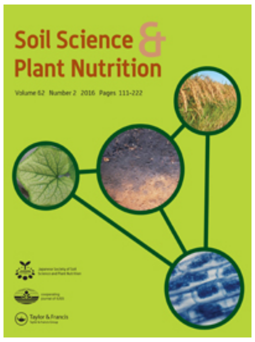

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ORIGINAL ARTICLE

Evolution of soil respiration depends on biological soil crusts across a 50-year chronosequence of desert revegetation

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ABSTRACT

Despite intensive study in recent decades, soil respiration rate (Rs) and its evolution accompanying vegetation succession remain perplexing. Using a 50-year chronosequence of sand-fixing revegetation in the Tengger Desert of China, we took intact soil columns of 20 cm in depth, incubated them at 12 levels of soil water content (0–0.4 m^3 m^{-3}) and at nine temperatures (5–45°C) in a growth chamber, and measured Rs. The results showed that Rs increased rapidly 15 to 20 years following revegetation but stabilized after 25 years. Rs for soils covered with moss crusts were markedly higher than those covered with algal crusts. Further, Rs correlated significantly with sand content (negatively) and fine particle contents (positively), and increased exponentially with increased soil organic matter (SOM) and total nitrogen (TN) contents. Soil texture had a stronger influence on Rs than did SOM and TN. Also, Rs increased linearly with increased coverage and depth of biological soil crusts, which had a more pronounced influence on Rs than did soil physicochemical properties. Our results suggest that the capacity of carbon sequestration likely increases during the 50-year period after revegetation because the linear increase in SOM outweighs the limited sigmoidal increase in Rs.

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KEY WORDS
sand-fixed dunes; soil organic matter; soil texture; the Tengger Desert

1. Introduction

Revegetation is a common and effective method to combat desertification in many arid regions of the world (Fullen and Mitchell 1994; Fearnehough *et al*. 1998). The adapted vegetation plays a vital role in soil rehabilitation, such as enhancing the soil carbon stock (Lal 2009) and production of desert ecosystems by stabilizing dune surfaces, preventing wind erosion and thus stabilizing the local desert ecosystem (Li *et al*. 2007). A non-irrigated revegetation system was established within the matrix of straw-checkerboards placed to stabilize sand dunes and to prevent the Baotou-Lanzhou railway from sand burial at the southeastern edge of the Tengger Desert of northern China (Qiu *et al*. 2004; Li *et al*. 2007). The initiation of revegetation on moving sand dunes (MSD) in different years beginning in the 1950s forms a 50-year chronosequence that is ideal for the study of ecological patterns and processes accompanying the succession of the plant-soil system (Fullen and Mitchell 1994; Li *et al*. 2007, 2012; Su *et al*. 2011; Zhang *et al*. 2012). Following revegetation on MSD, the increased water consumption led to a series of successions in the revegetation-soil system. The coverage of sand-fixed shrubs arrived at peak of 33% in about 15 years and then decreased to about 10% after 40 years, whereas natural invasive annual herbs increased their coverage with time of revegetation and dominated gradually on sand-fixed dunes (Li *et al*. 2007). Accompanying the succession of the vegetation and dustfall sedimentation, topsoil physicochemical properties recovered and biological soil crusts (BSCs) formed on the stabilized dune surface (Li *et al*. 2007). BSCs evolved from cyanobacteria crusts to mixed (green algae and diatoms) algal crusts, to lichen crusts and finally to moss crusts as time progressed, and displayed topographic differentiations due to micro-habitat difference after 25 years of revegetation (Li *et al*. 2010, 2012; Su *et al*. 2011; Zhang *et al*. 2012). Soil respiration rate (Rs), the flux of carbon dioxide (CO_2) from the soil to the atmosphere, is probably the least understood component of the terrestrial carbon cycle, and it may change the carbon sequestration potential of the soil (Raich and Tufekciogul 2000; Rey *et al*. 2011; Talmon *et al*. 2011). However, information is lacking on how Rs changes during the succession of the plant-soil system after dune stabilization (e.g., Zhang *et al*. 2013) and how it affects the carbon sequestration potential of the desert ecosystem.

Arid and semiarid lands are typically covered with discontinuous or patchy vegetation, and interspaces between vegetation are mostly covered by BSCs (Eldridge *et al*. 2002; Maestre and Cortina 2003; Belnap *et al*. 2005, 2006; Cable *et al*. 2011; Castillo-Monroy *et al*. 2011). Soil respiration from patches of BSCs mainly comes from microbial heterotrophs and autotrophic cryptogams, e.g., algae, lichens and mosses, which are responsible for a large proportion of landscape-scale CO_2 efflux due to the following reasons: (1) BSCs dominate the arid and semiarid regions, with more than 70% coverage (Belnap *et al*. 2005; Castillo-Monroy *et al*. 2011); (2) mosses, algae and cyanobacteria that comprise BSCs respond

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The supplementary material for this article is available online from

to rain and temperature pulses more rapidly than do vascular plants (Zaady *et al*. 2000; Eldridge *et al*. 2002; Sponseller 2007; Wilske *et al*. 2008; Thomas and Hoon 2010); and (3) compared with vascular plants, BSCs have a higher labile carbon content due to algal filaments, moss protonemata and rhizoids, and polysaccharides secreted by cyanobacteria, all of which are easily decomposable substrates for soil microbes (Thomas and Hoon 2010; Talmon *et al*. 2011). Thus, BSCs are expected to produce more important influences on microbial respiration than soil physicochemical properties in a water-limited ecosystem (e.g., Zaady *et al*. 2000; Castillo-Monroy *et al*. 2011; Zhang *et al*. 2013). In addition, soil texture, through changes in soil water, and nutrient and substrate availabilities, produces more profound influences on microbial respiration than do soil chemical properties such as soil organic matter (SOM) and total nitrogen (TN) (Austin *et al*. 2004; Cable *et al*. 2008; Potts *et al*. 2008; Rey *et al*. 2011; Talmon *et al*. 2011). Thus, BSCs are the most important factor impacting on Rs in water-limited ecosystems, followed by soil texture and soil chemical properties. Moreover, topographic differentiations of BSCs are supposed to have different effects on Rs, i.e., moss crusts have more labile carbon contents and thus have higher Rs rates than algal crusts do.

