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Review

Extracellular polysaccharides from cyanobacterial soil crusts: A review of their role in dryland soil processes

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ABSTRACT

Cyanobacterial soil crusts are a community of microorganisms living in the soil surface of different habitats worldwide. Through photosynthesis, cyanobacteria produce extracellular polysaccharides (EPS) increasing the soil carbon (C) pool as carbohydrates. The layer of polysaccharides also acts as a mechanical structure surrounding the filamentous cyanobacteria that together with the soil particles form stable aggregates in the topsoil thus decreasing C loss by erosion. Thus despite their apparent importance to the dryland system we have only a limited understanding of their role and possible applications in dryland soil environments. This review draws on these disparate sources of information in order to provide a summary of our understanding of the characteristics, behaviour and influence of cyanobacterial EPS in dryland soils and makes recommendations for further research.

1. Introduction

Biological soil crusts (BSC) form at the soil surface by an intimate association between mineral grains and organic matter (OM) with varying proportions of cyanobacteria, algae, lichens and mosses. They are a common feature of all dryland soils and have been investigated with increasing frequency with regard to their influence on erodibility (e.g. Belnap and Gillette, 1998; Bowker et al., 2008); nitrogen content (Belnap, 2003); soil respiration (Elbert et al., 2009; Thomas et al., 2008; Zaady et al., 2000) and soil moisture (Belnap, 2006). Correspondingly, there have been a number of recent comprehensive reviews on the role of BSC in the dryland landscape, notably Belnap et al. (2008), Bowker (2007), Büdel et al. (2009), Mager (2010b) and Viles (2008). The purpose of this review, however, is to synthesize our understanding of the characterisation, production and influence of extracellular polysaccharides (EPS) secreted by cyanobacteria on dryland soils.

Polysaccharides secreted by cyanobacteria form a mechanical structure surrounding the bacterial cells that together with the soil particles form a heterogeneous mass or aggregate in the topsoil (Mazor et al., 1996). Because dryland soils contain only small amounts of organic C, particularly humic substances, EPS is often a major source of C (Mager, 2010a). The amount of EPS produced by cyanobacteria in their natural environment, however, varies with soil type (Hu et al., 2002) and the biochemical composition of EPS is not specific for different cyanobacteria but controlled by environmental conditions and nutritional levels (Nicolaus et al., 1999). Thus predicting the amount and form of polysaccharides produced by soil cyanobacteria is challenging. Although there is increasing interest in the exploitation of microorganisms for the production of polysaccharides from a number of cyanobacteria for industrial applications (e.g. Otero and Vincenzini, 2003; Wolfaardt et al., 1999) there have been relatively few studies conducted on *in-situ* soils. Most studies on EPS synthesis have been conducted in a laboratory setting using individual strains of cyanobacteria and under controlled environmental conditions (i.e. light and temperature). Therefore, this review aims to summarise the role of EPS from cyanobacterial soil crusts.

2. The ecology of cyanobacteria

Cyanobacteria are the largest, most diversified, evolutionary most significant, and ecologically most successful prokaryotes on Earth. Cyanobacteria display considerable morphological diversity (Whitton and Potts, 2002) and may be unicellular (e.g. *Chrooccocus*) or filamentous (e.g. *Microcoleus*) occurring as single cells or grouped in colonies (e.g. *Nostoc*). Cyanobacteria not only exhibit morphological diversity but a complex metabolism. They are capable of photosynthesis, respiration (Fig. 1) and N_2-fixation and

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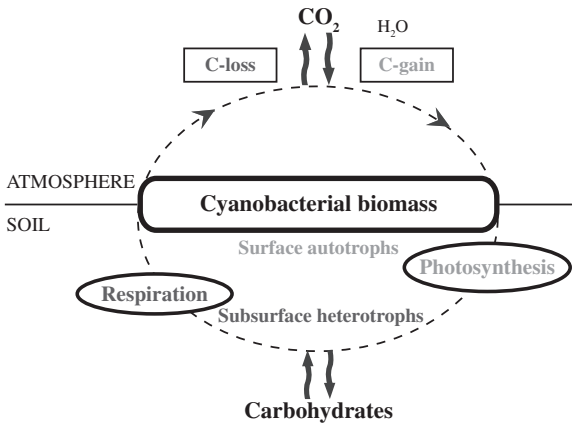

