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RESEARCH ARTICLE

Biocrust and sand burial together promote annual herb community assembly in an arid sandy desert area

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Abstract

Background Annual herbs are crucial components of sandy ecosystems and their community assembly in arid sandy dunes is an intuitive indicator of a degraded ecosystem's successful restoration. In sandy areas, biocrust and sand burial often co-occur, given the higher diversity and biomass of annual herbs where both factors co-occur than where either does alone. Yet our knowledge of the underlying mechanism is limited.

Methods A field survey was conducted to verify that the presence of biocrust and sand burial jointly promoted the assembly of herbs. And then controlled simulating experiments were conducted to investigate the individual and collective effects of three biocrusts (bare sand (control), cyanobacterial crust, and moss crust) and three depths (0 (control), 2.5, and 5 mm) of sand burial upon germination, growth of three annual herbs as well as the soil water and nutrition status in a revegetated area of the Tengger Desert.

Results Biocrust inhibited seed germination of the three annual herbs, but promoted their seedling growth. However, sand burial disrupted the inhibitory influence upon seed germination and strengthened the positive effects of biocrust on seedling growth of all species, by improving the availability of water and nutrients in upper soil.

Conclusion Mutual complementary effects of biocrust and sand burial promote the establishment, and overall recruitment success of annual herbs. This finding emphasizes the importance of buried disturbance of biocrust in plant community assembly processes, providing an approach to disentangle relationships between biocrust and vascular plants, and a new technique suggestion for ecological restoration in arid sandy areas.

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Introduction

Understanding the key factors and mechanisms promoting community assembly and configuration is a central goal of community ecology (Ejrnæs et al. 2006; Datry et al. 2016; Havrilla et al. 2018). Incorporating facilitation into ecological theory yields a paradigm whereby establishing positive interactions is key to explain the dynamics of ecosystem restoration (Bruno et al. 2003; Filazzola and Lortie 2014). In degraded sandy ecosystems, successful recruitment of plant populations has a positive impact on community restoration, biodiversity and ecological recovery (Becerra and Montenegro 2013). In degraded sandy ecosystems, the successful recruitment of species is a clear indicator of the facilitation effect, which to some extent positively impact community reconstruction, biodiversity, and ecological restoration; nonetheless, it is always challenging to distinguish which factors and mechanisms promote their successful recruitment. Plant recolonization is a useful mode to achieve ecological restoration in areas with low plant coverage and biodiversity, and the pathways and mechanisms of recolonization can provide basic guidance for various ecological restoration applications. Elton (1958) posits superior competitive ability as the main mechanism responsible for a recolonizer's success, for which resource competition (space, nutrients, water, etc.) is the most intuitive. Over the past two decades, increasing attention has been paid to the role of biocrust in mediating resource replenishment in sandy biomes (Havrilla and Barger 2018). This is especially true for annual herbaceous plants, being a specific highly sensitive and environmentally dependent group, whose settlement, establishment, growth, and reproduction are vulnerable locally changed resource levels (Golay et al. 2013; Kołodziejek 2017; Frei et al. 2018; Furey and Tilman 2021). In arid sandy areas, the fitness of annual herbs are often highly dependent on precipitation and ground surface conditions (Barbosa et al. 2019), which are niche-closer to surface-dwelling biocrust in physical distance when compared with deep-rooted shrubs (Li et al. 2010). However, most previous studies have focused on how biocrust affects the assembly of species without considering the recruitment of species (Song et al. 2017, 2022). Accordingly, the processes and mechanisms of biocrust affecting annual herb species recruitment in sandy ecosystems still remain unclear (Havrilla et al. 2018).

The successful recruitment of plant species is a pivotal marker of ecosystem restoration in sandy areas, contributing significantly to ecosystem function, biodiversity, nutrient cycling, and biomass (Ruesink et al. 2005). Mounting studies have shown that biocrust profoundly influences the settlement, establishment, and assembly of alien plants by altering the arid, harsh sandy environment (microenvironment) with limited resources (Belnap et al. 2006; Zhang and Nie 2011; Zhang et al. 2016; Havrilla and Barger 2018), particularly with respect to soil nutrient and water resource availabilities. Numerous studies have proven that biocrust plays key roles in dryland nutrient cycling (Bowker et al. 2008, 2014; Barger et al. 2016), by increasing the availability of soil carbon (Li et al. 2012), nitrogen (Barger et al. 2016; Rodriguez-Caballero et al. 2018; Su et al. 2021), and phosphorus (Zhang et al. 2012), to improve soil fertility and the levels of other mineral nutrients (Belnap and Harper 1995), and further modify the soil microclimate by altering soil hydrology and surface temperature (Belnap et al. 2006; Jia et al. 2014, 2019, 2020; Xiao et al. 2019; Li et al. 2018, 2021). Via these biological and mechanical improvements to the soil niche, biocrust can strongly influence the recruitment success of vascular plant species that coexist with them (Li et al. 2010; Zhang and Belnap 2015; Song et al. 2017; Havrilla et al. 2018).

Besides the positive impacts of biocrust on vascular plant establishment and assembly (Bowker et al. 2018, 2022; Muñoz-Rojas 2018; Muñoz-Rojas et al. 2018; Ferrenberg et al. 2018; Das et al. 2019; Vinoth et al. 2020), the species-specific (Li et al. 2005; Ahmadian et al. 2021) and general negative (Thiet et al. 2014; Kidron 2014; Gilbert and Corbin 2019) effects—on emergence, survival and growth—have also been observed, some of which are life-stage dependent (Zhang et al. 2016; Havrilla et al. 2018). For example, in the early stages of seedling establishment, biocrust influences seedling emergence in multiple ways, which often depends on the type of biocrust (Zhang et al. 2016). Biocrust community composition and micro-topography largely determine the roles that biocrust plays in seedling emergence. Related studies have shown that smooth or wrinkled biocrust may inhibit seed retention and radicle penetration into the soil profile (Clements et al. 2007), while biocrust with a rolling or pinnacle micro-topography may increase its capture and retention of dispersed seeds (Boudell et al. 2002). In addition, metabolites of microorganisms that inhabit biocrust may also directly affect rates of seed germination and survival. For example, toxins produced by cyanobacterial crusts may limit seed germination and seedling growth (Harper and Marble 1988). Subsequently, the biocrust provides a favorable microhabitat for seedling emergence by increasing levels of soil moisture and temperature (Zhang et al. 2016). Other studies have shown that differences in seed traits, such as size (Briggs and Morgan 2011) and external morphology, are also important drivers of how biocrust impacts seedling emergence (Zhang and Belnap 2015). Once seedlings are established, biocrust may provide favorable soil conditions for their onward growth by improving their access to soil moisture and nutrients. This latter benefit has been repeatedly confirmed in studies (Zhang and Nie 2011; Zhuang et al. 2015; Nevins et al. 2020). Likewise, the growth of vascular plants may benefit from the greater availability of soil resources provided by biocrust. Notably, Kidron and Tal (2012) reported that under conditions of difficulty in obtaining water resources, biocrust inhibited the assembly of herbs. Therefore, biocrust imposes differential effects (either positive or negative, or none) on herbaceous plant assembly, and the direction of such effects likely depends on common disturbances to biocrust, including fire (Brianne et al. 2020), trampling (Navarro-Perea et al. 2022), animal burrowing (Warren et al. 2021), and burial by wind-blown sand (Ma et al. 2021).

In sandy ecosystems, sand burial is a major factor controlling the distribution and composition of vegetation (Maun and Lapierre 1986). Previous studies confirm that sand burial can influence germination and seedling survival (Maun 1994) by changing aspects of the vascular plant microenvironment such as light (Brown 1997), temperature (Klimes et al. 1993), moisture (Ren et al. 2002), soil organic matter, and soil microbial activity (Maun 1998). Related research has also shown that seed germination and seedling growth are linked to the depth of sand burial (Su et al. 2007). Chen et al. (2023) identified a suitable sand burial depth that can reduce soil temperature and increase soil moisture, thus promoting seed germination, as well as seedling emergence and growth. However, when sand burial depth is too deep, it can result in insufficient light and reduced soil permeability, which can inhibit germination and emergence. For plant seedlings, their allocation of below- and above-ground biomass was found to vary according to sand burial depth (Zhu et al. 2005). However, because most research has focused on the single effect of sand burial or biocrust on the assembly of sand-fixing vegetation structure in sandy ecosystems (Guo et al. 2010), how they interact to alter the assembly of annual herbaceous communities in sandy areas is less reported, and less known.

