NATIONAL AERONAUTICS AND SPACE ADMINISTRATION

Technical Report No. 32-971

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ABSTRACT

In terrestrial desert environments, favorable microenvironments are found in the soil that promote the development of algae and associated organisms and a subsequent accumulation of organic matter. The most favorable habitats in desert soils occur in algal and lichen soil crusts, and on the undersurface of translucent or transparent materials partially imbedded in the soil surface. Algal abundance is increased and ecological factors are much less restrictive in these ecological niches than in the surrounding desert soil. Insolation is modified, more moisture is retained, desiccation is reduced, and organic matter accumulations are noticeable. Characteristics of translucent materials, such as white or milky quartz and chalcedony, which are partially imbedded in the surface of desert soils, permit the existence of mesophilic algal inhabitants, such as species of coccoid, blue-green algae, that do not normally occur as components of xeric soil populations. Other species are cosmopolitan forms occurring in a wide range of environments, including habitats at low or high elevations in hot or cold deserts. The probable occurrence of a number of translucent and transparent minerals in extraterrestrial soils and other geological materials may also provide a favorable ecological niche or microenvironment for organisms and associated organic matter in an otherwise harsh macroenvironment.

I. DESERT ENVIRONMENT

The search for life in our solar system will undoubtedly take place in extremely harsh environments. These environments may either represent or approximate deserts that possess unfavorable characteristics for the existence of life. Although terrestrial deserts may or may not have some of the attributes of extraterrestrial environments, knowledge and understanding of desert regions and their ecology on our own planet can provide valuable background information prior to detection of possible extraterrestrial organisms.

Terrestrial deserts are characterized by a combination of environmental factors that greatly limit the ability for organisms to survive, grow, and reproduce. When environmental factors are most adverse, no animals or macroplants are evident, and the life in desert regions is limited to microorganisms. When the environmental conditions are especially unfavorable, desert life forms can be restricted to specialized physiological groups of soil microflora; those that do occur may be of low abundance, irregularly distributed or, possibly, found only in favorable ecological microenvironments or niches. Biotic populations or communities that are able to exist under the harshest conditions in terrestrial desert regions are usually xeric ecotypes that are especially adapted to rigorous arid environments.

Some of the most restrictive environmental factors for life in terrestrial desert regions include water (quantity, quality, availability, and distribution), solar radiation (quality and intensity), temperature (extremes, mean diurnal and seasonal fluctuations), relative humidity (extremes, mean diurnal and seasonal fluctuations), wind (direction, intensity, and frequency), food supply (quantity, quality, and availability), and certain edaphic factors (especially stability of well-developed, favorable, interacting physical, chemical, and microbiological soil systems). Time is an important factor in all desert regions. The time during which an environmental factor is operative can be crucial, e.g., frequency and duration of drought, wind, and temperature extremes.

Water is commonly the most critical environmental factor. Biologically available water is frequently absent for an extended time period in most desert regions. Water is sometimes present as sudden deluges in temperate or tropical deserts, but it is irregularly distributed and rapidly lost through runoff or high rates of evaporation. In some desert regions, liquid water is present, but it is of an adverse quality for most organisms because of the kinds of salts or the total salt concentration. In polar deserts, a sufficient accumulation of water is usually present, but it occurs for extended time periods in an unavailable form as ice or snow. Salts can be a problem in polar regions as well as in temperate and tropical deserts, and the high osmotic pressure or imbalance of salts is too restrictive for most organisms. A few desert areas apparently have had little or no meteorological precipitation for decades. For example, the Tanezrouft in the southwestern Algerian Sahara, and parts of the Atacama–Loma Desert in Chile and Peru are noted as exceptionally dry and barren and are referred to as deserts within deserts (Ref. 1).

Other environmental factors that are restrictive for life in terrestrial desert regions frequently accentuate unfavorable moisture conditions. The solar radiation flux is commonly intense because the cloud cover is either negligible, thin, or irregular, and it does not appreciably intercept incoming ultraviolet and infrared rays. Temperatures are a limiting factor where there is a relatively high or low mean, thereby greatly influencing water availability and evapotranspiration rates. Relative humidity values of the air may sometimes be high but they are commonly low in most desert regions. Desert soil humidities may be high, despite extended periods of low air humidity (Ref. 2). Winds are frequently a noticeable feature in deserts, at times reaching high velocities, especially in polar and high mountain deserts. Whirlwinds ("dustdevils" or "winddevils") can be observed in hotter deserts. Winds tremendously increase the evaporation rate in deserts and also desiccate and abrade exposed surfaces of soils and plants during the intense transport of windladen debris.

The food supply in desert ecosystems and soils is frequently quite low. Food is a limiting factor to heterotrophic organisms because of the paucity and irregular distribution of organic matter and available water. Autotrophic organisms are also restricted by the lack of available water or the lack of available nutrients in sufficient quantity. An unfavorable ratio or balance of nutrients is not uncommon to desert regions. Many desert soils are fertile and have the ability to produce and sustain a biomass of macro proportions, but they are unproductive due to the lack of sufficient quantity and quality of water or accumulation of precipitated and unleached salts. Distinctive soil formation, which results in well-developed mature soils, is negligible in the harshest of terrestrial desert areas. A soil with the most favorable physical and chemical attributes presents the most favorable environments for organisms. Conversely, a soil with the most favorable characteristics for habitation of organisms has usually been developed under the influence of organisms. Other than organic matter and water, important soil factors for microorganisms are soil inorganics, reaction (pH), oxidation-reduction potential (Eh), temperature, aeration, and various biotic interactions.

II. DESERT MICROFLORA

Soil microorganisms are the only life forms which have been found to occur in some desert areas (Refs. 2, 3, 4).[1] The microflora found in desert areas includes various physiological and morphological groups. Desert microflora are commonly (1) bacteria (including heterotrophes, chemoautotrophes, aerobes, anaerobes, and microaerophils), (2) streptomycetes (various members of the actinomycetales), (3) fungi (especially ascomycetous molds), (4) algae, (5) myxomycetes, and (6) lichens. In some desert soils, especially with more favorable microenvironments and ecological niches, other microorganisms and microbiota are found, including myxobacteria, protozoa, nematodes, and numerous members of the Arthropoda. Desert soils have not been investigated for viruses, although blue-green algae, bacteria, and many other microorganisms are subject to virus attack (Ref. 5).

Semiarid and comparatively arid soils with 25- to 35-cm annual precipitation can have an abundance of bacteria and actinomycetes which may approach 1×10^6 or more per gram of soil (Ref. 6). In these same soils, the numbers of heterotrophic bacteria can approximate the abundance of chemoautotrophic bacteria.[1] Algal abundance at the surface 2 cm or less can approach that of the abundance of aerobic or microaerophilic bacteria. Algae decrease in abundance with depth of soil and may not be present below a depth of 0.5 to 3 m. Fungi and anaerobic bacteria may be abundant in more favorable desert soils, but have been found to be very few (< 10/gm of soil) in the most unfavorable desert soils so far investigated.[1]

In soils from harsh, desert environments, it appears that algae, and/or chemoautotrophic microorganisms are the most abundant groups present (Refs. 2, 7, 8, 9, 10).[1] The algae are filamentous blue-green or coccoid green forms. The chemoautotrophes are usually aerobic or microaerophilic, short or long bacterial rods and/or streptomycetes. The chemoautotrophes, which have been isolated and cultured from tropical or temperate desert soils, have been primarily metabolizers of sulfur or sulfur compounds (Refs. 8, 9, 10).[1] Studies of Antarctic soils have shown that sulfur and lactose metabolizers may be the most prevalent microorganisms in these soils (Ref. 11); algae were the only photosynthetic soil microflora present. The most abundant populations of desert microflora may or may not occur at the immediate soil–atmosphere interface (Refs. 2, 6, 9, 10). Knowledge and understanding of terrestrial desert soil microflora, their abundance, distribution, physiological and morphological characteristics, their biotic, edaphic, and other environmental relationships and interactions are far from complete.

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[1] JPL Desert Microflora Program, Unpublished Data, 1961 to Date.

III. DESERT ALGAL HABITATS

During the course of investigations on desert soils and microflora for the Desert Microflora Program, observations have been made on desert ecological niches, or microenvironments that are favorable for microorganisms (Ref. 2). When the overall environment of an area is extremely harsh, only microenvironments may have favorable conditions for the survival, growth and reproduction of desert microorganisms. Such habitats may have protective features which modify or shield microorganisms from unfavorable, or prolonged physical and chemical desert environmental factors. Although optimum conditions may not prevail, a favorable ecological niche can permit the development of a substantial population or community of microorganisms and a subsequent accumulation of organic matter.

The observations presented in this report are the result of continued studies on the properties of desert soils and their microflora relationships (Refs. 2, 3, 6, 7, 9, 10, 12, 13, 14, 15). Special attention has been given to the desert algae since they are the most abundant group of photoautotrophes present in surface layers of a number of desert soils. The observations reported here are also a continuation of previous efforts devoted to studying the occurrence, distribution, habitat, and kinds of algae occurring in the Sonoran Desert in Arizona (Refs. 16 through 22).

The algae of desert regions occupy a number of habitats, not all of which are xeric in nature. In general, these habitats can be categorized as follows: (1) permanent bodies of water such as lakes, streams, canals, ponds, wells, hot and cold mineral or freshwater springs, fumaroles, and cattle tanks (both natural and artificial), (2) intermittent streams and rain pools, and temporarily wet beds and banks of washes and ravines, (3) moist or dry exposed rock surfaces, either as epilithic or endolithic algal populations and communities or as lichen components, (4) epiphytic, as on various living xeric vascular plants such as cacti, and shrubs, xerophilous mosses and lichens, other algae, and also fresh or decomposed wood, (5) epizoophytic, as on various desert animals, such as tortoises or toads, (6) endophytic, including other algae, (7) almost negligible depressions in the soil microrelief where water stands for very short periods after rains, (8) subterranean components of the soil, sometimes to a meter or more in depth, (9) as components of algal or lichen surface soil crusts or strata and, (10) sublithophytes, growing around or under translucent or transparent materials—commonly minerals that rest on the soil surface or extend to some depth below the soil surface. Some desert algae also occur in aquatic or edaphic environments as halophytes, and in cold deserts, as cryophytes, growing on, in, or below ice or snow. This does not include all desert habitats, especially for hydrophytes and aerophytes, but it includes most of the environments that have been noted. There are also populations or communities of algae in deserts which exist as inhabitants of adjacent or overlapping ecosystems, such as saturated brine, salt, salt–soil interfaces or cryo-edaphic environments. Some desert microenvironments which contain algae are highly specialized, such as epizoophytic algae that occupy the shells of tortoises, or the thermophilic algae occurring in hot springs or around fumaroles. A number of desert algae are euryecological and they are ecophenes which may be similar or dissimilar in morphology. However, they may not necessarily have the same physiology since they have adapted to a wide number of diverse habitats (Refs. 23, 24, 25). In most cases, desert algae occupy environments where *available* moisture is present at some time during the life cycle, and light, temperature, nutrients and other physical, physico-chemical, chemical, and biotic factors are suitable for growth and reproduction.

Special attention has been given to the desert soil algae because they are the most abundant group of photoautotrophes present in surface layers of desert soils. Soil algae are present when no other chlorophyllous plants are evident in desert regions. Various accounts have been given of them as to their survival, abundance, or distribution in dry regions of this planet. Information has been given for their occurrence in Antarctica (Refs. 26, 27, 28), the Arctic (Refs. 29, 30), Australia (Refs. 31, 32), Chile (Refs. 33, 34), India (Refs. 35, 36), the Soviet Union (Refs. 37 through 46), the Sahara (Refs. 4, 47, 48) and South Africa (Ref. 49).[2] For Southwestern and Western United States, information is available on the occurrence or abundance of soil algae in arid or semiarid areas of the States of Arizona (Refs. 16 through 22, and 50, 51), California (Refs. 6, 52, 53), Colorado (Refs. 54, 55), Nevada (Refs. 52, 56, 57, 58), New Mexico, (Ref. 59), Oklahoma (Refs. 60, 61, 62), Utah (Ref. 63) and various western states (Ref. 64). Additional information has been obtained for the abundance and distribution of algae in arid and semi-arid soils of Baja California, Colorado, Hawaii, eastern Oregon, and Wyoming.[1] Soil algae, typical of other desert algae, are also abundant in semiarid soils at high altitudes in California (Refs. 12, 15).[1] The geographical distribution of many soil algae, including desert species, is apparently world-wide (Ref. 65).

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[2] An unpublished bibliography of 168 references on soil algae in Russia has been prepared by Dr. Herman Forest.

IV. XERIC ALGAL AND LICHEN SOIL CRUSTS

The first mention of conspicuous desert algal soil crusts was in 1907 (Ref. 66), although they were observed (but not understood to contain algae), some years earlier in South Australia (Ref. 67). This lack of attention to desert algal soil crusts is understandable, since algae were most frequently collected from marine, brackish, and freshwater habitats where growth was abundant and conspicuous (Ref. 68). Algae were collected mainly from regions of adequate rainfall, and soil algae were collected only when observed on ground which was moist for a substantial period or in association with other plants, such as lichens, liverworts, or mosses. It is mainly within the last 25 yr that desert algae have been observed, collected, cultured, isolated, and studied.

As noted previously (Ref. 16), algal and lichen soil crusts are of importance in arid and semiarid soils in regard to soil stabilization and erosion, water infiltration and penetration (Refs. 51, 59, 60, 69), reclamation of salty lands (Ref. 36), resistance to desiccation and prolonged drought (Refs. 31, 37, 51, 59), resistance to extreme soil temperatures (Refs. 2, 22, 53, 70, 71), diurnal freeze–thaw cycles (Refs. 12, 14), and in the colonization of denuded, eroded, or barren ground (Refs. 21, 29, 52, 66, 69, 72, 73). Algae, especially blue-green forms, are among the first colonizers of newly exposed, or bare and weathered rock, pumice, and ash, and raw soil-like materials (Refs. 29, 42, 74, 75, 76). They are also important forerunners to subsequent establishment of soil surfaces by mosses and seed plants (Ref. 60).

