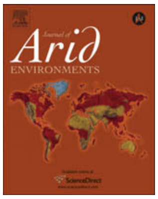
Journal of Arid Environments 73 (2009) 828–833

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv



Comparative study of nitrogenase activity in different types of biological soil crusts in the Gurbantunggut Desert, Northwestern China

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ARTICLE INFO

Article history:
Received 30 January 2008
Received in revised form
10 December 2008
Accepted 3 April 2009
Available online 21 May 2009

Keywords:
Acetylene reduction
Ecological function
Lichen-dominated crust
Nitrogen fixation

ABSTRACT

Biological soil crusts cover large areas of the Gurbantunggut Desert in northwestern China where they make a significant contribution to soil stability and fertility. The aim of this study was to quantify the potential nitrogen-fixing activity (NA) of different types of biological soil crusts in the Gurbantunggut Desert. The results suggest that NA (nmol $C_2H_4\ m^{-2}\ h^{-1}$) for each type of crusts was highly variable. Seasonal variation was also important, with all three types of crusts responding in a similar way to changes in environmental conditions. From March to May, NA was relatively low for all crust types. During this season, NA was 2.26×10^3 for cyanobacterial crust followed by lichen crust (6.54×10^2) and moss crust (6.38×10^2). From June to October, all crust types reached their highest level of NA, especially lichen crust and moss crust ($p < 0.01$). The NA of cyanobacterial crust (9.81×10^3) was higher than that of lichen crust (9.06×10^3) and moss crust (2.03×10^3). From November to February, when temperatures were consistently low (<0 °C), NA was at its lowest level, especially in cyanobacterial crust (4.18×10^2) and moss crust (5.43×10^2) ($p < 0.01$). Our results indicate that species composition is critical when estimating N inputs in desert ecosystems. In addition, all three types of crusts generally responded in a similar way to environmental conditions. The presence of N fixation activity in all crusts may contribute to the maintenance of fertility in sparsely vegetated areas and provide surrounding vascular plant with fixed nitrogen.

1. Introduction

Net primary productivity in terrestrial ecosystems is often limited by nitrogen availability (Vitousek and Howarth, 1991). During desertification of semi-arid grasslands, this limitation may intensify (Dregne, 1983), but relatively little is known about the factors affecting the nitrogen status of desert soils. Nitrogen inputs in arid lands result largely from N_2 fixation (Belnap, 2002b; Evans and Ehleringer, 1993; Rychert et al., 1978; Skujins, 1984) by biological soil crusts and free-living, heterotrophic bacteria (MacGregor and Johnson, 1971; Zaady et al., 1998). In desert ecosystems, nitrogen fixed by the heterocystic cyanobacteria (*Anabaena*, *Calothrix*, *Cylindrospermum*, *Dicothrix*, *Hapalosiphon*, *Nodularia*, *Nostoc*, *Plectonema*, *Schizothrix* and *Scytonema*) (Harper and Marble, 1988), non-heterocystous cyanobacteria (*Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phoridium* and *Tolypothrix*) (Belnap, 1996; Rogers and Gallon, 1988) and cyanolichens (*Collema* spp. and *Peltula* spp.) that occur in the biological soil crusts can be the major source of nitrogen (Evans and Ehleringer, 1993). This is especially true for regions where rainfall and inputs of N resulting from human activities are low. Cyanobacteria can also live epiphytically on soil mosses and lichens that have green algae as phycobionts; thus this consortium of organisms can also show N fixation activity (Peters et al., 1986).

Estimations of N_2 fixation by soil crusts in arid and semi-arid areas vary widely (Aranibar et al., 2003; Belnap, 2002b; Hartley and Schlesinger, 2002; Zaady et al., 1998). It is difficult to compare values which can be reported using different units of time, for example from hourly to annual rates, and at different spatial scales, for example from square centimeters to hectares (Aranibar et al., 2003). Although the importance of N_2 fixation in soil crusts has been widely studied in many deserts throughout the world, this has not been the case in China. Until now, most studies of nitrogenase activity in deserts in China were focused on legumes (Ci and Gao, 2005; Shen and Jing, 2003), and few mentioned the possible role of biological soil crusts in N_2 fixation (Li et al., 2001; Zhang et al., 2005).

