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Source: Rangeland Ecology and Management, 78(1) : 213-219

Published By: Society for Range Management

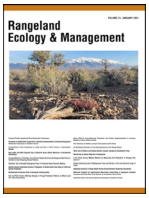
URL: https://doi.org/10.1016/j.rama.2020.08.010

Rangeland Ecology & Management 78 (2021) 213–219

Contents lists available at ScienceDirect

Rangeland Ecology & Management

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



Biological Soil Crusts of the Great Plains: A Review

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ARTICLE INFO

Article history:
Received 23 March 2020
Revised 22 July 2020
Accepted 27 August 2020

Keywords:
Aerobiology
Bacteria
Biocrusts
Bryophytes
Fungi
Terrestrial algae

ABSTRACT

Biological soil crusts (BSCs), or biocrusts, are composed of fungi, bacteria, algae, and bryophytes (mosses, etc.) that occupy bare soil, entwining soil particles with filaments or rootlike structures and/or gluing them together with polysaccharide exudates to form a consolidated surface crust that stabilizes the soil against erosion. BSCs are common in arid and semiarid regions where vascular plant cover is naturally sparse, maximizing the exposure of surface-dwelling organisms to direct sunlight. Although less prominent and less studied there, BSC organisms are also present in more mesic areas such as the Great Plains where they can be found in shortgrass and mixed-grass prairie, in the badlands of several states, where burrowing animals have created patches of bare soil, on damaged road-cuts, strip-mines, gas and oil drill pads, military training areas, heavily grazed areas, and burn scars. Even where BSCs are not readily visible to the naked eye, many of the organisms are still present. BSC organisms are passively dispersed to the Great Plains as airborne organismal fragments, asexual diaspores, or sexual spores that accompany wind-blown dust from as far away as northern China and Mongolia. BSCs can best be studied and managed by 1) acknowledging their presence; 2) documenting their diversity, abundance, and functional roles; and 3) minimizing unnecessary disturbance, particularly when the soils are dry. This paper describes the current knowledge of Great Plains BSCs in an effort to heighten awareness of these cryptic but crucial ecosystem components and to encourage new research initiatives to better understand and manage them in this biome. Some specific actions may include refined taxonomic and ecologic studies of BSC organisms in underexplored areas, particularly those previously less or not recognized as BSC habitat, and incorporation of techniques to sample airborne organisms.

Biological soil crusts—a general introduction

On a global scale, biological soil crusts (BSCs) develop when various combinations of diminutive organisms including fungi (free-living, lichenized, and mycorrhizal); bacteria (cyanobacteria, chemoheterotrophic and diazotrophic [nitrogen-fixing]); terrestrial algae (including diatoms); and bryophytes (mosses, liverworts, and hornworts) occupy the surface few millimeters of the soil, entwining and/or gluing soil particles with polysaccharide exudates into a stable surface layer. BSCs can be present in a wide array of ecological conditions, when and where aridity and/or physical disturbances have exposed the soil surface to colonization by BSC-forming organisms (Warren 1995). They are most recognized in hot or warm arid regions, semiarid regions, and dry but frigid polar zones where vascular plant cover and diversity are characteristically low, leaving areas of bare soil available for BSC colonization (Rosentreter and Belnap 2001).

Despite their small size, BSC organisms are crucial ecosystem components that perform essential functions important to ecosystem health and stability. The ecological roles of BSCs include the acquisition, accumulation, and cycling of essential airborne and soil nutrients; redistribution of precipitated water; and soil formation and stabilization (Warren 1995; Belnap and Lange 2001; Pietrasiak et al. 2013; Weber et al. 2016). BSCs and their ecological functions can be disturbed by a variety of natural and anthropogenic factors including, but not limited to, livestock grazing and trampling (Warren and Eldridge 2001), off-road vehicular traffic (Wilshire 1983), military training (Warren 2014), mining (Spröte et al. 2010), and fire (Johansen 2001).