Algae are an important source of organic matter in soils as indicated in previous reviews (Refs. 16, 77, 78). In this regard, desert regions of Southwestern United States have received attention as to the role of algae as constituents of algal and lichen soil crusts (Refs. 17, 51, 59). It has been found that these crusts, and filamentous blue-green algae isolated from these crusts, have the ability to fix atmospheric nitrogen (Refs. 50, 79, 80, 81). Soil algae, primarily filamentous blue-green algae and a few species of coccoid green algae, were the most conspicuous constituents of the algal flora in these soils (Refs. 17, 22). Algae were the only photoautotrophes present in barren, desiccated, well-drained desert soils in harsh desert environments. They were most conspicuous as constituents of soil rain crusts (Fig. 1), in temporary rain pools or favorable microrelief where they formed thin algal soil crusts (Fig. 2) and thick lichen soil crusts (Fig. 3). These crusts are evident on bare or eroded soil, sometimes as developmental stages between algal soil crusts and definitive, mature, crustose lichen crusts (Fig. 4). In other cases, they are present among xeric vascular vegetation (Fig. 5), although competition may promote vascular plants and gradually eliminate algae. Chemical analyses of these crusts show a comparatively high content of organic matter as indicated by determinations for accumulated organic carbon and organic nitrogen (Refs. 13, 16, 50, 51, 59). Surface crust samples contain more organic matter than the surrounding soil or the non-encrusted soil to some depth beneath the samples (Refs. 16, 50, 79).

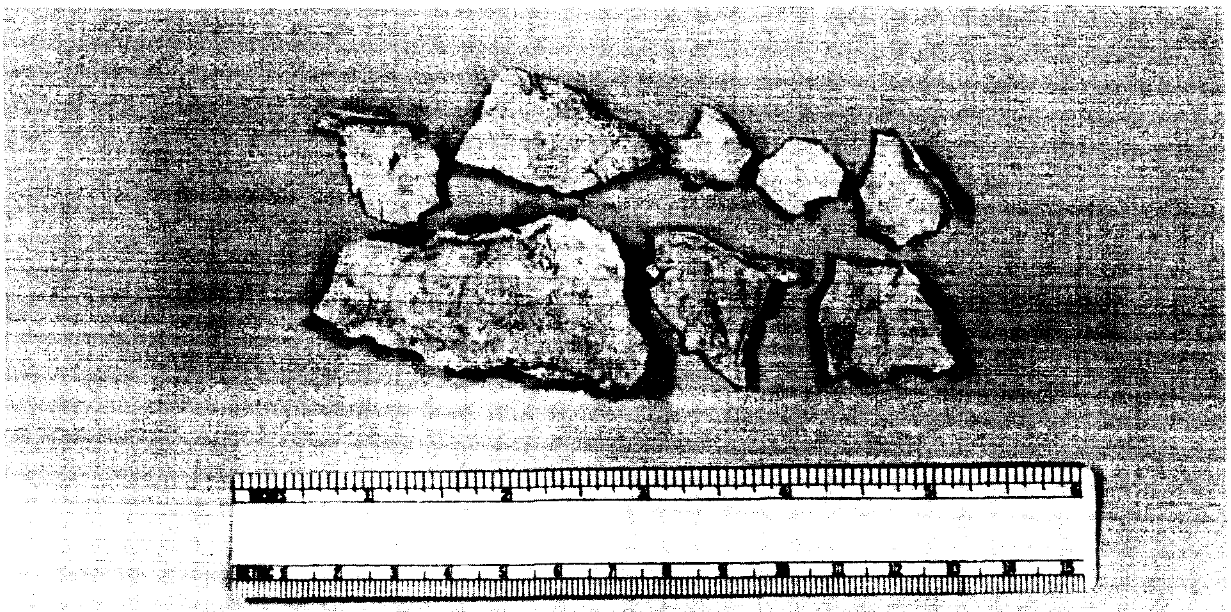

Fig. 1. Thin, curled soil rain crust from temporary rain pool near Lancaster, California, Mohave Desert: Bundles of twisted and intertwined trichomes and filaments of *Microcoleus vaginatus* were present as well as a few diatoms, *Navicula* sp., and trichomes of *Microcoleus lyngbyaceus*.

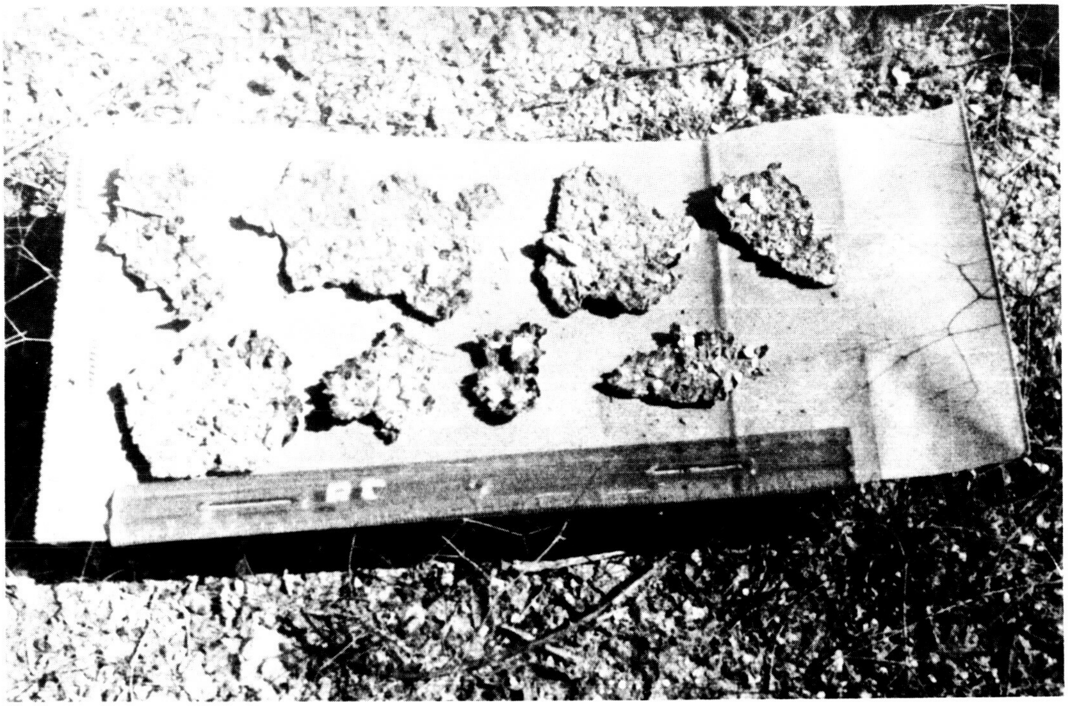

Fig. 2. Soil algal and lichen crusts with partially imbedded, small translucent stones, near Tucson, Arizona, Arizona Upland Desert: The algal community consisted of *Microcoleus* spp., *Oscillatoria brevis*, *Anacystis montana*, *Scytonema hofmannii*, *Nostoc muscorum*, *Schizothrix calcicola*, *Protococcus grevillei* and various diatoms.

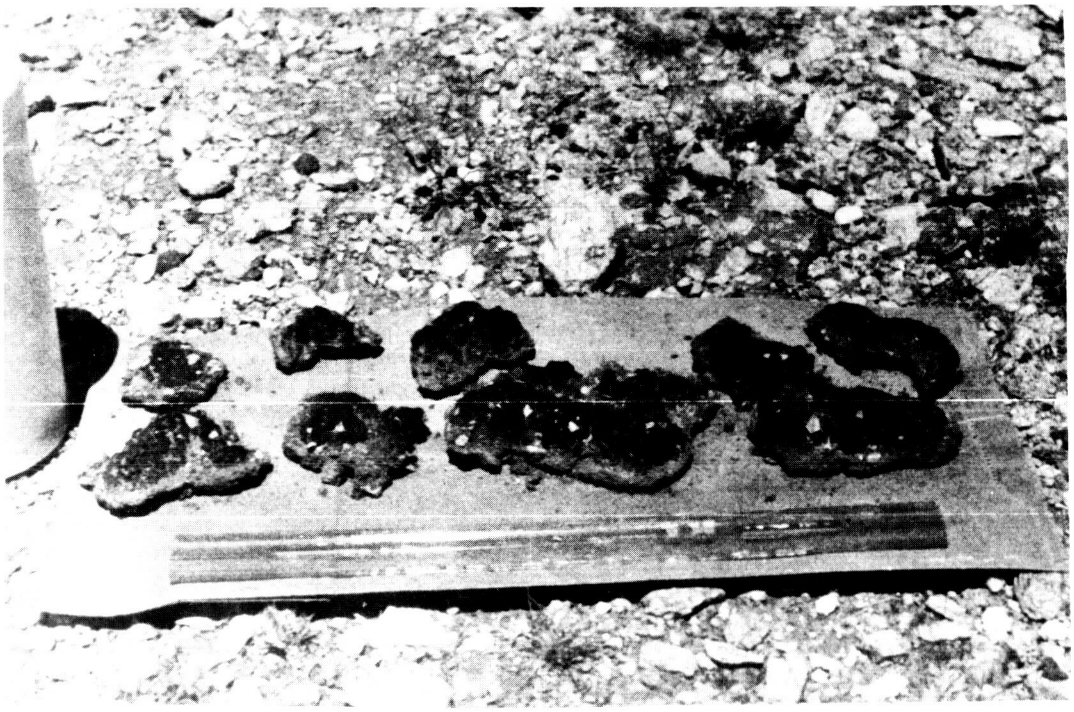

Fig. 3. Thick, lichen soil crusts containing small translucent stones which occurred on rocky soil, foothills of Santa Catalina Mountains, Arizona Upland Desert: The algal community consisted of *Microcoleus* spp., *Symploca Kieneri*, *Schizothrix calcicola*, *Nostoc muscorum*, *Scytonema hofmannii*, and coccoid forms of *Stichococcus subtilus*.

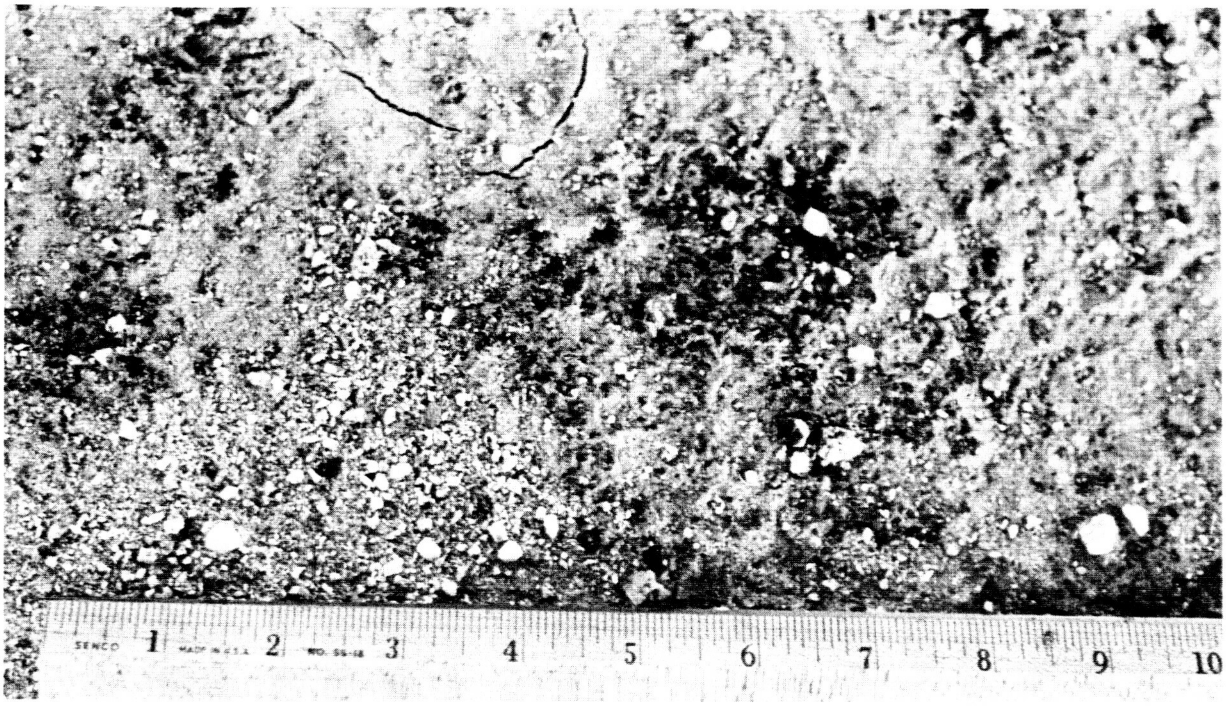

Fig. 4. Intact, cracked surface of algal soil crusts, premature lichen soil crusts, and partially imbedded and scattered translucent quartz stones, near Thermal, California, Colorado Desert: The algal community consisted of *Scytonema hofmannii*, *Nostoc muscorum*, *Schizothrix calcicola*, *Microcoleus chthonoplastes*, and *Protococcus grevillei*.

Fig 5. Xeric macrovegetation in association with algal and lichen soil crusts, foothills of Santa Catalina Mountains, Arizona Upland Desert: Cacti include *Opuntia santa-rita* and *Ferrocactus covillei*. Shrubs in background are *Fouquieria splendens* and *Larrea tridentata*.

