SOIL STABILIZATION BY A PROKARYOTIC DESERT CRUST: IMPLICATIONS FOR PRECAMBRIAN LAND BIOTA

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Abstract. A cyanophyte dominated mat, desert crust, forms the ground cover in areas measuring hundreds of square meters in Utah and smaller patches in Colorado. The algal mat shows stromatolitic features such as sediment trapping and accretion, a convoluted surface, and polygonal cracking. Sand and clay particles are immobilized by a dense network of filaments of the two dominating cyanophyte species, *Microcoleus vaginatus* and *M. chthonoplastes*, which secrete sheaths to which particles adhere. These microorganisms can tolerate long periods of desiccation and are capable of instant reactivation and migration following wetting. Migration occurs in two events: 1. immediately following wetting of dry mat, trichomes are mechanically expelled from the sheath as it swells during rehydration, and 2. subsequently, trichomes begin a self-propelled gliding motility which is accompanied by further production of sheath. The maximum distance traveled on solid agar by trichomes of *Microcoleus vaginatus* during a 12 hour period of light was 4.8 cm. This corresponds to approximately 500 times the length of the fastest trichome, and provides a measure of the potential for spreading of the mat in nature via the motility of the trichomes.

Dehydration resistence of the sheath modifies the extracellular environment of the trichomes and enables their transition to dormancy. Following prolonged wetting and evaporative drying of the mat in the laboratory, a smooth wafer-like crust is formed by the sheaths of *Microcleus* trichomes that have migrated to the surface. Calcium carbonate precipitates among the algal filaments under experimental conditions, indicating a potential for mat lithification and fossilization in the form of a caliche crust. It is suggested that limestones containing tubular microfossils may, in part, be of such an origin.

The formation of mature Precambrian soils may be attributable to soil accretion, stabilization, and biogenic modification by blue-green algal land mats similar to desert crust.

1. Introduction

Stabilization of some soils in the arid regions of the United States of America results from sediment trapping and accretion by blue-green algal communities. They form stromatolitic mats on land that are known as 'desert crust'. Desert crust (see Figure 1) is geographically widespread in the southwestern United States, having been reported in Oklahoma, Kansas, Texas (Booth, 1941), New Mexico (Shields *et al.*, 1957), and Idaho (Brock, 1975). This study reports new occurrences in Utah and Colorado.

A network of filamentous cyanophytes is responsible for consolidation of sand, and is frequently one to three inches deep. The crust may rest on rock (see Figure 2) or soil (see Figure 3) in areas of flat topography. It is absent from erosional channels and steeply sloping terrain. The mat's surface is typically rough and undulating, and is rigid, although the mat is fragile enough to disintegrate into sand when pressure is applied. Some polygonal cracking occurs which allows careful removal of intact chunks of the crust for structural analysis such as scanning electron microscopy (see Figures 4 and 5). The

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ground cover afforded by desert crust varies from meter square isolated patches on a Colorado grassland plateau to areas of several hundred square meters which occur throughout Canyonlands National Park in Utah.

Soil algae have been shown to be instrumental in soil binding and water retention (Booth, 1941) and to be important sources of fixed nitrogen (Shields *et al.*, 1957). In this study the stromatolitic nature of a modern terrestrial algal mat is recognized and observations are made on the species composition of the algal community, the adaptations of the algae to water shortage which prevails during extended periods of time in the desert, and their response to wetting and drying.

Blue-green algal stromatolites occurred in the marine subtidal and intertidal zones during the Precambrian, and continue to occupy similar niches in the Recent (e.g. Shark Bay and the Persian Gulf), and some of the Precambrian stromatolite-dwelling organisms have been shown to have modern morphological counterparts (Golubic, 1976; Golubic and Hofmann, 1976).

This paper discusses the evolutionary origins of desert crust algal mats and their possible role in the formation of Precambrian soils.

2. Materials and Methods

Pieces of dormant desert crust were collected dry in the field and stored near a window in an effort to simulate natural conditions of light. Mat placed in finger bowls was dampened with distilled water in order to achieve a laboratory simulation of the mat's response to rain. It was then allowed to dry gradually and completely.

Dry cyanophyte filaments were selectively plucked out of the natural field-collected mat for microscopic preparations using forceps. Small chunks of crust were wetted and transferred carefully through a series of droplets of distilled water to clean organisms of adhering sand particles, to enable photomicrography and identification of species.

Light microscopy and photomicrography were accomplished using a Zeiss Universal microscope with transmitted light, Nomarsky interference contrast, and phase contrast illumination (see Figures 6–15). Scanning electron microscopy was done on an AMR model 1000 SEM.