Interestingly, animal activity (Brown et al. 2012) and wind-sand movement (Ma et al. 2021) are the main causes of sand burial occurrence in the Tengger Desert (Jia et al. 2008, 2012), the Mu Us Desert (Bao et al. 2013), and the Ulan Buh Desert (He et al. 2012), resulting in varied depths of sand burial even after these degraded areas were restored in part and biocrust flourished following plantation establishment. Our field investigation revealed that annual herbs are more frequently found in sand-buried biocrust patches than in either biocrust or bare sand single patches in the Tengger Desert (Fig. 1), indicating a novel restoration guidelines to promote annual herb community assembly in an arid sandy desert area by creating the opportunity of the co-occurrence of biocrust and sand burial. Yet, whether the sand burial disturbance of biocrust promotes the recruitment of annual herbs in degraded sandy ecosystems, and the related mechanism involved, remains unknown. Therefore, in this study, our aim was to evaluate the single and combined effects of biocrust and sand burial on herb seed germination and seedling growth, in addition to simultaneously monitoring changes in soil moisture and nutrient conditions. Our main hypothesis was that biocrust and sand burial jointly promote the recruitment and assembly of the annual herb community by increasing soil water and nutrient availabilities. This follows from reports in the same study area that biocrust and sand burial can respectively enhance soil nutrients (Zhang et al. 2016) and alter soil moisture (Li et al. 2022).

Materials and methods

Study area

The study area is located at the southeastern margin of the Tengger Desert (37°28′N, 105°02′E; elevation: 1339 m), lying in the transition zone between

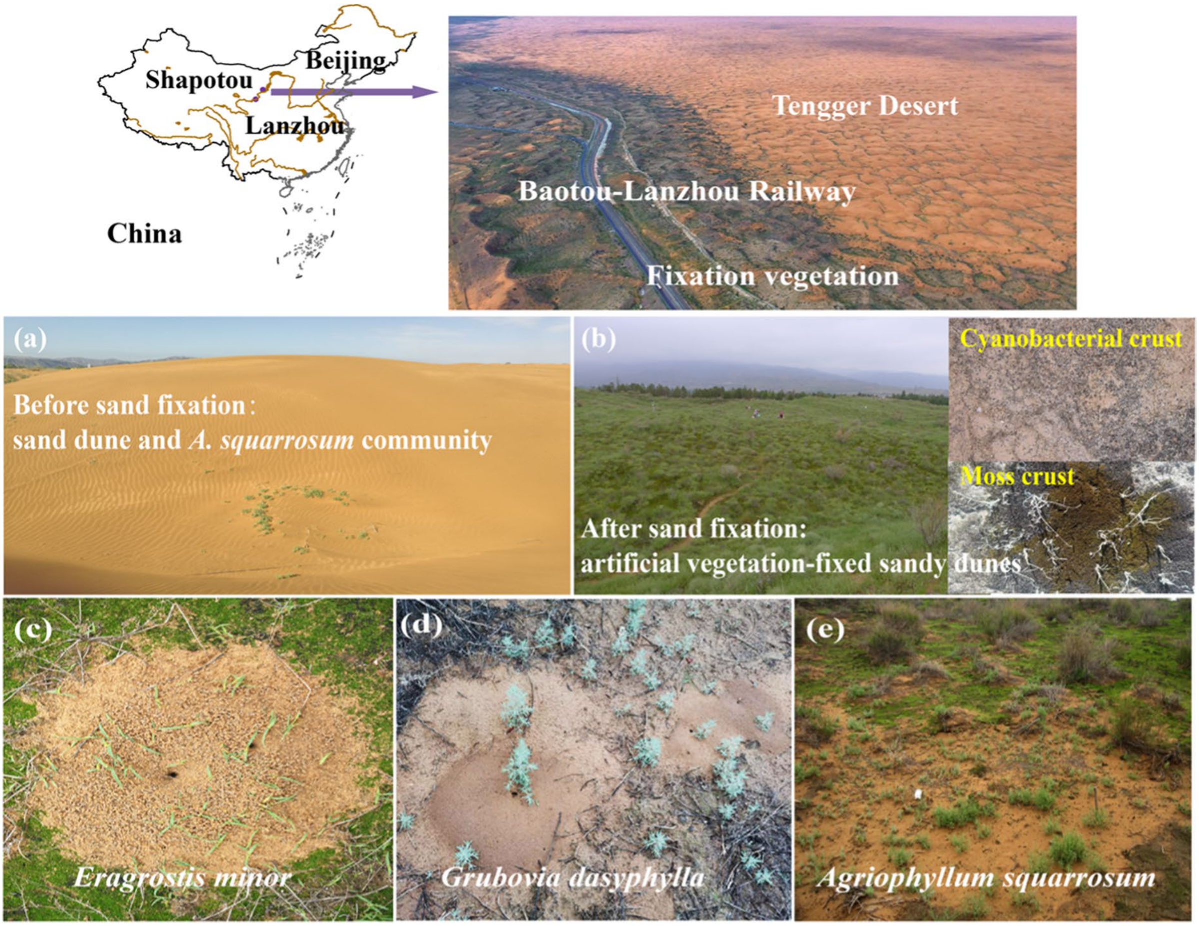

Fig. 1 Diagram showing the geographical location and main scenes of the revegetated area following shrub plantation establishment in the Tennger Desert. The annual herb species *A. squarrosum* is only found in the bare sand before revegetation occurred (**a**); with the formation of biocrust (**b**), *A. squarrosum* (**c**) suddenly disappeared while populations of *E. minor* (**d**) and *G. dasyphylla* (**e**) established in the ecosystem. However, when sand burial occurred on biocrust, the re-colonization of *A. squarrosum* soon followed

desert and desert grassland of the Alashan Plateau, where some areas have been transformed into desert dunes and the total vegetation coverage is <1% (due to natural and anthropogenic factors). Here, the average annual temperature is 9.6 °C, and average annual precipitation is 186.5 mm, mainly falling from May to September. Average annual potential evaporation is 2300–2500 mm; the prevailing wind direction is northwest, with an annual average wind speed of 2.9 m s^{-1} (Zhao et al. 2017).

In 1956, an artificial-vegetation protection system was established by erecting straw checkerboard and transplanting shrubs into the study area to protect the Baotou-Lanzhou railway line from sand burial (Fig. 1) (Jia et al. 2018). Later on, it was gradually expanded in different years (1956, 1964, 1981, and 1987) and now effectively constrains the threat of sand burial to the railroad's operation. This artificial revegetation became a successful example of the reversal of desertification, in that the mobile sand dunes have been successfully transformed into stable and productive ecosystems (Li et al. 2011), in which the structure and function of their vegetation zones has changed considerably over time. In tandem, biocrust has gradually formed and developed, whose total coverage now exceeds 70% in the revegetated area. Before the artificial planting, the initial vegetation cover was <1% and the sole herb species, *Agriophyllum squarrosum* (L.) Moq., was widely present (Li et al. 2012; Jia et al. 2018). However, as more biocrust formed and expanded, *A. squarrosum* was suddenly excluded from this ecosystem and its plant community gradually re-assembled. Meanwhile, more than five annual herb species have successfully colonized those restored areas. Sand burial is usually caused by two independent physical processes: wind erosion in spring and animal activity (ants, lizards, rabbits, etc. burrowing behavior) in summer and autumn (Jia et al. 2018). Interestingly, we found that biocrust disturbed by sand burial seemed to be more conducive to herbaceous plant establishment and assembly, and *A. squarrosum* revived. Table 1 presents detailed information on the field-observed associations between biocrust, sand burial, and their combination for the establishment of *A. squarrosum* and other two typical annual herb species in this region, *Eragrostis minor* Host. and *Grubovia dasyphylla* (Fisch. & C. A. Mey.) Freitag & G. Kadereit.