The focus of this paper is on the evolution of soil respiration in a 50-year revegetation chronosequence. Laboratory incubation of soil columns under varying soil water content (SWC) and temperature levels is considered a reliable method to characterize Rs (Davidson *et al*. 1998; Sponseller 2007; Wu *et al*. 2010). We studied soil respiration using intact soil columns sampled at 10 sites defining a gradient of ecosystem recovery: one site on MSD corresponding to time 0, eight sites on sand-fixed dunes (SFD) with an increase in time of recovery (e.g., 16–50 years after revegetation) and one reference steppe site (Ref) corresponding to undisturbed ecosystem, defined as a target for ecosystem recovery. The columns were incubated at different levels of SWC and temperature to measure Rs. We wanted to clarify: (1) how does Rs increase during the succession of the plant-soil system on dunes after stabilization? and (2) how do the changes in soil and BSC properties affect Rs? To address these questions, we posed the following hypotheses: (1) Rs rates increase with the succession of the plant-soil system after stabilization; (2) BSCs, soil texture and soil chemical properties have a decreasing importance on Rs; and (3) Rs dominated by moss crusts is higher than that dominated by algal crusts on SFD.

2. Materials and methods

2.1. Study sites

The Shapotou-Cuiliugou region is located at the southeastern edge of the Tengger Desert (37°32′–37°26′N, 105°02′–104°30′ E) at an altitude of 1300–1350 m above sea level. This area is typical of the ecotone between desertified steppe and sandy desert (Li *et al*. 2007). Annual mean temperature is 10.0°C, January mean temperature is −6.9°C and July mean temperature is 24.3°C. Annual mean precipitation is 186 mm and about 80% of this falls between May and September. Annual mean wind velocity is 2.9 m s^{-1}. Annual potential evaporation is about 2900 mm (Li *et al*. 2004). The main soils are Aridisols and Psamments based on the soil classification by United States Department of Agriculture (USDA) Soil Taxonomy (Soil Survey Staff 1993), and composed of fine sands with very uniform physicochemical properties. The Shapotou area is characterized by high, dense and continuous reticulate chains of barchan dunes that incline from northwest to southeast, representing a step distribution, with relative height difference of 15–20 m. Natural vegetation is dominated by *Hedysarum scoparium* Fisch. & C.A. Mey and *Agriophyllum squarrosum* (L.) Moq, with a cover of approximately 1% (Li *et al*. 2004).

To protect the Baotou-Lanzhou railway crossing the Tengger Desert, a non-irrigated vegetation protection system was established by planting xerophytic shrubs within the matrix of straw-checkerboards on moving sand dunes in 1956 and over the subsequent years of 1964, 1981, 1987 and 1990 (Li *et al*. 2004, 2007; Qiu *et al*. 2004). The sand-fixing practice resulted in herbs gradually settling on the dunes after the revegetation (Li *et al*. 2004). The protective vegetation has also promoted the deposition of air-borne dust onto the dune surface, and as more and more microorganisms propagated, BSCs developed (Li *et al*. 2007). After 25 years, moss and algal crusts dominate the sites. Moss crusts, primarily composed of *Bryum argenteum* Hedw. and *Didymodon constrictus* (Mitt.) Saito., mainly occur at windward (north-facing slopes) and hollow locations on the dunes. Cyanobacterial-algal crusts, mainly composed of filamentous cyanobacteria (accounting for 45.5%), green algae (18%), diatoms (27%) and *Euglena* sp. (9%), predominantly colonize the crest and leeward (south-facing slopes) (Li *et al*. 2010). For photos of BSCs at different topographic locations at SFD, refer to the Supplementary material, Fig. S1.

In the Cuiliugou area, west of Shapotou (the location of our stable-dune reference site), the common BSCs in the area include algae and cyanobacteria. The dominant species are *Anabaena azotica* Ley, *Microcoleus vaginatus* (Vauch.) Gom., *Hydrocoleus violaceus* Martens. and *Lyngbya crytoraginatus* Schk. (Li *et al*. 2010). Due to historical long-term dustfull sedimentation on the dune surface, the Ref site has deeper topsoil with improved physicochemical properties compared to sites on SFD (Zhang *et al*. 2012). The only exception is that the Ref site was not enclosed until 2002 and suffered from grazing, resulting in low coverage and less developed BSCs. In any case, Ref was defined as a target for ecosystem recovery to compare with different steps of recovery in the study.

2.2. Field methods

In Shapotou, eight sites on SFD (with a variety of time-since-stabilization and topographic locations) and one site on an MSD were selected for the study. A reference site (Ref) was set up on a north-facing slope (5–15°) of a stable dune in Cuiliugou. At the 10 sites, BSC coverage, BSC and subsoil depth, and shrub and herbaceous species coverage were measured in September 2006 (Table 1). In December 2006, soil samples of the 0–20 cm soil depth were collected at each site to analyze particle size (sand, silt and clay contents), SOM and TN. The detailed methods for measurements of BSCs, plants and soil physicochemical properties can be found in

Table 1. Study sites and their biological soil crusts (BSCs) and vascular plant characteristics.

Site classification								
Code	Year revegetated	Age of sand-fixed dunes (year)	Position	Moss coverage (%)	Algal coverage (%)	Depth of BSC and subsoil (cm)	Herb cover (%)	Shrub cover (%)
MSD	Moving sand dunes	0	Windward	0	0	0	< 1	< 1
A16[a]	1990	16	Hollow	2.3 ± 1.2	32.2 ± 5.3	1.23 ± 0.31	11.8 ± 10.0	30.7 ± 7.9
A19	1987	19	Windward	10.6 ± 2.4	33.8 ± 3.6	2.03 ± 0.54	7.2 ± 3.6	21.3 ± 18.6
A25	1981	25	Leeward	11.5 ± 3.6	60.1 ± 7.6	2.29 ± 1.12	17.3 ± 10.2	5.6 ± 4.3
M25	1981	25	Windward	33.4 ± 7.8	42.5 ± 8.5	2.50 ± 0.62	10.7 ± 5.0	6.5 ± 3.2
A42	1964	42	Crest	11.2 ± 8.9	61.2 ± 10.3	2.32 ± 0.63	12.5 ± 2.4	7.8 ± 3.7
M42	1964	42	Windward	78.3 ± 6.8	11.6 ± 2.4	3.89 ± 0.54	5.3 ± 1.2	6.7 ± 5.3
A50	1956	50	Crest	22.5 ± 3.7	56.4 ± 8.9	3.06 ± 0.63	15.8 ± 5.7	8.7 ± 3.3
M50	1956	50	Windward	83.7 ± 12.5	9.2 ± 4.3	3.69 ± 1.00	7.5 ± 0.7	12.0 ± 3.6
Ref	Reference site	/	North-facing slope	0.9 ± 0.5	19.4 ± 7.6	50.0 ± 12.1	15.3 ± 11.4	12.6 ± 7.7

[a]The capital letter of a site code refers to the type of BSCs on the sand-fixed dunes (A: algal crusts, M: moss crusts); the double-digit number represents the age of revegetation. Data extracted from Zhang *et al*. (2012).