The Gurbantunggut Desert (44°11′–46°20′N, 84°31′–90°00′E) is the largest fixed and semi-fixed desert in China with an area of 48,800 km^2. In recent years there has been a significant increase in

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0140-1963/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2009.04.002

utilization, in particular for livestock grazing, agricultural production and energy exploration. Soil surface disturbances associated with these uses have been repeatedly shown to convert species-rich biological soil crusts dominated by late successional lichens and mosses, to species-poor crusts dominated by early successional cyanobacteria. The recovery of disturbed biological soil crusts is extremely slow. In order to protect biological soil crusts in this desert, a number of projects have been undertaken to study their role in soil stabilization, increasing the fertility of soil, minimizing wind and water erosion and adding to soil organic matter (Zhang, 2005; Zhang et al., 2006). The purpose of this study was to quantify the nitrogen-fixing activity in different types of soil crusts in the Gurbantunggut Desert using acetylene reduction assays (ARA) and to discuss the factors influencing NA.

2. Materials and methods

2.1. Study area

The study was conducted in the Gurbantunggut Desert, which is situated in the center of the Jungger Basin, in the Xinjiang Uygur Autonomous Region of China. The Himalayan Range to the south produces a 'blocking effect', preventing moist air currents from the Indian Ocean reaching the area, and resulting in the vast expanse of arid terrain. Mean annual rainfall is approximately 79.5 mm, falling predominantly during spring. Mean annual evaporation is 2606.6 mm. The average annual temperature is 7.26 °C. Wind speeds are greatest during late spring, averaging 11.17 $\mathrm{m\,s^{-1}}$, and are predominantly from the WNW, NW and N directions (Zhang et al., 2007). Natural vegetation in the area is dominated by *Haloxylon ammodendron* and *Haloxylon persicum* (Chenopodiaceae), with a vegetation cover of less than 30%. The land is characterized by massive, dense, semi-fixed sand dunes with stable moisture content and covered by biological soil crusts consisting of various combinations of bacteria, cyanobacteria, algae, mosses and lichens. Scattered shrubs can be associated with the soil crusts. These biological soil crusts grow favorably during cool, wet, periods, in fall and early spring, utilizing not only rainfall, but also dew and fog (Du, 1990; Kidron et al., 2002; Zhang et al., 2002). The study was conducted in the southern part of the Gurbantunggut Desert which contains biological soil crusts typical of those (algae-dominated crust, lichen-dominated crust and moss-dominated crust) found throughout the desert (Zhang et al., 2002, 2004) (Fig. 1).

2.2. Field experiment layout

In 2003, a typical, longitudinal sand dune (44°32′30″N, 88°6′42″E) was selected as a permanent site. We selected an area covered only in biological soil crusts in order to avoid any complications from the presence of vascular plants. From the interdune area, we randomly selected ten 50 cm × 50 cm plots at approximately 10 m intervals. The thickness and cover of biological soil crust were recorded for each plot. Three types of soil crusts were collected from each plot between March 2005 and February 2006: (1) cyanobacterial crust which is heavily dominated by the cyanobacterium *Microcoleus vaginatus*. Sand particles are bound tightly not only by the fine filaments of this cyanobacterium but also by the mucilage it produces, thus protecting the sand surface from wind and water erosion; (2) lichen crust, which included *Collema tenex*, *Psora decipiens*, *Xanthoria elegans*, *Acarospora strigata*, and *Lecanora argopholis*. Lichen-dominated soil crust is the predominant type of biological soil crusts in the desert where different species of lichen can be black, white, brown, yellow or blue in color; (3) moss crust, which is mainly dominated by *Tortula desertorum* and *Bryum argenteum*.

Crust samples were collected by inserting a 5.4-cm diameter aluminium container into the soil crust, then carefully removing it to provide a sample of crust with a surface area of 22.89 $\mathrm{cm^2}$ and approximately 2 cm deep. Ten replicates from each type of crust were collected, making a total of 30 samples for each sampling period. These were transported without delay to the laboratory of the Xinjiang Institute of Ecology and Geography, Chinese Academy of Science in Urumqi.

2.3. Acetylene reduction activity

In the laboratory, the samples were analyzed immediately for nitrogenase activity (NA). NA was estimated using the acetylene reduction assay (ARA), based on the ability of the nitrogenase enzyme to catalyze the reduction of N_2 to ammonium (nitrogen fixation), as well as the reduction of acetylene to ethylene (Aranibar et al., 2003). Samples were placed in clear, 60-ml gas-tight tubes and the entire crust surface was equally and completely moistened with distilled water. Tubes were injected with enough C_2H_2 to create a 10% C_2H_2 atmosphere. After injection, samples were incubated for 24 h at 26 °C. Sub-samples (0.5 ml) of the head space within the tubes were analyzed for C_2H_2 and ethylene (C_2H_4) content on a Trace GC 2000 gas chromatograph, fitted with flame ionization detector, and Al_2O_3/S column, using N_2 as the carrier gas (1.5 ml/min). Results of the observed NA were expressed as ethylene production ($\mathrm{nmol\,C_2H_4\,m^{-2}\,h^{-1}}$) per unit time on a surface area basis (Belnap, 2002b).