Experimental design

A field survey and controlled simulation experiments were carried out to test the possible interactive effects of biocrust and sand burial upon the establishment and assembly of annual herbs in the vegetation restoration area of the Tengger Desert. Firstly, through a field survey, the relationships between the cover of sand burial, biocrust, and the species richness of the herbs was investigated, to provide preliminary direct evidence to test our initial hypothesis. Secondly, we designed a controlled experiment that simulated exposure to biocrust and sand burial to examine their interactive effects on the coupled dynamics of seed germination and seedling growth of the annual herbs, in addition to the environmental soil moisture and nutrient conditions, to explore the underlying mechanisms involved.

Field investigation

Five study sites were used: four differently aged sites planted with shrubs (respectively in 1956, 1964, 1981, 1987) plus one control site (a moving sand dune, non-planted). They were surveyed in September in three consecutive years, 2019, 2020, and 2021, these corresponding to years with wet (201.5 mm), dry (158.1 mm), and normal rainfall (186.5 mm) in the study area, respectively. Three 200 m-long parallel transects were randomly positioned along the revegetation area corresponding to different successional stages; the distance between the adjacent transects was at least 100 m. Then, sampling plots (each 10 m × 10 m) were set at 10-m intervals within each transect. We then divided the 10 m × 10 m sampling plots into 100 squares of 1 m × 1 m. The coverage of sand burial, and depth of sand burial (distance between the uppermost layer of buried sand to the lowest unburied soil surface using a straightedge), and the species richness (number of species) of herbs in each plot were recorded.

Controlled biocrust + sand burial treatment under two rainfall regimes

A factorial experiment was set up to test the effects of biocrust, sand burial, and their combination on seed germination and seedling growth of the three annual herbs. Two types of biocrust (cyanobacterial crust and moss crust) and bare sand (the control), were crossed with three sand burial depths (0 mm [control],

Table 1 Relationships between biocrust, sand burial, and their combination for the establishment of three dominant annual herbs in the revegetated area of the Tennger Desert

Annual herb species	Bare sand	Biocrust (after revegetation)	Biocust and sand burial co-occur (after revegetation)
Agriophyllum squarrosum	+	–	+
Eragrostis minor	–	+	++
Grubovia dasyphylla	–	+	++

+ represents the level of species establishment and assembly (+: weak; ++: strong); − represents the exit of the species from the ecosystem

2.5 mm, and 5 mm) under two rainfall gradients (5 mm or 10 mm once, at 3-day intervals). Each treatment combination had five replicates (Fig. 2). The total water amounts sprayed during the experiment's period were 190 and 380 mm, respectively representing the normal and double annual precipitation in the study area from 1990 to 2010 (Li et al. 2012; Jia et al. 2012). Sand burial depths were selected based on actual sand burial depths in the study area.

Biocrust sampling

In April 2020, 90 intact soil columns with 100% coverage of moss (n = 90) or cyanobacterial crust (n = 90), or with just bare sand (n = 90) were separately collected from the 1956 and 1987 restored vegetation area and flowing sand dunes, using cylindrical PVC tubes (diameter: 20 cm, height: 50 cm). Thus, a total of 270 samples were collected (Fig. 2). Before sampling, distilled water was slightly sprayed to ensure that the biocrust was intact, and not easily broken during the collection. All samples were transferred to the Water Balance Observatory of the Shapotou Desert Research Experiment Station of the Chinese Academy of Sciences (about 1 km from the sampling site). There, the 270 samples were placed below the ground surface, with the top 2 cm of each left exposed aboveground. Rain shelters were then placed at a height of 2 m above the bed of samples (Fig. 2). The soil surface surrounding the samples was paved with a straw curtain, which extended for 5 m beyond the shaded ground portion of the shelters, to prevent disturbance from sand particles from outside the experiment's area (Jia et al. 2018).

Herb seed collection

We chose three typical annual herbaceous plants (*A. squarrosum*, *E. minor*, and *G. dasyphylla*) in the revegetated area of the Tengger Desert. In 2020, mature seeds (seeds of uniform size and healthy fullness) of each species were harvested, air-dried, and stored (about 200-240 days) in seed bags for later use.

Seed germination and growth monitoring

Seed germination pretests were conducted by referring to the methodology of Song et al. (2022). These results showed that the germination rate of seeds of all three annual species reached more than 90%. 40 seeds of each herb were sown on three-treatment (cyanobacterial crusted, moss crusted and uncrusted bare sand) soil samples, respectively, ie., 40 seeds per PVC tube displayed in Fig. 2. To simulate the natural fall of seeds, no external force was applied to bring the seeds into contact with the soil. Then, the sand burial treatment of various depths (0 [control], 2.5, and 5 mm) were applied, using the method described by Jia et al. (2018). To do this, the sand was distributed gently and evenly over crusts allocated to each of the supply subgroups described above. Once the experiment began, the number of seeds germinating in each treatment combination was observed daily and the appearance of a seed's radicle was designated as seed germination success. If no new seedlings grew for 6 consecutive weeks, germination was no longer recorded. We then limited the number of seedlings in each tube

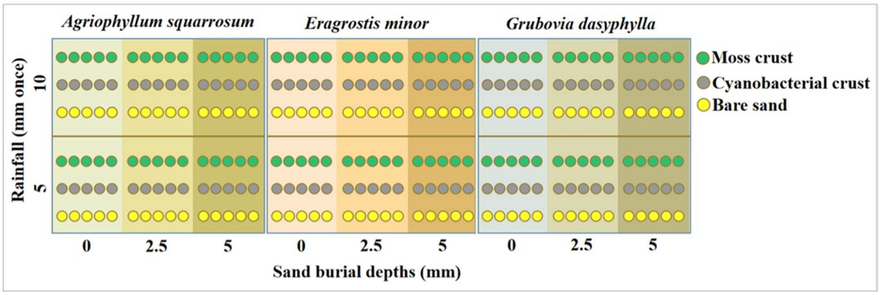

Fig. 2 Layout of the factorial experiment design. Emergence and growth of three annual herb species (*A. squarrosum*, *E. minor* and *G. dasyphylla*) on three successional stages of biocrust (bare sand [control], cyanobacterial crust, and moss crust) at three depths (0 (control), 2.5, and 5 mm) of sand burial and their combination under two rainfall regimes (5 mm and 10 mm once, at 3-day intervals)

to five at the most; any remaining seedlings that germinated later in the experiment was removed, to prevent any intraspecific competition among herbs in the limited tube space from affecting our experimental results. The entire experiment began on May 27 and ended on September 5. Seed germination rate was expressed as the ratio of the number of seeds germinating to the total number of seeds sown. At the experiment's end, we separately harvested the above-ground parts of seedlings in the PVC tubes, then dried at 70 °C for more than 48 hours until they were completely dry and then weighed.

Soil moisture and nutrient content measurements

We also studied the changes in soil moisture, water holding capacity, and nutrient content caused by biocrust, sand burial, and their treatment combinations, to control for their possible influence on herb growth. Specifically, we analyzed the responses of soil water content and nutrient content to the single and interactive effects of sand burial and biocrust under natural conditions in the three field-sampled areas—that restored in 1956 and 1987 and that with flowing sand dunes, respectively—during the same period in parallel to the above controlled experiment. Water monitoring probes, each consisting of a five-channel data collector (EM50, METER, USA), were set within four vertical soil layers (at 2, 5, 10, and 20 cm from the initial soil surface) in the cyanobacterial crust, moss crust and bare sand sampling areas, respectively. Then each location where moisture monitoring probes were installed received a sand burial treatment (the same as in the controlled experiment above). To ensure that the sand burial at the location of the moisture monitoring probes persisted and be not wind-blown away, in whole or in part, the sand burial treatments were set up in a circle with 1-m radius. The EM50 was set to measure moisture at a 60-min interval; hence, 24 soil moisture data points were recorded each day at each location. Finally, we calculated mean daily soil moisture during the experiment.