Zhang *et al*. (2012). Also, the water-holding capacity of 10 sites was measured using a pressure chamber (ceramic plate extractor Cat. #1500, Soilmoisture Equipment Co., Santa Barbara, CA, USA). Field capacity (SWC at −0.3 bar) at MSD was the least with 0.03 m^3 m^{-3} and that at Ref was largest with 0.25 m^3 m^{-3}; those at SFD sites ranged from 0.04 m^3 m^{-3} (A19) to 0.15 m^3 m^{-3} (M50). Wilting point (SWC at −15 bar) had less variation than field capacity; the corresponding values were 0.008, 0.016 and 0.036 m^3 m^{-3} of SWC for MSD, SFD and Ref, respectively.

At each site, three random samples of intact soil cores were collected in September and December 2006 and April 2007. Due to drought and poor adhesion of the sandy soil, water was applied prior to sampling. After the water had completely infiltrated into the soil profile, a polyvinyl chloride (PVC) column (inner diameter of 10 cm and height of 22 cm) was pushed into the soil to 20 cm in depth. Then the soil column was taken out and the bottom was covered tightly with a plastic cap. Also, soil samples at 0–20 cm depth were taken to measure SWC. After the soil columns were taken back to the laboratory, they were weighed immediately (each PVC column and the matched bottom lid were also weighed prior to sampling). Prior to incubation, all soil columns were placed outdoors to dry for at least a month.

2.3. Incubation experiment in laboratory

In this experiment, volumetric SWC gradient and temperature gradient were established. The water gradient included 12 levels of SWC (0.01, 0.02, 0.03, 0.04, 0.06, 0.08, 0.10, 0.15, 0.20, 0.25, 0.30 and 0.40 m^3 m^{-3}), and the temperature gradient spanned nine levels from 5 to 45°C in 5°C increments. For the three soil columns collected in September 2006 at each site, one did not receive water and was used as a control, while the other two were sprayed with distilled water. The second column was treated randomly as 0.01, 0.02, 0.03, 0.04, 0.06 and 0.08 m^3 m^{-3} of SWC, and the third was treated randomly as 0.10, 0.15, 0.20, 0.25, 0.30 and 0.40 m^3 m^{-3} of SWC. During water application, the soil column was placed on an electric balance with a precision of 0.01 g, and water was sprinkled gently on the soil surface. Weights of soil columns were recorded and columns were placed inside a plant growth chamber (Thermoline L + M, Thermoline Scientific Equipment Pty. Ltd, Australia) to incubate for 10 hr at the designated temperature, and then soil respiration rates (Rs) were measured using a LI-6400 Portable Photosynthesis System attached to a 6400–09 soil chamber (LI-COR, Inc., Lincoln, Nebraska, USA; Fig. S2). For each measurement, Rs values were recorded at 4-s intervals over an 80-s period, once steady-state conditions were achieved within the chamber. After Rs measurement at the designated temperature, the soil columns were moved outdoors for recovery for about 14 hr. When the Rs measurement at a designated soil temperature was completed, the above steps were repeated to finish measurements at all nine temperature levels (i.e., in 9 d), including two levels of SWC per round. From the second measurement, the control soil column was also applied with distilled water to maintain the weight during measurements involving all nine levels of the temperature gradient. It took 54 d to complete the measurements for all the samples collected in September 2006 (six rounds of the nine-level temperature gradient). After that, soil columns collected in December 2006 and April 2007 were treated by repeating the above steps.

The range of temperature in our study corresponded well to that of the field condition, but not for the SWC levels (Zhang *et al*. 2013). Most SWC values were less than 0.10 m^3 m^{-3}, and the maximum (0.23 m^3 m^{-3} of SWC) occurred at M25 site. Therefore, the control soil column we adopted in our incubation encompassed a wide range at low water conditions. During the experiment, air humidity and CO_2 concentration in the plant growth chamber were set to constant values of 50% and 380 μmol mol^{-1}, respectively. The incubation and measurement were conducted completely in the dark, so photosynthesis by crustal organisms was ignored. However, recovery of soil columns in the outdoors led to cryptogams assimilating atmospheric CO_2 to supplement soil carbon pool (e.g., Wilske *et al*. 2008), and ensured that the soil carbon pool is not easily consumed through Rs measurement. When all measurements were finished, the bulk soil was removed from the PVC columns, dried at 105°C for 48 hr and weighed to calculate the actual SWC.

2.4. Data processing and modeling of Rs

To facilitate data processing, the original 12 levels of SWC were merged into six (abbreviated W1, W2, W3, W4, W5 and

W6), i.e., the adjacent two levels were combined. The descriptive statistics of SWC within the six-level gradient are shown in the Supplementary material, Table S1. Then, a general linear model was performed on Rs, with sampling date, age of sand-fixed dunes, type of BSCs, temperature and soil water level as independent variables. The data included three sampling dates (September and December 2006, and April 2007), seven age classes of SFD [one MSD site, five SFD sites (data of two sites revegetated in the same year were merged into one) and one Ref site; here we consider MSD as having a minimum age (of zero) and the Ref site as having a maximum age], three types of BSCs (no crusts, algal crusts and moss crusts), nine levels of temperature and six levels of SWC.

To consider the effect of age of SFD on Rs, the data were measured at the same topographic location on MSD and SFD sites. These sites were MSD, A16, A19, M25, M42 and M50 (A: algal crust, M: moss crust; number refers to the age of dune revegetation), representing 0, 16, 19, 25, 42 and 50 years of dune revegetation, respectively. As we used the same topographic location, uniform aeolian sandy soil and the same method of dune fixation in different years, the space-for-time substitution approach in our work meets the assumption of chronosequence (Johnson and Miyanishi 2008). The Rs data measured in soil columns extracted from SFD chronosequence at nine temperature levels and six soil water levels were fitted by a Boltzmann's sigmoidal equation, because the parameters of the equation have specific physical meaning:

$$Rs = \frac{A_1 - A_2}{1 + e^{(t-t_0)/dt}} + A_2 \quad (1)$$

where t is the age of SFD ($0 \le t \le 50$ years), Rs is soil respiration rate (μmol CO_2 m^{-2} s^{-1}), t_0 is the center, dt is the width, A_1 is the initial Rs value: t (−∞) and A_2 is the final Rs value: t (+∞). The Rs value at t_0 is halfway between the two limiting values A_1 and A_2: Rs (t_0) = (A_1 + A_2)/2. The Rs changes drastically within a range of the t variable; the width of this range is approximately dt. A_2 represents the highest potential Rs of the SFD and is compared with Rs of the Ref using the T-test. Also, A_2 and the ratio of A_2 to Rs of the Ref were compared among temperature and water levels using one-way analysis of variance (ANOVA).