Converting C_2H_4 values is controversial, as the ratio used varies widely depending on the organism and habit conditions. The ratio of ethylene produced to N fixed varies widely for different soils, microbial communities and environmental conditions. In Sweden, conversion factors ranged from 1 to 15.7 for different soils and water contents (Nohrstedt, 1983), and in the high Arctic from 0.022 to 4 for different microbial communities (Liengen, 1999). However, existing literature commonly reports N_2 fixation applying the theoretical 3:1 ratio (Ischiei, 1980; Rychert and Skujins, 1974; Skarpe and Henriksson, 1986). For the purpose of comparison, this ratio was also used in this study to describe the nitrogen fixation activity associated with biological crusts.

2.4. Statistical analyses

All statistical analysis was done using an SPSS statistical package. ANOVA procedure was used to understand how crust types and sampling time affect NA. Tests of between-subjects effects showed the results more clearly. Results are reported as significant when $p < 0.01$ unless otherwise noted.

3. Results and discussion

3.1. The potential NA of different types of biological soil crusts

Rates of ethylene production (as indications of nitrogenase activity and N_2 fixation) are presented in Fig. 2. The results suggest that potential nitrogenase activity (NA) for each type of crust varied considerably depending on the season.

From March to May, rates of ethylene production were quite low for all crust types, but of these, the cyanobacterial crust reached the highest rate of ethylene production (2.26×10^3 $\mathrm{nmol\,C_2H_4\,m^{-2}\,h^{-1}}$), followed by lichen crust (6.54×10^2 $\mathrm{nmol\,C_2H_4\,m^{-2}\,h^{-1}}$). Moss crust produced the lowest rate (6.38×10^2 $\mathrm{nmol\,C_2H_4\,m^{-2}\,h^{-1}}$).

From June to October, each type of crust reached its highest rate of NA, particularly in the case of lichen crust and moss crust ($p < 0.01$). Ethylene production rates of cyanobacterial crust (9.81×10^3 $\mathrm{nmol\,C_2H_4\,m^{-2}\,h^{-1}}$) and lichen crust ($9.06 \times 10^3$ nmol

Fig. 1. Appearance of Gurbantunggut Desert (left) and distinguishing types of biological soil crust based on physical–chemical and microbiological parameters in this desert (Right). a. Algae-dominated crusts (light color, devoid of surface pigmentation; most abundant in the middle to the top of dunes); b. Lichen-dominated crusts (predominant type of biological soil crusts in the desert where different species of lichen can be black, white, brown, yellow or blue in color; most abundant in the middle-down to interdune areas); c. Moss-dominated crusts (scattered within the interdune areas) (Zhang et al., 2002, 2004).

$C_2H_4\,m^{-2}\,h^{-1}$) were much higher than those of moss crust (2.03×10^3 nmol $C_2H_4\,m^{-2}\,h^{-1}$).

From November to February, low temperatures (<0 °C) are responsible for the reduction of NA in all crust types, especially in cyanobacterial crust (4.18×10^2 nmol $C_2H_4\,m^{-2}\,h^{-1}$) and moss crust (5.43×10^2 nmol $C_2H_4\,m^{-2}\,h^{-1}$) ($p < 0.01$). This result is similar to previous studies conducted in Southeast Utah, USA, where it was found that low temperature (<1 °C) precluded NA in biological soil crusts (Belnap, 2002b). The variation of NA indicated that species composition, that is, whether the soil crust is dominated by algae, lichens or mosses, is critical when estimating N inputs from biological soil crusts in desert ecosystems. In addition, all three types of crusts generally responded in a similar manner to seasonal changes in weather conditions.

The data were analyzed using the ANOVA procedure of SPSS statistical package (Chicago, IL, USA). The results indicated that NA levels were significantly influenced by the time of year sampling took place and by crust type ($p < 0.01$). Tests of between-subjects effects showed significant type × time interactions on NA levels ($p < 0.01$) (Table 1).

Most studies in the Gurbantunggut Desert have concentrated on nitrogen fixation activity associated with legumes (*Astragalus lehmannianus*, *Eremosparton songoricum* and *Halimodendron halodendron*) (Guan et al., 1991) and terrestrial nitrogen-fixing cyanobacteria (*Nostoc commune*, *Nostoc flagelliforme*, *Microcoleus vaginatus*, *Scytonema ocellatum* and *Schizothrix mellea*) (Guan et al., 1995). The present study confirms that nitrogen fixation occurs in biological soil crusts in the Gurbantunggut Desert and that ethylene production rates vary from 1.8×10^2 to 2.8×10^4 depending on the type of soil crust (cyanobacterial, lichen or moss) and the seasonal climatic conditions at the time of sampling.