Fig. 1. Desert crust covers large areas in Canyonlands National Park, Utah. Fig. 2. Desert crust forming over flat rock. Fig. 3. Desert crust forming on sand. The mat can be several inches deep, and has a brittle, convoluted surface. Fig. 4. SEM of the experimentally wetted and dried crust shows a horizontal surface layer of cyanophyte filaments. Dried moss gametophytes are above, and sand grains are below. All scales shown indicate micrometers. Fig. 5. Beginning calcite precipitation in the surface layer of Figure 4. Fig. 6. Cross section of a large filament of *Microcoleus* which was resin-embedded, thin sectioned, and stained. More than forty trichomes are in a common sheath, which is actually a composite of smaller bundles that appear here as darkened rings. During dehydration, shrinkage of sheath material causes tubular spaces (arrow) to form around the trichomes. Fig. 7. Bundled trichomes of *Microcoleus vaginatus* (Vaucher) Gomont in a common sheath. Note the capitate, narrowing trichome tip characteristic of this species. All light photomicrographs are with Nomarski contrast illumination. Fig. 8. *Microcoleus chthonoplastes* Thuret. Trichomes end with a bullet-shaped end cell.


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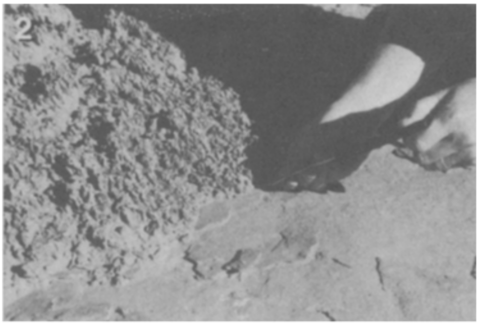
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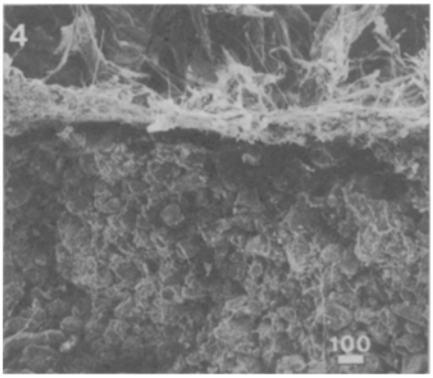
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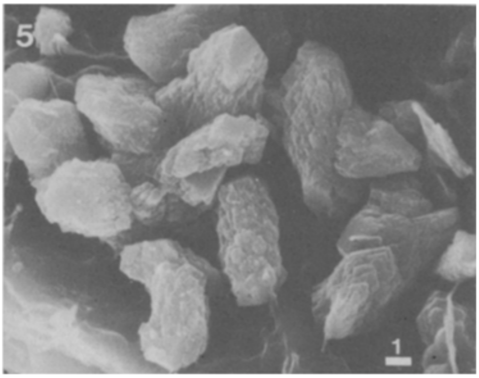
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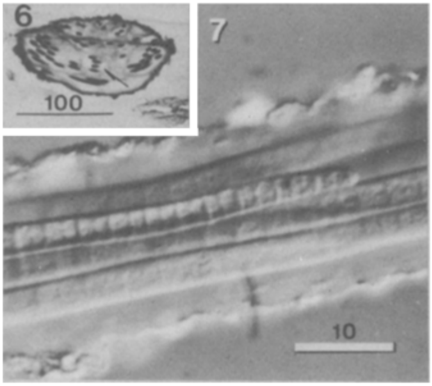
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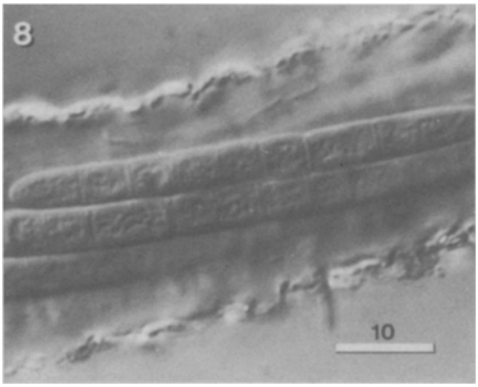
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Study of algal motility was conducted as follows: cyanophytes were tweezed from the dry mat and put on a dry slide. A coverslip was placed on top, and the microscope focused to 160x in order to best observe motility of entire trichomes. A drop of distilled water was touched to the edge of a coverslip, and by capillary action drawn beneath it. Maximum rates of gliding motility were measured directly by observation with the microscope and timing with a stopwatch. Long term migration, was followed by recording the position of trichomes on an agar surface at time intervals. This approach is a more valid basis for extrapolation to rates of migration in nature than using the maximum rates of gliding described above, because direct observation of trichomes showed that they move intermittently and at varying speeds.

The migration of trichomes over a period of several hours was observed by placing single dry filaments (each containing ca. 50–100 trichomes) at the center of twenty seven solid agar plates (BG-11 freshwater medium, see Stainer *et al.*, 1971, with 1.5% agar) under the following conditions: (1) the inoculation was made on seven plates in the dark and after 12 hours of darkness each plate was illuminated for 12 hours; (2) the inoculation was made on twenty plates in the light and after 12 hours of light the plates were placed in darkness for 12 hours. During periods of illumination plates were observed several times using a dissecting microscope. Plates kept in darkness were observed only at the end of the dark period. The migrating trichomes leave visible trails along the agar surface (as long as it is fairly solid). The lengths of the trails were measured (from the leading trichome to the point of the inoculum) and the average motility rate of that trichome was calculated in μm sec^{-1}.