To test the effects of BSCs on Rs, SFD sites of more than 25 years of age covered by different types of BSCs (i.e., A25 and M25, A42 and M42, A50 and M50) were selected. Rs of sites of the same age but with different BSCs were compared at four temperature levels (10, 20, 30 and 40°C) and six SWC levels using T-test. In total, 72 pairs of comparisons were conducted. Also, soil physicochemical properties (sand content, fine particle content, SOM and TN) of the SFD sites with the same age but different topographic locations covered by different types of BSCs were compared using one-way ANOVA. The relationships between soil physicochemical properties and age of SFD were fitted with linear or sigmoidal equations. Also, using averaged Rs as dependent variables, and soil sand content, fine particle content (silt + clay contents), SOM, TN, BSC coverage, and depth of BSCs and subsoil as independent variables, the linear or exponential equations were fitted. The best models were selected based on R^2 and statistical significance.

For the general linear model and all ANOVAs, multiple comparisons of means were conducted at α = 0.05 level using Tukey's post hoc test. Data were transformed as needed to ensure that they met normal distribution requirements. Statistical analyses and graphic plotting were conducted using SPSS 13.0 for Windows (SPSS, Chicago, IL, USA) and Origin 7.0 (OriginLab Corporation, Northampton, MA, USA), respectively.

3. Results

3.1. General behavior of Rs of samples from the study sites

With the general linear model, we found significant differences in Rs among temperature levels, among SWC levels, among age classes of SFD and among BSC types, but not among sampling dates. Also, all two- and three-way interactions were highly significant ($P < 0.001$) except for interaction among age, BSCs and temperature. Among the two- and three-way interactions including sampling date, the interaction was highly significant ($P < 0.001$) only when SWC was included, indicating that SWC treatment on soil columns is dependent on sampling date. The four- and five-way interactions were not significant except for the one case not including sampling date (Table S2).

Rs of the MSD (0.187 μmol CO_2 m^{-2} s^{-1}) was the lowest and was significantly lower than those of the SFD of 19 years or older and that of the Ref (Fig. 1). Rs of the Ref was the highest (0.462 μmol CO_2 m^{-2} s^{-1}) and was significantly higher than those of the SFD of less than 25 years of age. Also, Rs values of the SFD of 16 and 19 years of age were significantly lower than those of the SFD of 25 years or older. Rs of the MSD without crust cover was significantly lower than those of soil columns covered with BSCs, and also Rs of soil columns dominated by algal crusts (0.356 μmol CO_2 m^{-2} s^{-1}) was significantly lower than that of soil columns dominated by moss crusts (0.419 μmol CO_2 m^{-2} s^{-1}). Rs for the six SWC levels peaked at W5 (SWC averaged 0.226 m^3 m^{-3} and ranged from 0.178 to 0.266 m^3 m^{-3}) and showed significant differences among them except for W4 and W6. Rs increased exponentially with increased temperature and had significant differences between adjacent levels except for the four lowest temperature levels.

3.2. Rs in relation to the age of the sand-fixed dunes

With the aging of the SFD, the values of Rs under different water and temperature regimes all showed a slow initial increase up to 15 years after the establishment of sand-fixed vegetation, and then a rapid increase at 15 to 20 years of age (Fig. 2). After 25 years, Rs tended to a constant value and was not affected by the age of the SFD; Rs in W5 even surpassed the level of reference. The sigmoidal function (1) modeled the relationship between Rs and age of SFD very well, as indicated by the averaged R^2 of 0.564 and by the fact that all functions reached highly significant levels ($P < 0.001$; Table S3). We found that parameter t_0 averaged 17.8 years and ranged from 12.3 to 24.6 years, and the width of this range (dt)

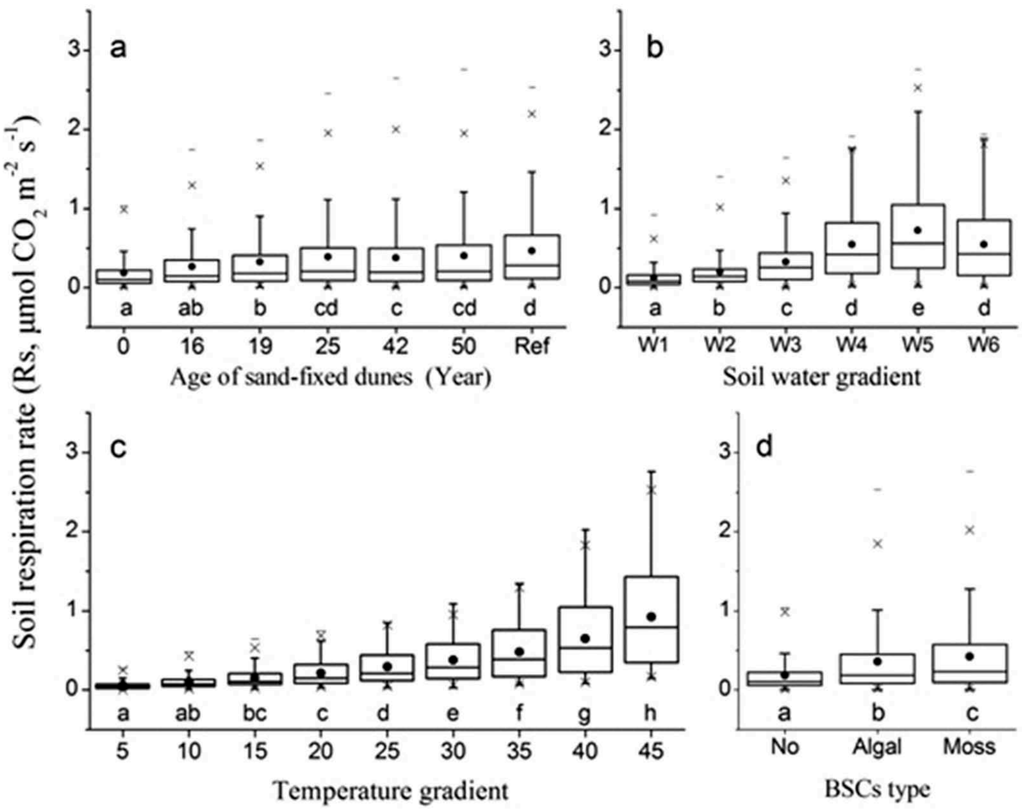

Figure 1. Soil respiration rate as a function of (a) age of sand-fixed dunes (including the reference site, Ref), (b) soil water content, (c) soil temperature (in °C) and (d) type of biological soil crusts (BSCs). For all box plots, filled dot denotes mean; in-box line denotes median; extended whisker is for standard error (SE); box range covers the first and third quartiles; product sign ("×") stands for 99% confidence limit; and the bars are for maximum and minimum. Age of sand-fixed dunes in (a): 0 refers to MSD; 16 and 19 refer to A16 and A19 sites; 25, 42 and 50 include of data of two sites revegetated in same year (i.e., A25 and M25, A42 and M42, A50 and M50). Type of BSCs in (d): no crust shows data of MSD; algal crusts show data of A16, A19, A25, A42, A50 and Ref sites; moss crusts show data of M25, M42 and M50 sites. Different letters in the same panel mean significant differences at the $P < 0.05$ level.