Fig. 1. The C cycle associated with cyanobacterial soil crusts. Atmospheric CO_2 is fixed by cyanobacteria when combined with water to produce oxygen and carbohydrates (C gain). C respiration uses oxygen in order to release CO_2 back to the atmosphere through microbial respiration (C loss).

can contribute significant quantities of C and N to the dryland ecosystem (Tandeau de Marsac et al., 2001). The ability to adapt to fluctuations in environmental conditions is also related to the expression of the cyanobacterial genome and to fundamental adaptations of the circadian rhythm (Terauchi and Kondo, 2008). The cyanobacterial circadian rhythm is a periodical cycle of about 24 h that controls metabolic and genetic functions (Mann, 2000). For example, cyanobacteria are able to combine photosynthesis and respiration (Terauchi and Kondo, 2008) and fix atmospheric N_2 under conditions of N limitation in differentiated cells (heterocysts) whose sole function is N_2-fixation (Luque and Forchhammer, 2008). Some non-heterocystous cyanobacteria (i.e. *Microcoleus*) even have particular physiological strategies which permit them to fix N_2 aerobically and without a heterocyst. Because the heterocyst is photosynthetically inactive when exposed to O_2, photosynthesis and N_2-fixation may be separated temporally rather than structurally (Terauchi and Kondo, 2008).

Cyanobacteria are able to grow in nearly all environments, in part because of their low nutritional requirements but also because they have evolved to sense and respond to changes in their environment making them extremely resilient and adaptable. For example, they are capable of thriving in dryland soil surfaces which experience large variations in the intensity and spectral quality of incident light (which could result in photo-oxidation and UV radiation stress), nutritional conditions (i.e. N starvation) and diurnal large fluctuations of temperature (i.e. heat, cold, drought), moisture and humidity (Tandeau de Marsac and Houmard, 1993). EPS are fundamental to this adaptability allowing cyanobacterial cells to glide along a matrix of EPS to optimal microenvironments within the soil (see Section 3.2).

2.1. Carbon metabolism

Cyanobacteria are photosynthetic prokaryotes (autotrophic) with a highly effective CO_2 concentrating mechanism as their preferred growth metabolism (Fig. 1). Recent research has hypothesized that C from EPS is the primary substrate respired in the pulses of CO_2 typically observed after heavy rainfall on dryland soils (Thomas and Hoon, 2010; Thomas et al., 2008). Photosynthesis by terrestrial cyanobacteria requires water as electron donor. Light is absorbed in the surface by chlorophyll *a* to generate NADPH that reacts through an electron transport chain to produce ATP, which is then used to reduce CO_2 to carbohydrates accumulating C as carbohydrates and energy reserve for cells (Bertocchi et al., 1990) that can be readily utilised by other soil organisms. Through photosynthesis, cyanobacteria are therefore capable of increasing the C content in the surrounding soil (Fig. 1) and this source may form a significant portion of total soil organic C (SOC) (Mager, 2010a).

Rates of photosynthesis vary with cyanobacterial species abundance and composition due to their different metabolic requirements. A comparative study by Garcia-Pichel and Belnap (1996) of the photosynthetic activity of three species of cyanobacteria (*Microcoleus*, *Nostoc* and *Scytonema*) from south-eastern Utah show that rates of C fixation by *Microcoleus* are generally lower than other species due to their reduced biomass and chlorophyll *a* content in comparison to the other two species. Temperature has also been shown to affect cyanobacterial photosynthetic activity. Although cyanobacteria have a wide range of temperature tolerances, Zhao et al. (2008) have shown that variations in the rate of photosynthetic recovery after a dormant phase in *Nostoc flagelliforme* are due to different water absorption rates at higher temperatures. Thus whilst higher temperatures may lead to an increase in photosynthetic rates because of faster water adsorption, ultimately the duration of active photosynthesis will be significantly reduced because of more rapid rates of desiccation. These adaptations indicate that cyanobacteria are not only capable of surviving a wide range of environmental conditions but that they can continue to contribute to CO_2 fixation and ultimately to SOC over those conditions.

