Environmental Science

AIMS Environmental Science, 8(5): 498–516.
DOI: 10.3934/environsci.2021032
Received: 07 September 2021
Accepted: 26 September 2021
Published: 12 October 2021

http://www.aimspress.com/journal/environmental

Review

Atmospheric transport and mixing of biological soil crust microorganisms

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Abstract: Biological soil crusts (BSCs) are created where a diverse array of microorganisms colonize the surface and upper few millimeters of the soil and create a consolidated crust. They were originally described from arid ecosystems where vascular vegetation is naturally sparse or absent. They have since been discovered in all terrestrial ecosystems. Where present, they perform a variety of important ecological functions, including the capture and accumulation of water and essential plant nutrients, and their release in forms useful to vascular plants. They also stabilize the soil surface against wind and water erosion. BSC organisms include fungi (free-living, lichenized, and mycorrhizal), archaea, bacteria (cyanobacteria and chemotrophic and diazotrophic bacteria), terrestrial algae (including diatoms), and bryophytes (mosses and worts). BSC organisms reproduce primarily asexually via thallus or main body fragmentation or production of asexual spores that are readily dispersed by water and wind. Asexual and sexual propagules of BSC organisms are commonly lifted into the air with vast quantities of dust from the world's arid areas. BSC organisms and/or their propagules have been detected as high as the stratosphere. Some have also been detected in the mesosphere. Airborne dust, microorganisms, and their propagules contribute to the formation of essential raindrop and snowflake nuclei that, in turn, facilitate precipitation events. While airborne in the atmosphere, they also reflect the sun's rays passing laterally through the troposphere and stratosphere at dawn and dusk, often causing brilliant colors at sunrise and sunset.

Keywords: aerobiology; fungi; archaea; bacteria; terrestrial algae; bryophytes; dust; ecological roles

1. Introduction

Biological soil crusts (BSCs) are comprised of diverse and highly integrated communities of microorganisms that effectively occupy and stabilize soil surfaces against the forces of wind and water erosion. Generally, their environmental parameters vary in soil chemistry, texture, and structure depending on the specific combination of organisms present and local environmental conditions. Organisms commonly comprising BSC communities include various combinations or subsets of fungi (free-living, lichenized, mycorrhizal), archaea, bacteria (cyanobacteria, and chemoheterotrophic and diazotrophic bacteria), terrestrial algae (including diatoms), and bryophytes (mosses and worts) [1]. BSCs and their component organisms have global distributions, occurring ubiquitously anywhere that aridity and/or disturbance have reduced vascular plant cover, but are best developed and recognized in arid and semiarid environments where competing vascular plant cover is naturally limited [2–4]. The composition and ecological functions of BSCs in arid environments have been well-documented, and are discussed below.

In soils with large and/or numerous pores, i.e., those with a sand content that exceeds ~80%, cyanobacteria, fungal hyphae, filamentous terrestrial algae, and root-like structures produced by lichenized fungi and bryophytes, and polysaccharide exudates produced by cyanobacteria and fungal hyphae tend to clog or obstruct soil pores, thus limiting water infiltration. However, in soils with a sand content of less than ~80%, BSC filaments, soil binding exudates, and roots and/or root-like structures contribute to the formation of stable soil aggregates, thus increasing the number and size of soil pores and, thereby, enhancing water infiltration, redistribution, and storage [5].

BSC organisms contribute to soil surface stability in three ways. First, the presence of larger and more vertical vegetative structures such as those produced by lichen and moss thalli tend to dissipate the kinetic energy of wind, falling raindrops, and surface flow of water, thus reducing the potential for soil erosion [6,7]. Second, even where such vegetative structures are absent, many BSC communities contribute to an irregular soil surface micro-topography that dissipates the velocity of wind and water flow. Third, BSCs contribute to the mechanical and chemical aggregation of soil particles, particularly in soils with finer texture. For example, bryophyte rhizoids, lichen rhizines, fungal hyphae, filamentous cyanobacteria and algae typically form a dense living mesh that stabilizes soil particles [8–10]. Extracellular polysaccharide exudates produced by some BSC organisms, particularly cyanobacteria, also contribute to the formation of soil aggregates. McCalla (1946) [11] was among the first to show that soil aggregates formed in association with bryophytes, algae, and fungi were more resistant to erosion by rainfall than aggregates formed through physical processes without the stabilizing influence of BSC organisms. Osborn (1952) [12] subsequently demonstrated that the occurrence of a cyanobacteria-dominated soil crust in deteriorated rangeland habitats significantly reduced splash erosion by raindrops. Furthermore, Osborn (1952) [12]s howed that greater rainfall intensity was required to initiate splash erosion on crusts dominated by bryophytes and lichens than on cyanobacteria-dominated crusts or bare ground. The presence of BSC organisms significantly contributes to both the living cover and the irregular structure of the soil surface, thus causing water to pool on the surface of BSC dominated soils, and facilitating increased infiltration and subsequent storage of water in sub-surface soil pores [5].