Rain crusts, algal and lichen soil crusts in xeric environments vary in their appearance. Rain crusts, which are most conspicuous in shallow, temporary, drying pools, contain algae and usually present a smooth, soil-colored stratum that warps and curls upwardly and breaks into polygonal fragments (Fig. 1). These crusts usually warp upwardly because of differential drying between the upper and lower surface of the crusts. Differential drying is promoted by differences in temperature, moisture and aeration between the upper and lower surfaces of the crusts, and the abundance of organic matter and finer-sized distribution of soil particles on the upper surface of the crusts. These crusts are more or less attached by coarse soil particles and microbial organic matter to the underlying soil strata. Algal soil crusts also have an appearance similar to that of the surrounding soil surface, or else they are darker, appearing as dark "burned" reddish, brownish, or blackish strata [Ref. 19 (see Fig. 4)]. Upon closer examination, some crusts may show a *fuzzy* growth of entwined filaments of scytonematoid species. Phormidioid, lyngbyoid, microcoleioid, schizothricioid, and oscillatorioid species may also exhibit this phenomenon within crusts. Lichen soil crusts are usually more conspicuous (Fig. 3) than rain crusts or algal soil crusts and their distribution and occurrence is more common at the base of hills and mountains and along the banks of washes and ravines or other drainage areas where the soil is protected from erosion (Fig. 6). Lichen soil crusts remain moist for a longer period than algal soil crusts. They are usually more dense, thicker and elevated, extending farther above, as well as below, the soil surface than the algal soil crusts. Some are 2 to 5 cm thick. They are commonly of a dark brownish or blackish color, although some are lighter in color, and even pinkish or whitish when sporulating (Fig. 7). The surface of many crustose soil lichens is dissected into numerous small polygons. After precipitation, soil lichens become more greenish in appearance following active photosynthesis by algae. Moisture collects in minute cracks between the polygons and new algal growth fills the cracks and spreads freely over the lichen and onto the adjacent soil surface.

As can be observed for algal soil crusts, the undersurface of soil lichen crusts as compared with the

Fig. 6. Close-up of translucent stones in field of quartz and algal and lichen soil crusts, Atomic Energy Commission Test Site, Nevada, Great Basin Desert (after Drouet, 1958): One of the most prominent algal components was *Protosiphon cinnamomeus.*

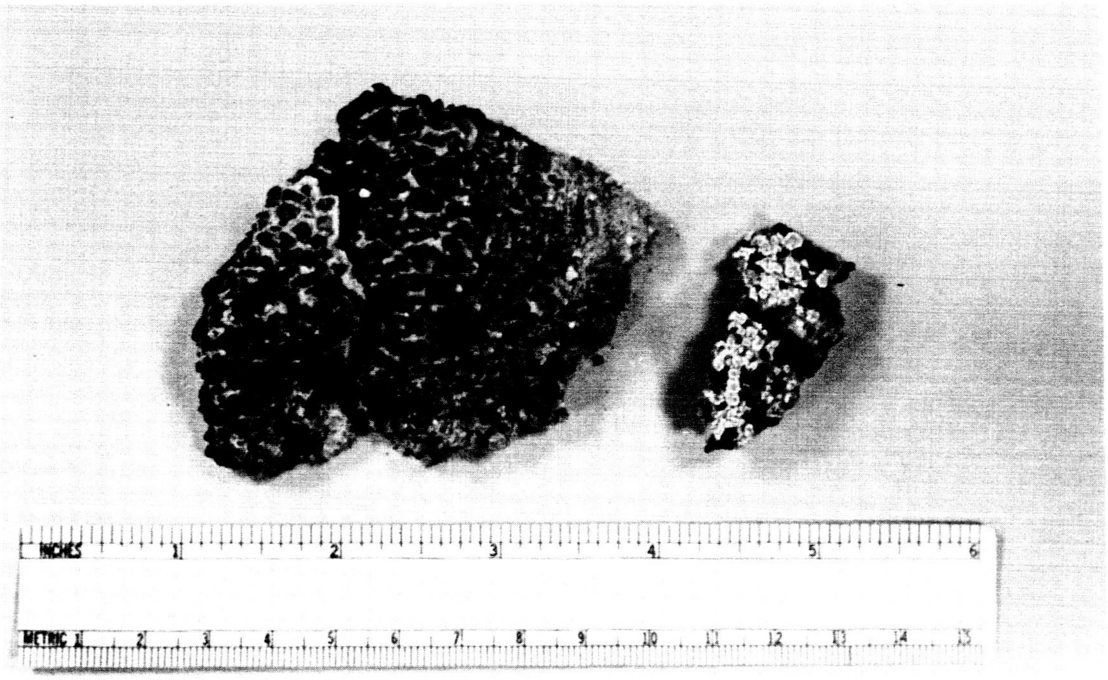

Fig. 7. Desiccated uppersurface of thick lichen soil crust near Thermal, California, Colorado Desert: Light-colored pink fruiting bodies of ascomycetous fungus are evident on small fragment. Aggregations of a lichenized coccoid green alga were observed.

uppersurface, is different in color, has a dense, fuzzy accumulation of organic matter, and is more porous and granular in appearance (Fig. 8). Also, as noted previously (Refs. 51, 82), the undersurface of crusts shows considerable matting and adherence of soil particles by mold mycelia and sheaths of algal filaments. Sometimes the lichen crust, extending above the soil surface, separates from the crusts beneath it, and it becomes hollow and folded, presenting a chambered appearance in cross-section (Fig. 9). Fracture of the upper, separated layer and opening of the chamber to the atmosphere results in death of the fragment, evidently through adverse effects of desiccation and insolation.

Fragmentation serves as a physical method for soil lichen propagation. Fragments of lichen may become transported to other areas especially when erosion is active. These fragments then serve as *seeds* for growth of new lichens on the soil. Small translucent stones or gravel can sometimes be observed in association with these crusts (Figs. 2, 3, 4). The translucent materials are usually an intimate component of the crusts, and when the crusts are dislodged from the soil surface, these materials are also removed along with the intact crust. An examination of the translucent stones or gravel shows that there is frequently a coherent boundary layer of conspicuous organic matter between the soil and the larger particles of translucent materials. Where topography, drainage, moisture conditions, and other environmental conditions are favorable, a continuous stratum of an irregular microrelief of algal and lichen soil crusts and translucent stones (Fig. 6) can develop (Ref. 56).

Although the algal soil crusts are sometimes transitory in desert soils and their maintenance is highly dependent on a period of available moisture, they are oftentimes less noticeable after the soil surface is dry. Within a period of one or more days, they may no longer be evident as a distinctive feature of the soil surface and have either been removed through erosional processes of abrasion and transport by wind and wind-borne debris, or they may have lost moisture, chlorophyll is no longer conspicuous, and crusts have become undistinguishable from the rest of the soil surface. Sometimes differential cracking and shrinking of the soil surface is an evidence of algal crusts (Fig. 4).

As lichenization increases, especially with prolonged water availability, the crusts become more mature and fully developed (Fig. 3). Individual crusts may become confluent and stability is considerably increased, resulting in a greater resistance to soil erosion. Erosive forces may leave remnants of surface soil as pedicels topped by lichen crusts extending several or more centimeters

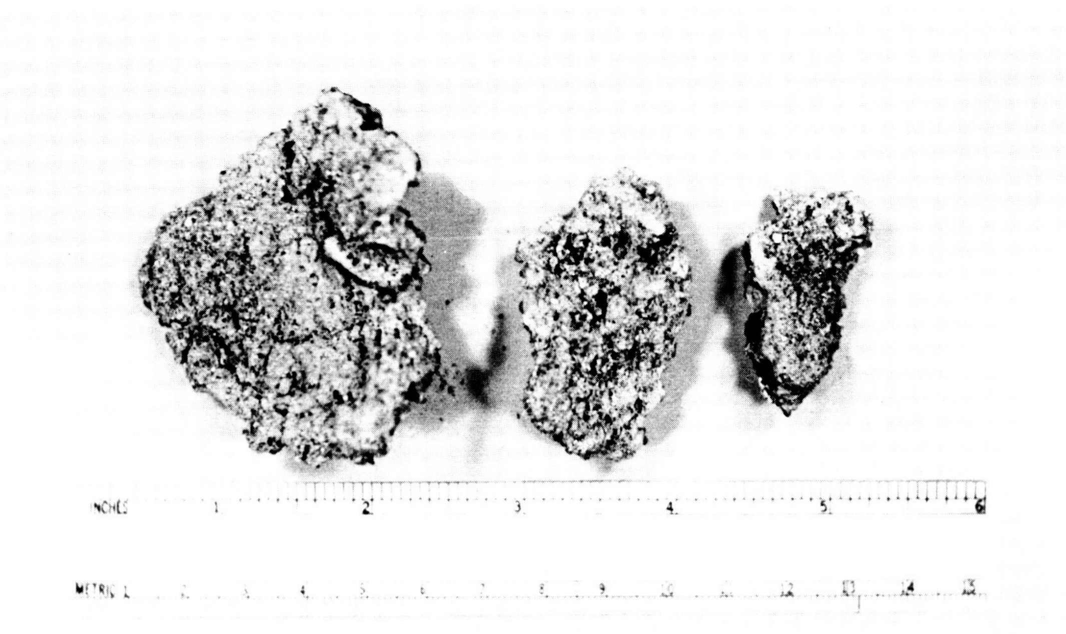

Fig. 8. Undersurface of adherent, porous, matted organic matter of lichen soil crust shown in Fig. 7.

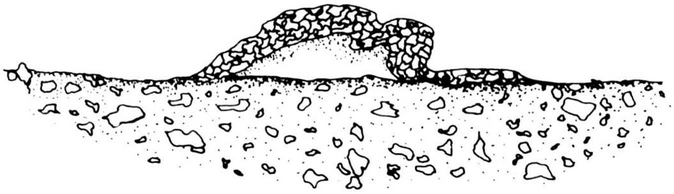

Fig. 9. Diagrammatic cross-section of vesiculated lichen soil crust.

above an area of surrounding soil surface. In some areas, these resistant structures have been observed to extend up to a decimeter above the soil surface, resembling conspicuous capped pinnacles in an area of eroded soil microrelief. Elevated pedicels capped by translucent stones are occasionally observed.

Rain crusts, algal and lichen soil crusts and the algal growth surrounding translucent stones are important reservoirs of algae that spread across the desert soil when meteorological precipitation or other supplies of moisture are available. Depending on the past history of wetting and drying, the time period of extended moisture availability, mechanical intensity of the precipitation, and periods of drought, the oscillatorioid soil algae in desert regions can form a conspicuous blue-green or green growth on the soil, in rain-pools, drainage systems and temporarily inundated rocks. The algal cover has been macroscopically observable in 15 min following a desert cloudburst (Ref. 2). Part of this rapid response of soil algae is due to the mechanical dispersion and separation of the algae from soil particles following the forceful, disruptive action of raindrops and rapidly moving sheets of water which move by gravity flow across the soil surface. Another contributing factor to the rapid appearance of desert algae following the application of moisture to the soil is the fast action exhibited by the gelatinous algal sheaths and colony material for the imbibition of water, which is subsequently followed by a softening and/or swelling of algal material and the backward and forward movement of trichomes. Finally, there is an *explosive*, or sudden, propelled discharge of the trichomes of blue-green algae into the aqueous medium. Although not as rapid in response, the colonial, coccoid and botryoid green algae, especially *Protococcus grevillei* and *Protosiphon cinnamomeus*, form zoospores (Chlamydomonad stage) within spore-mother cells. These subsequently enter the aqueous phase in the soil and are dispersed to other environments by flagellated cells. Following the cessation of available moisture in desert soils, subsequent changes occur in soil algae. These changes include the development of thickened cell walls and an increase in the sheath and colonial gelatinous material which is again formed around trichomes and filaments of blue-green algae and the vegetative cells of coccoid and botryoid green algae. Formation of pigments and vacuoles are additional features observed with time of quiescence. This cyclic process of activity, growth, and reproduction, and cessation of discernible motility is repeated in desert soils whenever water is again available, even after years of desiccation. For example, desert algal soil crusts that had been air-dry for four years, and then remoistened, showed activity and new growth within 24 hours. Remoistening of the same crusts after another four year interval of drying again caused activity and new growth to be evident within 24 to 48 hr.[1]

Ability of some algae to survive long periods of desiccation was shown by revival of a dried herbarium specimen of *Nostoc commune* that was 107 yr old (Ref. 19). Part of this same algal specimen had been previously revived after 87 yr of storage (Ref. 83). A longevity record for algae in arid and semiarid soils was recently established (Ref. 84). Algae from soils in California were regenerated after air-dry storage of 65 to 85 yr as museum specimens. The algae included common soil species found in desert areas, such as *Protosiphon cinnamomeus*, *Schizothrix calcicola*, *Nostoc ellipsosporum*, and *Microcoleus* spp.[1] However, abundance of desert algae in some air-dry stored soil samples has been found to decrease after storage of 2 to 4 yr.[1]

Response to moisture by desert algae is also observed to some extent in the dark, but is probably more of a physical phenomenon due to the stimulus and solvent action of water which results in a release of trichomes.

V. ALGAE COMPONENTS OF ALGAL AND LICHEN SOIL CRUSTS

Only a few species of algae are apparently present in temperate and tropical desert algal and lichen soil crusts, although a number of species have been listed by various collectors as occurring in desert soils (Refs. 4, 17, 56, 59). It has also been stated that in polar deserts only a few species of algae are present (Refs. 26, 28, 70). It is only recently that this list of species has been further delimited, because it has been determined that numerous described taxa of oscillatoriaceae are ecophenes (Refs. 23, 24, 25).[3] Variants of the taxa differ in many cases only because of emphasis given to differences in the nature of their habitat, whether microenvironmental or macroenvironmental, and the apparent influence of environmental factors upon certain differences in morphological and physiological features.