Cyanobacteria also have the ability to grow in the absence of light (such as in the subsoil) through respiration using the photosynthetic electron transport chain and polysaccharides as an energy source (Peschek et al., 2004). Because light inhibits respiration and O_2 inhibits photosynthesis, the occurrence of these two processes simultaneously in the same compartment is a good demonstration of the metabolic complexity of cyanobacteria (Terauchi and Kondo, 2008). The possibility that the processes of photosynthesis and respiration share certain components (i.e. the electron transport chain) also indicates that these two processes of energy conversion are functionally related (Peschek et al., 2004). As shown in Fig. 1, the combination of photosynthesis and respiration in terrestrial environments means that cyanobacterial competition for growth is vertically stratified (Garcia-Pichel and Pringault, 2001). With the availability of soil moisture, surface autotrophic cyanobacteria grow through photosynthesis while subsurface heterotrophic cyanobacteria grow through respiration (Terauchi and Kondo, 2008).

3. Extracellular polysaccharides from soil cyanobacteria

3.1. Composition of EPS

Polysaccharides are polymers consisting of chains of monosaccharide or disaccharide units joined by glycosidic bonds with different number of C (e.g. six for a hexose such as glucose). Whereas numerous laboratory studies have characterised EPS in single strains of cyanobacteria, only one study to our knowledge, has attempted to characterise cyanobacterial EPS from soil crusts (Mazor et al., 1996) and they remain very poorly documented. The layer of EPS can present different morphological forms, either capsules surrounding the cells and soil grains or a slime or sheath loosely surrounding the colony (De Philippis and Vincenzini, 2003). Although these morphological forms have been characterised in the laboratory for isolated species of cyanobacteria, they have also been observed in cyanobacterial soil crust samples from dryland soils (Fig. 2) (Mager, 2009). The characteristics of EPS produced by the same species of cyanobacteria can be significantly different depending on the growth settings (Brüll et al., 2000; Huang et al.,

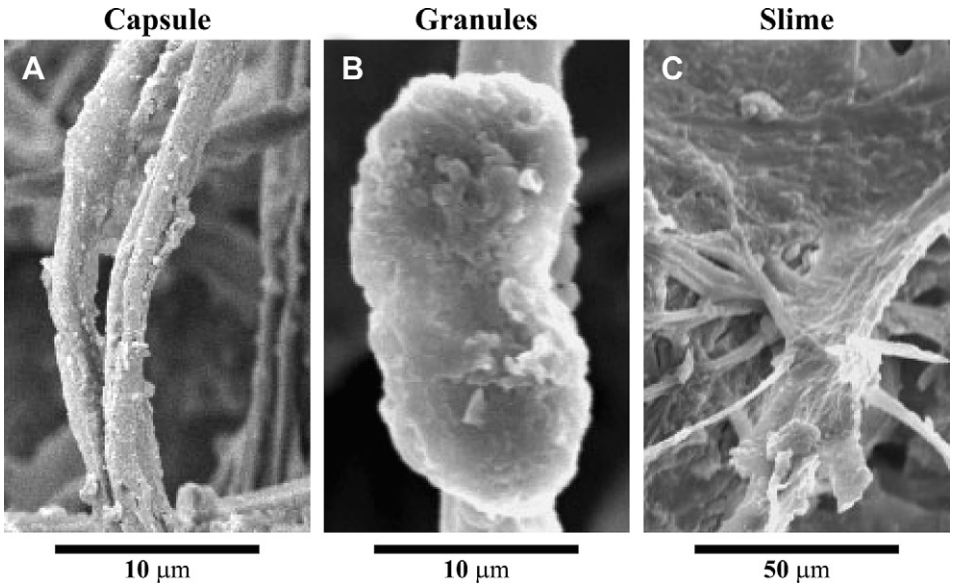

Fig. 2. EPS forms found on cyanobacterial soil crusts. SEM images of different morphological forms of EPS produced by cyanobacterial soil crusts in Kalahari Sand soils.

1998; Nicolaus et al., 1999). Under laboratory conditions with no nutrient limitations, more complex products may be formed, induced by different growth medium, than in nutrient limited conditions often found in dryland soils. Thus *in-situ* EPS synthesis is more likely to lead to the production of only essential products, such as glucose and galactose, required by the cyanobacteria (Brüll et al., 2000).