BSC organisms also contribute to the accumulation, fixation, and processing of a variety of soil nutrients, ultimately making them available to the associated vascular plants [13]. For example, free-living and symbiotic diazotrophic bacteria and archaea fix atmospheric nitrogen, some of which is subsequently taken up by vascular plants [14]. Photoautotrophic BSC organisms fix and store organic carbon while co-occurring prokaryotic decomposers and saprophytic fungi extract energy from decaying organic matter, and thus cycle carbon as CO_2 back into the atmosphere [15]. Essential micronutrients are also accumulated, stored, and released by BSC organisms [16,17], including Ca, Cu, Fe, K, Mg, Mn, Na, and Zn, among others [18]. The contributions of BSC organisms to the community-level availability of mineral nutrients is directly related to their capacity to bind with fine soil particles. Negatively charged clay particles, bind to the gelatinous sheaths and polysaccharide exudates produced by cyanobacteria as well as the hyphae of free-living and symbiotic fungi that, in turn, bind with and accumulate positively charged essential mineral nutrients [10]. The weathering of essential minerals from rock substrata is enhanced by the production and release of weak organic acids produced by some BSC organisms, particularly lichen mycobionts [19,20]. Polysaccharide exudates produced by cyanobacteria act as chelating agents, sequestering and releasing micronutrients [21,22]. Considered together, improved water infiltration into the soil profile, soil stabilization against the action of wind and water erosion, and the enhanced accumulation and availability of essential nutrients, combine to provide critical support for the establishment and survival of vascular plant seedlings [23–25]. Results may vary depending on the nature and timing of critical events and processes.

The various BSC microorganismal groups share several common characteristics, including tolerance to desiccation, extreme temperatures, and ultraviolet (UV) solar radiation, as well as production and excretion of various soil-binding chemistries, preferential utilization of asexual reproduction, a pattern of aerial dispersal over impressive global distances, and a universal vulnerability to various kinds of anthropogenic disturbances. Beyond those already described, BSC communities perform several other essential community level ecological functions, including the enhancement of vascular plant seed germination and seedling survival [26–28]. Many BSC organisms are photoautotrophic (e.g., cyanobacteria, eukaryotic algae, and bryophytes) which fix, accumulate, and distribute organic carbon in a variety of forms and in connection with various community-level processes. Other BSC groups (e.g., free-living and symbiotic diazotrophic bacteria and archaea) fix atmospheric nitrogen and release organic nitrogen into the soil environment.

In addition to arid environments where BSCs were originally described, they are also abundant in semiarid climates, particularly in vascular plant communities dominated by shrubs with significant inter-shrub spaces commonly occupied by BSC communities. Some BSC organisms, particularly bryophytes, also commonly occur beneath the shrub canopy [29,30]. This type of community structure minimizes competition for direct sunlight while generally providing for a more equitable distribution of other essential resources. Biological soil crusts are also known to occur on the sand dunes and beaches of both lakes and oceans [31–36]. They have been reported to occur on as mine spoils [37,38].

The authors of the present paper have each been involved in various aspects of BSC research for 40+ years each. However, beginning in 2018, they began a new line of investigation regarding aerobiology and passive restoration of BSC communities [39]. This adjustment in research direction was initiated with the intent of exploring answers to previously unanswered questions about how BSC propagules are effectively and broadly distributed across earth landscapes. There are interesting similarities in the taxonomic composition and diversity of BSC organisms in widely disparate geographic locations, including at bipolar, intercontinental, and interhemispheric scales. While BSCs have generally been reported from arid and semiarid habitats globally, the authors have observed or collected BSCs throughout most of the United States, including Florida and Hawaii, which are seldom considered arid. They have also seen or collected them in Chile, England, Germany, and Iceland. They are also aware of collections from many other parts of the world that are neither arid nor semiarid. They finally arrived at the conclusion that BSC organisms are not limited to arid and semiarid environments. Indeed, they are geographically universal. However, how they are transported and distributed on a global scale is poorly understood – a question that is the focus of this paper. They have explored this question to a limited degree previously [1,39]. The intent with this paper is to address the issue in more detail by specifically exploring patterns and processes of aerial dispersal on a global scale. Some novel and poorly documented functions of BSC organisms are described in the following two sections.