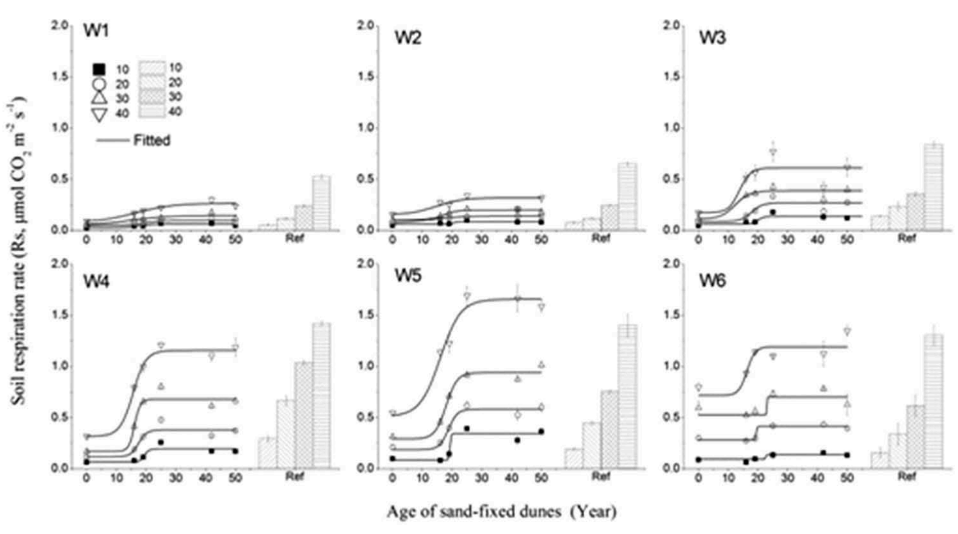

Figure 2. Relationships between soil respiration rate (Rs) and the age of sand-fixed dunes (including the reference site) within a four-level temperature gradient (10, 20, 30 and 40°C) and a six-level soil water gradient (W1, W2,…W6; averaged soil water content (SWC) values were 0.014, 0.036, 0.071, 0.130, 0.226 and 0.352 m^3 m^{-3}, respectively; see Table S1). Data are shown as means ± standard error (SE).

averaged 2.2 years, meaning that Rs increased rapidly for the 17–19 years after the establishment of sand-fixed vegetation.

The highest potential Rs of the SFD (A_2) and Rs of the Ref did not differ significantly (T = −1.81, $P = 0.076$), confirming our results that Rs of the SFD older than 25 years tended to reach a constant value approaching the value of the Ref. A_2 increased exponentially with increasing temperature (F = 16.0, $P < 0.001$), and was significantly affected by SWC (F = 15.4, $P < 0.001$), peaking at W5 of the SWC gradient. Also, the ratio of A_2 to Rs of the Ref was significantly affected by SWC levels

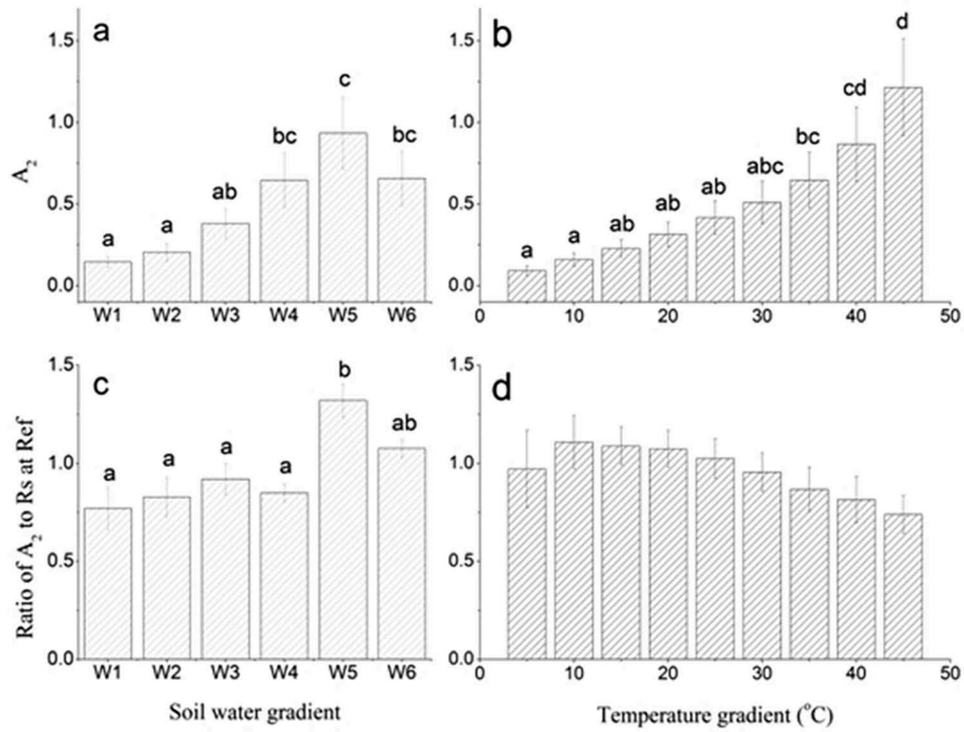

Figure 3. The highest potential soil respiration rate (Rs) at sand-fixed dunes (A_2) obtained by the sigmoidal function (Equation 1) at different levels of (a) soil water content and (b) temperature, and the ratio of A_2 to Rs at the reference site (steppe) in relation to (c) soil water content and (d) soil temperature. Data are shown as means ± standard error (SE) with different letters in the same panel denoting significant differences at the $P < 0.05$ level.

($F = 7.44$, $P < 0.001$) and peaked at W5 of the soil water gradient (Fig. 3).

3.3. Effect of biological soil crusts (BSCs) on soil respiration (Rs)

Seventy-two comparisons of Rs between different types of BSCs on SFD of the same age were made (Fig. 4). Soil columns dominated by moss crusts had significantly higher Rs than those dominated by algal crusts in 45 pairs, while 25 pairs showed no significant difference in Rs between the two types of BSCs. Soil columns dominated by moss crusts had significantly lower Rs than those with algal crusts in only two pairs.