Some of the functions of EPS are non-specific and are shared by the whole range of polysaccharides while other roles are specific to the structure of the EPS (Mozzi et al., 2001). For example, similar structures may share specific roles (e.g. forming gel) while having different physical properties (e.g. rheology) (Nicolaus et al., 1999). Understanding the complexities of microbial processes and environmental controls on the dynamics of EPS production within a soil crust community is therefore essential before progress can be made on predicting the amount or form of EPS produced in dryland soils. For example, in drylands there is a tight linkage between the C and N inputs by cyanobacterial soil crusts and the nature and magnitude of rainfall pulses (Austin et al., 2004). Therefore, the EPS produced in cyanobacterial soil crusts is likely to be affected both by changes in moisture availability and N levels. The following sections evaluate the existing published studies on the effect of environmental conditions on EPS synthesis.

3.2. Soil moisture and EPS synthesis

In drylands, the major constraint to soil microbial activity is moisture availability. EPS are hygroscopic and attract and absorb water from the surrounding environment (Potts, 2001). Cyanobacteria also track moisture in soils. Garcia-Pichel and Pringault (2001) showed how cyanobacteria were able to migrate to the soil surface when wet and move back down the subsoil upon subsequent drying in order to avoid desiccation and photo-damage. Between rainfall events cyanobacteria can remain indefinitely in a desiccated state, partly because of the protection afforded to the cells by the EPS (Potts, 2001).

Changes in soil moisture content also affect the physiological functioning of crust organisms and EPS synthesis. Cyanobacteria present daily cycles of metabolic activity related to changes in moisture availability in the soil surface (Mazor et al., 1996), thus the reactivation of cyanobacterial metabolism depends on the amount of moisture available (Lange et al., 1994; Satoh et al., 2002). Early morning humidity and dew has been shown to provide enough moisture to stimulate activity (e.g. Lange, 2003; Thomas et al., 2008). In some cases, liquid water has proven to be necessary to reactivate photosynthesis by soil cyanobacteria (Lange, 2003).

The availability and absorption of moisture triggers different metabolic processes in cyanobacteria (i.e. photosynthesis, respiration and N_2-fixation). During rewetting experiments using *Nostoc*, Scherer et al. (1984) found that respiration recovered within minutes but that photosynthesis recommenced approximately 1 h after and N_2-fixation several hours after hydration. Further studies have revealed that the recovery process of the metabolic pathways depends on the amount of water available for photosynthesis (Lange, 2003). Colonies of isolated cyanobacteria (*Nostoc commune*) were subjected to different amounts of water (Satoh et al., 2002), from one-fourth to three-fourths of the dry weight of the colony. The highest amount of water was required for full recovery of photosynthesis. Satoh et al. (2002) thus suggested that the physical structure of the EPS is the main contributing factor to the amount and absorption kinetics of moisture allowing cyanobacteria to absorb many times their dry weight in water.

The amount and frequency of rainfall events in drylands is likely to have the most significant impact on EPS synthesis and whether C sequestration or loss occurs (Fig. 1). In the western United States, frequent moisture pulses were found to increase microbial respiration (C loss) resulting in large effluxes of CO_2 (Belnap et al., 2004). Net photosynthesis (C gain) was only initiated in response to very small changes in soil moisture content. Recent studies in Kalahari Sand soils (Thomas et al., 2008) have also found evidence of the complexity of the metabolic responses of cyanobacterial soil crusts to rewetting. Thomas et al. (2008) measured C fluxes from the cyanobacterial soil crust with similar moisture pulses but during different seasons. They found net C gains to the soil (net cyanobacterial photosynthesis) upon surface wetting when subsoils were dry, but that in generally moist conditions there was net respiration. Because cyanobacteria are vertically stratified in the soil (Garcia-Pichel and Pringault, 2001), only surface autotrophs are likely to respond to light wetting, leading to C gain, whilst deeper soil moisture penetration will also activate subsoil heterotrophs leading to net respiration (Thomas and Hoon, 2010; Thomas et al., 2008). Although cyanobacteria are able to synchronise both photosynthesis

and respiration (Terauchi and Kondo, 2008), which could explain the apparent C gain and loss from the soil, rates of photosynthesis and respiration remain unknown and Thomas et al. (2008) found no clear correlation between environmental conditions and soil efflux. Although CO_2 fluxes give an indication of the main processes and conditions of C gain and loss from dryland soils, these fluxes can change rapidly, with both uptake and release occurring simultaneously and are thus difficult to interpret.