2. Cloud condensation, raindrop, and ice nuclei

In 1978, a student from Montana, USA flew over a farm field collecting air samples while attempting to obtain samples of a bacterium that might also serve as cloud and ice nuclei while airborne. The idea lay dormant for 30+ years but has now reemerged. *Pseudomonas* and other microorganisms are now commonly recognized as cloud and ice nucleating agents [40]. BSC organisms and their propagules are now recognized for the critical role they play as cloud condensation nuclei, and raindrop and ice nuclei in the atmosphere [41–43]. Specifically, fungi [44,45], archaea [46], bacteria [47–49], algae [50,51], and bryophyte fragments [52] have been identified as frequent, viable contributors to cloud condensation and ice nucleation. Clouds form as moist air reaches a saturation point and condenses onto small solid airborne particles, thus forming tiny droplets that initiate cloud formation [53] eventually increasing in size until they fall as precipitation. In cold climates, bioaerosol particles serve as ice nuclei, contributing to the formation of snowflakes [54,55]. BSC organisms often reach the atmosphere with airborne dust and, in combination, they serve as condensation nuclei [57,58], as can pollen [59], smoke particulates [60–62], and sea salt aerosols [63–65]. The presence of condensation nuclei is essential, without which there would be no precipitation [66].

3. Aesthetics of airborne BSC organisms at dawn and dusk

Most of us, at one time or another, have noticed the colors of the sky at dawn and/or dusk. These color patterns result from the presence of dust, along with airborne microorganisms, and other particulates suspended in the atmosphere that scatters the sun's rays [67,68]. The process is referred to as Rayleigh scattering [69] where sunlight passes obliquely through the relatively thin (~50 km) band composing the troposphere and stratosphere where most dust and microorganisms accumulate. This effect often results in a variety of spectacular colors at sunrise and sunset [70–72]. Early in the morning and late in the evening, as the sun rises or sets, its rays traverse a much greater horizontal distance (hundreds or thousands of kilometers) than at mid-day when they traverse vertically only from the top of the stratosphere to the Earth's surface (a mere 50 km), encountering an abundance of solid atmospheric particles including dust and airborne microorganisms. As the distance increases, it is increasingly scattered [743 by concentrated airborne particles.

4. How BSC organisms become airborne

Biological soil crust organisms living at or near the soil surface are susceptible to being dislodged and subsequently suspended by wind [74–76]. Given their small size and minimal weight, they are easily suspended and transported. Because reproduction by BSC organisms is largely asexual [1], asexual spores and thallus fragments are even smaller and lighter. Laminar airflow over an unconsolidated soil surface can easily dislodge BSC organisms. As the wind encounters rocks, vegetation, and other surface features, turbulent airflow occurs, lifting BSC organisms and their reproductive propagules farther from the surface. Warm air rises, carrying the lightweight particles even higher. In arid areas, where BSCs often occur, dust devils, or tornadic bodies of rotating air, can lift dust and associated BSC organisms up to a height of 2 km [77]. All BSC organisms, once airborne, are ubiquitous or nearly ubiquitous inhabitants of the atmosphere, at least through the stratosphere, e.g., fungi [45,78], archaea [79,80], bacteria [81,82], algae [83,84], and bryophytes [85,86].

5. Characteristics of bioaerosols

Bioaerosols, or airborne microorganisms, collected from the Earth's atmosphere include essentially all groups of BSC organisms, including archaea, bacteria, fungi, algae, and bryophytes in the form of sexual and/or asexual propagules, including spores, group-specific specialized reproductive structures, or thallus fragments, all of which have been shown to regenerate viable organisms [87]. They include both unicellular and multicellular organisms that range in size from <1 μm and larger [88]. Given the small size and weight of BSC propagules, they are easily suspended and carried aloft by surface winds – depending on wind speed and air temperature parameters [88]. Airborne microorganisms have also been shown to pass through multiple generations while airborne [89].