In addition, to assess the changes in the water holding capacity and nutrient content of surface soil layer caused by biocrust, sand burial, and their combination, we measured the water potential characteristics and nutrients of shallow soil layer (0–5 cm) under each treatment. At the experiment's end, soil samples were collected from each sampling area at different sand burial depths. Ten replicate soil samples were then randomly taken for each treatment and brought back to the laboratory, half of which were used to determine soil water potential and the other half to measure soil nutrient content. In this experiment, the soil water potential were measured using the GQT1-WP4 device (range: 0–40 MPa, precision: ± 0.1 MPa, resolution: 0.01 MPa; DECAGON,USA). By following the method of Sun et al. (2010), we drew the water characteristic curve during soil dehumidification. The empirical equation $y = ax^{-b}$ was used for that fitting, where y is the soil water content, x is the soil water potential, and both a and b are estimated model parameters.

Soil organic matter (SOM) was determined by dichromate oxidation; total nitrogen (TN) was determined by micro Kjeldahl method; total phosphorus (TP) was determined by alkali diffusion method; total potassium (TK) was determined by HF-HCLO$_4$ method; effective nitrogen (AK) was determined by alkali diffusion method; effective phosphorus (AP) was determined by NaHCO$_3$ digestion and Mo-sb colorimetric method (for methodological details, refer to Bao 2005).

Data analysis

Differences in herb coverage, richness, biocrust coverage, and sand burial coverage among the different successional stages of revegetation were analyzed using one-way repeated-measures ANOVA for three consecutive years. The effects of biocrust, sand burial, and their interaction on soil moisture, soil nutrient content (SOM, TN, TP, TK, AK and AP), as well as the germination rate and aboveground biomass of the three annual herbs, were tested using two-way ANOVAs. Data normality and equality of error variances were checked by Shapiro-Wilk test and Levene's test separately before data analysis. Least significant difference test was used for pairwise comparisons of means, with a significance level set at 0.05 (P value threshold). All statistical analyses were performed using SPSS 22.4 software (IBM SPSS Inc., Chicago, IL, USA).

Results

Relationship of herbaceous coverage and abundance with biocrust and sand burial coverages

With the succession of vegetation following shrub plantation establishment, coverage of herb plants, biocrust, and sand burial (bare sand not considered) all gradually increased, as did the herb richness (Fig. 3). Herb coverage changed significantly with the annual rainfall amount, being significantly higher in 2019 and 2021 than in 2020 (Fig. 3a-c, $P < 0.05$). In addition, herb coverage and richness increased as the coverage of biocrust and buried-sand increased during the succession of artificial sand-fixing vegetation. Interestingly, even in three years with different rainfall levels, our field surveys revealed a similar phenomenon of more annual herbaceous plants (e.g. *A. squarrosum*, *E. minor*, and *G. dasyphylla*) colonizing patches where biocrust and sand burial occurred simultaneously, this phenomenon was more obvious in years with better rainfall (Fig. 3).

Effects of biocrust and sand burial on seed germination of three annual herbs

Biocrust and sand burial jointly enhanced the germination rates of the three herbs (Fig. 4). Under normal conditions of rainfall (i.e., 5 mm once) moss crust significantly reduced seed germination of three herbaceous species, while cyanobacterial crust significantly reduced the seed germination of *A. squarrosum*, yet had no significant effect on that of both *E. minor* ($P = 0.06$) and *G. dasyphylla* ($P = 0.06$). Deep sand burial (5 mm) significantly increased the seed germination of *G. dasyphylla*, while shallow sand burial (2.5 mm) had no significant effect on the seed germination of any of the three herbs *A. squarrosum* ($P = 0.48$), *E. minor* ($P = 0.28$) and *G. dasyphylla* ($P = 0.25$). Interestingly, a complementary effect arose under the combination of biocrust and sand burial, in that the seed germination of all three herbs increased (Fig. 4a, c, e and Table S1).

Under more applied rainfall (10 mm once), moss crust significantly reduced germination of all three herbs, whereas cyanobacterial crust had no significant effect on seed germination of any of the three herbs *A. squarrosum* ($P = 0.33$), *E. minor* ($P = 0.19$) and *G. dasyphylla* ($P = 0.93$). Deep sand burial significantly increased the germination of *A. squarrosum* and *E. minor*, but it did not significantly affect that of *G. dasyphylla* ($P = 0.09$). Shallow sand burial enhanced the seed germination of all three herbs. Importantly, sand burial eliminated the inhibitory effect of moss crust on the germination of all three herbs and both factors together promoted the germination of these species (Fig. 4b, d, f and Table S1).

Effects of biocrust and sand burial on growth of three annual herbs

Biocrust and sand burial generally increased the aboveground biomass of the three herb species (Fig. 5). Under normal conditions of rainfall (i.e.,

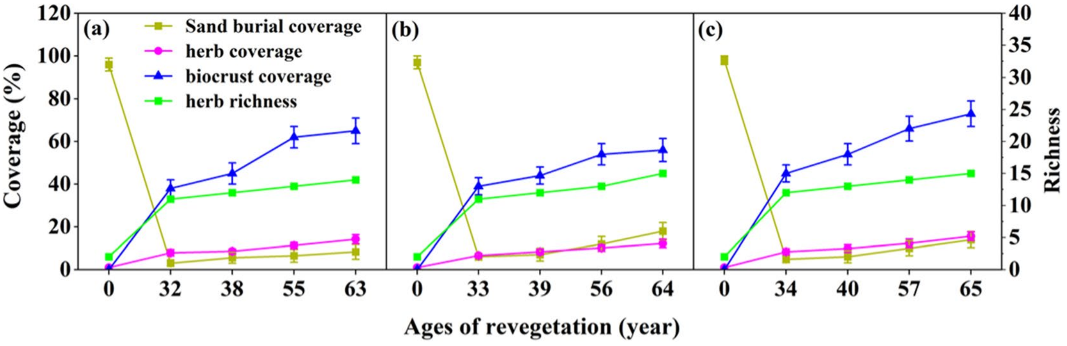

Fig. 3 Dynamics in the coverage of biocrust, sand burial, and herbs as well as richness of herbs in different successional stages: flowing sand dune [0], 1987 [32–34], 1981 [38–40], 1964 [55–57], and 1956 [63–65] of sand-fixing vegetation in 2019 (**a**), 2020 (**b**), and 2021 (**c**). Bars represent one SE of the mean