3.3. Soil nitrogen and EPS synthesis

After water, soil N availability is a critical limiting resource for dryland functioning (Schlesinger et al., 1996). The availability of N in dryland soils is controlled by mineralization and nitrification rates, where N inputs occurs as deposition (N compounds found in dust, rainfall water and in dung and urine by livestock) and by biological fixation by bacteria and legumes (Hawkes, 2003). Cyanobacteria are the most abundant and efficient N_2-fixing organisms and are thus of particular importance in environments which are poor in combined-N sources, such as dryland soils. Cyanobacteria, however, require C as an energy source for N metabolism. Although N metabolism is controlled by C/N ratios in the soil (Luque and Forchhammer, 2008) the precise proportion of N and C required for optimal metabolism under changing environmental conditions remains unknown. Changes in available N levels where cyanobacterial soil crusts are present could have an effect on EPS synthesis. This is particularly important as the EPS produced by cyanobacteria could serve as a C source for N metabolism or as a C sink when C/N metabolism is unbalanced by low N availability (Otero and Vincenzini, 2003). In return, the C/N balance in crusts will ultimately affect nutrient availability in the topsoil.

Dryland soils are characterised by an imbalance between high rates of N input and low levels of soil N (Schlesinger et al., 1996), suggesting that much of the fixed N must be loss by leaching (discussed in more detail later) or to the atmosphere. Cyanobacteria are capable of using both inorganic and organic sources of combined-N (i.e. ammonium, nitrate and urea) (Luque and Forchhammer, 2008). Cyanobacteria take up N compounds from the environment and convert them intra-cellularly to ammonium which is ultimately assimilated into cellular material. Ammonium is the preferred form of combined-N for cyanobacteria, inhibiting the use of any other form of N in its presence. In the absence of ammonium, cyanobacteria can utilise other N forms (i.e. nitrate) that are subsequently reduced to ammonium (Luque and Forchhammer, 2008). Depletion of combined-N sources leads cyanobacteria to use molecular dinitrogen as N source (N_2-fixation).

N_2-fixation requires the highest amount of energy from the N-assimilatory pathways in cyanobacteria and is therefore related to the availability of C from the polysaccharides (Luque and Forchhammer, 2008). Rates of N_2-fixation by cyanobacteria are difficult to compare as published rates are usually derived from occasional measurements and not seasonal variations. The most common method used to monitor N_2-fixation is the acetylene reduction technique, sometimes, but not always, in conjunction with ^{15}N isotope data. Both techniques have methodological problems in that, not only are they dependent on the experimental conditions but also on the microbial diversity of the crust (Staal et al., 2001). The amount of acetylene reduced to ethylene is proportional to N_2-fixation but reported conversion rates vary considerably (Belnap, 2003). Similarly, changes in the ratio of $^{14}N–^{15}N$ can provide information on N_2-fixation rates but analysis costs often restrict sample size and the data are at best semi-quantitative.

A large number of cyanobacterial species have been studied to determine whether N speciation has an effect on the composition of the polysaccharides produced. For example, cultures of *N. commune* grown in media with and without N (mainly ammonium and nitrate) have different ratios of polysaccharides to cyanobacterial biomass and carbohydrate composition (Brüll et al., 2000; Huang et al., 1998). Huang et al. (1998) found that in the presence of combined-N, the EPS to microbial biomass ratio increases and that a more complex polysaccharide structure was produced. Brüll et al. (2000) also suggested that changes in N metabolism might influence carbohydrate yield, where in the absence of N, only basic products were synthesised in contrast to more complex structure in the presence of combined-N.

Otero and Vincenzini (2003) also evaluated the effect of N source and light intensity on the synthesis of EPS with three strains of the genus *Nostoc* under laboratory conditions. High light intensities enhanced total carbohydrate synthesis and led to some structural changes of the EPS (from capsulated to non-capsulated; see Fig. 2) in response to nitrate availability. Because N_2-fixation is inhibited in the presence of ammonium or nitrate (Luque and Forchhammer, 2008), the loss of capsulated polysaccharides affects the activity of the nitrogenase (N_2-fixing enzyme) inside the heterocyst. Their findings thus provide evidence of a correlation between EPS synthesis and N_2-fixation in the presence of nitrate. They suggested that EPS is produced only when fixed C exceeds the amount of N available in the culture medium. In other words, during conditions of low N availability, EPS serves as a sink for excess fixed C (Otero and Vincenzini, 2003). It remains unclear, however, whether cyanobacterial responses to N availability would be similar under field conditions.