Bioaerosols often accompany wind-eroded sediment from windstorms as reported from various parts of the world [90]. Dust and accompanying BSC organisms may be transported by wind on scales ranging from centimeters to thousands of kilometers, a process that has been ongoing for at least a millennium [91]. Primary sources of dust arriving in the mid-latitudinal United States are transported by western trade winds blowing from the Taklamakan and Gobi Deserts of China and Mongolia [92–94] via the Pacific Dust Express, so named by the National Aeronautics and Space Administration [95,96]. Dust originating in Asian deserts is deposited in western North America [97–99]. Dust and accompanying microorganisms arriving in the Caribbean and the southeastern United States generally originate from the east, specifically the Saharan Desert via the Saharan Air Layer [100–102].

Dust generally originates from arid landscapes and/or areas of disturbed or otherwise destabilized soil surfaces. Dust originating in the deserts of Northern Africa routinely arrives in the Caribbean and southeastern United States, bringing with it an impressive array of bacterial and fungal propagules [103,104]. At a conservative estimate of 10,000 microorganisms per gram of soil, that would be equivalent to 10 quadrillion microbes. While UV radiation from the sun may kill some microbes during the 5–7 day journey across the Atlantic Ocean, a huge number makes landfall in the Americas [103]. Worldwide, billions of tons of dust and vast numbers microorganisms are aerosolized each year [105]. Dust storms from different parts of the world transport unique microbial communities [106].

Dust storms and sandstorms also carry billions of microbes that come from harsh environments and survive the stressful journey of thousands of kilometers through the troposphere [107]. Airborne dust commonly originates in all arid areas of Earth. In addition to the Asian and Saharan Deserts, dust is commonly reported from the North American arid areas of the Mojave, Sonoran, Chihuahuan, and Great Basin Deserts [108,109], the Namib Desert of southwestern Africa [110], the Great Victoria Desert of Australia [111], the Atacama Desert of western South America [112,113], and interior Antarctica [114,115].

6. Reproduction of BSC organisms

Warren et al. (2019b) [1] reported that while specific modes of reproduction vary between BSC organisms, many groups demonstrate both sexual and asexual reproductive patterns. Asexual processes such as fission, cloning, budding, mitotic cell division, formation of specialized asexual spores, and thallus fragmentation represent the most common reproductive approaches across BSC organismal groups. Asexuality among BSC organisms is not a negative alternative to sexual reproduction. Indeed, asexually reproducing microbial communities are known to reproduce successfully even at low population densities, while also demonstrating impressive potential for both diversity and rarity [116]. BSC prokaryotes and eukaryotes with dominant haploid generations, readily express genetic variation through mutations, thus providing the genetic raw material essential for developing potentially valuable adaptations through natural selection. Eukaryotic BSC organismal groups commonly reproduce a variety of both sexual and asexual propagules. Sexual reproductive cycles among eukaryotic BSC organisms follow a basic pattern involving alternation of haploid and diploid generations with a wide variety of group specific patterns. Cycling between haploid and diploid generations is accomplished by the meiotic division of the diploid generation followed by the fusion of sex cells produced mitotically by the haploid generation. Among eukaryotic BSC organisms, in addition to mutations, meiosis also produces a significant source of genetic variation through generic recombination essential for the evolution of useful adaptations by natural selection. Almost exclusively, BSC reproductive propagules (both sexual and asexual) are dispersed aerially, often over impressive distances [117] – between countries, climates, continents, hemispheres, and poles.

7. Atmospheric structure

The Earth's atmosphere is organized conceptually by the National Aeronautics and Space Administration (NASA) and the global astrophysicist community into multiple concentric regions or layers based on approximate distances from the Earth's surface, i.e., the troposphere, stratosphere, mesosphere, thermosphere, and exosphere (https://www.nasa.gov/mission_pages/sunearth/science/atmosphere-layers2.html). The troposphere, the first atmospheric layer, extends from the Earth's surface up to approximately 12 km. Most weather phenomena, including convection, turbulence, and clouds occur in the troposphere layer, although some phenomena may extend into the next layer or lower stratosphere. Generally, bands of circumpolar trade winds in the troposphere occur between 30 °north and 30 °south latitudes, straddling the equator, and blow from east to west. As those winds reach 30 ° north or south latitude, they are affected by the Coriolis force [118], a phenomenon related to the rotational pattern of the planet that causes the winds to reverse direction between 30 °and 60 °north or south latitudes. The winds reverse again between 60 °north and south latitude and the respective poles. The trade winds derive their name from the role they played in intercontinental commercial trade via windblown sailing ships on the world's oceans many years ago. Jet streams generally occur in the tropopause, the boundary layer between the top of the troposphere and the bottom of the stratosphere; they are meandering air currents reaching speeds of 110+ mph (177+ kph) (https://scijinks.gov/jet-stream/). They generally blow from west to east, and meander between continents and hemispheres. Air temperatures in the troposphere generally decline with altitude.