Table 2 compares the results of the present study to earlier studies on ethylene production rates from deserts around the world. The Gurbantunggut Desert is similar to other cold deserts (e.g. the Colorado Plateau and the Great Basin Desert of North America), which receive most of their precipitation during winter.

3.2. The factors influencing NA of different types of biological soil crusts

Biological soil crusts throughout the Gurbantunggut Desert have a similar species composition (Table 3) (Zhang, 2005; Zhang et al., 2005), but the species occur in different proportions in different regions (Zhang et al., 2007). The different combinations of species are likely to influence the NA level of a given biological soil crust. Cyanobacteria in biological crusts of the Gurbantunggut Desert include 77 species belonging to 25 genera and 6 families. They are dominated by the filamentous cyanobacteria, such as the large,

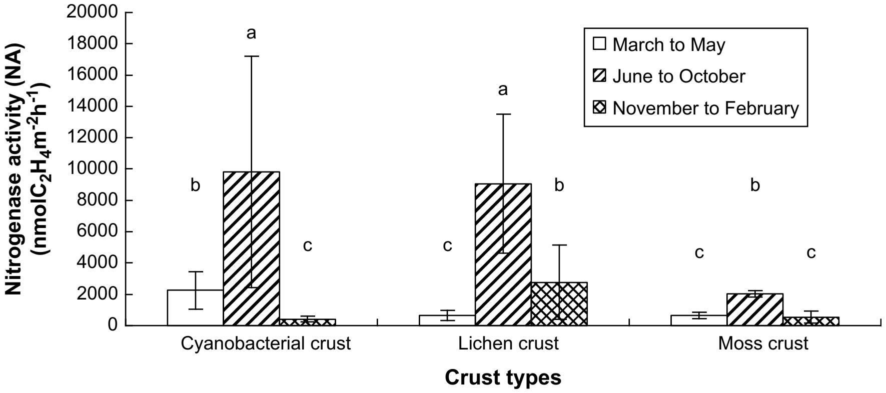

Fig. 2. Potential nitrogenase activity (NA) for each type of crust varied considerably depending on the season. Different letters indicate significant differences ($p < 0.01$ in all cases).

Table 1
Tests of between-subjects effects showed significant type × time interactions on NA levels.

Source	Type III sum of squares	df	Mean square	*F* value	Sig.
Corrected model	0.107[a]	8	1.34E−02	11.942	0
Intercept	5.488	1	5.488	4902.736	0
Sampling time	5.49E−02	2	2.75E−02	24.532	0
Crust type	9.94E−03	2	4.97E−03	4.439	0.016
Sampling time × crust type	2.96E−02	4	7.39E−03	6.6	0
Error	6.27E−02	56	1.12E−03		
Total	7.589	65			
Corrected total	0.17	64			

[a] *R* squared = 0.63 (adjusted *R* squared = 0.578).

highly mobile, non-heterocystic *M. vaginatus* (Vauch.) Gom. Lack of heterocysts means this species must employ other means of excluding oxygen, such as creating micro-anaerobic zones in the soil, either in closely packed filaments of multiple organisms or within the extra-cellular polysaccharide sheaths surrounding the cyanobacteria (Belnap, 2002a; Belnap and Gardner, 1993; Steppe et al., 1996). However, in this study, the relatively high ethylene production rates of cyanobacterial crusts in the Gurbantunggut Desert, suggest that their N-fixing capacity is greater than that of cyanobacterial crusts in other cool deserts around the world. Lichen crusts in this study showed higher ethylene production rates, suggesting that N inputs from N_2-fixing lichens such as *Collema tenax* are very important for this desert ecosystem. In contrast, the lowest ethylene production rates in this study were observed in moss crusts, probably because N fixation occurs in cyanobacteria growing in association with mosses, either as epiphytes or in the soil rather than in the mosses themselves. Nitrogen fixation has been shown to occur in crusts that include both mosses and cyanobacteria (Peters et al., 1986), but the N_2-fixing ability of moss crusts is significantly lower than that of cyanobacterial crusts and lichen crusts as presented in this study.