Nitrogen not only affects the composition of EPS but the biomass of carbohydrates produced. Contradictory results have shown enhanced carbohydrate synthesis under both low levels and high levels of N (Gordillo et al., 1999). Cultures of the cyanobacteria *Spirulina platensis* show greater carbohydrate synthesis under enhanced CO_2 availability and N sufficiency, but decreased carbohydrate synthesis under N limitation and high CO_2 (Gordillo et al., 1999). The results suggest that an increase in atmospheric CO_2 enhances photosynthesis by cyanobacteria with N sufficiency. To date there is no clear relationship between the source (i.e. ammonium and nitrate) and amount of N and EPS synthesis in mixed cyanobacterial soil crusts.

4. Function of EPS in dryland soils

4.1. Nutrient sequestration

Nutrients in dryland soils are concentrated in the topsoil, partly due to nutrient absorption by soil particles but also because of the widespread presence of cyanobacterial soil crusts (Thomas and Dougill, 2007). By preventing nutrient losses to the subsoil, BSC are able to increase nutrient availability suggesting that nutrient cycling adjacent to BSC is topsoil dominated. Carbohydrates produced by cyanobacterial soil crusts in the south-west Kalahari are topsoil concentrated with an exponential decrease with depth, where the carbohydrate content in the surface can represent up to 75% of the total SOC (Mager, 2010a).

Elevated atmospheric CO_2 concentrations have been shown to influence microbial rates of decomposition and nutrient transformations by affecting water use efficiency (Housman et al., 2006). It is expected that changes in environmental conditions could affect the synthesis of EPS and therefore alter the ability of cyanobacterial soil crusts to retain nutrients in the topsoil. Because soil water content affects the synthesis of EPS, the ability of cyanobacterial soil crusts to store nutrients in the crust will ultimately depend on how changes in precipitation affect the metabolic activity of BSC organisms. The relationship between microbial activity and seasonal

distribution of small and large precipitation events has direct implications for the system C and N balance (Austin et al., 2004). The C balance of dryland soils is determined by differences between CO_2 fixation by plants and BSC, and respiration (both by plants and BSC) and soil heterotrophs (Tandeau de Marsac et al., 2001). All these metabolic processes require the availability of moisture.

Elevated nutrient concentrations within cyanobacterial soil crusts has been suggested to give a competitive advantage to adjacent plants as nutrients in the crust become available for plant use (Harper and Belnap, 2001). Because N_2-fixation in cyanobacterial soil crusts is highly dependent on C levels, fixation rates are highest after photosynthesis has replenished cyanobacterial C stores. The EPS matrix thus immobilises nutrients within the soil crust both physically (by trapping nutrient-enriched dust grains) and chemically (through glycosidic bonds) acting as a sink and preventing losses from the system (Hawkes, 2003; Veluci et al., 2006). Although BSC can increase N input into the soil through N_2-fixation, much of this N is released almost immediately to the surrounding soil (Belnap, 2003), suggesting that fixed N must be lost to the atmosphere or by leaching.

4.2. Erodibility

Dryland soils, because of their characteristically limited OM and fine grained particles, are generally poorly aggregated and highly erodible. Patchy vegetation cover also means that soils are often exposed to wind and water making them susceptible to erosion. Cyanobacteria and particularly cyanobacterial EPS play a critical role in stabilizing dryland soil surfaces thus preventing the undesirable consequences of erosion (such as nutrient and OM loss, dust generation and crop damage). The ability of cyanobacterial filaments to create surface aggregates and increase soil stability is closely associated with the number/biomass of cyanobacteria in the soil (Belnap and Gillette, 1998) and the EPS produced (Wolfaardt et al., 1999). EPS have thus been used as a proxy measure of soil stability in the field (Belnap et al., 2008; Bowker et al., 2008). The presence of cyanobacteria producing EPS may not only enhance the stability of the soil but of other non-filamentous cyanobacteria. EPS acts as a binding matrix between the filamentous cyanobacteria and the soil particles, providing a substrate for the cyanobacteria and a skeleton and cementing to the upper layer of the soil (Mazor et al., 1996). The layer formed by the polysaccharides provides greater compressive and tensile strength leading to soil particle aggregation and stabilisation of the surface (Hu et al., 2002).