The next atmospheric layer is the stratosphere. It is located above troposphere, beginning at about 12 km and extending to approximately 50 km above the Earth's surface. The stratosphere is minimally susceptible to vertical mixing, and lies in horizontal strata, hence the name *strato*sphere. Wind speeds in the stratosphere can reach 220 km per hour (130 mph). Occasionally, tropospheric and the stratospheric air-masses mix, particularly when strong Polar-night Jet Oscillations correspond to the strong downward movement of stratospheric air-masses, typically associated with significant increases in stratospheric ozone levels [119]. Due to low humidity conditions, there are generally few clouds in the stratosphere. There are no storms or turbulence there to mix the air, so cold, heavy air is at the bottom of the layer and warm, lighter air is at the top. The stratosphere is perhaps most noteworthy for the presence of the ozone layer located about 25 km above the Earth's surface. This is the layer where approximately 90% of atmospheric ozone is concentrated. The ozone layer absorbs much of the solar ultra-violet (UV) radiation from the sun and protects life on Earth from the harmful effects associated with prolonged exposure to UV radiation.

Above the stratosphere is the mesosphere. It begins at about 50 km altitude and extends to about 80 km above the Earth's surface. The mesosphere is the coldest atmospheric layer. At the top of the mesosphere, the temperature falls to a low of −90 °C. Most meteors approaching the Earth's surface from outer space vaporize in this layer. Knowledge about the mesosphere is limited due to accessibility issues associated with sampling methods.

Above the mesosphere is the thermosphere which begins at about 80 km altitude and ends at about 700 km altitude. As the name implies, temperatures in the thermosphere are very hot, reaching 2,000 °C or higher. The northern and southern lights, or aurora borealis and aurora australis, respectively, occur in the thermosphere as charged particles (electrons) collide with oxygen and nitrogen molecules, exciting them to higher energy states and emitting photons or light (https://pwg.gsfc.nasa.gov/polar/telecons/archive/PR_E-PO/Aurora_flyer/aurora-flyer_p2.doc.pdf).

The exosphere is the outermost layer of the atmosphere, beginning at about 700 km altitude and ranging up to about 1000 km above the Earth's surface. This atmospheric layer serves as the transition zone between the Earth's atmosphere and outer space, and reaches temperatures of up to 1,700 °C. Only the lightest gases occur in the exosphere, i.e., helium, hydrogen, traces of carbon dioxide, and elemental oxygen. The density of the exosphere is so low that it is difficult to determine where this layer ends and outer space begins.