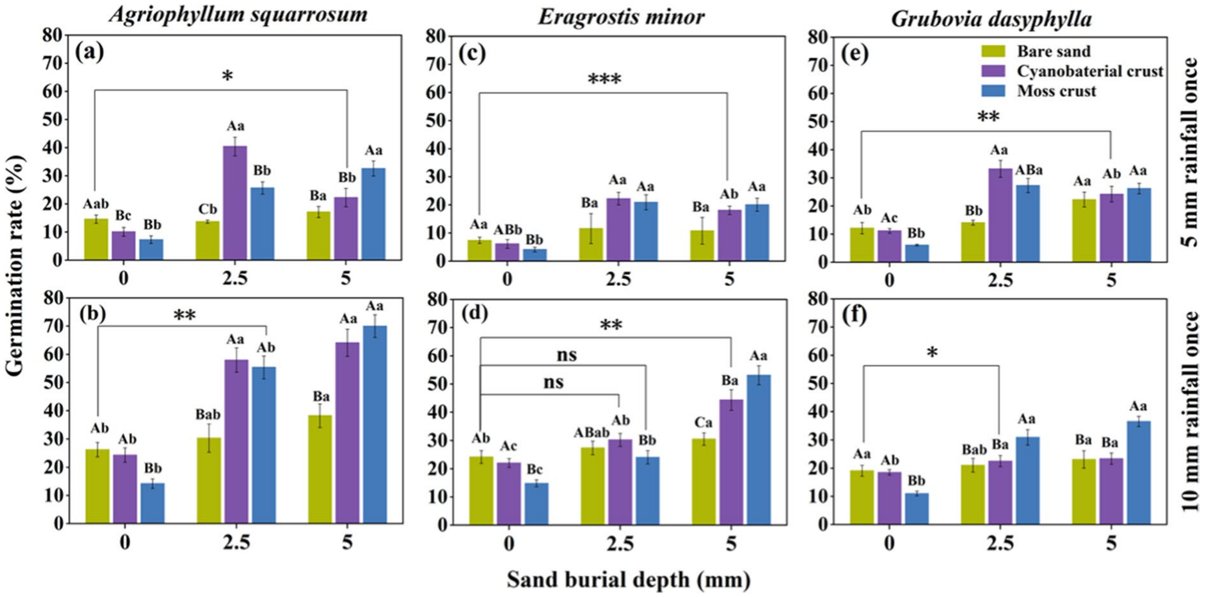

Fig. 4 Effects of three successional stages (bare sand [control], cyanobacterial crust, and moss crust) of biocrust at three sand burial depths (0 [control], 2.5, and 5 mm) on seed germination rates of *A.squarrosum* (**a** and **b**), *E. minor* (**c** and **d**), and *G. dasyphylla* (**e** and **f**) under two simulated rainfall regimes (5 and 10 mm, each once, at 3-day intervals). Uppercase letters indicate significant differences between crusts types within groups ($P<0.05$); lowercase letters indicate significant differences between the different depths of sand burial between the groups ($P<0.05$); asterisks indicate significant differences between bare sand and different combinations of sand burial and biocrust (* $P<0.05$; ** $P<0.01$; *** $P<0.001$; ns, no significant difference). Bars represent one SE of the mean

5 mm once), moss crust led to a greater biomass of *A. squarrosum* and *E. minor*, whereas *G. dasyphylla* was negligibly affected ($P=0.29$). Cyanobacterial crust significantly increased the biomass of *A. squarrosum*, but had no significant effect on *E. minor* ($P=0.14$) or *G. dasyphylla* ($P=0.74$). Deep sand burial and shallow sand burial significantly enhanced the biomass of individual plants of all three herbs. Moreover, a higher biomass for each herb species was found when both biocrust and sand burial were concurrently present (Fig. 5a, c, e and Table S1).

Under more applied rainfall (10 mm once), both types of biocrust improved the growth of *E. minor* but had little effect on *A. squarrosum* ($P=0.07$). Sand burial at either depth favored the accumulation of plant biomass in all three species. When biocrust and sand burial were simultaneously present, the same patterns were found between wetter and normal rainfall conditions; i.e., combination of biocrust and sand burial augmented the biomass of the three studied annual herbs (Fig. 5b, d, f and Table S1).

Effects of biocrust and sand burial on soil moisture

Biocrust had a positive effect on daily soil moisture at different depths, in the order of moss crust > cyanobacterial crust > bare sand (Fig. 6a). When sand burial occurred, there was a greater increase in soil water content of soil covered by either biocrust; furthermore, these increases were related to the type of biocrust and sand burial depth. Specifically, soil water content of the treatment combinations was ranked as follows: moss crust + deep sand burial > moss crust + shallow sand burial > moss crust > cyanobacterial crust + deep sand burial > cyanobacterial crust + shallow sand burial > cyanobacterial crust > bare sand.

The regression analysis yielded soil water characteristic curves under different treatment combinations. The equation $y=ax^{-b}$ describes very well the relationship between soil water potential and water content (Table S2). The soil moisture characteristic curves under different treatment combinations all showed the same trend: rapid decline, then slow decline, and then basically a smooth flatter trend

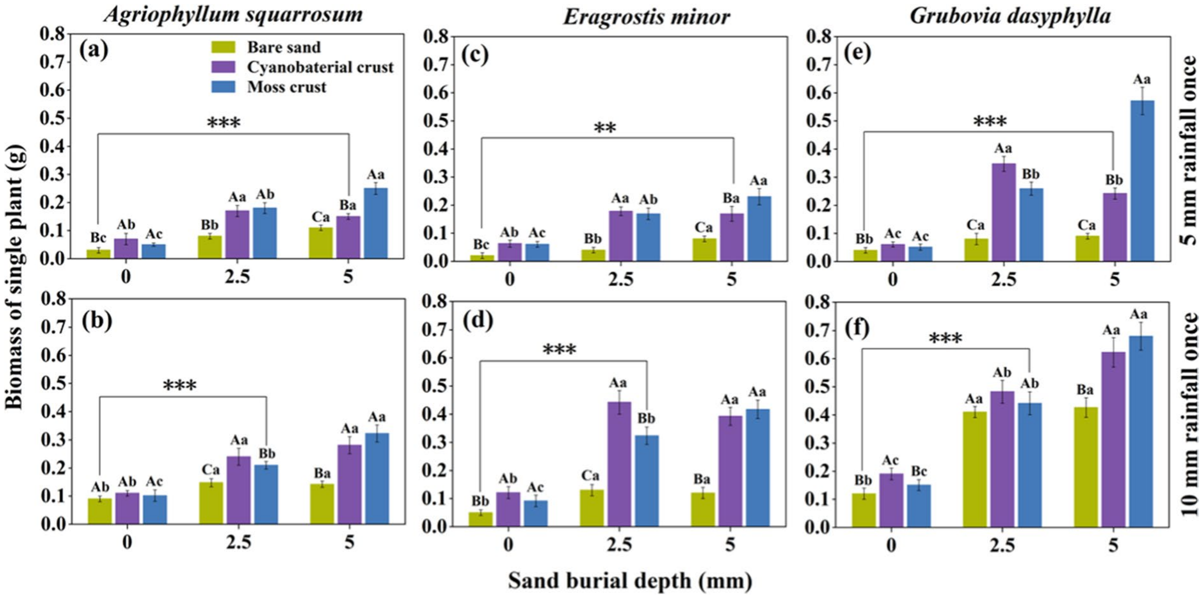

Fig. 5 Effects of three successional stages (bare sand [control], cyanobaterial crust, and moss crust) of biocrust and three sand burial depths (0 [control], 2.5, and 5 mm) on seedling biomass of *A. squarrosum* (**a** and **b**), *E. minor* (**c** and **d**), and *G. dasyphylla* (**e** and **f**) under two simulated rainfall regimes (5 and 10 mm, each once, at 3-day intervals). Uppercase letters indicate significant differences between crusts types within groups ($P < 0.05$); lowercase letters indicate significant differences between the different depths of sand burial between the groups ($P < 0.05$); asterisk indicate differences between their interaction sand burial×biocrust and bare sand (Duncan's multiple range test, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, no significant difference). Bars represent one SE of the mean

(Fig. 6b). According to their estimated parameters, the water holding capacity of soil was in the order of moss crust + deep sand burial > moss crust + shallow sand burial > cyanobacterial crust + deep sand burial > moss crust > cyanobacterial crust + shallow sand burial > cyanobacterial crust > bare sand (Table S2). Therefore, these results demonstrated that the joint presence of crusts and sand burial increased the water holding capacity of soil and, accordingly, its moisture content.

Effects of biocrust and sand burial on soil nutrients

Soil nutrient contents—TN, TP, TK, AP, AK, and SOM—were positively affected by biocrust, and this further augmented by sand burial (Fig. 7). However, these two positive effects differ among different biocrust type and burial depth combinations. The TN content increased significantly more under moss crust than cyanobacterial crust when sand burial occurred ($P < 0.05$). For AP, the increase effects from cyanobacterial crust were dramatically strengthened by shallow burial only ($P < 0.05$), not deep burial ($P > 0.05$), while the enhancement of AP by moss crust was found not to be statistically reinforced by burial irrespective of its depth ($P > 0.05$). For TP and AK, moss crust significantly increased their respective content ($P < 0.05$), while cyanobacterial crust did not significantly change the TP content. When sand burial did occur, under both types of biocrusts the TP content was augmented. For both TK and SOM, their increase under either biocrust was more pronounced when sand burial disturbance had occurred ($P < 0.05$).