Bundled trichomes were embedded and sectioned for light microscopy. However, the embedding method described below also provides a specimen preparation suitable for transmission electron microscopy. When trichomes migrate on agar they tend to move together in streams. Streams were fixed with glutaraldehyde (2.5%), covered with a drop of warm liquid agar, and a block of agar containing the trichomes was cut out of the plate (see Rippka *et al.*, 1974). This block was then stained with OsO_4, transferred through cacodylate buffer and then a dehydration series of gradually increasing ethanol concentration, placed in propylene oxide, and then a 1:1 mixture of propylene oxide and liquid epon 812 resin. The block was then transferred twice into pure epon before curing in an oven at 60°C for three days. The resulting hard plastic block was then sectioned on an M-1 microtome, cutting cross-sections through a *Microcoleus* filament. The thin sections were stained with toluidene blue (see Figure 6).

3. Results and Discussion

3.1. THE SPECIES COMPOSITION OF THE ALGAL MAT COMMUNITY

The Utah and Colorado desert crust microbial communities are predominantly prokaryotic. Two species of filamentous cyanophytes, *Microcoleus vaginatus* (Vaucher)

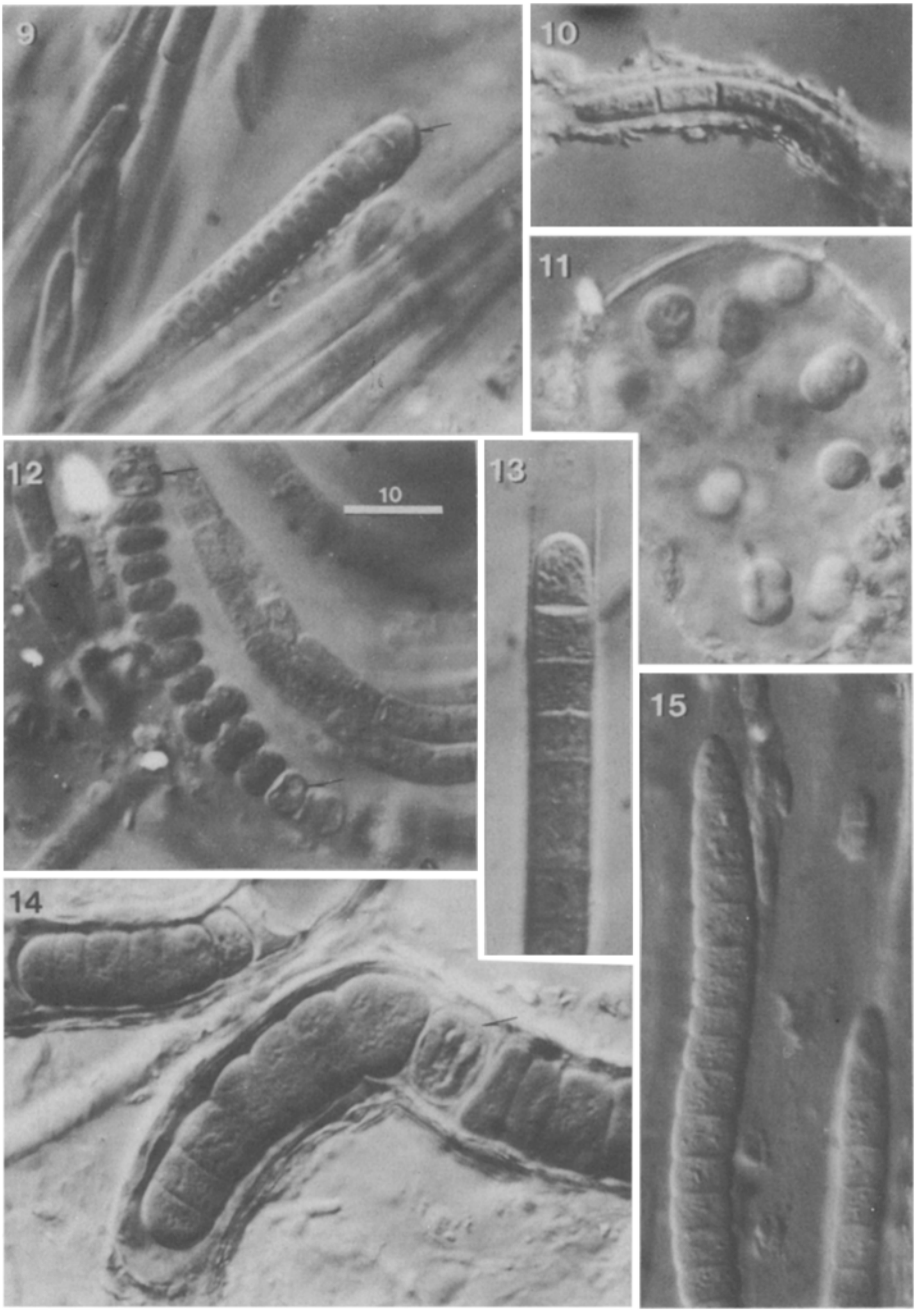

Fig. 9. *Calothrix pulvinata* Bornet-Thuret surrounded by trichomes of *Microcoleus chthonoplastes*. Heterocysts, sites of N_2 fixation, are marked with arrows in Figures 9, 12, and 14. Fig. 10. *Schizothrix penicillata* (Kützing) Gomont. Fig. 11. *Gloeocapsa nigrescens* (Vaucher) Novaček. Fig. 12. *Nostoc commune* Vaucher surrounded by trichomes of *M. chthonoplastes*. Fig. 13. *Phormidium retzii* Gomont. Fig. 14. *Scytonema tenellum* Gardner (has dark brown sheaths). Fig. 15. *Schizothrix subconstricta* Golubic.

Gomont (see Figure 7) and *M. Chthonoplastes* Thuret (see Figure 8), are the dominant organisms in both mats, and are responsible for approximately 90% of the organic material. *Microcoleus* is characterized by multiple trichomes that are bundled in a common sheath (see Figures 6, 7, and 8). Other species that are present in the Utah crust (which will be discussed for the remainder of this paper) are *Calothrix pulvinata* Bornet & Thuret (see Figure 9), *Schizothrix penicillata* (Kützing) Gomont (see Figure 10), *Nostoc commune* Vaucher (see Figure 12), *Gloeocapsa nigrescens* (Vaucher) Novǎcek (see Figure 11), *Phormidium retzii* Gomont (see Figure 13), *Scytonema tenellum* Gardner (see Figure 14), and *Schizothrix subconstricta* Golubic (see Figure 15). *Scytonema* and *Calothrix* are usually found at the surface of the mat while all others commonly occur beneath the surface.

The surface of the desert crust, when viewed with a dissecting microscope, consists of tightly packed sand, white sheaths abandoned by *Microcoleus*, dark brown sheaths of *Scytonema* and *Calothrix* which frequently contain trichomes, and small clumps of the foliose lichen *Collema*. When teased apart, the desert crust is seen to be composed of a dense mesh of filaments, many of which are dark green, to which grains of sand adhere. They are filaments of *Microcoleus*.