The moisture content of the organism ultimately controls both the duration and the rate of N fixation (Belnap, 2003), as cyanobacteria and cyanolichens in biological crusts are only physiologically active when wet (Kershaw, 1985; Nash, 1996). After the application of water the increase in nitrogenase activity, may reflect the activity of N_2-fixing micro-organisms after extended drought (Hartley and Schlesinger, 2002). The Gurbantunggut Desert is located at the transitional belt between Central Asia and Middle Asia. The climate of the Gurbantunggut is characterized by aridity, with very low precipitation, extremely high evapotranspiration, strong winds, intense radiant heat and light from the sun, and extreme variation in temperature. The climate is typical of a continental desert, however, precipitation is predictable and seasonal, with rain and snow falling in winter and spring (Zhang and Chen, 2002). Water in liquid form necessary for N_2-fixing biological crusts can be derived from rainfall, snow melt, dew, or fog. In order to better understand how ethylene production rates differed within each sampling times, ten-year (1991–2000) average monthly temperatures and precipitation from a location near the Gurbantunggut Desert (44°06′00″N, 89°20′24″E) are presented in Fig. 3. While temperatures are highest between May and September and precipitation highest between May and August, there is some overlap, with NA at the highest rate for all crust types between June and October.

Table 2
Reported ethylene production rates (C_2H_4 nmol m^{-2} h^{-1}) for different deserts around the world.

Research sites	Ethylene production (nmol m^{-2} h^{-1})	References
Chihuahuan Desert	$1.0 \times 10–2.0 \times 10^5$	Hartley and Schlesinger (2002)
Sonoran Desert	$6.4 \times 10^4–7.8 \times 10^5$	MacGregor and Johnson (1971)
Great Basin Desert	$4.0 \times 10–9.0 \times 10^5$	Belnap (1996), Jeffries et al. (1992), Rychert and Skujins (1974)
Negev Desert	$3.4 \times 10^5–1.8 \times 10^6$	Zaady et al. (1998)
Kalahari Desert	$6.0 \times 10^5–6.8 \times 10^6$	Skarpe and Henriksson (1986)
Sahel Desert	$1.0 \times 10–4.2 \times 10^4$	Issa et al. (2001)
Tucson Desert	7.8×10^5	MacGregor and Johnson (1971)
Colorado Plateau	$2 \times 10^4–5.8 \times 10^5$	Eskew and Ting (1978)
Gurbantunggut Desert	$1.8 \times 10^2–2.8 \times 10^4$	This paper

The Gurbantunggut Desert is similar to other cold deserts (e.g. the Colorado Plateau and the Great Basin Desert of North America), which receive most of their precipitation during winter.

Table 3
The species composition of the three different types of biological soil crust in the Gurbantunggut Desert.

Crust type	Main composition species
Moss crust	*Tortula desertorum*, *Bryum argenteum*, *Tortula muralis*
Lichen crust	*Collema tenax*, *Psora decipiens*, *Xanthoparmelia desertorum*, *Diploschistes muscorum*
Cyanobacterial crust	*Microcoleus vaginatus*, *Microcoleus paludosus*, *Anabaena azotica*, *Porphyrosiphon martensianus*, *Xenococcus lyngbyge*

Nitrogen fixation by biological crusts was higher from June to October than at any other time of the year and this corresponds with the period of higher rainfall. Soil moisture enhances the metabolic activity of N_2 fixers directly and promotes nitrogenase activity by increasing C and energy supplies. Aranibar et al. (2003) assumed that the number of rainy days represented half the number of days during which biological soil crusts were at field capacity, because biological crusts have the potential to rapidly absorb water, swell to several times their original volume and subsequently retard their dehydration rate (Campbell et al., 1989). Higher inputs of water can also affect N_2 fixers indirectly by stimulating net primary production thereby increasing the inputs of soil organic matter, and by transporting dissolved organic carbon and nutrients down slope (Wierenga et al., 1987). Although the absence of nitrogenase activity in dry soils suggests that moisture is the primary factor limiting N_2 fixation in desert soils, where soils are wet for long periods of time, continuously high soil moisture may reduce overall N fixation, while alternation between wet and dry soils, a characteristic of most deserts, may lead to greater N fixation rates per unit ‘moist soil time’ than those of wetter regions (Belnap, 2002b).

N fixation rates are also generally controlled by temperature (Belnap, 2002b). Optimum minimum air temperatures for nitrogen fixation in cyanobacteria and cyanolichens in biological crusts reported globally range from 20 to 30 °C (Du Bois and Kapustka, 1983). In this study, ethylene production rates in all three types of crusts reached their highest NA from June to October with temperatures in the vicinity of 20 °C whereas *Stigonema* and *Scytonema* crusts from the tropics showed no NA at 0 °C (Ischiei, 1980). In contrast, freezing can damage nitrogenase in *Nostoc* (Du Bois and Kapustka, 1983; Scherer et al., 1984). Low temperatures can reduce photosynthetic rates and thus reduce available ATP and reductant pools, creating a lag time after freezing before N fixation is initiated (Kershaw, 1985). We consider low temperatures (<0 °C) to be the most likely reason for the marked decrease in ethylene production rates for all three types of crusts between November and February. In winter, the darker color of later successional lichen crusts may make them and the soils beneath them, relatively warmer than lighter colored, early successional cyanobacterial crusts, thus the warmer temperatures of the darker lichens would have the potential to enhance photosynthesis and lead to greater quantum