3.4. Soil physicochemical properties in relation to the age of the sand-fixed dunes

Soil physicochemical properties showed remarkable evolutionary patterns with the increasing age of the SFD. Fine particle content (silt + clay content) followed a sigmoidal trend with SFD age, increasing from 0.7% at the MSD site to 23.4% at the M50 site, and was significantly lower than the value at the Ref site (40.4%; Fig. 5). Twenty-five years after the initial stabilization, the windward side of SFD dominated by moss crusts had significantly higher fine particle content and significantly lower sand content than the leeward or crest covered by algal crusts (fine particle contents: $F = 17.0$, $P < 0.001$; sand content: $F = 8.46$, $P = 0.005$). SOM showed a significant and linearly increasing trend in the 50-year chronosequence, from 0.62 g kg^{-1} at the MSD site to 1.96 g kg^{-1} at the M50 site, and was significantly lower than the value of the Ref (4.58 g kg^{-1}). Similar to SOM, TN also showed a significant and linearly increasing trend with SFD age, although no significant topographic differences were found for SOM or TN.

3.5. Relationships between averaged Rs with soil and BSC properties

Soil respiration was tightly correlated with soil and BSC properties based on determination coefficients and significance (Fig. 6). Rs correlated negatively with sand content and positively with fine particle content, and increased exponentially with increased SOM and TN contents. It appears that soil texture had a stronger influence on Rs, considering the higher R^2 values and higher levels of statistical significance than those of the correlations of Rs with SOM and TN. Also, averaged Rs increased linearly with increased coverage of BSCs and depth of BSCs and subsoil when the Ref site was excluded (due to low BSC coverage and greater depth of BSCs and subsoil as compared to the SFD).

4. Discussion

Establishment of sand-fixing revegetation with straw checkerboards on moving sand dunes in the Tengger Desert has facilitated dustfall accumulation and BSC development, and thus improved topsoil physical, chemical and biological properties (Fearnehough *et al*. 1998; Li *et al*. 2007; Su *et al*. 2011; Zhang *et al*. 2012). The change in BSCs and soil properties

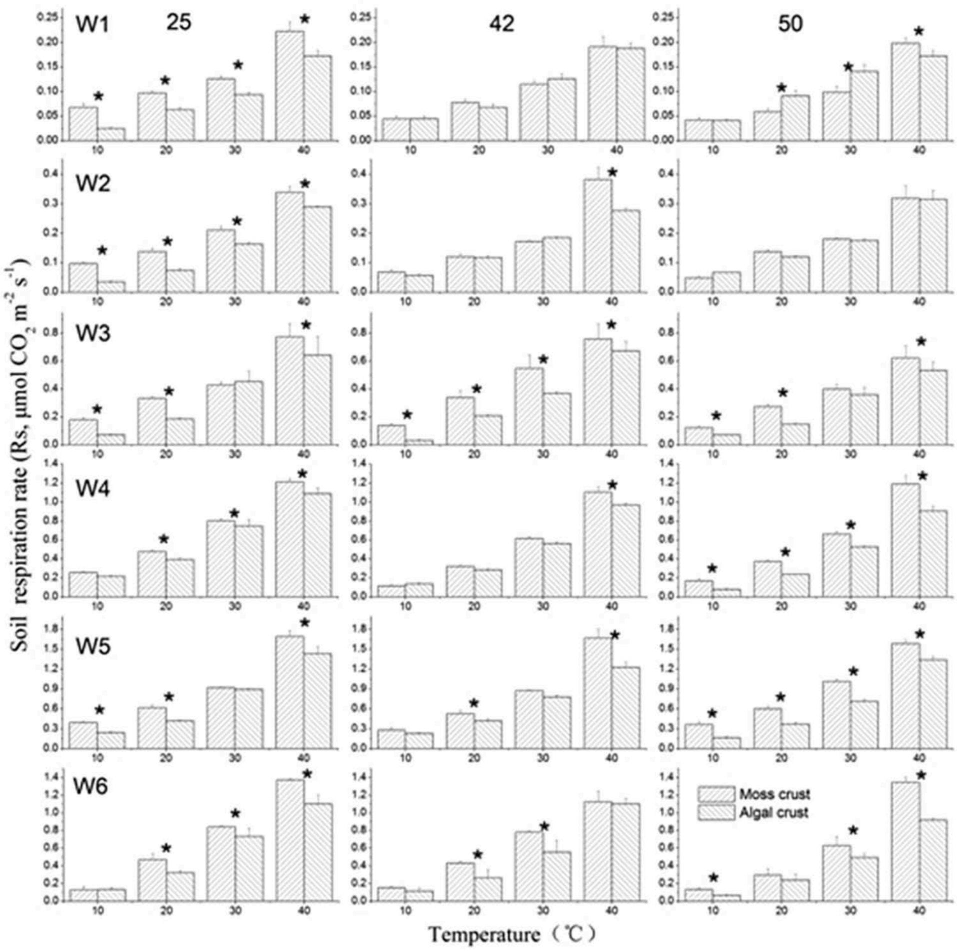

Figure 4. Comparison of soil respiration rate (Rs) measured on soil columns collected from the sand-fixed dunes of the same age (25, 42 and 50 years) but covered by different types of biological soil crusts (moss or algal crust) in a four-level temperature gradient and a six-level soil water gradient (W1, W2,…W6). Data are shown as means ± standard error (SE) with the symbol "*" denoting significant difference at the $P < 0.05$ level.

combined with the succession of sand-fixing revegetation has improved soil functions such as Rs.

Following revegetation on moving sand dunes, the coverage and biomass of shrubs peaked in about 15 years, and began to decrease thereafter (Li *et al*. 2004). The annual herbaceous species dominated over the deep-rooted shrubs after 30 years (Li *et al*. 2004). The stage in which Rs had the fastest recovery rates (15–20 years of age) corresponded well to the stage in which revegetated shrubs were dying (Fig. 2), indicating that the soil was receiving abundant shrub litter for decomposition. After 25 years of revegetation, Rs tended to reach a constant value approaching that of the Ref (Fig. 2 and 3), at which stage annuals gradually dominated on SFD, e.g., annual stage. It is likely that the soil was receiving stable litter input from shrubs and annuals and thus exhibited stabilized respiration.

The recovery of soil respiration differed from that of soil physicochemical properties, most of which showed the fastest recovery over the initial 15 years (Li *et al*. 2007). Also, an earlier study at our sites showed that oxidase activities, such as phenol oxidase and catalase, had the fastest recovery during the initial 19 years (Zhang *et al*. 2012), a trend different from that of Rs. However, the stage in which activities of hydrolases, such as α-amylase, alkaline phosphohydrolase and sucrase, had the fastest recovery rates (19–25 years; Zhang *et al*. 2012) corresponded well to the fastest recovery of Rs (Fig. 2), suggesting that the decomposition of fresh (shrub) litter was the main reason for elevated Rs at this stage of ecosystem recovery.