Even though similar in morphology, the same algal species has been described as a distinct taxon on the basis of its existence in different environments, e.g., *Microcoleus chthonoplastes* in salt water and salty soil = *M. lacustris* in fresh water (Ref. 85). In some specialized habitats, such as hot springs, the morphology of the same species is different from that of its ecophene in surrounding desert soil, and the same species has been described as a distinct taxon on the basis of its differences in morphology, e.g., filamentous *Schizothrix calcicola* in calcareous soils, = filamentous and "branched" *Plectonema nostocorum* in nonsalty soils and freshwater environments = filamentous *Phormidium valderianum* or various bacillarioid and coccoid *Synechococcus* spp. in hot springs or other thermal habitats. It is evident that a number of algal species are euryecological.

For the blue-green algae, it is now evident that the most abundant species in desiccated desert soils and algal and lichen soil crusts are a few species of filamentous forms. These are frequently *Schizothrix calcicola*, *Microcoleus chthonoplastes*, and *M. vaginatus*. (See Appendix B.) All three species are also the most abundant terrestrial species in Antarctica (Ref. 26). These taxa have been listed as occurring in such diverse habitats as permanent and temporary freshwater environments, marine, brackish, and other salty environments, dry or moist, hot or cold, and salty soils, rocks, ice, water of thermal environments, calcareous and silicious substrata and various plants, including other algae. Other prominent filamentous blue-green algae include *Nostoc muscorum* (= *N. linckia*, = *N. humifusum*, = *N. microscopicum*), *Scytonema hofmannii*, (= *S. ocellatum*, = *S. guyanense*), *Porphyrosiphon fuscus*, and *Microcoleus paludosus*.[1] These taxa may occur as single populations in soil crusts or as communities of mixed algal taxa and other microflora and microfauna. *Schizothrix calcicola* is a dominant constituent of many soil crusts, and it also inhabits the colonial mucilage and sheaths of

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[3] Personal Communication. Dr. Francis Drouet, Research Fellow, Department of Botany, Academy of National Sciences of Philadelphia, October 29–31, 1965; March 16, 1966. The number of species of Oscillatoriaceae can be reduced to 23.

other algae, frequently becoming evident following culture of soil crusts and culture of algal isolants from the crusts. It can also be considered as a climax species, both in nature and in algal cultures. All of the blue-green algae in desiccated desert crusts are non-sporeformers.[4] Crusts or soils which are moist for longer time periods may contain additional filamentous species, such as sporeforming *Nostoc ellipsosporum*, oscillatorioid species such as *Symploca Kieneri*, *S. muscorum*, *Oscillatoria brevis*, *Microcoleus lyngbyaceus*, and *Schizothrix macbridei*, rivularioid *Calothrix parietina* and coccoid species such as *Anacystis montana*, *A. thermalis*, *Coccochloris peniocystis* and *C. stagnina*. Morphology of representative blue-green algae and some of their ecological relationships have been given previously (Ref. 86). See Appendix B for figures of some blue-green algae occurring in desert soil crusts and diaphanous substrata.

Green algal components of algal and lichen soil crusts are either coccoid species or else they are other filamentous or botryoid species that exist in the crusts in the coccoid form. Filamentous forms of green algae are found only in soil which is kept moist over an extended time period or near a constant source of available moisture, such as along the bank of a perennial stream or seepage from cliffs. *Protococcus grevillei* or other protococcoid forms are the most common green algal components of desert soil crusts. However, *P. grevillei* cannot be easily distinguished in desert soils from coccoid forms of *Protosiphon cinnamomeus* (Ref. 56).[5] In more favorable habitats, and sometimes in culture, *P. cinnamomeus* becomes more characteristically botryoid. This botryoid form is observed in cultivated agricultural soils in desert regions, e.g., the Citrus Experiment Station at Mesa, Arizona (Ref. 16). *Phytoconis botryoides* (= *Protococcus viridis*), *Palmogloea protuberans* [= various *Gloeocystis* spp., (Ref. 87)], and *Chorella vulgaris* are also found in soil crusts, as well as coccoid or few-celled forms of normally filamentous *Stichococcus subtilus* (= *Chlorococcum humicola*) (Ref. 87). See Appendix B for some green algae common in desert soil crusts and diaphanous substrata.

Representative families of other algae are occasionally found in desert soil crusts. These can include the xanthophycean *Botrydium granulatum*, various englenoids, desmids and diatoms. All of these latter algae prefer soils contaminated with fecal matter such as cattle dung. A number of diatoms have been noted in desert soils, including moist soil crusts (Ref. 16). *Navicula* spp. are the most common (Ref. 17).

Most of the algae in Southwestern United States desert soil crusts tend to become parasitized, eventually developing into distinctive crustose soil lichens. However, this phenomenon was not reported for the Sahara Desert, and according to Killian [as stated in a paper by Thornton (Ref. 88)] no symbioses between algae and fungi were found. The algal components of soil lichen crusts are coccoid or few-celled, even though the unlichenized algae can be filamentous species such as *Nostoc muscorum* or *Scytonema hofmannii*. In their coccoid states as lichen components, these filamentous blue-green algae then resemble typical coccoid myxophyceae such as *Anacystis montana*, *A. marina*, *Coccochloris stagnina*, or *C. peniocystis*. These species tend to become more easily lichenized than the active, faster-growing and more readily motile taxa of the *Oscillatoriaceae*, e.g., *Microcoleus vaginatus*. Green algal components of soil lichen crusts are usually vegetative forms of *Protococcus grevillei*, *Protosiphon cinnamomeus*, and *Phytoconis botryoides*, which are also widely distributed in nonencrusted soils.

A variety of associated microflora and microfauna are found in desert soil crusts, especially as the moisture status becomes more favorable. These include an abundance of bacteria (such as nitrogen-fixing *Radiobacter* spp.), members of the Actinomycetales, Myxomycetes, Myxobacteria, mites, protozoa (especially ciliates and amoebae), nematodes, and moss associates. A desert soil crust can become a rich community of abundant microflora and microfauna which does not occur elsewhere in desert soils, except in association with translucent materials or other favorable microenvironments.

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[4] *Nostoc* spp. occurring in desert soil crusts have been most frequently identified as sporeforming *N. muscorum* or non-sporeforming *N. commune*. *N. muscorum* rarely forms spores in desert soil crusts and is, therefore, commonly identified as *N. commune*. Following the culture of crusts, spores and germlings may be observed under favorable conditions, and during the proper stage in the reproductive cycle, the *Nostoc* sp. subsequently is shown to be *N. muscorum*.

[5] Other coccoid green soil algae, such as those from various Western States, have been identified as various species of *Neochloris*, *Spongiochloris*, *Botrydiopsis*, *Radiosphaera*, *Chlorosarcina*, *Chlorosarcinopsis*, and *Friedmannia* (Refs. 89, 90). It is highly desirable to undertake periodic and prolonged observation of spherical members of the Chlorococcaceae before species are identified (Ref. 91).

VI. OCCURRENCE OF DIAPHANOUS SUBSTRATA IN DESERT SOILS

Diaphanous materials that are partially imbedded in the surface of desert soils are favorable habitats or microenvironments for abundant growths of algae and associated organisms. All of these materials possess the quality of diaphaneity—the property of some minerals to transmit light. These minerals are subsequently divided into two classes: (1) transparent materials, or those minerals which transmit light so that the outline of an object viewed through it is perfectly distinct, and (2) translucent materials, or those minerals which will transmit light, but the object cannot be seen through it (Ref. 92). Many soil minerals are opaque, and will transmit no light, even at the thinnest edges of the minerals.

The most common diaphanous minerals that have been observed in desert soils, including Western and Southwestern U.S., are usually translucent. Natural transparent minerals are infrequently found, although some varieties of volcanic glass or thin chips of obsidian and imperfect calcite crystals have been found. In general, the most frequently occurring translucent minerals in association with algae are white or milky quartz (Figs. 4, 6, 10 and 11), chalcedony (Figs. 12, 13 and 14-c), shell fragments of various molluscs [snails and bivalves (Figs. 15, 16)], gypsum (Fig. 14-a), agate (Fig. 14-b) and thin bone fragments from animal remains (Fig. 14-d). Other translucent animal remains may include teeth, egg shells, feathers, and shed skins of reptiles. Salt evaporites or salt crusts on the soil surface in some desert regions provide translucent substrata for microorganisms (Figs. 17, 18 and 19).[1] Dolomite and calcite are also suitable translucent minerals habitats, and in some cases, algae can be found under thin sections of micas or feldspars. In general, the two types of rocks which are important in lichen ecology are calcareous and silicious materials (Ref. 93). These same two types of rocks are also important in algal ecology.

A number of less common minerals possess the quality of diaphaneity, but are relatively less frequently found (primarily because they are collected or mined for personal or commercial reasons).[6]

Fig. 10. Milky white quartz-stones and adherent organic matter in association with algal and lichen soil crusts near Thermal, California, Colorado Desert: Fluorescence microscopy showed that the algae were primarily lyngbyoid filaments of *Scytonema hofmannii* and a few isolated cells of a coccoid green alga.

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[6] There are a number of transparent and translucent minerals. A survey of 200 minerals shows that only 50 are completely opaque. Sixty are transparent or translucent, 21 are translucent or opaque, and 42 occur in forms which may be transparent, translucent or opaque (Ref. 94).

Fig. 11. Large algal and lichen encrusted translucent quartz-stones removed from a quartz field at White Mountain Range, California [(elevation, 12,800 ft) Knife length = 7 cm]: On the undersurface of the smaller stone, *Nostoc muscorum* (as a form of *N. microscopicum)* and *Schizothrix calcicola* occurred as bright blue-green growths. At the air-stone-soil interface of the same stone, *Protococcus grevillei* was highly parasitized or lichenized. On the larger stone, *N. muscorum*, *S. calcicola* and *Phytoconis botryoides* were abundant. A few diatoms and filaments of *Calothrix parietina* were also present.

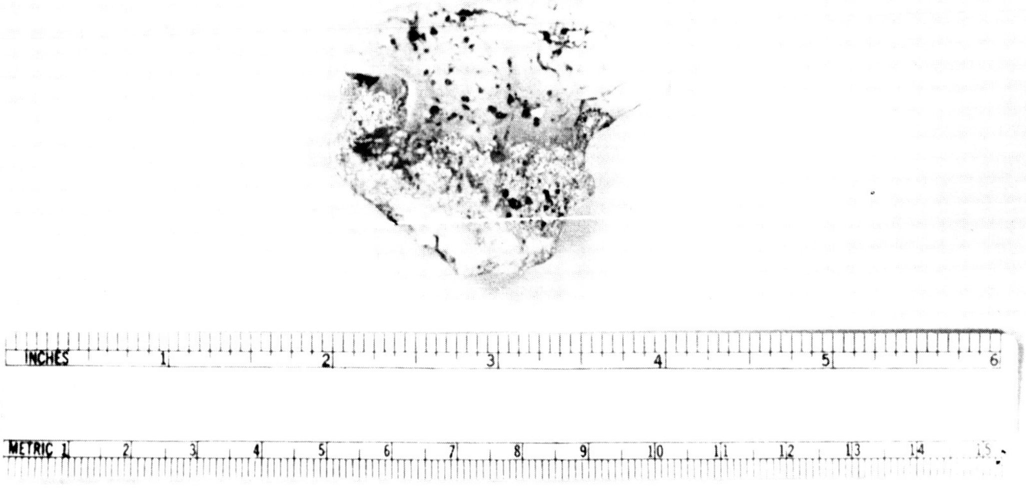

Fig. 12. Uppersurface of cavitated translucent chalcedony of extensive occurrence near Needles, California, Colorado Desert: Colonies of encrusted, highly pigmented and thickly ensheathed filaments of *Schizothrix calcicola* and a few trichomes of *Nostoc muscorum* were evident as dark, rounded or thread-like, tightly-adherent accumulations in exposed surface cavities of the partially imbedded stone.

Fig. 15. Under- and uppersurfaces of ancient weathered seashells which provided translucent substrata for algal habitation on sandy desert soil, near Thermal, California, Colorado Desert: Algae included primarily twisted and entangled dark brownish heterocysted filaments of *Scytonema hofmannii* and filaments of *Schizothrix calcicola*.

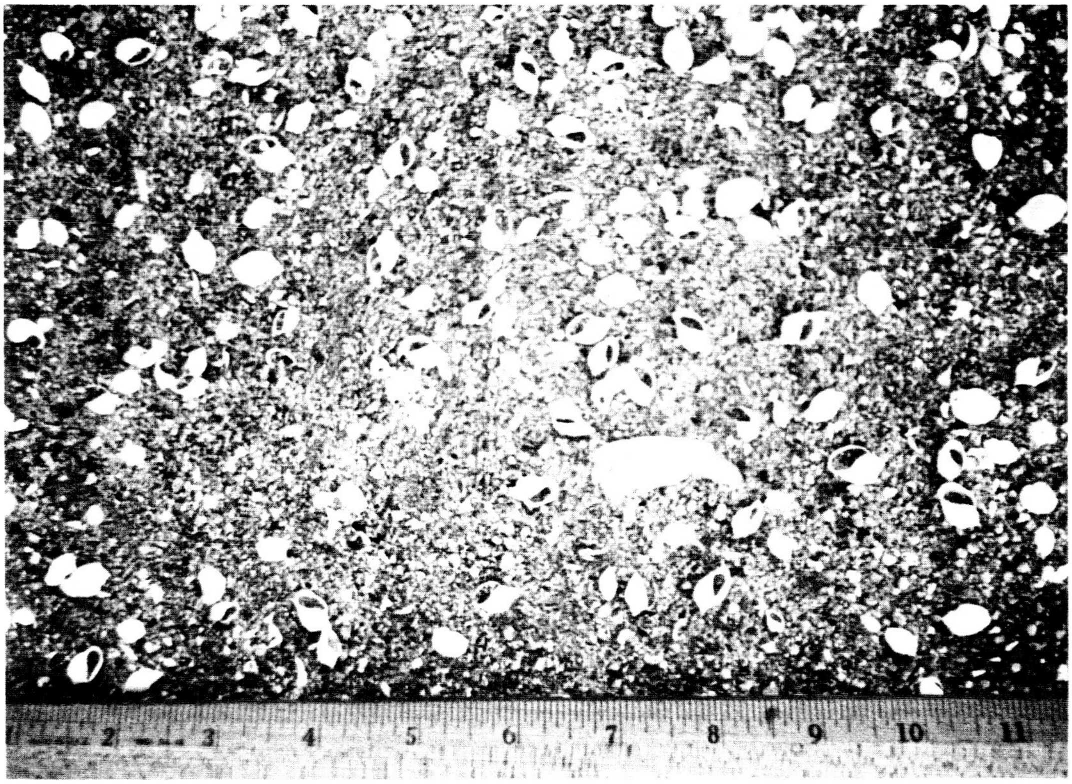

Fig. 16. Ancient seashells which provided a microgreenhouse environment for desert algae as distributed on the surface of sandy soil near Thermal, California, Colorado Desert.