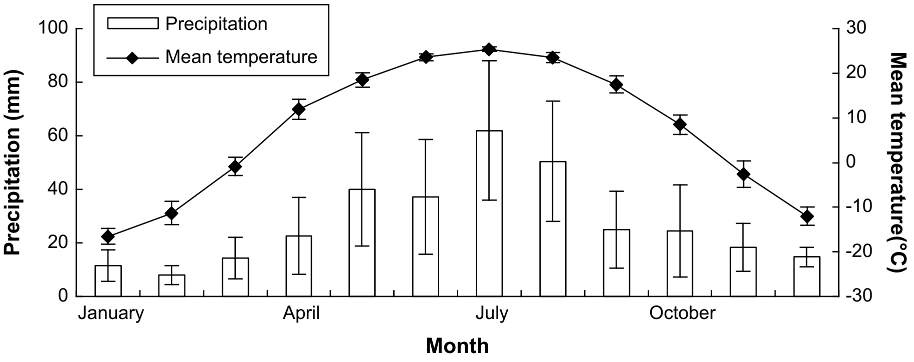

Fig. 3. Ten-year (1991–2000) average monthly temperatures and precipitation from a location near the Gurbantunggut Desert (44°06′00″N, 89°20′24″E).

efficiency (Housman et al., 2006). This may account for later successional lichen crusts in our study having higher NA than cyanobacterial crusts in the coldest period of the year between November and February. The lighter color of early successional cyanobacterial crusts may also increase albedo and therefore decrease soil temperatures with a resulting effect on metabolic processes including nitrogen fixation (Nash, 1996).

One of the major problems facing the world is to limit air borne particles, not only those produced by industry but also those originating from desert lands. N fixed by well established cyanobacterial and lichen crusts can also lead to the development of healthy moss crusts. The rough surface topography of both lichen and moss crusts, when compared to the smooth surface topography of cyanobacterial crusts, plays a major role in minimizing soil erosion, by water but more importantly by wind (Zhang et al., 2006), consequently stabilizing desert sands and soils and reducing the quantity of air borne particles. Well developed biological soil crusts can also provide a seed bed for vascular plants, and nitrogen fixed by soil crusts can be utilized in the subsequent growth of, for example, perennial grasses and shrubs, all of which contribute to the stabilization of desert dunes (Zhang et al., 2005). If the crusts are damaged, for example by the hard hoofs of grazing animals, by cultivation for agricultural purposes or by oil exploration, then there is nothing to stop the dispersal of sand and soil particles into the atmosphere. In contrast to the situation in the north and centre, we predict that in the southeast, the increasing human disturbances of the soil surface will degrade the quality and abundance of biological soil crusts. This will significantly diminish the potential benefit that nitrogen fixed by biological soil crusts could contribute to the environment. Earlier studies have demonstrated that cool desert sites show significantly greater decline in NA after disturbance than hot desert sites (Belnap, 2002a) and although human disturbances do not directly remove surface material, they still can have a profound impact on soil resources and nutrient cycles. Decreased N_2 inputs from crusts can have long-term effects on the physical condition of soils and on plant growth. Disturbance of biological soil crusts also decreases soil stability and albedo, both of which can influence N inputs and N cycles (Belnap, 1996; Belnap and Gillette, 1998; Williams et al., 1995).

This study confirms NA of biological soil crusts in the Gurbantunggut Desert for the first time. In the Gurbantunggut Desert, biological soil crusts which can fix N_2 contribute to maintaining the fertility of sparsely vegetated areas and also provide a source of nitrogen for vascular plants. The major factors controlling N fixation rates are moisture, temperature and the species composition of the soil crusts. As recovery times in desert ecosystems can be extremely slow, effective management of this vast resource will require considerable effort to preserve the structure and function of the ecosystem as it is now. Reduction in N input from biological soil crusts can have major implications for the environment and therefore the preservation of biological soil crusts in good condition should be of foremost consideration in land management decisions.

Acknowledgments

We gratefully acknowledge two anonymous reviewers for their valuable comments on the manuscript. We would like to thank the National Research Station of Fukang Desert Ecosystem. This work was supported by the National Basic Research Program (No.2009CB825104), the Key Knowledge Innovation Project of the Chinese Academy of Sciences (No. KZCX2-YW-336) and the National Natural Science Foundation of China (No. 40771114). The authors gratefully acknowledge Pan Borong, Pan Huixia, Zhang jing, Zhang Binchang, Wei Meili and Zhou Xiaobing for their assistance in field sampling and laboratory work.