3.2. THE EFFECT OF WETTING AND EVAPORATION ON THE MAT

Fluctuation in salinity of the water retained in the desert soil takes place following every rain. First, a flushing of the mat with freshwater occurs, followed by a gradual increase in salinity due to solution of soil salts in interstitial water. They eventually form a brine, and, ultimately, precipitate as evaporation proceeds. A laboratory simulation of this process was conducted by placing an intact piece of mat in a finger bowl, and wetting it with distilled water. Within hours following wetting, a noticeable 'greening' of the newly glistening surface of the mat occurred, a phenomenon also described by Brock (1975). This 'greening' is actually due to the migration of *Microcoleus* trichomes from the interior of the mat to the surface. As the experiment progressed evaporation was retarded in the fingerbowl by covering it with glass. A community succession ensued, beginning with the appearance of leafy moss gametophytes. Soon after, a stalked sporophyte generation arose and fungal mycelia appeared. After several weeks of drying, the surface of the experimental mat was noticeably whiter than it had been before wetting. Patches of dark green were still visible, but these were mainly in depressions. Months later, the surface was almost entirely white except for the dry brown 'forest' of moss gametophytes. The white color was due to the empty white sheaths of *Microcoleus*. The smoother, rounded surface of the experimental mat is very hard and resistant to pressure compared with the brittle and fragile surface of desert crust collected in the field. Figure 4 shows a scanning electron micrograph of a vertical section through the hardened mat of the fingerbowl experiment. At the top, the bases of moss gametophytes rest on the horizontal layer which is composed mainly of strands of empty *Microcoleus* sheaths. When this mat was treated with dilute hydrochloric acid bubble formation occurred. Calcium carbonate had precipitated in the layer of abandoned algal sheaths (Figure 5); as a result of the prolonged wetness soil salts went into solution, they traveled toward the surface of the mat via capillary water transport as evaporation progressed and precipitated there.

3.3. THE RESPONSE OF THE CYANOPHYTES TO WETTING

The most significant biological property of desert crust is its ability to switch almost instantly from a dry dormant state to an active state. This is characterized by the striking motility of *Microcoleus* trichomes when wetted. Trichomes do not move when they are dry. Upon wetting, trichome motility occurs in two consecutive events which have different causes: (1) mechanical expulsion of trichomes due to swelling of the common sheath as it rapidly imbibes water; and (2) a self-propelled gliding motility of the trichomes. The process of trichome release from the common sheath is independent of the gliding motility of individual trichomes.