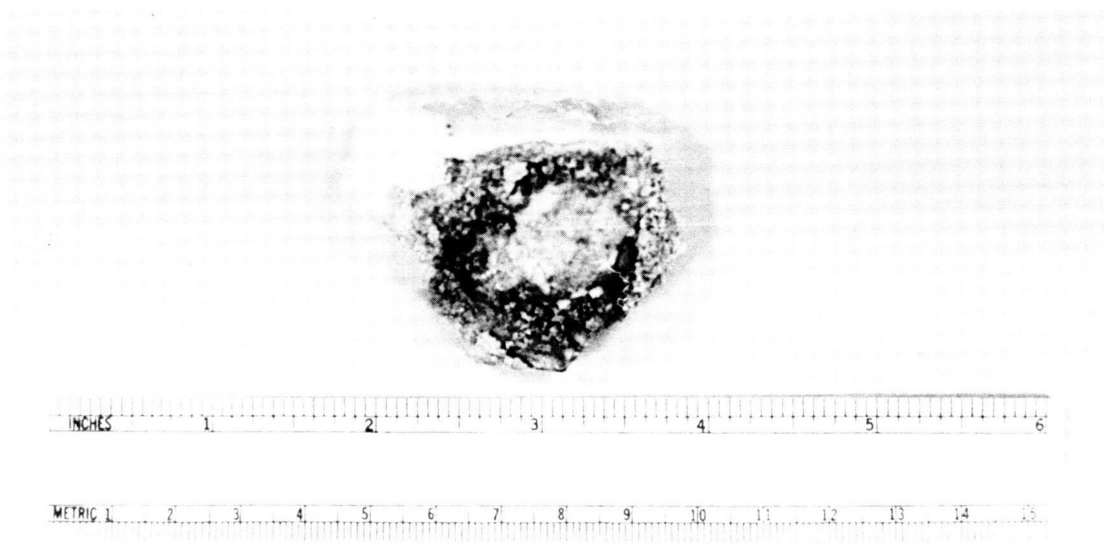

Fig. 13. Undersurface of translucent chalcedony stone of Fig. 12 shown with matted, dark, adherent organic matter accumulation. Thickly ensheathed and dark yellowish brown pigmented *Nostoc muscorum* and *Scytonema hofmannii* were the primary algal constituents, and some *Schizothrix calcicola* and *Microcoleus chthonoplastes* were also present.

Fig. 14. Translucent minerals serving as algal habitats which were obtained from the Arizona Painted Desert: From left to right, (a) platey gypsum, (b) agate from desert pavement, (c) botryoidal chalcedony, and (d) thin bone fragment.

Fig. 17. Vertical bank of eroded terrace covered by translucent salt evaporite, Death Valley National Monument, California: Salt scraped away from surface of bank shows a hard, dense, moist, sodium-permeated soil. Fresh algal growth occurred on the soil surface under salt which provided a greenhouse type environment.

Fig. 18. Thin, sodium salt-encrusted irregular microrelief on moist soil containing algae beneath salt crusts, Death Valley National Monument, California: Algal components included *Schizothrix calcicola* and small orangish-brown aggregates of *Protococcus grevillei.*

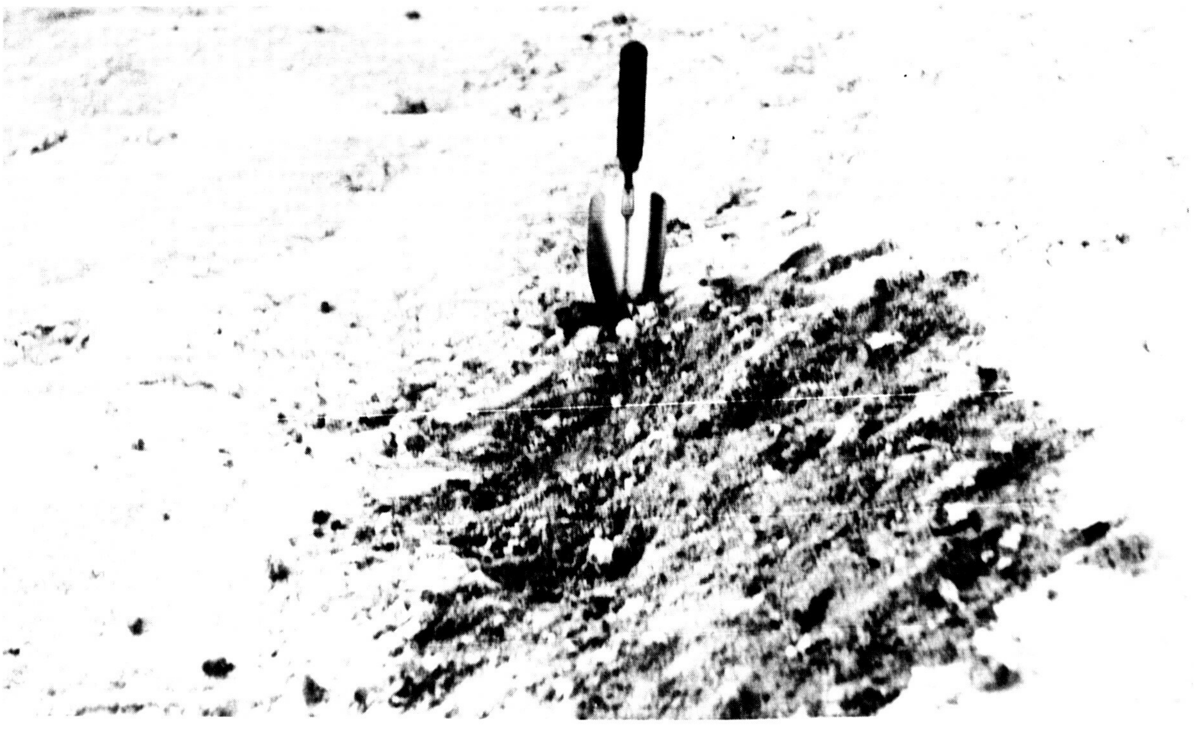

Fig. 19. Fluffy, translucent gypsous salt evaporite in cooling pond from thermal spring, The Big Spring, Hot Springs County State Park, Thermopolis, Wyoming: Algae included *Anacystis montana, Schizothrix calcicola*, and various diatoms, especially *Fragilaria* sp.

Additional common diaphanous materials found in some desert areas are due to occupation and activities of man. In paths of travel, or at permanent or temporary dwelling sites, man disposes of a number of manufactured translucent or transparent materials. The most common materials are usually transparent, and have consisted of glass (e.g., fragments of windows and bottles) and, more recently, pieces of transparent plastic, such as are used to package food or household items. These materials serve as efficient habitats for soil algae in desert areas, along with natural geologic minerals, bone fragments, or other animal products.

In the laboratory, the phenomenon of algae growing under diaphanous materials can be observed in various culture situations. Algae grow through the pores of filter paper in moist culture chambers (Ref. 95). Algae can also form abundant green growth under the filter paper, on the glass surface of moist chambers and culture tubes, and also, through and under a layer of approximately a centimeter of translucent silicious coarse sand in sand–water cultures.[1]

In cold regions, especially in mountains and polar areas, a unique diaphanous environment is provided for algae in association with ice and snow where they occur either on the surface, within the material, or underneath it, and at the ice–snow and associated soil or water interface. These algae are usually described as "green, red or yellow snow or ice phenomena," depending on the pigments developed by various algae in association with their particular substrate. These algae have been reported for cold areas, such as snowfields and icefields of various mountains of Alaska (Ref. 96), as well as mountains in the Alps (Ref. 97), cryoenvironments in the Antarctic (Refs. 71 and 98 to 100), and in ice flows of the Arctic (Refs. 30, 101). A summary of ice and snow algae in Antarctica has been given recently (Ref. 102).[7] Algae in cryoconite have also been described in Greenland (Ref. 103). In polar regions, a prolific growth of diatoms can be found beneath sea ice.

Algae can sometimes be found under ice in favorable microenvironments in arid areas (Ref. 52). At high elevations in the White Mountains of California, algae were found growing in snow, in meltwater at the edge of melting snowdrifts, under ice formed from melting snow, and on soil at the snow–soil interface.[1] Reddish algae were found directly on ice or snow, but the same coccoid or chlamydomonad forms lost carotenoid pigments in meltwater and soil and were of a green color.[1] Microscopic examination showed that the reddish algae were obviously true coccoid green algae.

All of the diaphanous materials have the ability to transmit light to some extent. Part of the light is reflected from the surface of the material and that which enters the material is refracted. The transparent materials, because they are of a less dense medium than the translucent materials, will consequently transmit more light and have a higher index of refraction (n). Nevertheless, most of the translucent minerals, when exposed at the soil surface, will transmit a sufficient quality and intensity of light to a significant depth beneath the soil surface for activity of microorganisms.

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[7] *Nostoc commune* and *Schizothrix calcicola*, two common blue-green algae in Antarctica, as well as the Arctic, were examined in the herbarium of Dr. Francis Drouet. The specimen was collected by Chief Warrant Officer Robert I. Ward on January 15, 1957 at Ross Island, at latitude 78°50′. It was reported that the entire plant was about 20 ft in diameter and resembled a miniature forest. Plant habitat was at a temporary pond, which was frozen over. Growth extended 2 to 3 in. above the ice, as well as 2 to 3 in. into, and below, the ice.

VII. GEOLOGICAL DISTRIBUTION OF DIAPHANOUS SUBSTRATA AS ALGAL HABITATS

The occurrence of diaphanous substrata in desert areas is dependent on a number of factors such as mineral formation, weathering, erosion, deposition, and the activities of man and other animals. These materials are found in all climatic zones including tropical, temperate, and polar regions. Sometimes fragments of translucent minerals are found widely scattered, and they are isolated on the soil surface without any other rocks in evidence, as quartz fields (Fig. 6), or else they may occur in association with other more or less opaque rocks. More commonly, they are found with other rocks on the soil surface (Fig. 4) and in formations as desert pavement (Figs. 20, 21).

One of the earliest reports of translucent minerals as a favorable habitat for algae was under dolomite stones

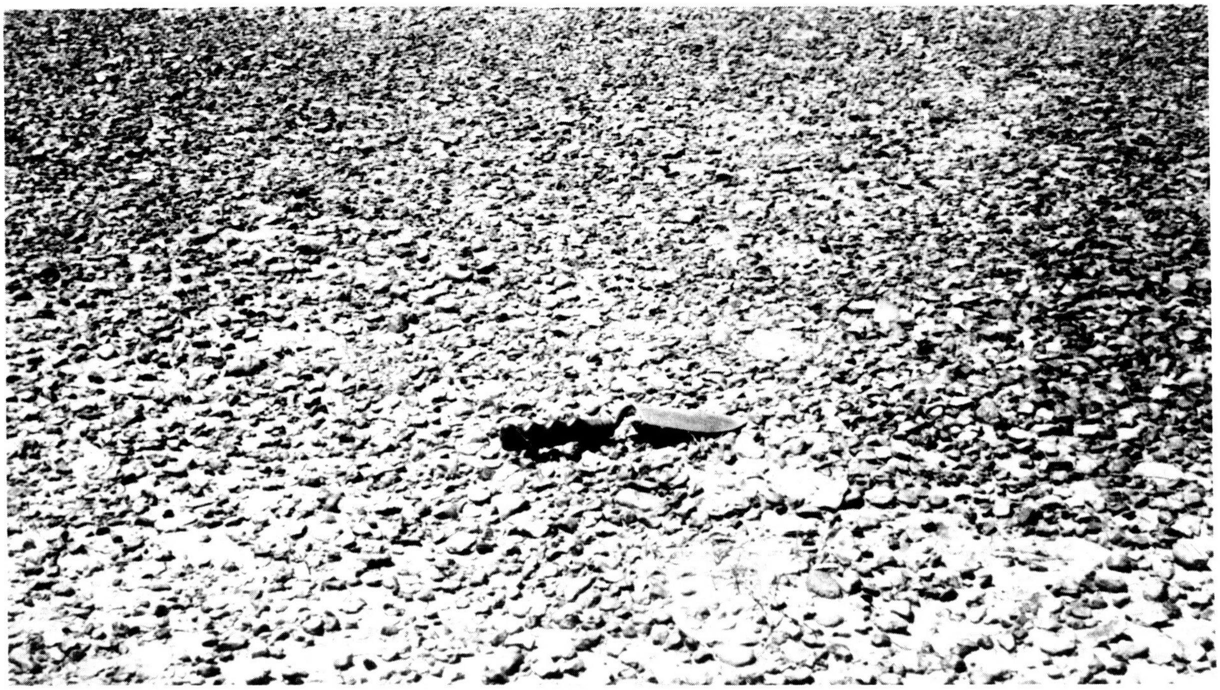

Fig. 20. Polished, wind-scoured, pebbly desert pavement containing irregularly distributed opaque and translucent stones, near Leupp, Arizona, Arizona Painted Desert: Nonadherent algae were found under chips of translucent agate.