8. The occurrence of BSC organisms in the atmospheric layers

The atmosphere is considered by some to be the ‘last extreme environment’, due in large part to temperature extremes and high levels of ultraviolet radiation particularly in the upper portions of the earth’s atmosphere [120]. Nevertheless, biological material is considered universally present in the atmosphere [121]. All groups of BSC microorganisms have been found as airborne propagules up to at least the mid-stratosphere [84,122,123]. Although diverse groups of bacteria and fungi have been collected from the troposphere [124], they have also been collected from a wide range of elevations in the stratosphere over India using hot air balloons [125]. The density of microbes in the troposphere varies little between the lower troposphere (2–5 x 10^5 cells/m^{-3}) and the tropopause (1 x 10^6 cells/m^{-3}), but declined to 8 x 10^4 cells/m^3 in the stratosphere at 35–38 km altitude [126]. Chen et al. (2012) [127] measured airborne microorganisms near ground level in Guanghzou, China during the summer and found markedly greater concentrations of bacteria than of fungi. Spores of two strains of yeast (fungi) from a high elevation site in the Atacama Desert survived stratospheric balloon flights into the upper stratosphere (severe desiccation, low atmospheric pressure, low temperature, and high UV exposure) [128]. Viable bacteria and fungi are also reported to occur in a stratospheric transoceanic bridge between Asia and North America [78,129]. Bacterial taxa collected from below and above the tropopause, an area corresponding to the upper tropospheric and lower stratospheric layers of the atmosphere, were highly similar [130]. When exposed to conditions typical of the upper stratosphere - including reduced atmospheric pressure, low temperatures, extreme desiccation, and high levels of UV radiation, 99.9% of *Bacillus subtilis* spores were killed [131]. Nicholson et al. (2000) [132] reported similar results. In contrast, bryophytes propagules have been shown to tolerate all extraterrestrial stresses except for UV radiation [133], suggesting that UV radiation may be the critical factor limiting global atmospheric transport of BSC propagules [131]. The ozone layer is located in the mid-stratosphere and serves to attenuate most UV radiation, suggesting that the possibility of viable bacteria occurring above that layer is unlikely. However, at least some species of lichens have been shown to survive UV exposure [134]. A number of studies have demonstrated the presence of both bacteria and fungi in the stratosphere. It is likely that bacteria can survive conditions in the upper stratosphere [135], although it is not clear if the samples were collected above or below the ozone layer [136]. Moist vegetative shoots of three or four species of bryophytes have been shown to survive after two hours in the harsh conditions of the stratosphere while showing initial stages of regeneration, suggesting the potential for wide-range aerial dispersal by bryophytes [137].

9. Biosphere

The biosphere defines the physical and functional limits of life on Earth and was originally thought to have an upper atmospheric limit of about 12 km above the Earth’s surface, thus within the troposphere. The biosphere likely originated billions of years ago and included ancient prokaryotes such as bacteria and archaea, all capable of surviving without molecular oxygen. Over time, some groups of prokaryotes likely evolved the capacity to use sunlight to synthesize simple sugars by extracting hydrogen from water and carbon and oxygen from carbon dioxide, and subsequently releasing the oxygen from the water into the atmosphere as O_2. These photosynthetic prokaryotes were abundant, and over time, changed the chemical environment of the biosphere by contributing a significant amount of molecular oxygen to the atmosphere – a condition that ultimately resulted in conditions suitable for sustaining new and more complex forms of life on the Earth. Recently, the vertical dimensions of the biosphere have been reevaluated and some have suggested that those portions of the atmosphere protected by the ozone layer of the stratosphere may also be part of the biosphere [138]. As exploration of the stratosphere above the ozone layer and into the mesosphere has increased, a growing number of viable airborne microorganisms have been collected and identified from the upper stratosphere and lower mesosphere [135,139]. It has been suggested that the dark pigments in cells from these parts of the atmosphere could protect resident cells from the harmful effects of UV radiation [140].

After being exposed for 2 weeks to Mars-like conditions (severe desiccation, high UV radiation, and temperature extremes) on the surface of an Earth-orbiting FOTON-M2 Russian satellite, dormant lichens were found to have remained dormant, with no ultrastructural changes in either symbiont, and thalli generally remaining viable as measured by chlorophyll fluorescence [141]. The International Space Station (ISS) orbits the Earth at approximately 400 km (250 mi) above the Earth, within the thermosphere (85–690 km). Dust samples collected from the ISS have been stored for 12 years, and still contain viable bacteria and fungi [142], suggesting the possibility of extraterrestrial BSC organisms. Cosmic dust samples were collected from the surface of the ISS by a crew member during a spacewalk. These samples were subsequently analyzed for bacterial DNA and a gram-negative bacterium of the genus *Delfia* was identified. This bacterium was genetically similar to a gram-negative bacillus collected in surficial microlayers from the Barents and Kara sea coastal zones in Russia [143].

10. Ozone hole

In 1957, the British Antarctic Survey began to monitor ozone levels at the Halley Bay ground station in Antarctica with the intent of better understanding ozone concentrations at ground level and in the atmosphere above the station. Since the mid-1970s, NASA has used satellites to monitor atmospheric ozone. In 1985, scientists first reported what they assumed was a 'hole' or a depleted area in the ozone layer of the stratosphere over the South Pole [144–146]. That discovery led to worldwide panic, with fears of high levels of skin cancer in humans caused by increased UV radiation associated with depletion of the ozone layer. Consequently, the global 'Montreal Protocol on Substances That Deplete the Ozone Layer' was signed in 1987, phasing out the production and use of chlorofluorocarbons (CFCs) and halons that were thought to be the leading causes of ozone depletion. A subsequent decline of 98% in the production and use of ozone depleting substances was correlated with a reversal of the depletion pattern associated with the hole in the ozone layer over Antarctica [148]. However, at least part of the ozone layer depletion pattern may be attributed to a significant relationship with the polar vortex, as a longer, stronger, and later breakup time of the polar vortex each year has also been connected to ozone depletion [148].