When a dry filament of *Microcoleus* is plucked from the mat and mounted dry for microscopy an immediate imbibition of water occurs as it is added, and the polysaccharide sheath swells to several times its original volume within seconds. The forces which result cause an explosive expulsion of the trichomes at rates of hundreds of microns per second.

Understanding of how the trichome propulsion occurs is based on observation of dehydrated, embedded filaments that have been thin sectioned and stained for light microscopy. A cross-section through a common sheath of *Microcoleus* shows that it is a composite of several smaller bundles, each visible as a dark ring. During dehydration the sheath pulls away from the trichomes it contains, leaving a space (Figure 6, arrow). Water enters such a tubular space by capillarity and the sheath expands in an inward as well as an outward direction during rehydration. This results in pressure on the trichomes which squeezes them out of the sheath. Usually, after a lag period of seconds to minutes, gliding motility of trichomes begins.

The mechanism of gliding motility is still a subject of debate. Cyanophyte trichomes have no visible locomotive structures and the theories that have been proposed were reviewed by Doetsch and Hageage (1968). *Microcoleus* trichomes move with a rotating motion forward or backward, frequently reversing direction.

There is no gliding of trichomes when desert crust is dehydrated; water, then, is one trigger for gliding motility. Figure 16 shows that light as well as water is a trigger for motility. It is a graph of the rate of gliding motility of the fastest *Microcoleus vaginatus* trichome (from a group of 50–100) that migrated on one illuminated agar plate for 12 hours before being placed in darkness for 12 more hours. It sometimes rains at night in the desert so we questioned whether light is necessary for trichome motility. Some trichomes that were plated in darkness and exposed to light only at the moment of observation were found to have migrated even in the absence of light, although the distance traveled was significantly shorter than in the daylight experiments. Figure 17 shows that water in the absence of light is a trigger for motility, although it is the initial

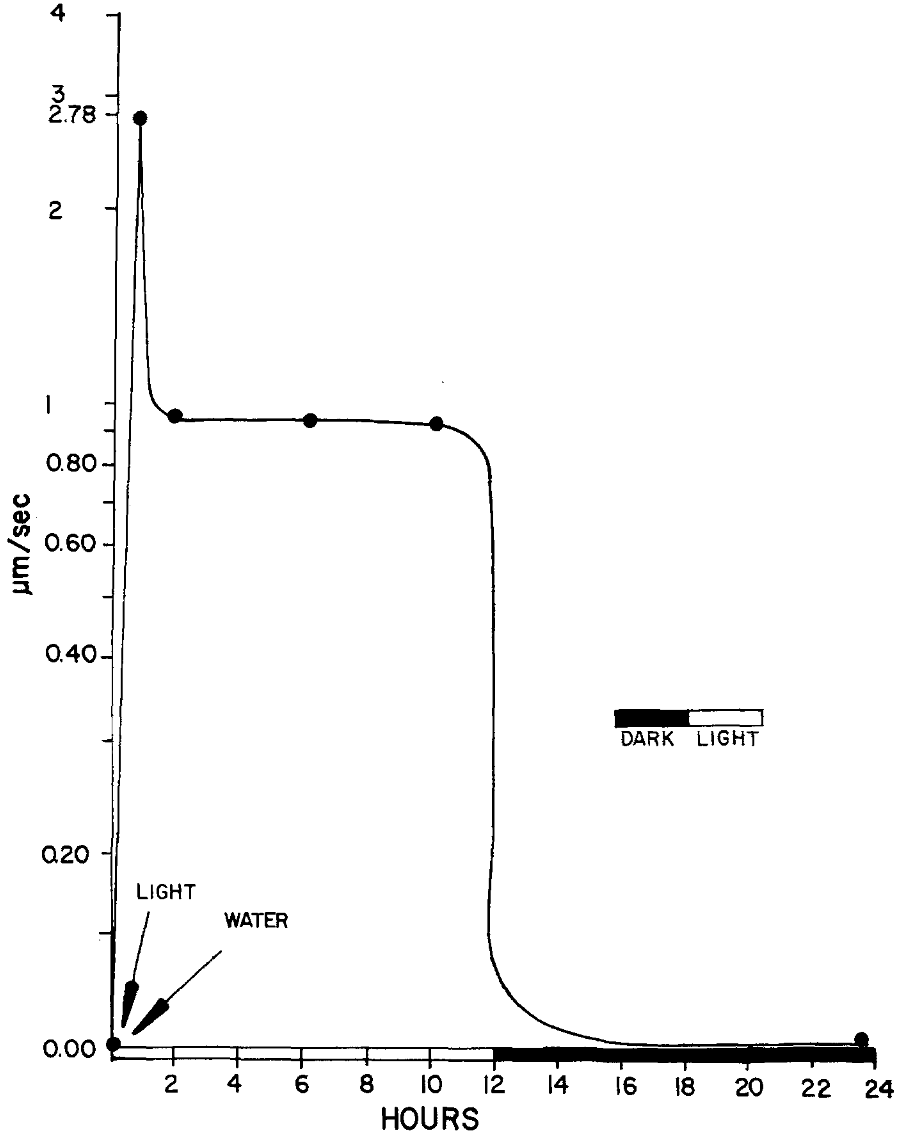

Fig. 16. Rates of gliding motility of a trichome of *M. vaginatus*: highest immediately following wetting on an illuminated agar plate. No motility occurred in the dark.