Filamentous cyanobacteria, such as the genus *Microcoleus*, are responsible of forming a mat on the surface soil during times of available moisture and moderate weather. Filamentous cyanobacteria posses a greater capacity to entangle the surface grains as they can reach between soil grains or deeper layers of the crusts, even during drought conditions. This distinction between cyanobacterial forms and the formation of surface aggregates has been demonstrated by wind tunnel experiments by McKenna-Neuman et al. (1996) and Hu et al. (2002). Both studies used cultures of isolated filamentous cyanobacteria (*Lyngbya*, *Microcoleus* and *Nostoc*) grown for between five and seven weeks respectively on unconsolidated sand during greenhouse experiments. After crust development, they were subjected to varying degrees of particle abrasion. Additional experiments were carried out by Hu et al. (2002) where colonies of filamentous cyanobacteria were grown for one year in field plots. McKenna-Neuman et al. (1996) found that filamentous cyanobacteria had greater flexibility than green algae, while Hu et al. (2002) suggested that filaments are responsible for providing tensile strength to the soil. The tensile strength imparted by the filaments was found to increase with time as crusts grew and the electrochemical affinity between EPS and soil particles developed. Xie et al. (2007) also investigated the compressive strength of three cyanobacteria in the field and found a higher compressive strength with increasing cyanobacterial biomass. As the cyanobacterial biomass increased gradually, more EPS was released forming more soil aggregates. Recent studies in the Kalahari found that aggregated soils are more resistant to erosion than single particles of sand, silt or clay and is closely related to the presence of filamentous cyanobacteria and the EPS produced (Thomas and Dougill, 2007).

Aggregate stability can be maintained over time and under adverse conditions of varying rainfall patterns, temperatures and light intensities. This property is especially important during periods of drought, where cyanobacteria may be the only living organisms capable of stabilising the soil surface (Belnap and Gillette, 1998). A well-developed aggregate could maintain soil cohesion and resistance from wind erosion throughout the year, as they often form a continuous cover in plant interspaces (Hu et al., 2002). This resistance to erosion, however, is limited not only by edaphic factors but disturbance levels by livestock and game.

Disturbance history is therefore important to spatial heterogeneity of crust organisms because the integrity of the crust is vulnerable to both small and large scale disturbance (Belnap and Gillette, 1998). The most common disturbance to BSC in drylands is trampling by livestock. Trampling generates physical breakage of the EPS matrix, decreasing aggregate stability. The decrease in aggregate stability not only reduces crust cover but affects the development and functioning of BSC. BSC are also vulnerable to disturbance by wind erosion (Belnap and Gillette, 1998), removing the biological material from the soil surface or covering the surface with sediments resulting in crust burial.

Recovery rates, given no further disturbance, vary with BSC species composition. Recovery rates of cyanobacterial soil crusts are relatively quick (several months) depending on intensity of disturbance and conditions after disturbances (Thomas and Dougill, 2007) compared to very slow recovery rates (several years) of lichen-dominated crusts (Lalley and Viles, 2008). Removal of cyanobacteria from the crust and loss of fine soil particles to which nutrients are bound reduces site productivity and exposes unprotected subsurface soils to wind erosion (Evans and Belnap, 1999). Ultimately, crust disturbance not only affects soil water content, nutrient availability and accelerated soil loss through erosion but can result in decreased physiological functioning of the cyanobacteria resulting in the interruption of the feedbacks between biotic and abiotic components of the system.

