the formation of a BSC layer and soil configuration transformations changed soil water-holding capacity, infiltration processes and the redistribution of precipitation. This meant that the vegetation had to adapt to the changing soil hydro-

logical environments over the long term [10,11,20,28,111].

Eight to 10 years after the re-establishment of vegetation, shrubs dominated the landscape and coverage quickly increased to more than 15%–25%. After 40 years, more than 14 species naturally occurred in the sand-stabilized dunes. However, the planted shrub coverage decreased to 6%–9% and herb coverage was three to four times greater than the shrubs. After 30 years, the natural vegetation was dominated by the herbaceous synusium, which covered 25%–30% of the area and replaced the sand-stabilized shrubs [10,57,58]. The herb vegetation provided suitable habitats for other species. After 46 years, 28 bird species, 50 insect species and 23 animal species were identified in the revegetated dunes. The significant change in species diversity verified, to a certain degree, that the vegetation evolved from simple sand-stabilized shrubs to steppe desert vegetation dominated by herbaceous synusium and cryptogams and also led to the transformation of the relatively barren dune environment into a desert ecosystem with a complex structure, composition and function [79].

3.4 Relationship between vegetation pattern and hydrological processes

Most desert or sand ecosystems are regulated and controlled by abiotic factors, especially by limited water, which means that the land cannot support large areas of relatively homogeneous and continuously distributed higher plants communities. Water movement, both run-on and run-off, and water redistribution between plant patches were used to model the source-sink relationships with material and energy flows [6,63]. In simulation experiments, 55% of the applied water became runoff on the BSC patches and was redistributed to the shrub patches. More than 75% of the sediments, 63% of the soil carbon, 74% of the nitrogen and 60% of the dissolved nutrients in the runoff from the BSC patches were delivered to shrub patches. During smaller precipitation events (with a rainfall intensity of 2.8 mm h⁻¹), in the BSC patches, 32.9% of the water became runoff, which delivered 37.1% of the total sediments, 30.3% of the total soil carbon, 48.3% of the total nitrogen and 30% of the dissolved nutrients to the shrub patches, compared to bigger precipitation events (with a rainfall intensity of 5.7 mm h⁻¹) where 18.9% of the water became runoff, which delivered 31.1% of the total sediments, 9.84% of the total soil carbon, 19.0% of the total nitrogen and 10% of the dissolved nutrients to the shrub patches [112].

The spatial distribution differences between BSCs were caused by long-term adaption to changes in the hydrological environment. On a small-scale, the changes in ground surface properties, such as various micro-geomorphological changes, e.g. changes in the size of desert shrub soil mounds, would effectively increase dustfall input and deposition onto the topsoil. On a medium-scale, the windward sides, leeward sides, crests and hollows of sand-stabilized

dunes were covered by different types of BSC. The four orientations of shrub mounds and the different topographies of the dunes produced significantly different BSC types and changed species diversity, coverage and biomass [7]. This led to a change in micro-climate conditions at the small and medium-scale, such as changes in shading, humidity, temperature and UV radiation intensity, etc. Furthermore, it resulted in changes to the composition, structure and the ecological functioning of BSC communities. Meanwhile, micro-geomorphology, through resource redistribution, such as redistributions of N, P, K nutrients and water, increased soil property heterogeneity. Dustfall input increased the percentage of silt and clay particles in the soil, the soil nutrient and carbon contents and the water-holding capacity. It also changed the soil physical, chemical and biological properties. These changes can account for the vegetation pattern at the micro-geomorphological scale [63].

4 Future research prospects

The plants used to revegetate the desert regions of China underwent considerable change according to some survival indices and biomass and coverage levels during the initial stages were maintained at relatively high levels. Today the vegetation has stabilized and is sustainable, especially with regards to composition, structure and function. The transformation shows that the ecohydrological processes in desert plant-soil systems gradually change and these changes have now been recognized. Considering the existing problems and the lack of vegetation in desert areas, the following topics need to be further researched.

4.1 Scaling up and down

Scaling up or down is always the most difficult part of the arid ecohydrological process. Because different researchers have worked at different scales, the results of their research are not always comparable. For example, morphological adjustment is the main way that plants adapt to water variation at the individual level. However at the community level, regeneration and succession is driven by variations in the water environment, which are determined by vegetation patterns and dynamics [11]. It is thus clear that the determining factor at one level may not be the determining factor at other levels, and the scaling often results in the loss of spatio-temporal data information. Some new research method applications, such as extrapolation and microform [113], RS and GIS techniques, isotope tracer, dendro-chronological dating and networking research across a number of scales may make scaling-up and down easier.