exposure to light that causes a significantly greater response. Following a 12 hour dark period in which group migration of trichomes had taken place, an average rate of 0.2 µm sec^{-1} was determined for the trichome in the lead. Then, this exemplary agar plate (as all others in the same test group) was exposed to light and observed continually. During the first 15 minutes there was a sharp increase in the leading trichome's rate of movement up to 11.0 µm sec^{-1}. Movement then slowed down to an average of 0.4 µm sec^{-1} until the end of the light period. This is twice the average rate for the dark period.

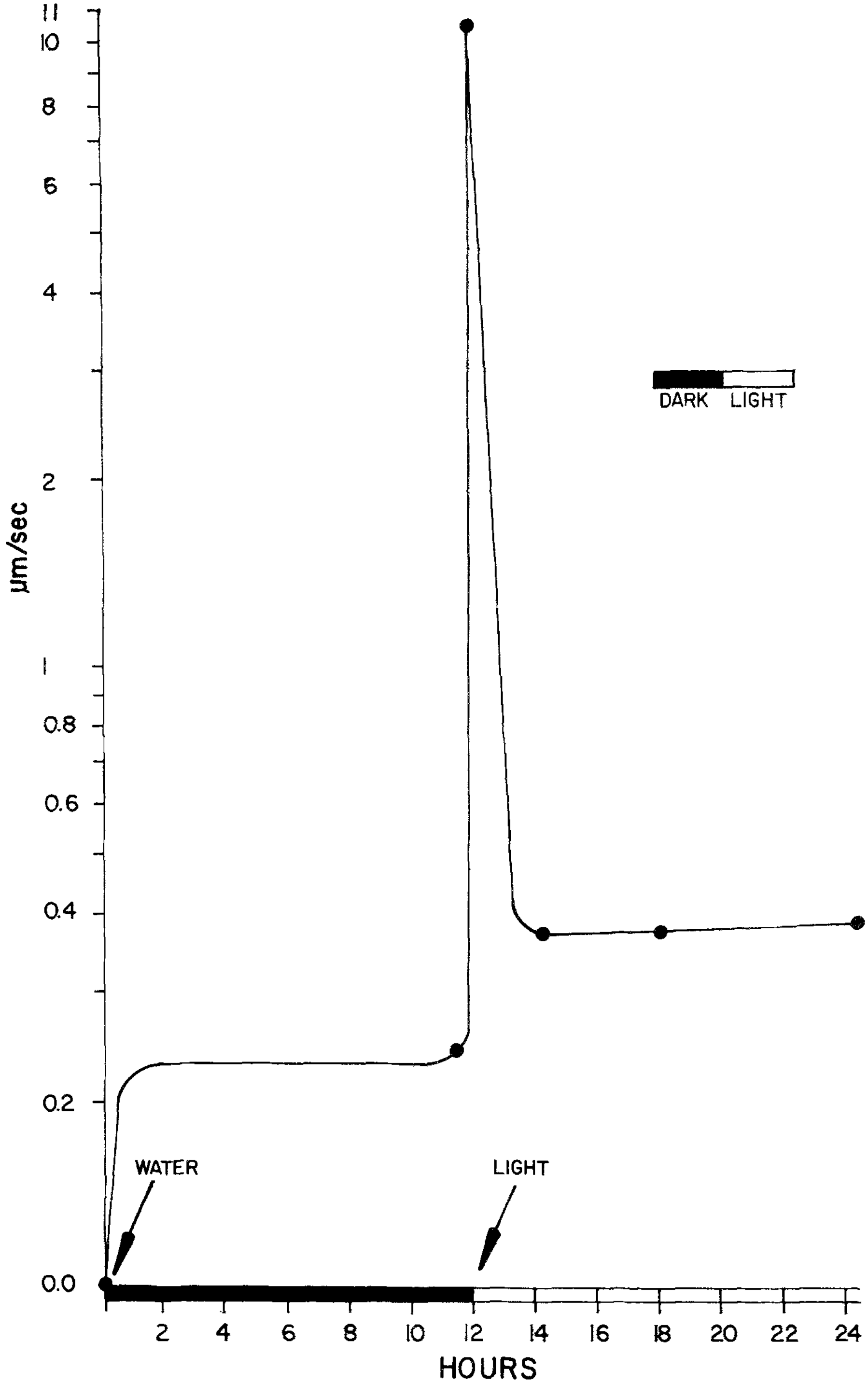

Fig. 17. Gliding motility of a trichome of *M. vaginatus* wetted in darkness on agar and subsequently exposed to light. Average speed was recorded for the dark period. The onset of light caused a burst of activity which then slowed down to a rate about twice that of the dark period.