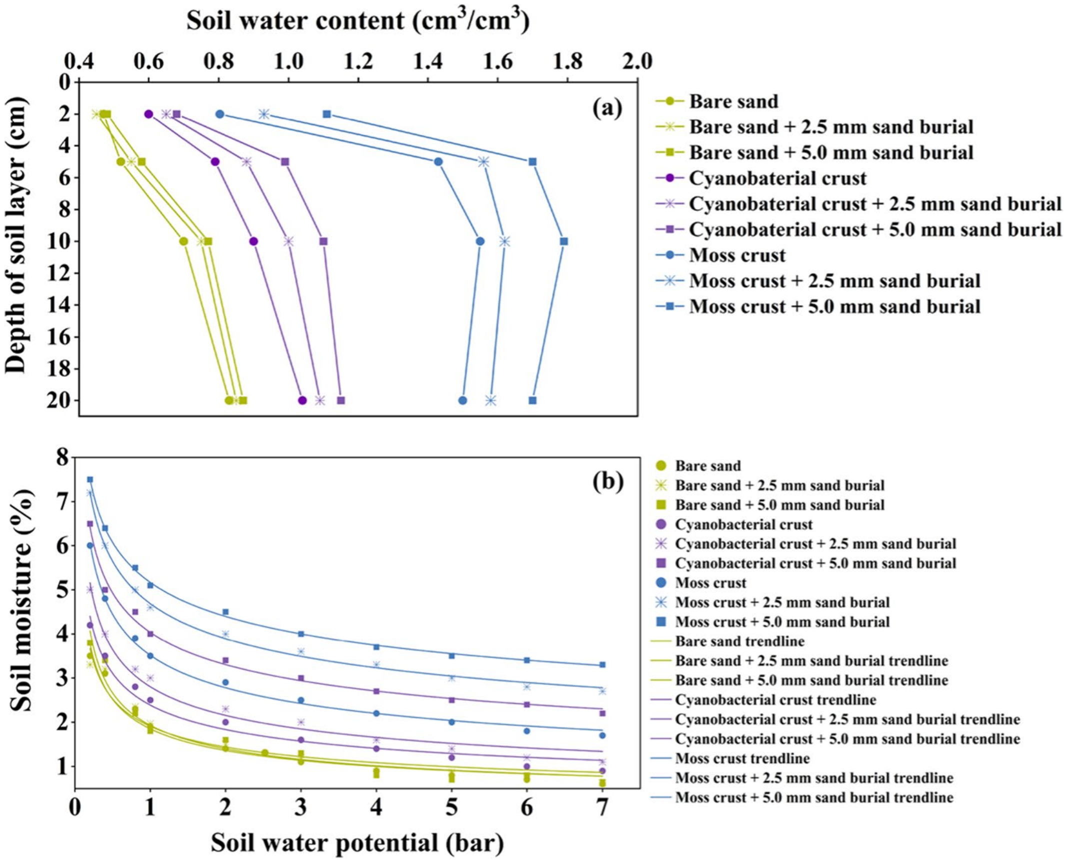

Fig. 6 Changes in soil water at 2, 5, 10, and 20 cm depths (**a**) and fitted moisture characteristic curves (**b**) of the surface soil layer (0–5 cm) covered by bare sand (no biocrust [control]), cyanobacterial crust, and moss crust, combined with 0 (control), 2.5, and 5 mm depth of sand burial

Discussion

Herbaceous community assembly is a key indicator of ongoing ecosystem restoration in degraded sandy areas (Hai et al. 2004). Our results showed that an inhibitory factor for annual seed germination (i.e. a biocrust surface) can be turned into a strongly promoting factor when subjected to interaction with a disturbance factor occurred (i.e., sand burial of biocrust). Our field survey found that the herbaceous coverage and richness increased with the increase of biocrust coverage in the long-term succession of vegetation planted to fix moving sand (Fig. 1). The improved soil moisture and nutrition conditions in the near-surface soil niche created by biocrust and an appropriate sand burial (depth of sand <5 mm) disturbance explains the successful recruitment, assembly, and replenishment of the annual herb community in the studied arid sandy desert (the Tengger Desert).

Effect of biocrust on annual herb assembly in sandy desert

Many factors can influence the colonization of annual herbs, among which the plants' own biological characteristics and functional traits often play an initial pivotal role (Alvarez et al. 1974; Burylo et al. 2007; Crawford and Whitney 2010), such as seed dispersal and propagation (Howe and Smallwood 1982; Kumar and Reddy 2011), resource access and competition (Hambäck and Beckerman 2003), etc. Flowing sand is essential for the germination of *A. squarrosum*, while biocrust is a prerequisite for *E. minor* and *G. dasyphylla* to germinate (Fig. 3). This may

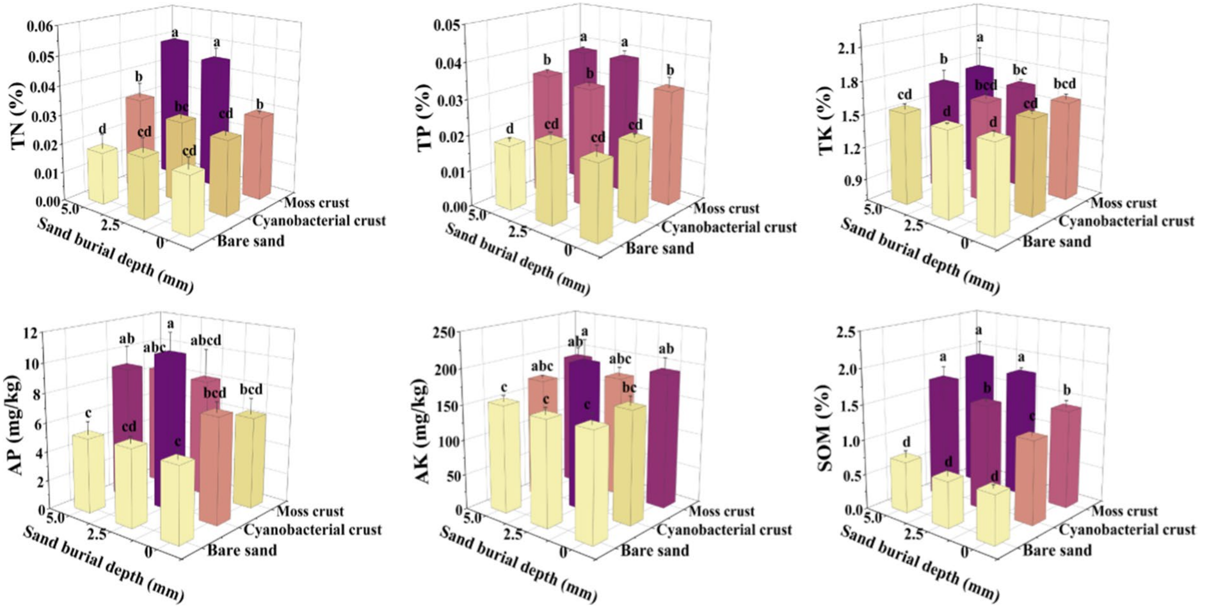

Fig. 7 Changes in nutrient contents of the surface soil layer (0–5 cm) covered by bare sand (no biocrust [control]), cyanobacterial crust, and moss crust, combined with 0 (control), 2.5, and 5 mm depth of sand burial. Different lower case letters indicate significant differences among different sand burial depths, biocrust types and their combination at the $P < 0.05$ level. Bars represent one SE of the mean