References

Aranibar, J.N., Anderson, I.C., Ringerose, S., Macko, S.A., 2003. Importance of nitrogen fixation in soil crusts of southern African arid ecosystems: acetylene reduction and stable isotope studies. Journal of Arid Environments 54, 345–358.

Belnap, J., 1996. Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial–lichen soil crusts. Biology and Fertility of Soils 23, 362–367.

Belnap, J., 2002a. Impacts of off-road vehicles on nitrogen cycles in biological soils crusts: resistance in different U.S. deserts. Journal of Arid Environments 52, 155–156.

Belnap, J., 2002b. Nitrogen fixation in biological soil crusts from southeast Utah, USA. Biology and Fertility of Soils 35, 128–135.

Belnap, J., 2003. Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management, vol. 150. Springer, Berlin, pp. 241–261.

Belnap, J., Gardner, J., 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53, 40–47.

Belnap, J., Gillette, D.A., 1998. Vulnerability of desert soil surfaces to wind erosion: impacts of soil texture and disturbance. Journal of Arid Environments 39, 133–142.

Campbell, S.E., Seeler, J., Goulic, S., 1989. Desert crust formation and soil stabilization. Arid Soil Research and Rehabilitation 3, 217–228.

Ci, E., Gao, M., 2005. Research advances in the effects of environmental factors on the symbiotic nitrogen fixation of legumes. Acta Botanica Boreali-Occidentaria Sinica 25 (6), 1269–1271.

Dregne, H.E., 1983. Desertification of Arid Lands. Harwood Academic Publishing, New York, p. 242.

Du, X.H., 1990. Study on topsoil crust in sandy land. Chinese Journal of Desert Research 10, 31–37.

Du Bois, J.D., Kapustka, L.A., 1983. Biological nitrogen influx in an Ohio relict prairie. American Journal of Botany 70, 8–16.

Eskew, D.L., Ting, I.P., 1978. Nitrogen fixation by legumes and blue-green cyanobacterial–lichen crusts in a Colorado Desert environment. American Journal of Botany 65, 850–856.

Evans, R.D., Ehleringer, J.R., 1993. A break in the nitrogen cycle in arid lands? Evidence from N^{15} of soils. Oecologia 94, 314–317.

Guan, G.L., Wang, W.W., Yang, Y.S., 1991. Resources of the Nitrogen-fixing Organisms in Xinjiang Arid Area. Scientific Press, Beijing, pp. 5–45.

Guan, G.L., Yang, Y.S., Guo, P.X., 1995. The group and distribution of terrestrial nitrogen-fixing blue alga and its effects on environment in the arid area of Xinjiang. Arid Zone Research 12 (1), 1–6.

Harper, K.T., Marble, J.R., 1988. A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller, P.T. (Ed.), Vegetation Science Applications for Rangeland Analysis and Management. Kluwer, Dordrecht, pp. 135–169.

Hartley, A.E., Schlesinger, W.H., 2002. Potential environmental controls on nitrogenase activity in biological crusts of the northern Chihuahuan Desert. Journal of Arid Environments 52, 293–304.

Housman, D.C., Powers, H.H., Collons, A.D., Belnap, J., 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. Journal of Arid Environments 66, 620–634.

Ischiei, A.O., 1980. Nitrogen fixation by blue-green cyanobacterial soil crusts in Nigerian savanna. In: Rosswall, T. (Ed.), Nitrogen Cycling in West African Ecosystems. Royal Swedish Academy of Sciences, Stockholm, Sweden, pp. 191–198. 450.

Issa, O.M., Stal, L.J., Défarge, C., Couté, A., Trichet, J., 2001. Nitrogen fixation by microbial crusts from desiccated Sahelian soils (Niger). Soil Biology and Biochemistry 33, 1425–1428.

Jeffries, D.L., Klopatek, J.M., Link, S.O., Bolton, H., 1992. Acetylene reduction by cryptogamic crusts from a blackbrush community as related to resaturation and dehydration. Soil Biology and Biochemistry 24, 1101–1105.

Kershaw, K.A., 1985. Physiological Ecology of Lichens. Cambridge University Press, Cambridge, p. 293.

Kidron, G.J., Herrnstadt, I., Barzilay, E., 2002. The role of dew as a moisture source for sand microbiotic crusts in the Negev Desert, Israel. Journal of Arid Environments 52, 517–533.

Li, X.R., Jia, Y.K., Long, L.Q., 2001. Advances in microbiotic soil crust research and its ecological significance in arid and semiarid regions. Journal of Desert Research 21 (1), 4–11.

Liengen, T., 1999. Conversion factor between acetylene reduction and nitrogen fixation in free-living cyanobacteria from high arctic habitats. Canadian Journal of Microbiology 45, 223–229.