The maximum distance traveled by a single trichome of *Microcoleus vaginatus* was 4.8 cm! Many trichomes are nearly 1 mm long, thus, such a trichome is capable of traveling about 500 times its own length on agar in one day. Assuming that slime production is continuous, the resulting 4.8 cm long thread is capable of trapping soil particles. Although it is not known whether rates of migration on agar are comparable to rates of migration on soil, they do provide a measure of potential for mat expansion. Desert crust formation and expansion does not depend directly on the growth and division rates of the organisms that make it, but rather, on their gliding motility and the accompanying production of a sheath which they continually abandon while migrating. It is the sheath which actually binds the mat, and represents the trails of single organisms which are capable of moving for days. Wind transported sand grains and clay particles adhere to the moist, sticky sheath and remain tightly bound to it as drying and sheath polymerization occurs. In this way soil accretes and is stabilized. The stabilized soil is very resistent to erosion by wind and water. Booth (1941) showed that when a similar mat and adjacent barren soil in Kansas were subjected to large amounts of forcefully applied water, the run-off from the barren soil was muddy while that of mat stabilized soil was quite clear.

3.4. THE RESPONSE OF THE CYANOPHYTES TO DRYING

The effect of dehydration on the metabolic activities of the *Microcoleus* dominated desert crust was studied by Brock (1975) who tested the mat's ability to photosynthesize under conditions of reduced matric and osmotic water potential by measuring the production of chlorophyll. Brock dehydrated entire pieces of mat either by absorption (reduction of matric water potential), or by wetting it with water of increasing salinity (reduction of osmotic water potential). Matric reduction caused a precipitous decrease in production of chlorophyll by the organisms at −10 bars, while osmotic reduction of water potential caused an *increase* in chlorophyll production from 0 to −20 bars, and thereafter, at lower osmotic water potential values, chlorophyll production decreased markedly. Brock calculated the water potential of sea water to be −28 bars and concluded that desert crust is not active at marine salinities. However, according to conversion tables (Hale, 1965) a salinity of 30–35‰ (average salinity of the ocean) corresponds to a water potential range of −20 to −25 bars. The photosynthetic activity of the mat that Brock measured was high within this range. It is interesting to note that while *Microcoleus vaginatus, Schizothrix penicillata, Gloeocapsa nigrescens, Nostoc commune*, and *Scytonema tenellum* are freshwater cyanophytes, other members of the mat community (e.g. *Microcoleus chthonoplastes, Schizothrix subconstricta*, and *Calothrix pulvinata*) commonly occur in marine environments. In fact, the Sippewisset Marsh intertidal algal mats (Wood Hole, Massachusetts) contain a large proportion of *Microcoleus chthonoplastes.* This species is also present in benthic mats of Solar Lake (Israel) near the surface of the pond (Campbell, unpublished observations) which undergoes seasonal fluctuation in salinity that culminates in precipitation of salt at the boundaries of the pond (Cohen *et al.*, 1977). Thus, the species composition of the Utah desert crust makes it well adapted to fluctuations in salinity, especially because the two dominating species may have different salinity optima (*Microcoleus vaginatus* vs. *M. chthonoplastes).* However, both species react to reduced matric water potential by dehydration and sudden collapse of the sheath with an accompanying loss of metabolic activity.

The ultrastructure of the cyanophyte sheath is a finely meshed network of thin fibrils (Fogg *et al.*, 1973). In desert crust, as dehydration occurs, this polysaccharide network collapses on itself, and, as a result, it increases in density which serves to slow additional water loss. Due to its small size, changes in the sheath morphology of *Microcoleus* are difficult to observe. However, observations of a marine *Rivularia* sp. during alcohol dehydration showed that from 0 to 95% ethanol no perceptible alteration of the size or shape of sheaths occurred. Then, as the ethanol concentration increased, the sheath suddenly collapsed to about 75% of its original size (Campbell and Golubic, unpublished observations). This indicates that strong molecular forces in the sheath bind water and maintain the sheath in expanded form until a critical amount of water is removed. If a similar affinity for water is characteristic of the *Microcoleus* sheath, the effective result would be hydrated surroundings for the trichomes up to the moment that the sheath collapse occurred. Such a mechanism could be instrumental in allowing sufficient time for the trichomes to slow or switch off their metabolic activity as dehydration ensues, thereby modifying the harsh desert climatic extremes.

The sudden and rapid changes in availability of water in the desert preclude colonization of soil by cyanophytes that are exclusively aquatic. Only those cyanophytes which produce sheaths can survive rapid desiccation and are competitive. Except for *Gloeocapsa*, all others in the assemblage are motile, either as fully differentiated trichomes or in their juvenile hormogonal stages. Resumption of metabolic activity upon rehydration is evidenced by the immediate migration of trichomes (following mechanical expulsion from a common sheath) and the accompanying renewed production of hygroscopic sheath. Rapid resumption of metabolic activity, gliding motility, and tolerance to drying are adaptations which allow the formation and spreading of vast communities of the prokaryotic primary producers that blanket otherwise barren terrain in an environment which fluctuates between the inundation of flash floods and long periods of drought.