Fig. 21. Mixture of loose, translucent and opaque rocks at edge of talus slope, near Mammoth, Arizona, Arizona Upland Desert: Algae and lichens composed of *Scytonema hofmannii*, *Nostoc muscorum*, *Schizothrix calcicola* and *Microcoleus* spp., occurred around and underneath translucent minerals, especially chalcedony. Shrubs of *Larrea tridentata* are in the background.

in the mountains of South Tyrol (Ref. 104). Endolythic and epilythic algae were also found on silicious and calcareous rocks in Yugoslavia (Ref. 105), in the Alps (Refs. 106, 107), and in the mountains of Northern Bohemia (Ref. 108).

In a semi-desert area in New South Wales, Australia, it was observed that algae could be found in dry localities as a subsurface covering of quartz pebbles (Ref. 31). It was also noted that cow teeth and a kangaroo skull provided a similar favorable habitat for soil algae! In other dry areas of New South Wales, it was found that the highest frequency of algae, including nitrogen-fixing species, occurred under an extensive field of translucent quartz-stones (Ref. 32). A similar property of light transmission was found to occur to a depth of 1 cm in sandy soils (Ref. 109).

In the Atacama Desert region, near Antofagasta, Chile it was found that desert algae existed under translucent sand, as well as stones (Refs. 33, 34, 110). Several new species were reported, and their mode of existence described. One species was a mesophilic alga. Moist salt was the most conspicuous algal habitat.[1]

An extensive investigation was undertaken in the South African Desert with regard to algal and lichen associations with translucent quartz-stones (Ref. 49). A number of algae and fungi were found attached to the undersurface of the stones, although some growth was supported on the exposed surfaces of the stones. Surface growth was permitted by indirect transmission and refraction of light through the stone to organisms sheltered within cavities or depressions in the stone and covered by a protective mat of organic matter on the upper surface. Plants associated with stones in this desert area were appropriately designated as *Fensterpflanzen* or window plants.

Polar regions, which are unique terrestrial deserts, also contain translucent materials (not including ice and snow) that have adherent algae and lichens either within cracks of rocks or attached to the undersurface. In the Antarctic, it was found that the assimilative portion of lichens was sometimes confined to cracks between rock crystals (Ref. 111), or else under them (Refs. 99, 112). The undersurface of loose rubble, scree and marble chips on flat ground supported a luxuriant lichen vegetation (Ref. 28). On one group of Antarctic Islands, the Ongul Islands, algae were not found on the exposed surface of stones but underneath them, only, where parts of the stones were buried in the sand (Ref. 113). There are many stones and salts in arid regions of Antarctica, similar to those in other arid areas (Ref. 114). Undoubtedly, some of these will provide favorable habitats for algae.

Translucent quartz and chalcedony were described as favorable habitats for organisms in the Great Plains Region of the U.S. (Ref. 115). It was observed that mosses, primarily, and algae, secondarily, were the main contributors to *pebble peat* beneath translucent pebbles, which were slightly imbedded in soil in semiarid regions. However, in arid regions, algae were replaced by mosses beneath the stones (Ref. 115).[1]

Algal associations with the undersurface of translucent minerals have been observed especially in the Southwest. Algae have been found under gypsum crusts in the White Sands National Monument (Ref. 59), in the Atomic Energy Commission Nevada Test Site (Refs. 56, 58), the Sonoran Desert of Arizona (Refs. 2 and 16 through 22), and Death Valley National Monument (Ref. 53), as well as various desert regions that have been investigated for the Desert Microflora Program (Fig. 4, and Figs. 10 through 21).[1] Soil algae and lichens have been found in additional arid and semiarid areas in the United States, such as the Great Basin Desert, Arizona Upland Desert, Oregon Desert, Colorado Desert, Yuma Desert, Mohave Desert, Painted Desert and Wyoming Red Desert.[1] Algae and lichens were also observed in association with the undersurface of translucent materials at elevations of 10,000 to 14,250 ft in the relatively arid White Mountain Range of California.[1] At elevations above 12,000 ft, algae were found under and circumscribing milky quartz (as well as on, in, and under ice and snow). At lower elevations, algal accumulations were found either associated with dolomitic limestone or under partially imbedded Indian arrowheads made from obsidian!

For tropical areas with adequate rainfall, algae are seldom reported as inhabiting the undersurface of translucent materials. This may be because abundant growth of other organisms covers the stones (Ref. 115). However, calcicolous blue-green algae have been reported for Java, which grew below the surface of limestone, as well as within the material and on its exposed surfaces (Ref. 116).

VIII. ECOLOGICAL FACTORS OF DIAPHANOUS SUBSTRATA

Ecology of organisms associated with diaphanous substrata in desert soils is not completely known or understood, but it is commonly recognized that an ecological niche exists which is a favorable microenvironment for algae, lichens, and associated organisms.

The more recognizable environmental factors are general biotic and non-biotic parameters which influence or limit the growth, reproduction, and survival of all soil microorganisms. However, some factors are intensified or modified in the environment around the translucent materials, as compared with the surrounding soil. These factors include, primarily, the nature of the substrate, moisture and humidity, temperature and insolation, alteration of light intensity and wavelength, organic matter accumulation, and nutrition, certain modifications of soil physico-chemical and chemical factors, and biotic factors which are demonstrated by increase in the abundance, diversity, and activity of microbiota on a community level.

A. Properties of Common Translucent Substrata

In desert areas, translucent minerals that are observed in the soil are, primarily, silicious or carbonaceous. Quartz (Figs. 6, 10, 11) and chalcedony (Figs. 12, 13, 14-c) are two of the most typical silicious translucent minerals encountered in desert areas that serve as favorable habitats for algae. Known properties of these two minerals that are more or less relevant to understanding the nature of the substrate and its influence on soil organisms are discussed below.

Normally, quartz is colorless and transparent, with a vitreous luster. Although there are a number of varieties and subvarieties of quartz found in desert soils, the most favorable quartz varieties for algae have been found to be either fine-grained white quartz, pigmented by admixed clayey material, or those varieties that, because of the scattering of light by minute cavities or flaws, appear white, milky white, or grayish white. The white color of granular massive quartz tends to become more uniform with decrease in grain size. Less Ti and Al are found in quartz varieties associated with algae than in varieties not so associated. In nature, the massive type of quartz is found in such geological strata as pegmatites and hydrothermal veins (Ref. 117).

Quartz and the other polymorphs of silica, which are not coarsely or finely crystallized, are highly transparent for visible wavelengths. However, this property is altered by variations in crystallization, mineral size, shape, flaws, cavities, and impurities which will influence the growth of desert algae. In the ultraviolet, it is much more transparent than most such crystalline substances as certain varieties of glasses or liquids; but in the range of short ultraviolet, the absorption of quartz is appreciable—which undoubtedly is a factor that protects the algae underneath quartz stones. Exposure to short-wave ultraviolet radiation, as well as to heat, tends to decolorize or increase the violet coloration of quartz (Ref. 117). In the infrared, the absorption of the ordinary ray is greater than the extraordinary ray.

Quartz of the colorless variety is an optically positive, uniaxial substance, with optical properties varying slightly with temperature and the substitution of Al or Si. For white light at room temperature, the indexes of refraction are $\epsilon = 1.553$, $\omega = 1.544$ with a birefringence of 0.009. The birefringence of quartz decreases with increasing wavelength and the change is relatively rapid at short wavelengths. Quartz also possesses the ability to rotate the plane of polarized light. It does not ordinarily fluoresce in either short-wave or long-wave ultraviolet radiation, although inclusions or impurities can result in a demonstration of this property.

Chalcedony is a fine-grained variety of quartz; agate is one of the common subvarieties of chalcedony. In desert soils, chalcedony usually occurs as isolated fragments or crusts with an irregularly rounded, botryoidal, or warty surface (Figs. 12, 14-c). Chalcedonic silica occurs in many types of geologic environments, and it is generally deposited at relatively low temperatures and pressures (Ref. 117). In geologic strata, it occurs as pendant masses, stalactite formations, irregular grape-like sheets, reniform, irregular or rounded isolated masses of concretionary origin, or weathered-out cavity fillings, and sinter-like deposits, as veinlets and interstitial cement.

In consolidated geological strata and soils, chalcedony occurs as geodes and pseudomorphs after other minerals, especially calcite and fluorite, and as a replacement of these and other minerals, as well as fossil shells and some petrified wood. Chalcedony may be associated with zeolites, carbonates and chloritic or celadonitic alteration products. Many fine-grained varieties of quartz, including chalcedony, because of their physical and chemical stability, occur in detrital and residual deposits. Lavas, acidic igneous rocks, and volcanic ash are among some of the geologic deposits where chalcedony is also found.

Chalcedony and its subvarieties have a fibrous structure that gives them properties of subtranslucence or translucence. The color of chalcedony is usually rather pale, including shades of gray, grayish blue, grayish white, and milky white to almost colorless. It is more or less porous, which is important in the retention of water for the growth of algae and associated organisms, and the subsequent accumulation of organic matter. Pores may either be isolated, or tubular and thread-like. In milky material, its chemical composition approaches 99% SiO_2, with some impurities such as H_2O, and Fe_2O_3 or Al_2O_3 and other oxides. Dehydration is accompanied by a decrease in refractive index. Indices of refraction are similar to those for quartz, but cannot be measured accurately. Divergence of optical properties from those of ordinary quartz is caused essentially by disoriented aggregates of fibers (Ref. 117).

Chalcedony is weakly affected by ultraviolet radiation, and varieties of chalcedony, including agate and opal, fluoresce a yellowish green to green, especially in short-wave ultraviolet radiation, whereas others may show a white or cream to dull yellowish-orange fluorescence.[1] A large part of the water in chalcedony may be lost by desiccation at room temperature or at oven-dry temperature (105°C). Its solubility is increased in alkaline solutions, which may be a factor in salty desert soils.

B. *Field Studies and Observations*

Field studies and observations of algae associated with translucent materials generally have not been extensive, especially from the ecological viewpoint. Some of the most obvious factors which are altered or modified by the translucent substrata, as compared with the surrounding soil, include light transmission, temperature, and moisture relationships (solclime), and organic matter–biotic relationships and associations.

Light quality and intensity are obviously altered after passage through translucent materials, as indicated previously. In the field, it can be observed that some light can pass through milky or white quartz as thick as 2 to 4 cm (Ref. 56).[1] At higher elevations, it has been found that the depth of light penetration is apparently increased (Fig. 11). The depth to which light can penetrate through quartz-stones can be determined by an examination of the undersurface for an accumulation of organic matter (Fig. 22). The adherent accumulation of organic matter is often delimited on the undersurface of the deeper, imbedded stones, and it exists as a thickened band or ring of dark material. At some depth below the partially buried stone, where light penetration is either nil or insufficient for growth of algae, there may be a bare area of stone with no adherent organic matter (Fig. 22).

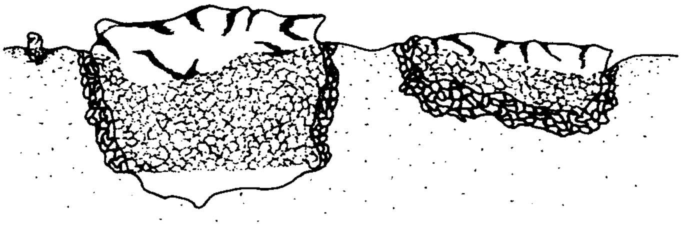

Fig 22. Diagrammatic cross-section of milky quartz-stones partially imbedded in soil and covered with algal-organic matter.

An examination of typical quartz-stones, which supported an undersurface growth of algae, has shown that light is transmitted from the ultraviolet to the near infrared (Refs. 49, 118). Although some ultraviolet may be transmitted, a number of desert algae apparently either are resistant to ultraviolet radiation or are protected by a thin layer of soil particles (Ref. 14). The organic matter and nontranslucent soil particles may give some protection to algae, but in some cases, it has actually been found that ultraviolet irradiated blue-green soil algae will increase in both biomass and abundance as compared with non-irradiated soil algae (Ref. 119). Ultraviolet trained strains of blue-green algae have been grown in the laboratory (Ref. 120). Blue-green algae are known to have the ability to adjust to varying light intensity and quality, and are better adapted than other algae to utilize all available light within a wide range of habitats (Ref. 121). Studies of quartz-stones and their algal associates in the South African Desert revealed that if only 10% of the incident sunlight were transmitted through the stones, this amount of radiation would be sufficient for algal assimilation (Ref. 49). It was also shown that the quality of incident light was altered, so that reddish-yellow or violet light was received under translucent stones, and this was sufficient for algal activities (Ref. 49).

Insolation is modified by translucent substrata in desert areas. Desert soils are commonly light colored and absorb less energy than darker soils; but reddish and yellowish soils, which are found in many desert regions, will show a more rapid rise in temperature than will white soils (Ref. 122). To a considerable extent, translucent stones show the same insolation and temperature effects as do white soils; but they also have a greater ability to reflect incident radiation, while also refracting and dispersing part of the transmitted light. In tropical soils of West Africa, it was found that quartz-stones have lower temperatures than the surrounding soil and, thereby, provide a more favorable temperature environment for algae (Ref. 123). At night, the organic matter surrounding the stones will cool off more slowly than the barren soil. Blue-green algae probably show a greater response to high summer temperatures than high light intensities in transparent aqueous media (Ref. 124).