A report on carbon fixation of BSCs in the same 50-year chronosequence suggested that net photosynthetic rate and annual carbon fixation of cyanobacterial-algal crusts showed increasing linear and exponential trends, respectively, with recovery time (Su *et al*. 2011). Also, net photosynthetic rate and annual carbon fixation by BSCs were correlated significantly with crust cover. These findings support our results that Rs increased linearly with BSCs coverage (Fig. 6). However, different from the recovery of Rs, annual carbon fixation showed a slow recovery rate in 15 to 26 years after revegetation and a high recovery rate in 43 to 51 years at our study site (Su *et al*. 2011). From the same site, Li *et al*. (2012) also found that annual carbon fixation by lichen-moss crusts dominating the late successional stage more than doubled that of the cyanobacterial-algal crusts dominating the early successional stage (26.8 vs. 11.4 g C m^{-2} yr^{-1}). This implies that the carbon fixation capacity of the plant-soil system does not decrease with succession in spite of a decrease in vascular vegetation coverage. Also, carbon uptake by BSCs likely outweighed the

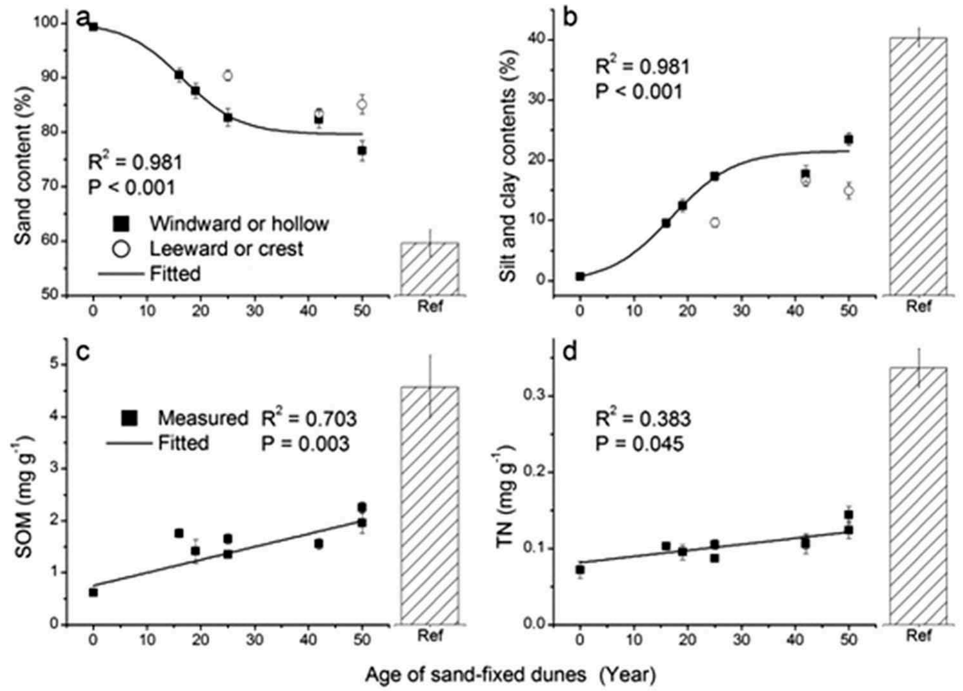

Figure 5. Relationships between soil physicochemical properties and the age of sand-fixed dunes (SFD). For (a) sand content and (b) silt and clay contents, only data from 25-year-old windward SFD were used because of significant differences between topographic locations. For (c) soil organic matter (SOM) and (d) total nitrogen (TN), averaged data of topographic locations at 25-year-old SFD were used because of no significant difference between them. Data are shown as means ± standard error (SE).

respiratory losses, as indicated by the linear increase in SOM across the 50-year chronosequence (Fig. 5). Together with the limited sigmoidal increase in Rs (Fig. 2), our results suggest that the capacity of carbon sequestration likely increases with the succession of the sand-fixing revegetation.

BSCs affect Rs through their high labile organic carbon input, e.g., polysaccharides secreted by cyanobacteria to the soil (Thomas and Hoon 2010; Talmon *et al*. 2011). With the development of SFD, coverage and depth of BSCs increased, which were coupled linearly with Rs (Fig. 6). This indicates that BSC recovery was important for the recovery of Rs. Generally, with the increase in coverage and depth of BSCs (especially BSC depth), the soil texture changes due to dustfall settlement on the dune surface (Fearnehough *et al*. 1998; Li *et al*. 2007; Zhang *et al*. 2012). However, when BSC coverage reaches a certain level, for example 70% at SFD sites of 25 years of age (M25 and A25), soil CO_2 efflux is likely mainly fueled by carbon input by BSCs (Li *et al*. 2012). This could be the main reason why Rs of the SFD sites of more than 25 years of age tended to a constant value approaching that of the Ref (Fig. 2 and 3), indicating that 25 years could be an age threshold marking the stationary soil respiration status of the SFD in the Tengger Desert. Soil columns from the windward side of SFD had significantly higher Rs than those from the leeward side and crests on dunes stabilized in the same year (Fig. 4), suggesting the impact of the composition and coverage of BSCs on Rs. Generally, the windward sides of SFD of more than 25 years of age had higher coverage and depth of BSCs, were dominated by moss crusts (Table 1), and had fine-textured surface soil as well (Fig. 5) compared to leeward sides or crests of SFD of the same age. Compared to algae, moss species have a higher biomass (Li *et al*. 2010, 2012), and thus more litter input to the soil. Also, this supports our third hypothesis that soil covered with moss crusts has higher Rs rate than that dominated by algal crusts.

Soil respiration was influenced differently by various soil physical and chemical properties. It increased significantly and linearly with increased fine particle content. Recent studies in water-limited ecosystems have shown that, through changing soil water, nutrient and substrate availabilities, soil texture would lead to changes in soil processes, especially Rs (Austin *et al*. 2004; Cable *et al*. 2008; Potts *et al*. 2008; Rey *et al*. 2011; Talmon *et al*. 2011). This supports the "inverse-inverse texture" hypothesis; i.e., soil microbial activity should be higher on fine-textured soils because of enhanced water-holding capacity and high nutrient availability, especially if these resources are concentrated in the surface layers (e.g., BSC formation and development on dune surfaces) where the highest density of soil microbes occurs (Austin *et al*. 2004; Cable *et al*. 2008). Besides, change in soil texture on SFD was involved in topographic location, e.g., windward sides accumulated more fine soil particle than leeward sides or crests did (Fig. 5). This is a possible reason why moss crusts prefer to form on the windward side due to its high water-holding capacity and nutrient availability, and thus higher Rs compared to the leeward side or crest. However, our finding of the significant exponential relationships between Rs and soil chemical properties, such as SOM and TN, is new. Our results show that SOM and TN (as indicators of soil nutrient availability) exhibited a linearly increasing trend in the 50-year revegetation chronosequence (Fig. 5). However, Rs increased linearly during the initial 25 years, after which Rs became similar among three older