3.5. THE FOSSILIZATION POTENTIAL OF DESERT CRUST

Desert crust does not normally lithify. It is a fragile structure, and a transient phenomenon which is easily trampled. However, the fingerbowl experiment showed that carbonate may precipitate in the mat. Similar conditions of prolonged wetting and then drying in nature could allow formation of caliche. If this process were repeated many times a carbonate rock could result, similar to that described by Swineford *et al.* (1958) who proposed a subaerial caliche development for limestone formations of the Great

Plains. Sufficient fossilized microflora had been previously found at the same site by Elias (1931) that he termed it "algal limestone". Swineford *et al.* denied finding microfossils and also rejected the lacustrine environment of deposition that had been postulated by Elias, arguing that the time of deposition occurred at the close of the Pliocene "at the culmination of a time trending toward aridity in the Great Plains". They noted shrinkage cracks, barite and calcite veins, and rotated blocks which they said were attributable to "successive episodes of desiccation, shrinkage, solubilization and reprecipitation". Although the limestone studied by Swineford *et al.* need not have required the presence of an algal mat such as desert crust for its formation, it is important to note that the presence of such a mat could be responsible for, or indicative of calcrete formation under similar conditions. James (1972) and Krumbein (1968) discuss the possible involvement of microorganisms in the production of some calcrete carbonates. Krumbein and Lange (in press) show direct involvement of blue-green algae in the formation of "desert stromatolites" of Israel. These observations indicate that even a fragile terrestrial desert crust community has a preservation potential and may appear in fossil calcrete deposits as lithified microscopic tubes (sheaths) and cellular remains of algal trichomes. Thus, a reexamination of calcrete limestone previously identified as resulting from abiogenic subsoil caliche formation is warranted.

3.6. PRECAMBRIAN SOILS

The colonization of land in the early Precambrian by prokaryotic, lithophytic assemblages similar to those that presently occur on alpine cliffs was suggested by Golubic and Campbell (1979). This proposal was based on the morphological similarity of *Eosynechococcus moorei*, a marine intertidal cyanophyte in the Precambrian Belcher Island Formation, to *Gloeothece coerulea*, a modern freshwater lithophyte.

Schopf (1968) suggested that "Oscillatorian gliding" may have enabled early colonization of land surfaces. The present study has established the adaptational value of gliding motility and the accompanying sheath production in the modern oscillatoriacean cyanophyte *Microcoleus* for colonization of barren land and accretion of soil. The antiquity of *Microcoleus vaginatus*, one of the desert crust species, has been invoked by Schopf's interpretation of the Late Precambrian *Cephalophytarion grande* (Schopf, 1968).

Several cyanophytes show extreme morphological conservatism, i.e. they have maintained species level similarity over time spans of billions of years (Knoll *et al.*, 1975; Golubic and Hofmann, 1976; Golubic and Campbell, 1979). It is important to note that some of these fossil-Recent counterparts, *e.g. Palaeolyngbya barghoorniana-Lyngbya estuarii* and *Eoentophysalis belcherensis-Entophysalis major*, have continued to inhabit marine intertidal environments since the Precambrian, while others occurred in the intertidal zone of Precambrian seas but have terrestrial (or freshwater) modern equivalents. The intertidal *Cephalophytarion grande* and the soil dwelling *Microcoleus vaginatus* represent another such case, illustrating that the evolutionary transition of cyanophytes from the marine environment to freshwater-wetted land was initially achieved by organisms that had occupied intertidal niches where they were exposed to a daily alternation of wetting and drying, and wide ranges of salinity. Such organisms would have been preadapted for invasion of dry land. In desert crust, one co-dominant species is *Microcoleus vaginatus*, a freshwater alga, and the other, *M. chthonoplastes*, is marine. Both are capable of tolerating the wide fluctuation in salinity that occurs in the wetted desert soil, although they probably have different optima. With respect to salinity fluctuation, dehydration, and rehydration, the desert soil is comparable to the intertidal sands.

Fisher (1965), Roscoe (1969), Tappan and Loeblich (1971), Kalliokoski (1975), and Fryer (1977) have noted or discussed the occurrence of mature Precambrian paleosols. D. Grandstaff (personal communication, 1979) has recorded the presence of 0.25% reduced organic carbon in analyses of a 15m thick, subaerially formed paleosol from the Precambrian (2.4 billion years old) Blind River Formation of Ontario. What was the source of organic matter in the subaerially formed soil? It is now proposed that terrestrial blue-green algal mats may have been responsible for the accumulation, stabilization, and biogenic modification of mature Precambrian soils. In its ecological function the modern *Microcoleus* dominated desert algal mat provides a representative model for such an ancient subaerial microbial community.

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