Algae in dry soil may withstand temperatures up to 100°C for short time periods (Ref. 125). Temperatures of 110°C may kill all soil algae (Ref. 126). Surface temperatures of desert soils have been found to be 40 to 80°F higher than air temperatures 3 ft above the soil surface, even at high altitudes (Ref. 2). In Death Valley, soil surface temperatures as high as 190°F have been recorded (Ref. 127). Desert soil algae would undoubtedly have the ability to withstand high soil temperatures, even though insolation is modified by translucent substrata.[8] Desert soil algae have been found to survive autoclaving at 115°C for 20 min in fluid thioglycollate medium and to show subsequent normal growth.[1] The moisture status around translucent minerals partially imbedded in the surface of desert soils is much more favorable than in barren soils without such minerals. Following the application of moisture or meteorological precipitation to the environment of translucent stones imbedded in the soil, it can be observed that with time, the evaporation around the stones is reduced and observable moisture is retained for a greater period than in the surrounding desert soil. Although inherent properties of the translucent minerals are partly responsible for a reduced rate of evaporation and greater moisture retention (especially in chalcedony), hygroscopicity of the adherent organic matter surrounding the stones is of more importance. The slower rate of desiccation of the environment around translucent stones imbedded in desert soils is quite similar to that observed for conspicuous or well-formed, desert algal and lichen soil crusts.[1]

The combined moisture-organic matter environment of translucent stones also results in an increased specific heat capacity. This capacity would be much greater than in the surrounding mineral soil, as shown by a comparison of the specific heat of sand, 0.19; clay, 0.21; and peat, 0.25 to 0.48 (Ref. 128). Temperatures of the undersurface of organic matter coated, translucent substrata will be lowered, partly due to evaporation effects from moist materials around the stones but, also, partially due to a higher specific heat than in the surrounding mineral soil.

Translucent substrata partially imbedded in desert soils function as a moisture-gathering mechanism. Water can be accumulated in the organic matter coating of translucent stones as moisture is sorbed from the surrounding soil (Ref. 49). During the night, when air temperatures are cooler, it has been found that the translucent stones can also function as a condensation apparatus (Ref. 32). Condensed dew can then be stored in the organic matter around the stones. A more favorable moisture regime can provide a much longer period for growth and reproduction of soil algae, as indicated by the formation of spores and sexual stages around quartz-stones as compared with non-quartz inhabited soil. Increased moisture capacity and availability would also account for the occurrence and abundance of mesophilic soil algae in addition to xerophilic forms (Ref. 49).[1]

Organic matter accumulation around translucent substrata in desert soils is one of the obvious results of a more favorable microenvironment (Figs. 6, 10, 11, 13, 15). Except for some algal and lichen soil crusts, the organic matter around translucent stones is the most abundant accumulation of organic matter derived from, or composed of, soil microorganisms. The thickness of adherent organic matter formed by soil algae, mosses and other soil microflora may reach a thickness up to 1 cm or more around the stones (Ref. 115).[1] Organic matter content around the stones can be much higher than the surrounding highly mineral desert soils. This organic layer expands when moist and contracts when drying, forming cracked polygonal patterns when subject to desiccation.

Although the organic matter around translucent substrata is composed of living microbiota, as well as their remains and products, the most active algal growth or

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[8] A specimen of *Nostoc muscorum* (recorded as No. 21, *N. spongiiforme*) was examined in the herbarium of Dr. Francis Drouet. The specimen was collected by Dr. N. L. Gardner on May 27, 1930, from water at 94.5°C along the upper tract to the spring, Arrowhead Hot Springs, San Bernardino County, California. An examination of the specimen showed typical trichomes, filaments, and spores, both free and imbedded, within yellowish-brown gelatinous material. A variety of diatoms were also observed. So far as is known, this is the highest aqueous temperature in nature from which an algal specimen has been collected.

assimilation is at the stone–organic matter interface. Sometimes, when the stones are dislodged from the soil, the green algal layer is retained in the soil, thereby outlining the cavity of the removed stone. Nonmucilaginous algae, as well as moss protonema, may not adhere to the translucent substrata as tightly as other algal forms, such as the various mucilaginous oscillatorioid species.

Organic matter around translucent substrata undoubtedly modifies or intensifies certain desert soil characteristics that influence the activities and existence of soil microbiota. Nitrogen fixing species, e.g., *Azotobactor* and *Clostridium*, may be subcultured from the organic matter around translucent stones in desert soils (Ref. 32), but they have not been found to be present in soil algal and lichen crusts (Refs. 50, 51). Certain soil algae may grow prolifically in soil, even though they do not receive light energy. Facultative heterotrophy by soil algae in organic matter could be undertaken if the algae were associated with obligate heterotrophic bacteria (Ref. 129). It is probable that a heterotrophic mode of existence could occur for soil algae in the organic matter surrounding translucent minerals. In one case, it was found that a chlorophyllous protococcoid green alga, isolated from a desert soil crust, could be cultured in a moist chamber in the dark when grown on filterpaper in association with myxobacteria also obtained from a desiccated piece of wood in the Sonoran Desert (Ref. 16).

Certain physico-chemical and chemical factors would be altered in the organic matter around translucent substrata as compared with the surrounding mineral soil. The organic matter accumulation increases the ion exchange capacity and the consequent ability of this material to hold and supply nutrients or ions to microorganisms. The oxidation-reduction potential (Eh) as well as the pH of the soil could be modified or reduced. However, it is evident that the blue-green soil algae around translucent substrata are not appreciably affected by differences in pH of organic matter from that of the surrounding desert soil, which is usually neutral or basic in reaction. Blue-green algae grow best when the pH is 6.8 to 8.5, although they can grow at pH values between 4 and 5 (Ref. 8) and up to pH 13 (Ref. 130). Algal photosynthesis raises the pH, but humic acids could modify this effect. The soil undoubtedly exerts some buffering action on the organic matter surrounding translucent substrata. Dissolved salts in organic matter may or may not have an important influence on the soil algae, since a number of the same algal species occurring in desert soils can also exist in stony brines (Refs. 131, 132) as well as salty desert soils or salt ponds.[1,9] Common species of desert algae were observed in the Atacama Desert to be growing on the surface of moist salt, within it, and under it to depths of 15 cm.[1]

Other characteristics of translucent substrata that are important for algae include the size, shape, irregularities, and degree or extent of contact of the translucent substrata with the soil. Stones may be relatively large (Fig. 11) or relatively small, falling within the category or size range of soil particles. In the latter case, an admixture of translucent materials and soil can form a favorable ecological niche which is composite or intermediate between soil algal and lichen crusts and translucent substrata [Refs. 33, 34 (Fig. 23)].

Size of translucent material and its relationship to the soil is important for algal growth. It has been found that the larger the stone, the greater the algal abundance [Ref. 32 (Fig. 11)].[1] In all size classes of translucent substrata, portions of materials that do not touch the soil surface or those that merely rest on the soil surface either do not support a growth of algae or else limit their abundance [Ref. 32 (Figs. 10, 11, 12)].[1] However, surface concavities in translucent materials may protect a few algae (Fig. 10) and permit a pad of algal growth on, and within, translucent substrata (Ref. 49).[1]

Altitude of the site may or may not have an effect on the development of soil algae around or underneath translucent substrata.[10] In the White Mountains of California, at an elevation of 12,800 ft, a white quartz-stone field was examined. Stones in this field that were comparable in size, shape, distribution, and arrangement with those occurring in desert soils at lower elevations

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[9] Two specimens of *Nostoc muscorum* (Nos. 10-9 and 11-1) were observed in the herbarium of Dr. Francis Drouet. This alga was cultured from the extremely salty, low altitude Dead Sea by Benjamin Elazari-Volcani at the Daniel Sieff Research Institute, Rehovoth, Israel, in November, 1943 and July, 1944. Germinating spore stages were observed in material dated November 12, 1943. The Dead Sea occurs at a level of 1,286 ft below the level of the Mediterranean Sea and has a solid-matter content of 25%. It is six times as salty as other seas, contains primarily NaCl, and has a specific gravity of 1.199.

[10] Algal specimens of *Nostoc commune* were examined in the herbarium of Dr. Francis Drouet; these had been collected during the Yale North India Expedition by Prof. G. Evelyn Hutchinson in Ladak, a frontier district of East Kashmir State, North India. One plant was listed as having been obtained on July 12, 1932 from wet rocks on the south side of Thogmar La (Orototse La) Pass, south of Orototse Tso at elevations of 17,800 and 18,100 ft (Ref. 133). So far as is known, these are the highest elevations at which growths of algae have been found.

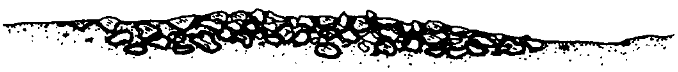


Fig. 23. Diagrammatic cross-section of algal soil crust formed by "cementation" of translucent quartz-grains with organic matter and soil particles.

in temperate regions did not support an algal growth on their undersurfaces; only the larger stones supported an abundant biomass of algae. This biomass was also heavily lichenized at the air–stone–soil interfaces (Fig. 11). Fresh algal growth also occurred to a much greater depth beneath the surface of the stone than in lower elevations in temperate deserts. No snow or ice algae were observed on one volcanic peak in the Atacama Desert at elevations of 16,500 to 20,200 ft, although they have been noted at lower elevations in other studies.[1]

Hardness and chemical nature of the translucent substratum are not known to have an appreciable effect on the development of algae in desert soils. The property of diaphaneity is evidently more important for desert algae than hardness or chemical composition (Ref. 134).[1] In Normandie, it was found that, for epilithic algae exposed on rock surfaces, the hardness of the rock definitely influenced the abundance and nature of algal growth (Ref. 135).

Rock hardness was found to have an effect on epilithic algae investigated in Yugoslavia (Ref. 105), but silicious and calcareous rocks of the same degree of hardness had relatively the same amount of algal growth. Insolation was of more importance than chemical composition in determining growth of algae on the surface of exposed rocks (Ref. 105).

IX. ALGAE ASSOCIATED WITH DIAPHANOUS SUBSTRATA

The same algal taxa or species that occur in desert algal and lichen soil crusts are found in association with diaphanous substrata imbedded in desert soils. The algae may exist as single populations or as communities with other algae and various non-algal microflora and microfauna associates. The desert algae around and underneath translucent substrata in desert soils are primarily filamentous blue-green and coccoid green forms. However, additional species are found which do not normally occur in soils or soil crusts that are subject to long periods of desiccation. These algae may be found in desert, as well as non-desert, soils which contain moisture that is available for an extended time period. The filamentous blue-green algae include nostocoid, scytonematoid, rivularioid, and oscillatorioid species. However, the coccoid blue-green algae, *Anacystis* spp. and *Coccochloris* spp., may form abundant populations; they may also occur as associates with other xeric algae around translucent substrata. *Anacystis marina,* the smallest coccoid blue-green alga which is in the size range of bacteria, was found only around and under translucent substrata which were imbedded in otherwise desiccated desert soils.

Some of the filamentous blue-green algae occurring with translucent substrata demonstrated certain morphological variations and were either larger or smaller than forms occurring in the surrounding desert soils. *Scytonema hofmannii,* for example, would show overlapping morphological characteristics typical of the larger filaments of S. *guyanense* or crustose filaments of S. *crustaceum.* Filaments of S. *hofmannii* were also more lyngbyoid. The *N. microscopicum* or *N. macrosporum* forms of *N. muscorum* were also more noticeable, as well as the smaller filamentous forms resembling *N. humifusum. Calothrix parietina,* which prefers a more mesophilic environment, was not encountered in soil crusts subject to prolonged desiccation, but it was sometimes found underneath translucent stones, as well as in moist soil crusts.

In many of the blue-green algae associated with translucent stones, as well as in desert soil crusts, it was noticed there were certain morphological changes that occurred compared to aquatic species. There was an increase in the formation of dark brownish and yellowish pigments which are probably reserve food materials, and also an increase in the abundance of granules and vacuoles. Granule content of nondesert soil algae is known to increase following desiccation (Ref. 136). The same phenomenon is observed in desert soil algae.[1] A reddish color may also occur in soil algae subject to desiccation (Ref. 66).

In desert soil algae, reddish color, or an increase in carotenoid pigments, occurs following desiccation and/or salt accumulation.[1] Soil algae in a nonsaline sandy desert soil (No. 1-2) were subjected to salt concentrations of 1 to 10%, NaCl, $CaCl_2$, $MgSO_4$, and $NaHCO_3$. There was a decreased rate of algal growth in all salt solutions and also a decrease in algal abundance compared with growth in nonsalty solutions. Algae grew in 4 or 5% NaCl, $CaCl_2$, and $NaHCO_3$, and in 10% $MgSO_4$. Concentrations of 1% salt gave the algae (especially *Protococcus grevillei*) a definite pigmentation which was observed as a mat of reddish-orange algal growth. Algal growth in relatively nonsalty solutions did not exhibit this effect.[1]

A greater variety of distinct protococcoid and botryoid forms of green algae developed under diaphanous substrata and in desiccated soil crusts. These forms may represent the more recognizable stages of coccoid green algae that have been described as *Bracteacoccus* spp., *Spongiochloris* spp., *Dictyococcus* spp. and *Chlorococcum* spp. [not represented as *Sticochococcus* spp. (Refs. 89 to 91)].

Certain coccoid green algal forms were observed *only* in association with diaphanous substrata in desert soils. *Trochiscia* spp., for example, were found in desert soils only underneath translucent quartz and chalcedony, but not in the surrounding nonstoney soils.[1] However, various described types of *Trochiscia* may actually be spiny or knobby zygote (zygospore or hypnospore) stages of non-stichococcus *Chlorococcum* spp. It has been reported that in soil, *Trochiscia* cells give rise to *Chlorococcum* individuals (Ref. 137).