Within the continental United States, BSCs are common in all of the major arid areas including the Great Basin and Colorado Plateau Deserts, which frequently freeze and experience snow dur-

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https://doi.org/10.1016/j.rama.2020.08.010
1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management.

Figure 1. Examples of Great Plains biological soil crusts at various scales: **a,** The vagrant lichen, gray-green *Xanthoparmelia* spp., covers the ground, creating a green carpet in front of this person on badland soils east of Salmon, Idaho; **b and c,** Vagrant lichens and cyanobacterium *Nostoc commune* (*white arrow*) growing among the grass in Montana; **d,** Close-up of the vagrant lichen *Xanthoparmelia* sp. (1-cm squares); **e,** Short mosses, including *Bryum* sp. and a yellow crustose lichen, *Fulgensia* spp. (*white arrow*) on soil between the grass and fringed sage; **f,** Squamulose (scale) lichens, *Cladonia* sp. (*white arrow*) growing with grass and fringed sage; **g,** Short mosses; **h,** Three common Great Plains BSC mosses from left to right: *Ceratodon*, *Bryum*, and *Syntrichia;* **i,** free-living cyanobacteria *Nostoc commune* (*white arrow*) growing with grasses and *Syntrichia* moss.

ing the winter, and the warmer Chihuahuan, Sonoran, and Mojave Deserts, which less frequently freeze and where the majority of precipitation falls as rain (Rosentreter and Belnap 2001). They are generally less visually prominent in the Great Plains than in more arid regions where vascular plant cover is characteristically lower and there is less competition for direct sunlight and bare soil conditions. Yet they are present there (**Fig. 1**). The objective of this review is to describe the BSCs of the Great Plains so that they can emerge from their scholarly obscurity and be recognized for the ecological roles they perform there. By making observers more aware of their presence and importance, it is hoped that further research efforts regarding their geographic distribution and ecological functions in the Great Plains will be initiated.

BSC distribution and abundance in the Great Plains

The Great Plains are characterized by cold, dry winters and hot, humid summers, with an average annual temperature of 8°C. Rainfall is concentrated in the summer. Shortgrass prairie rainfall averages 250 mm annually. Annual precipitation in mixed-grass prairie averages 350–580 mm. Grasses are typically short, and cover is sparse. The Great Plains evolved with periodic fire and grazing by herds of buffalo *(Bison bison)* unlike other arid and semiarid regions of the western United States (Mack and Thompson 1982). Biological soil crusts in this ecosystem are unique in that they appear to be adapted to the summer rainfall, periodic fire, and livestock disturbance (Rosentreter and Belnap 2001).

Most rangeland research in the Great Plains and elsewhere has focused on vascular plant communities and the ungulates that consume them. The presence and roles of soil microbial communities have received less attention relative to what drives their abundance, distribution, and ecosystem functionality. Still, BSCs of the Great Plains can occur in the interspaces between bunchgrasses and shrubs (see Fig. 1), but in contrast to their more arid counterparts, Great Plains BSCs are not as prominent. However, regardless of their cryptic appearance, BSCs constitute an important ecosystem component that merits scientific attention. The earliest research regarding the effect of BSCs on soil hydrology was conducted in the Red Plains region of Oklahoma, stretching from southern Kansas, through Oklahoma, and into Texas (Booth 1941), before labeling soil with a biologically crusted layer of surface soil as “biological soil crusts.” The research showed that early successional algae enhanced water infiltration into the soil, thus reducing runoff and concomitant soil erosion. Yet our understanding of how BSCs contribute to ecosystem functionality and health in other regions of the Great Plains is far from comprehensive and based on only a handful of studies. A more complete characterization of their communities and ecological functions is warranted. Here we review the historical and current knowledge of Great Plains BSCs.