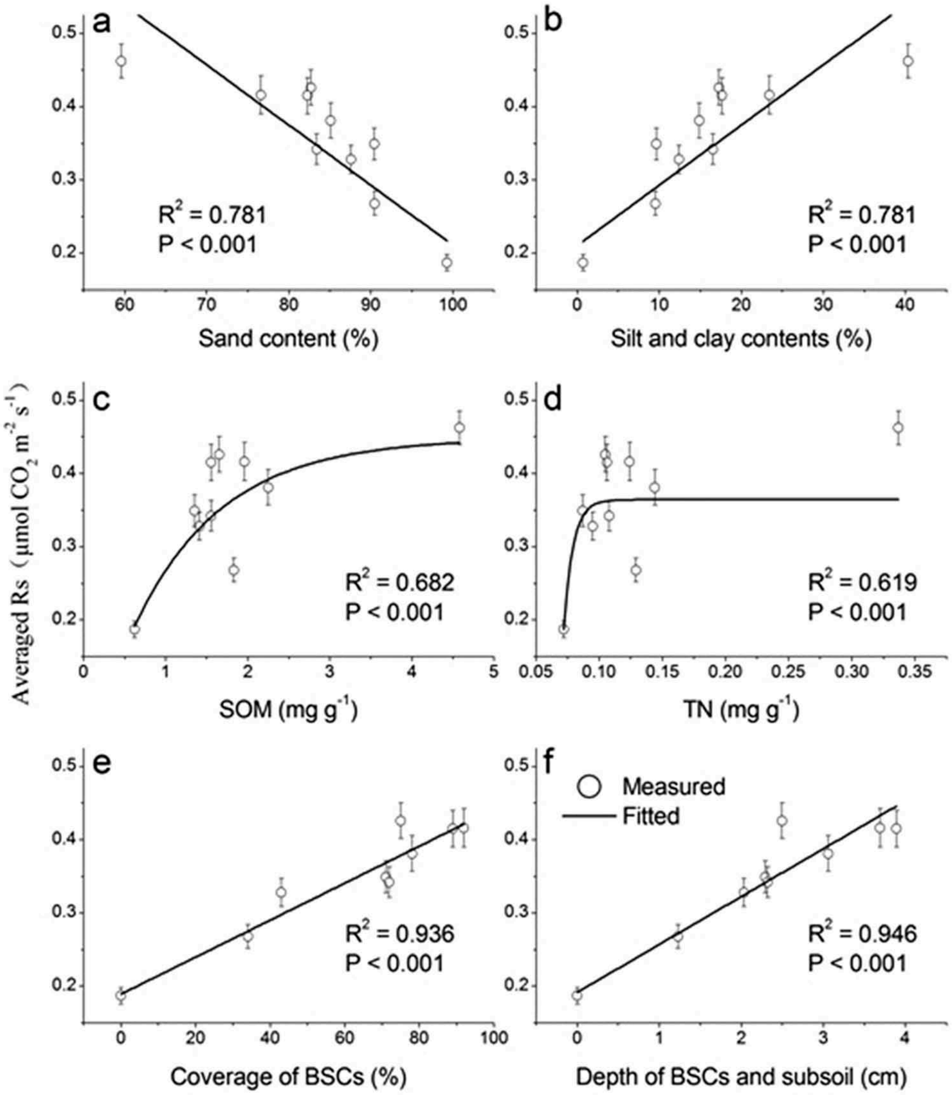

Figure 6. Relationships between average soil respiration rate (Rs) and (a) sand content, (b) silt and clay contents, (c) soil organic matter (SOM), (d) total nitrogen (TN), (e) coverage of biological soil crusts (BSCs) and (f) depth of BSCs and subsoil. In modeling the relationships between averaged Rs and BSCs properties, the reference site (Ref) was excluded due to lower BSC coverage and much greater depth of BSCs and subsoil than SFD. Data are shown as means ± standard error (SE).

SFD sites of 25, 42 and 50 years and approached that of the Ref (Fig. 2). This asymptotic behavior of Rs was further confirmed by the numerical similarity between the highest potential Rs of the SFD (A_2) and Rs of the Ref (Fig. 3). Overall, our results indicate that soil texture has stronger influence on Rs than on soil chemical properties, verifying our second hypothesis.

Our experiment showed that sampling date has no influence on Rs. The result did not support the former theory that BSCs are very dynamic and their composition can change in a period of months, as shown in North America (Belnap *et al.* 2006). The limited effect of sampling date in our experiment may be attributed to the fact that the sampling dates were from autumn to spring, a period characterized by scarce rainfall and low temperature, which inhibited BSC growth. However, the interaction between sampling date and SWC treatment on soil columns was very significant. Many field observations showed that, in comparison to wet soil, dry soil responds more sensitively in Rs to rainfall pulses or increasing SWC (Sponseller 2007; Cable *et al.* 2008; Talmon *et al.* 2011; Zhao *et al.* 2014). This is confirmed in our study as the driest soil collected in December 2006 (SWC = 0.01 m^3 m^{-3}) also had a more sensitive response in Rs to soil water treatment, compared with soils collected from two wetter periods (SWC of 0.11 and 0.08 m^3 m^{-3} for September 2006 and April 2007, respectively).

5. Conclusions

The establishment and succession of sand-fixing revegetation on moving sand dunes profoundly influenced soil respiration (Rs) due to BSC formation. Rs increased rapidly in the 15 to 20 years after dune revegetation, but stabilized after 25 years. The unique aspect of this study is that Rs exhibited an exponential relationship with SOM and a linear relationship with soil fine particle content. However, SOM shows an increasing linear trend during the 50-year sand-fixed revegetation chronosequence, implying that the capacity for carbon sequestration likely increases with succession of the sand-fixing revegetation. The result emphasizes that revegatation practices implemented in deserts have vital roles in soil rehabilitation and increasing carbon sequestration capacity with succession of revegetation (Lal 2009). Alternatively, BSC formation and development on dune surfaces are the key to the recovery of Rs in the 50-year chronosequence. Meanwhile, soil texture affects Rs by changing soil water, nutrient and substrate availabilities which is universal in water-limited ecosystems (e.g., Austin *et al.* 2004; Cable *et al.* 2008; Potts *et al.* 2008; Rey *et al.* 2011; Talmon *et al.* 2011), and more research is needed to clarify the underlying mechanisms.

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