be related to their differential adaptation abilities to sand burial (which happens frequently in flowing sand areas) and the biocrust-created niche among the three herb species. In addition to their inherent biological factors, changes in external environmental conditions may also affect the colonization of annual herbs. The establishment of plant communities could be relieved by one or more nurse plant species (Ren et al. 2008). Numeorus studies have shown that tall shrubs are nurse plants for some annual herb species under extreme climate and resource conditions in sandy areas (Filazzola and Lortie 2014; Sotomayor et al. 2014; Madrigal-González et al. 2020). Legumes can also reportedly act as potential nursing plants, improving the survival and growth of target species, by supplying nitrogen and shade in arid desert habitats (Filazzola and Lortie 2014). Accordingly, in the present case, the establishment of annual herbs in the revegetated area of the Tengger Desert may also have been positively influenced by a benign microenvironment provided by the nursing plants (shrubs such as *Hedysarum scoparium* and *Caragana korshinskii*), which is conducive to both the seed germination and seedling growth of herbs. It is worth noting that the shrubs' cover and spatial proportions are small in extent due to severe water and soil resource constraints, whereas biocrust can occupy larger areas of the interspaces between shrubs. We therefore ask an interesting question: could biocrust consisting of a community of tiny organisms (non-vascular plants) on the soil surface serve as a composite nurse plant for annual herbs? We found that the effect of biocrust on the assembly of annual herbaceous plants depends on their early life stages: seed germination and seedling growth (Figs. 4 and 5). The effect of biocrust on seed germination of the three annual herbaceous species was consistent; i.e., moss crust significantly inhibited the seed germination of *A. squarrosum*, *E. minor*, and *G. dasyphylla*, and cyanobacterial crusts had a less inhibitory effect than moss crusts. This is similar to the findings of Song et al. (2022) and Gilbert and Corbin (2019) but not those of Muñoz-Rojas et al. (2018) and Godínez-Alvarez et al. (2012). As reported by Zhang and Nie (2011), the inhibitory effect of biocrust may be related to plant species and crust type. Studies have shown that the emergence of large-seeded plant species, especially those with appendages (e.g., awn), is usually inhibited by biocrust (Belnap 2006; Zhang and Belnap 2015). However, in our study, seed weight and biocrust type appear to be the critical factors determining whether biocrust inhibits germination (Fig. 4): for the lighter seeds of *A. squarrosum*, *E. minor*, and *G. dasyphylla*, they incurred difficulty in coming into contact with the soil beneath the moss crusts, thus leaving their seeds exposed to the surface and unable to absorb sufficient water for germination (Havrilla and Barger 2018). In addition, the results also showed that the germination of seeds of all three herbaceous species on both crusted and bare soils increased significantly with a higher rainfall amount. However, compared with cyanobacterial crust, germination of their seeds was inhibited more by moss crust (Fig. 4). This is due to the fact that cyanobacterial crust provide better soil moisture availability for three annual herbs' seeds, thus increasing their germination rates, while moss crust still left the seeds exposed to the surface and easily dried and generated a shorter duration of wetness (Kidron 2014).

Once vascular plants are established, biocrust may provide favorable conditions for their survival and growth (Belnap et al. 2006; Boeken 2008; Zhang et al. 2016). The present study showed that the presence of moss and cyanobacterial crusts favored the growth of *A. squarrosum* and *E. minor*, but had little effect on the growth of *G. dasyphylla* (Fig. 5). Many greenhouse and field studies have confirmed such positive effects (Godínez-Alvarez et al. 2012; Zhang and Nie 2011) that may also be species-specific (Lan et al. 2014). For example, in North American cold deserts, the biomass of plants is higher in biocrust-covered soils than in adjacent bare areas (Belnap and Harper 1995). Similarly, in the Gurbantungut Desert of northwestern China, the presence of biocrust was associated with higher biomass of herbaceous plants (Zhang and Nie 2011).

Effect of sand burial disturbance of biocrust on annual herb assembly in sandy desert

Under certain conditions, the colonization success of annual herbs also depends on the weakening and removal of factors that inhibit their germination and growth, where disturbance may act as one of a naturally occurring selection (Havrilla et al. 2018). Biocrust exposed to sand burial disturbance was more suitable than bare soil for the establishment and assembly of all three annual herbaceous species (Fig. 1c, d, e; Table 1). The occurrence of a sand burial disturbance event interfered with negative effect of moss crust that typically inhibits seed germination and enhanced the positive effect of growth promoting of all three herbs (Figs. 4 and 5). In this study, sand burial disturbance increased the germination of all species, especially when sand burial depth was high, which may be divided into two processes to explain that pattern. Firstly, seeds on the surface of moss crust are brought into contact with soil under sand burial pressure, thus exposing them to the required moisture conditions for germination. Secondly, moss and cyanobacterial crusts under sand burial disturbance are able to reduce evaporation, retain more moisture, and increase the temperature required for seed germination (Couradeau et al. 2016; Kidron and Tal 2012). Further, the seedling growth response of all three annual herb species to sand burial disturbance on biocrust was consistently positive, and this beneficial effect was bolstered by wetter conditions (Fig. 5). This outcome could be linked to less water infiltration into deep layer under frequent sand burial disturbances, which would later effectively prevent evaporation from biocrust and increase soil nutrients'content (Figs. 6 and 7). Also, the alleviation of competition for resources between the biocrust and the herb under drier conditions is a plausible contributing factor as well, suggesting that biocrust may facilitate the establishment of herbs when coupled with sand burial disturbance event. This could offer a novel pathway for ecosystem restoration in desert areas.

In many desert areas, biocrust is an important biological indicator of the reversal of desertification (Bowker et al. 2014, 2018) and sand burial is a common disturbance events that biocrust incurs (Jia et al. 2014). For example, in the Negev (Littmann and Ritter 1997) and the Namib (Bristow and Lancaster 2004), sand burial disturbance is often viewed negatively, or unwanted, in terms of ecological restoration construction. However, this study shows that biocrust (especially moss crust) under sand burial disturbance strengthened ecosystem recovery by facilitating the germination and growth of three annual herbaceous species. Of course, too deep and chronic sand burial would induce the death of plants if they cannot emerge from the buried sand (Maun 1998). In our study, when sand burial happens it is shorter in duration and shallower in depth, which is critical for the herb community to assemble and thrive.

Mechanism and ecological significance of biocrust and sand burial collectively promote annual herb assembly in arid sandy desert

Habitat improvement is one pivotal way of enabling the successful establishment and assembly of annual grasses, this resulting from the facilitation effects generated or the removal of inhibiting factors. In this study, biocrust and sand burial are natural phenomena that typically co-occur in sandy ecosystems, and their mutual complementary effects promote the successful establishment and assembly of annual herbaceous plants (Figs. 4 and 5). It is well known that water and nutrients are key resources and drivers of plant establishment in desert environments. However, in most desert ecosystems, their infertile sandy soils hardly provide enough water and adequate nutrient conditions for vascular plants; hence, biocrusts formed in this area are critical for increasing the water holding capacity and nutrient content of dryland soils. In general, biocrust's positive effect on vascular plant growth is attributed to its improved soil nutrient content and soil water retention (Zhao et al. 2016; Rodriguez-Caballero et al. 2018; Li et al. 2018; Su et al. 2021). Several studies have found that plant community assembly benefits from the availability of soil resources provided by biocrusts (Belnap et al. 2016; Chen et al. 2020). We did find, however, a negative effect of biocrust on vascular plant, in that herb seeds' germination was limited by biocrust, perhaps because of the higher competitive ability for water by biocrust than seeds (Kidron 2014). In natural conditions, as biocrust forms, the diversity and activity of animals increases in tandem (Li et al. 2011). Multiple mechanisms underlying the disturbance of biocrust facilitating seedling emergence have been proposed (Belnap et al. 2016). An intact biocrust may foster resistance to invasive alien plants by reducing resource availability to vascular plants (Belnap 2006). Disturbance may reduce competition for nutrients, water, space, and light between herbaceous plants and biocrust, which may partially explain that phenomenon (Zhang et al. 2016). The introduction and emphasis the effects of sand burial interference in this study, may provide a new promising aspect to disentangle the vague relations between biocrust and vascular plants.