MacGregor, A.N., Johnson, D.E., 1971. Capacity of desert cyanobacterial crusts to fix atmospheric nitrogen. Proceedings – Soil Science Society of America 35, 843–844.

Nash III., T.H., 1996. Lichen Biology. Cambridge University Press, Cambridge, p. 320.

Nohrstedt, H.Ö., 1983. Conversion factor between acetylene reduction and nitrogen fixation in soil: effect of water content and nitrogenase activity. Soil Biology and Biochemistry 15, 275–279.

Peters, G.A., Toia Jr., R.E., Calvert, H.E., Marsh, B.H., 1986. Lichens to *Gunnera* – with emphasis on *Azolla*. Plant Soil 90, 17–34.

Rogers, L., Gallon, J., 1988. Biochemistry of the Algae and Cyanobacteria. Clarendon Press, Oxford, 374 pp.

Rychert, R., Skujins, J., 1974. Nitrogen fixation by blue-green cyanobacterial–lichen crust in the Great Basin Desert. Proceedings – Soil Science Society of America 38, 768–771.

Rychert, R., Skujins, J., Sorensen, D., Porcella, D., 1978. Nitrogen fixation by lichens and free-living microorganisms in deserts. In: West, N.E., Skujins, J.J. (Eds.), Nitrogen in Desert Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, p. 307.

Scherer, S., Ernst, A., Chen, T.W., Böger, P., 1984. Rewetting of drought-resistant blue-green algae: time course of water uptake and reappearance of respiration, photosynthesis and nitrogen fixation. Oecologia 62, 418–423.

Shen, S.H., Jing, Y.X., 2003. Present status and development of biological nitrogen fixation research in China. Chinese Science Bulletin 48 (6), 535–540.

Skarpe, C., Henriksson, E., 1986. Nitrogen fixation by cyanobacterial crusts and by associative-symbiotic bacteria in Western Kalahari, Botswana. Arid Soil Research and Rehabilitation 1, 55–59.

Skujins, J., 1984. Microbial ecology of desert soils. Advances in Microbial Ecology 7, 49–92.

Steppe, T.F., Olson, J.B., Paerl, H.W., Litaker, R.W., Belnap, J., 1996. Consortial N_2 fixation: a strategy for meeting nitrogen requirements of marine and terrestrial cyanobacterial mats. FEMS Microbiology Ecology 21, 149–156.

Vitousek, P.M., Howarth, L.R., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115.

Wierenga, P.J., Hendricx, J.M., Nash, M.H., Ludwig, J., Daugherty, L.A., 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. Journal of Arid Environments 13, 53–63.

Williams, J.D., Dobrowolski, J.P., West, N.E., 1995. Microphytic crust influence on interrill erosion and infiltration capacity. Transactions of the American Society of Agricultural Engineers 38, 139–146.

Zaady, E., Groffman, P., Shachak, M., 1998. Nitrogen fixation in macro- and microphytic patches in the Negev Desert. Soil Biology and Biochemistry 30, 449–454.

Zhang, L.Y., Chen, C.D., 2002. On the general characteristics of plant diversity of Gurbantunggut sandy desert. Acta Ecologica Sinica 22 (11), 1923–1932.

Zhang, Y.M., 2005. The microstructure and formation of biological soil crust in their early developmental stage. Chinese Science Bulletin 50 (2), 117–121.

Zhang, Y.M., Cao, T., Pan, B.R., 2002. A preliminary study on bryophyte associated with formation of soil crust in south fringe of Gurbantunggut Desert in Xinjiang, China. Acta Botanica Boreali-Occidentalla Sinica 22, 18–23.

Zhang, Y.M., Chen, J., Wang, X.Q., 2007. The spatial distribution patterns of biological soil crusts in the Gurbantunggut Desert, Northern Xinjiang, China. Journal of Arid Environments 68, 599–610.

Zhang, Y.M., Pan, H.X., Pan, B.R., 2004. Distribution characteristics of biological soil crust on sand dune surface in Gurbantunggut Desert, Xinjiang. Journal of Chinese Soil and Water Conservation 18, 61–64.

Zhang, Y.M., Wang, H.L., Wang, X.Q., 2006. The microstructure of microbiotic crust and its influence on wind erosion for a sandy soil surface in the Gurbantunggut Desert of Northwestern China. Geoderma 132, 441–449.

Zhang, Y.M., Yang, W.K., Wang, X.Q., 2005. Influence of cryptogamic soil crusts on accumulation of soil organic matter in Gurbantunggut desert, northern Xinjiang, China. Acta Ecologica Sinica 25 (12), 3420–3425.