4.3. Soil hydrology

Drylands are water-limited ecosystems characterised by variability in the magnitude, frequency and timing of precipitation events (Schlesinger et al., 1996). It is the nature of precipitation in drylands that allows soil crust organisms to thrive because they are able to exploit relatively short periods of optimal conditions (such as those following rainfall when soils are moist) as well as survive long periods of desiccation. A fundamental adaptation to this rainfall regime is the heterogeneous cover of vascular plants which allows light to reach the soil surface and provides the opportunity for autotrophic organisms to populate plant interspaces. Upon hydration EPS has been found to repair photosynthetic apparatus damaged during the state of dormancy (Harel et al., 2004) thus ensuring the maintenance and rapid return of physiological activities. As a defence mechanism, EPS also helps limit UV damage to the cyanobacteria (Ehling-Schulz and Scherer, 1999) by acting as a buffer zone between the environment and the cell. EPS produced by soil cyanobacteria will also influence different aspects of soil hydrology, including water infiltration, absorption and retention (Belnap, 2006; Eldridge et al., 2000; Mager, 2010b).

The EPS matrix absorbs and delays water movement through the soil by becoming more massive and less fibrous (Potts, 2001). Water absorption by EPS provides a cellular buffer for the cyanobacteria by regulating the uptake and loss of water from the cells. Water absorption thus creates a microenvironment that holds water for longer periods and dries more slowly than its surroundings, decreasing or at least delaying evapotranspiration losses within the crust layer (Potts, 2001). The water retained in the EPS matrix not only reduces evaporation losses but potentially increases the water-holding capacity of the soil (Mager, 2010b). For example, cyanobacterial soil crusts have been found to increase time of water retention within the surface by decreasing soil porosity and bulk density and by increasing OM and cation exchange capacity (Mager, 2009).

Higher volumes of rainfall can result in increased nutrient leaching from the soil surface. Johnson et al. (2007) evaluated possible losses of N from BSC in drylands, suggesting that the movement of N within soils covered by BSC is more related to climate (i.e. precipitation) than to biology (i.e. denitrification rates). Nitrate is typically very soluble and mobile in solution, and excess nitrate is readily leached when soils are saturated with water. Because drylands are characterised by short periods of soil moisture availability, it is difficult to expect significant rates of leaching. This relationship suggests that nutrient leaching is very low or undetectable during dry conditions in drylands (Austin et al., 2004).

The presence of BSC could potentially prevent leaching losses on these vulnerable areas. Cyanobacterial soil crusts are thought to immobilise nutrients in the surface that would otherwise be loss by leaching (Hawkes, 2003). Only recent studies have evaluated the role of BSC in N leaching from the soil surface (Veluci et al., 2006). Different BSC, dominated by mosses or lichens were evaluated for their potential to immobilise N in the surface. Leaching of N (ammonium and nitrate) was higher in bare and moss-dominated soils, but significantly reduced in lichen-dominated crusts. Potentially, the presence of cyanobacterial soil crusts could not only improve the fertility of the soils they colonise (Mager, 2010a) but also limit losses of N and C by leaching (Mager, 2009).

5. Summary and conclusions

Cyanobacterial soil crusts are particularly prevalent in dryland soils because a discontinuous vegetation cover allows more light to reach the soil surface. Cyanobacteria are able to survive the extreme conditions of the soil surface in part because EPS secretions provide a stable substrate and buffer cells from extremes of temperature, light and desiccation. Through their photosynthetic mechanism, cyanobacteria accumulate carbohydrates (EPS) as C and energy reserve for cells (Housman et al., 2006).

While several studies have addressed the ability of BSC to maintain or improve soil biochemical properties with moisture availability, most studies acknowledge the role of EPS in structuring BSC (e.g. Mazor et al., 1996). BSC are only recently known to immobilise excess N in the surface due to the production of EPS within the crust layer (Veluci et al., 2006). Whether cyanobacterial soil crusts also act to immobilise carbohydrates in the surface remains unknown.

The prevalence of cyanobacterial soil crusts is also essential in maintaining surface stability and decreasing the effect of erosion on dryland soils (Thomas and Dougill, 2007). Absence of these crusts can lead to increased erosion, resulting in loss of OM, water availability, fine soil particles and nutrient content (Belnap and Gillette, 1998). The survival of cyanobacterial soil crusts in dryland soils and their roles in dryland surface processes is related to the production of EPS. However, most studies related to the EPS surrounding microbial cells are based on laboratory isolations and cultures of cyanobacteria, or the effect of culturing conditions on the EPS production. It is clear that in order to better understand the role of cyanobacterial soil crusts on soil C storage and availability of carbohydrates and N, soil hydrological properties and surface stability we need to include further field studies regarding EPS dynamics.

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