Our results showed that the presence of both moss crust and cyanobacterial crust increase the daily water content of shallow soil, but the increased effect of cyanobacterial crust on the daily water content of shallow soil was not statistically significant (Fig. 6a), results consistent with those of most previous studies (Zhang et al. 2016; Adessi et al. 2018). Moreover, the presence of biocrust increases the water holding capacity of soil, especially when sand burial disturbances occur (Fig. 6b), which provides better water resources for seed germination and seedling growth of herbs. In addition, the presence of moss crust and cyanobacterial crust improved soil nutrient conditions (by further increasing TN, TP, TK, AP, AK, and SOM) (Fig. 7), which is consistent with other work (Barger et al. 2016). For example, Zhang and Belnap (2015) found that biocrust markedly increased the uptake of N and K by herbaceous plants in the Gurbantunggut Desert and their work revealed that soil nutrients are limiting factors for the early growth of desert herb species, especially AP and AK. More interestingly, the daily water content of the shallow soil covered by moss crust and cyanobacterial crust increased significantly with increasing depth of sand burial (Fig. 6a). Similarly, cyanobacterial crust and moss crust under sand burial disturbance apparently increased soil nutrient content (especially SOM) (Fig. 7). The better water and nutrient conditions for herbs colonizing sand burial patches facilitated their subsequent growth. Surprisingly, this differs from our previous findings, where sand burial significantly reduced the nutrient content of soil covered by biocrust (Liu et al. 2022). This discrepancy is likely linked to the shorter time and shallower depth of the sand burial treatment used in the present study.

A mechanistic model can to some extent express the relationships between sand burial disturbance of biocrust, topsoil processes, and herb species' establishment, assembly, and recruitment (Fig. 8). Bare sand is clearly not conducive to herb establishment and settlement. Biocrust improves moisture and nutrient conditions in the surface soil layer which is essential for the germination and growth of annual herbs, and promotes seedling growth, but inhibited seed germination due to competition for resources between biocrust and annual herbs (Kidron 2014). However, when the sand burial disturbance on biocrust happens, the nutrient and water conditions are increased considerably more and this also provides burial conditions for seeds exposed on the surface. The final outcome is the augmented germination and seedling growth of herb seeds, which should enhance

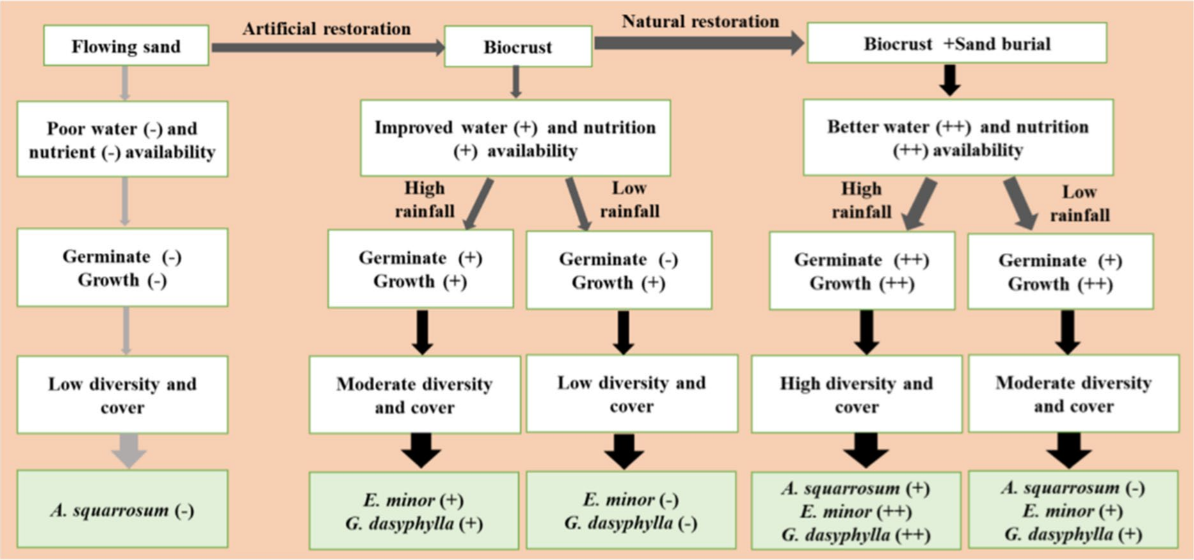

Fig. 8 Inferred mechanism, based on our study's results, by which biocrust and sand burial collectively promote annual herb community assembly in the revegetated area in the Tengger Desert. The -, +, and ++ represent the level of resource availability and germination and growth in the sequence of -<+<++

the establishment, settlement, assembly, and recruitment of seeds that are trapped by biocrust. This could explain the phenomenon of alien herbaceous species' entry into this ecosystem via exposed crusts among artificial sand-fixing shrubs in the Tengger Desert exposed to sand burial disturbance events. Likewise, it could provide a new timely reference for investigating and interpreting ecological restoration in other similar arid areas whose herb community assembly has similar trajectories or processes involved.

Our results indicate that sand burial disturbance to biocrust in the interspace among artificially planted shrubs contributes to the successful recruitment of annual herbaceous species. The formation and colonization of biocrust following plantation establishment magnifies the capture of dispersed herb seeds and simultaneously creates better moisture and nutrient conditions for their growth (Fig. 5); that was augmented by sand burial, besides providing suitable burial conditions for the germination of herb seeds (Fig. 4). This arguably enhances herbaceous diversity in the sand-fixing vegetation zone to some extent, which was witnessed by our field investigation shown in Fig. 1. In particular, the later successional stage moss crust was more favorable than earlier successional stage cyanobacterial crust to the recruitment success rate of the herbs *A. squarrosum*, *E.minor*, and *G. dasyphylla*. This can be partly explained by the fact that the deep sand burial caused by ant burrowing activities facilitated seed burial, infiltration of precipitation, and overall improvement of water and nutrient resources by biocrust. To a certain extent, this supplements the sand burial caused by the burrowing behavior of ants, leading to preferential infiltration flow that promotes water acquisition by deep-rooted shrubs (Li et al. 2011), especially for the restoration of sandy grasslands already originally scarce in herbaceous plants. The sand burial depths investigated in this paper are in the range of <5 mm, which is close to the average sand burial thicknesses caused by ant burrowing in the study area. However, in wind-prone areas with high speed winds, sand burial depth often exceeds the ability of annual herbs' bud and stem leaf to penetrate above the sand they are buried in, causing them to inevitably die (Sykes and Wilson 1990). This results in the widespread phenomenon of a dearth of annual herb plants in flowing sandy dunes (Kidron 2014).

Our results uncovered an interesting pathway or mechanism by which annual herbs could enter into sandy ecosystems (Fig. 8), demonstrating the importance of co-occurrence of biocrust and sand burial in shaping plant community structure, and providing a novel technique for ecological restoration that could be applied in the future to reverse desertification. The hospitable contribution arising from combining biocrust and sand burial to promote herb assembly may also be tailored as potential technology or technique suggestion for application in restoration practices. Artificially cultured cyanobacteria and moss biocrusts can be inoculated on a degraded sand surface, after which annual herb seeds and < 5 mm sand were sprayed, in that sequence, to mimic and trigger the natural restoration process of annual herb community establishment mediated by biocrust and sand burial. Of course, this restoration technique suggestion would be most effective in the rainy season given better performance of germination and growth of annual herbs under wetter conditions.

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Author contribution YHG, RLJ designed the research. YHG, RLJ, YZ, LNZ, WXY performed the experiments, YPL, YZ, YSW, HTY, LCL analyzed the data. YHG, RLJ, YZ,YLD and YPL wrote and participated to the revision of the manuscript.

Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval Not applicable.

Competing interests The authors declare that they have no conflict of interest.

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