An opportunity exists to research the consequences of a reduced ozone layer by studying the impact of increasing levels of UV radiation on BSC organisms *in situ*. Due to the 'ozone hole' in the stratosphere above Antarctica, scientists have been investigating the impact of increasing UV levels on various life forms, including BSC organisms. Initial results showed that many of the organisms have adapted by developing a cryptoendolithic growth habit [149], increasing the production of enzymatic antioxidants [150], and producing UV-absorbing/screening pigments and carotenoids [151–153]. Some BSC organisms have also been shown to reduce UV impact through the formation of clumps or aggregates [154]. Some BSC organisms have evolved adaptations to counteract the negative effects of increased exposure to ultraviolet radiation by (1) moving vertically up or down in the substrate column to avoid stressful exposure to UV radiation, and (2) evolving molecular repair mechanisms in situations where UV exposure is unavoidable [155]. Whether these adaptions arose before or after the discovery of the ozone hole is unknown, but the issue does raise questions about whether the ozone hole is strictly a recent phenomenon. Some have suggested that the ozone hole is a Black Swan event, i.e., a rare, improbable, and unpredictable outlier event [156,157]. Indeed, it seems several important questions remain unanswered. First, and most relevant to this paper, are questions about whether the UV-related defensive adaptations employed by BSC organisms and other microorganisms are new or have existed for millennia. Second, is the question of whether the first appearance of the ozone hole was truly novel, or whether it was a recurring phenomenon that grew and subsided regularly on a time scale much longer than modern humankind can imagine.

Regardless of the answers to these questions, while the Antarctic ozone hole is shrinking, possibly due to implementation of the Montreal Protocol, a large hole recently opened in the Arctic, possibly caused by cold temperatures and the strong vortex at the North Pole [158]; https://science.nasa.gov/nasa-reports-arctic-stratospheric-ozone-depletion-hit-record-low-march). This, plus the fact that the Arctic ozone layer appears to thin at least once per decade, seems to call into question the previously reported rationale for the human-related cause of the Antarctic ozone hole. It is quite possible that the occurrence and strength of the polar ozone layer is strongly influenced by the polar vortex [148].

11. Conclusion

Biological Soil Crusts (BSCs) occur where small, often microscopic, living organisms occupy and stabilize the upper few millimeters of the soil. First recognized and described in arid areas, they have since been identified globally, wherever aridity and/or physical disturbance have left at least portions of the soil surface bare. Biological organisms associated with BSCs typically include archaea, bacteria (cyanobacteria, and chemoheterotrophic and diazotrophic bacteria), fungi (free-living, lichenized, and mycorrhizal), and bryophytes (mosses and worts). They provide essential ecological services including soil stabilization against wind and water erosion, and the acquisition, distribution, and storage of soil water and essential nutrients used by vascular plants. From where and how they are transported to viable habitats raises important questions seldom seriously considered by BSC afficionados. BSC organisms are readily dislodged from arid or disturbed soil surfaces. BSC organisms are transported globally via trade winds in the troposphere (150 – 900 m altitude) and jet streams in the tropopause (6,000 – 15,000 m altitude) and are subsequently deposited globally. Most airborne organisms reproduce asexually via asexual spores, thallus fragments, specialized reproductive structures generated by fission/budding and mitotic cell division among eukaryotic groups. Most airborne propagules are accompanied by windborne dust from distant locales such as the Saharan and Asian deserts, and other arid regions around the world. Together, the microorganisms and dust particles play an essential role as cloud and condensation nuclei, without which precipitation as rain or snow would be eliminated. The particles also play a critical role in scattering the sun's rays to create colorful sunrises and sunsets.

Acknowledgments

This research was supported in part by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent any official USDA or U.S. government policy.

Conflict of interest

All authors declare no conflicts of interest in this paper.

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