The more favorable microenvironment which surrounds translucent substrata in desert soils undoubtedly provides an ecological niche which allows time for development of spores or sexual stages in blue-green and green algae. As was found for moist soil crusts, more abundant and diverse groups of non-algal forms also developed in the community of microorganisms around diaphanous substrata. Moss protonema, resembling filamentous green algae, can be found in this more favorable microenvironment, but not in the surrounding desiccated desert soils. Nematodes, various mites, protozoa, and other feeders are apparent in these microenvironments, especially following the addition of moisture.

X. CONCLUDING REMARKS

Terrestrial deserts provide one of the harshest environments for life. Water, its content and availability, is commonly the most critical factor. If water is present, other environmental factors, such as intense solar radiation, extreme temperatures, winds and high evaporation rates, and the presence of salt accumulations in the soil can adversely influence the soil moisture status which is critical for organisms.

In the harshest terrestrial deserts, such as in parts of the Atacama and Sahara deserts, there is little or no evidence of macrobiota, and life forms are restricted to soil microbiota. The microbiota usually consist of xeric ecotypes which are especially adapted to the rigorous arid environment. Desert soil microflora are commonly bacteria, streptomycetes, fungi, algae, lichens, and sometimes myxomycetes. In some desert soils, algae and chemoautotrophic bacteria have been found to be the most common life forms. The algae are the most abundant group of photoautotrophes, and they are usually filamentous blue-green or coccoid green forms. The chemoautotrophes are usually aerobic or microaerophilic, short or long, bacterial rods and/or streptomycetes.

Desert algae occupy a number of habitats, not all of which are xeric in nature. Habitats may range from arid soils and rocks to intermediate mesophilous environments, as well as various fresh, mineral, salty, cold or hot hydrophilous situations. Local characteristics of the habitat and dependency of organisms upon a good quality of sustained water supply may determine that non-xeric species can exist in a favorable microenvironment surrounded by the harsh macroenvironment.

In arid and semi-arid soils in various desert regions, it has been found that algae, as well as other associated microflora, exist in algal and lichen soil crust. These crusts have important influences on soil stabilization as well as erodibility, water infiltration and penetration, and they serve as forerunners to subsequent establishment of barren or eroded soil by higher plants. Algal and lichen soil crusts are one of the most important sources of soil organic matter in desert regions.

Algae in the crusts consist primarily of filamentous blue-green species, such *Nostoc muscorum, Scytonema hofmannii, Schizothrix calcicola, Microcoleus vaginatus,* and *M. chthonoplastes,* and protococcoid and botryoid green algae, such as *Protococcus grevillei* and *Protosiphon cinnamomeus. N. muscorum* and *S. hofmannii* have been isolated from desert soil crusts, and have demonstrated the ability to fix atmospheric nitrogen, thereby increasing the organic matter content of soil crusts. The oscillatorioid forms are the most active. Following the addition of moisture, they can spread across the soil surface within a short time period. All of the blue-green and green algae in desert soils tend to become parasitized by fungi or lichenized. This is particularly true of the slower growing forms, such as *N. muscorum* and *S. hofmannii,* as well as the coccoid green algae.

Diaphanous substrata, especially white or milky quartz and chalcedony, present one of the most favorable habitats for algae in desert soils. Environmental factors of light intensity and quality, temperature, and moisture status are modified or enhanced so as to permit the existence of an increased abundance and diversity of soil algae and associated organisms within a *microgreenhouse* environment. Organic matter of microbiotic origin is subsequently accumulated around translucent substrata to a depth that is limited by the penetration of light sufficient for algal photosynthesis and assimilation.

As a result of the more favorable environment surrounding translucent materials imbedded in the surface of desert soils, algal forms can be found which do not normally occur in desert soils that are subject to periods of prolonged or immediate desiccation. These algae can include blue-green coccoid forms, such as *Anacystis montana* and *A. marina, Coccochloris stagnina,* and *C. peniocystis.* There is, also, a greater variety of green algal forms present which show the development of Trochiscia-like sexual stages. The more favorable temperature–moisture (solclime) relationships around the translucent materials partially imbedded in the surface of desert soils undoubtedly permit the existence of abundant populations of mesophilic as well as xeric soil algae.

Although thermal environments may provide favorable habitats for life on other planets (Ref. 138), microenvironmental habitats such as algal and lichen soil crusts and translucent substrata should not be overlooked in the search for extraterrestrial organisms and organic matter. A number of geologic materials possess the property of transparency or translucency and similar minerals may occur in extraterrestrial environments, surrounded by organisms and organic matter. As can be observed in both hot and cold terrestrial deserts at both high and low elevations, these materials can provide microenvironments or ecological niches for an abundance and diversity of soil microflora and an accumulation of organic matter which is not found in the surrounding arid soils. Provision or application of a simulated transparent or translucent material, such as a thin sheet of clear plastic, on an extraterrestrial soil surface may provide a favorable habitat for photoautotrophes. This layer of plastic may also entrap CO_2 at the soil surface to show a higher concentration than in the surrounding air.[1]

Moisture is a critical factor for life, and because it has been found that translucent substrata can serve as a water-gathering mechanism in terrestrial desert soils, this same mechanism may also function in highly arid extraterrestrial environments to accumulate moisture. Sufficient moisture could then be available to permit survival and to support growth of organisms in a favorable microenvironmental situation.

APPENDIX A

Synonyms for Three Common Species

Synonymity for each of the three common species of Oscillatoriaceae in soil (Refs. 23, 24, 25) is given here:

A. *Schizothrix calcicola (Ag.)* Gom.

Amphithrix janthina
A. violacea
Lyngbya contorta
L. Diguetii
L. distincta
L. epiphytica
L. infixa
L. Lagerheimii
L. purpurea
L. Rivulariarum
L. Simmonsiae
L. versicolor
Oscillatoria subtillissima
Phormidium cebenennense
P. Crosbyanum
P. foveolarum
P. fragile
P. luridum
P. minnesotense
P. muciocola
P. persicinum
P. tenue
P. treleasei
P. valderianum
Plectonema Boryanum
P. calothrichoides
P. Golenkinianum
P. norvegicum
P. Nostocorum
P. purpureum
P. roseolum
P. terebrans
Pseudonocobyrsa fluminensis
Schizothrix Braunii
S. coriacea
S. Cresswellii
S. fasciculata
S. fragilis
S. Heufleri
S. lacustris
S. lacustris var. lacustris
S. lacustris var. caespitosa
S. lardacea
S. lateritia
S. Lenormandiana
S. nigrovaginata
S. pulvinata
S. roseola
S. rubra
S. septemtrionalis
S. tinctoria
Symploca dubia
S. elegans
S. parietina
S. thermalis
Tapinothrix Bornetii

B. *Microcoleus chthonoplastes (Mert.) Zanard.*

Hypheothrix longiarticulata
Microcoleus lacustris
M. rupicola
Oscillatoria laetevirens
O. luteola
O. salinarum
Phormidium californicum
P. subuliforme
P. Weissii
Schizothrix arenaria
S. Californica
Sirocoleum guyanense
Symploca cartilaginea
S. laete-viridis

C. *Microcoleus vaginatus (Vauch.)* Gom.

Hydrocoleum homoeotrichum
Lyngbya aerogineo-caerulea
Microcoleus vaginatus var. vaginatus
M. vaginatus var. monticola
Phormidium autumnale
P. favosum
P. incrustatum
P. incrustatum var. incrustatum
P. incrustatum var. cataractum
P. Setchellianum
P. subsalsum
P. toficola
P. umbilicatum
P. uncinatum
Oscillatoria amoena
O. beggiatoiformis

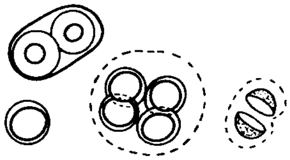
APPENDIX B

Common Algal Constituents

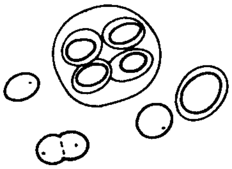
Common algal constituents of desert algal and lichen soil crusts and diaphanous substrata are the following:

Anacystis marina
Anacystis montana
Coccochloris stagnina
Nostoc muscorum
Scytonema hofmannii
Schizothrix calcicola
Porphyrosiphon fuscus
Microcoleus vaginatus
Microcoleus chthonoplastes
Microcoleus paludosus
Palmogloea protuberans
Protococcus grevillei
Protosiphon cinnamomeus
Phytoconis botryoides
Chlorella vulgaris
Trochiscia hirta

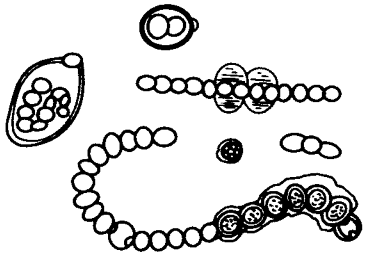
ANACYSTIS MARINA, × 1250



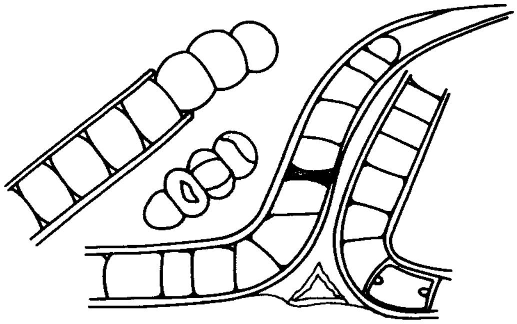
ANACYSTIS MONTANA, × 1250



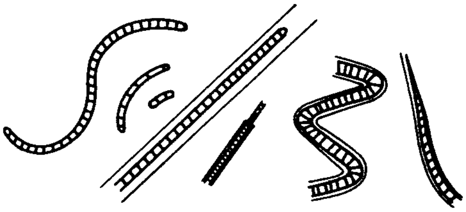
COCCOCHLORIS STAGNINA, × 1250



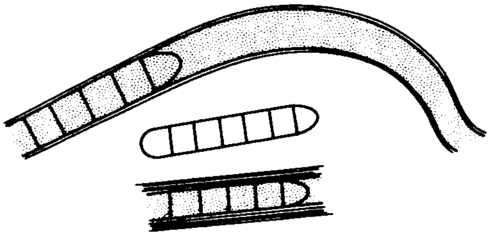
NOSTOC MUSCORUM, × 500



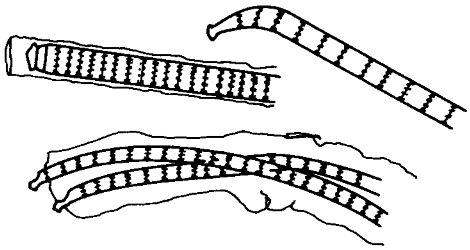
SCYTONEMA HOFMANNII, × 500



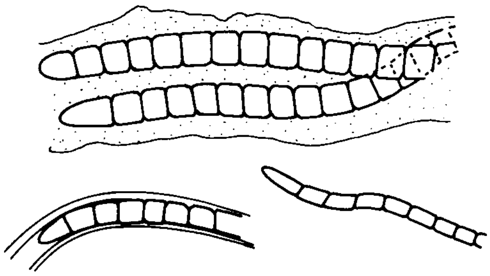
SCHIZOTHRIX CALCICOLA, × 1250



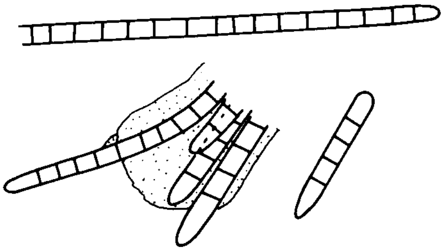
PORPHYROSIPHEN FUSCUS, × 500



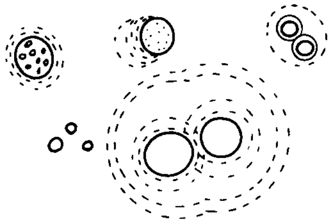
MICROCOLEUS VAGINATUS, × 500



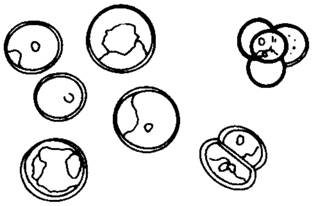
MICROCOLEUS CHTHONOPLASTES, ×500



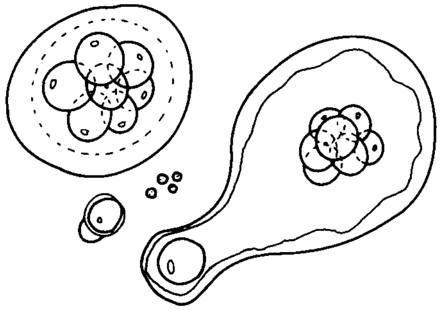
MICROCOLEUS PALUDOSUS, ×500



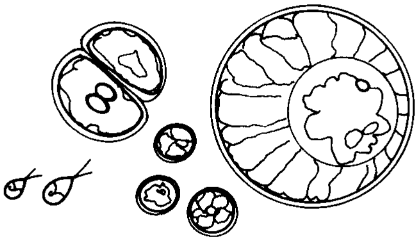
PALMOGLOEA PROTUBERANS, ×500



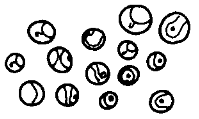
PHYTOCONIS BOTRYOIDES, ×500



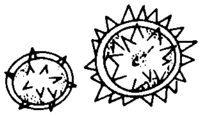
PROTOSIPHON CINNAMOMEUS, ×200



PROTOCOCCUS GREVILLEI, ×1000



CHLORELLA VULGARIS, ×1250



TROCHISCIA HIRTA, ×500

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