4.2 Ecohydrological effects of BSCs

BSCs are the major component in sand-stabilized dunes and have a vital role to play in arid ecohydrological processes

[114]. BSCs dominated by algae and lichen decreased precipitation infiltration and increased runoff, which benefitted vascular plant patches as they gained water and nutrients [115–117]. However, the effect of BSCs on hydrological processes is confused by underlying soil physiochemical properties, especially soil texture [118,119]. The difficulty is how to discriminate between the effects of BSCs and the underlying soil texture on hydrological processes, such as infiltration and runoff. Recently, an investigation found that the windward sides and the hollows in sand-stabilized dunes, 40 years after the re-establishment of vegetation, were mainly covered by moss crusts, while the leeward sides and the crests were dominated by algae crusts [7]. The topographical differences in BSCs may reinforce the topographical and hydrological processes, and further affect the vegetation patterns and processes in sand-stabilized dunes. It may be that polysaccharides secreted by algae prevent infiltration and thus increase runoff [120,121]. However the water transmitting functions of rhizoid and protonema mosses have been shown to improve infiltration [35,121]. We believe that the topographical differences in BSCs will change the hydrological and ecological processes in sand-stabilized dunes. Finally, the hydrological threshold levels and how they are affected by BSCs also need to be determined, which will provide useful information and suggestions for future studies and vegetation restoration projects.

4.3 Hydrological control of vegetation patterns and processes

The patch patterns of desert vegetation, namely tiger and banded patterns are the result of hydrological and ecological processes and display comparable stability under extreme drought and grazing pressure. Recently, scientists have focused on the direct and indirect influences vegetation patches and bare patches (or BSC patches) have on infiltration, runoff, erosion, soil water and productivity after precipitation events [122–124]. Furthermore, the influences of extreme precipitation events and extreme drought on vegetation pattern are key research fields for domestic and overseas scientists [125]. However, in the past these studies mostly concentrated on vegetation patterns at a certain stage in time, whereas there have been few long-term ecological investigations into the long term effects of hydrology on vegetation pattern dynamics. So future investigations should pay more attention to some major areas of hydrological research, such as the effect of long-term hydrological processes, especially variations in mutual transformation and flow in “rainwater-plant water-soil water-underground water”; the regeneration, survival and mortality of sand-fixed plant populations; the inter, intra and substitutional relations between annual plants species and cryptogams and the relationships between hydrological and ecological processes. Moreover, clarification of the eco-hydrological mechanism driving vegetation patterns and dynamics is needed if re-

vegetation practices are to be sustainable.

4.4 Building the eco-hydrological model

Ecological processes and hydrological processes interact closely with material and energy flows. Building an eco-hydrological model is a necessary and efficient way to measure eco-hydrological thresholds for vegetation stability and to predict future trends. Precipitation is vital for water replenishment in arid regions and is characteristic of strong spatio-temporal heterogeneity and randomness [126]. The randomness profoundly affects vegetation patterns and dynamics, is the core driving forces behind ecosystem succession and is the major reason why different plant function groups are able to co-exist [127]. In the past, research on plant-water relations concentrated on the composition of plant function groups and ecosystem productivity adaption to precipitation under set water conditions [128]. However, given the unique plant community patterns and hydrological processes in arid desert regions, scientists now prefer to consider the water response and feedback mechanisms in plants from stochastic eco-hydrological viewpoints. Some studies built a kinetic model and analyzed vegetation patterns and dynamics on the basis of the feedback between hydrological processes and vegetation [77,78,129,130] or interpreted the ecological pattern formation process in arid regions, as controlled by hydrology, using a conceptual model such as “Trigger–transmit–reserve–pulse” (TTRP) [122–124]. However, the former does not embody the stochastic attributes of precipitation, which is the best way to describe the hydrological characteristics in arid regions, while the latter was only a conceptual model. Hence, there is a need to create a stochastic hydrological model based on the actual conditions found in desert areas and to quantitatively describe the hydrological processes controlled by pulse precipitation. This can then be combined with the models for vegetation and patch dynamics. By doing so, an eco-hydrological model reflecting the responses of plants to water variation can be built that fits the pattern and dynamics of sand-fixed vegetation driven by water. The ecohydrological mechanisms behind sand-fixed community stability sustainability and succession could then be identified.

4.5 Sand-fixed vegetation stability, sustainability and ecosystem management measures

The ecological threshold for water resource utilization by sand-fixed vegetation should be determined through experimentation on natural vegetation. The influence and regulation thresholds for ecosystem management (such as by population adjustment, optimizing function group configurations and diversity restoration, plant-soil system recovery and stabilizing the soil environment) with regards to water balance should be discussed. A model for the optimum effective use of the plant-soil system should be built, and then

effective, sustainable ecosystem management counter measures for restoring sand-fixed revegetation-soil systems can then be formulated.

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