BSCs in the prairie ecosystems of the Great Plains

Extensive stretches of prairie ecosystems occur in the Great Plains from Canada south to New Mexico and Texas. Much of the limited BSC research in the Great Plains has been focused on shortgrass and mixed-grass prairie. Much of the western edge of the Great Plains is a naturally occurring shortgrass prairie where the primary grasses are short and seldom form a solid continuous ground cover, leaving considerable areas of bare soil available for colonization by BSC organisms (Rosentreter and Belnap 2001). Yet

BSCs are sometimes difficult to recognize in this ecosystem. Lichen and moss growth may be concentrated near shrubs and bunch grasses, which may visually hide the presence of BSC organisms. Interspaces may be colonized by algal BSCs, which constitute the most inconspicuous BSC type, which is easily overlooked. Fire is known to negatively affect BSC organisms (Johansen 2001; Warren et al. 2015), and recovery can vary for these ecosystem components. Two privately managed pastures east of Fort Collins, Colorado showed no difference in vegetation cover and composition (Warren, unpublished data). However, once BSC composition was assessed, one pasture contained a much higher presence of lichens compared with the other adjacent pasture (Warren, unpublished data). An investigation into fire history of these pastures revealed that the pasture without lichens had been burned the previous year, while the pasture with abundant lichens had not.

Common BSCs in prairie systems include many species bryophytes and lichens. Common bryophytes include species in the genera *Bryum*. *Ceratodon*, *Pterygonerum*, and *Syntrichia*. Frequently observable lichens include *Fulgensia* spp., *Heppia* spp., *Petula* spp., *Psora* spp., *Placidium* squamulosum (Ach.) Breuss, and *Collema tenax* (Swartz) Ach. The *Collema* lichen is composed of a fungal symbiont of the same name and a nitrogen-fixing cyanobacterial symbiont, *Nostoc commune* Vaucher ex Bornet and Flahault. It is critical in areas with few nitrogen-fixing vascular plants (Looman 1964; Freebury 2014).

Knowledge of BSC cyanobacterial and terrestrial algal diversity is limited in the Great Plains. One of the earliest works on algae in Colorado agricultural soil documented 19 species of cyanobacteria, one diatom, and one green alga in Great Plains habitats (Robbins 1912). In 1943, the cyanobacterium *Schizothrix macbridei* was reported as occurring in silty soil crusts in Nebraska and Colorado (Drouet 1943). The author also listed *Symploca kieneri* as a cyanobacterial species that could be found in sandy depressions in Nebraska. Durrell (1959) later floristically surveyed 239 soil samples from Colorado ranging from cultivated soils to barrens, alpine, and montane soils, as well as soils from sagebrush and grasslands. He found 85 algal species, of which 17 were later classified as cyanobacteria. Specific locational information was not provided. The author combined his records into broad habitat categories, such as “soil under sagebrush,” “soil under saltgrass,” and “soil under buffalograss.” Cyanobacterial species found in habitats within the Great Plains included *Anacystis thermalis* cf. *major* (Lagerheim) Drouet and Daily 1956, *Lyngbya versicolor* Gomont 1892, *Nodularia harveyana* Thuret ex Bornet and Flauhalt 1886, *Nostoc muscorum* C. Agardh ex Bornet and Flauhalt 1888, *Nostoc paludosum* Kützing ex Bornet & Flauhalt 1886, *Phormidium tenue* Gomont 1892, *Phormidium* spp., and *Schizothrix* spp. (Durell 1959). Schulten (1985) reported five cyanobacterial genera, *Nostoc*, *Microcoleus*, *Oscillatoria*, *Phormidium*, and *Scytonema*, on a sand prairie on a river terrace in southeastern Iowa. There were no descriptions, illustrations, or photographs associated with this work, and species identity of the cyanobacteria was unclear. The only recent study using a modern taxonomic treatment by applying the polyphasic approach to cyanobacterial systematics is the work of Pietrasiak et al. (2014a) in which the authors described a new *Symplocastrum torsivum* N. Pietrasiak & J. Johansen 2014 species from the US Department of Agriculture−Agriculture Research Services Central Plains Experimental Range site near Fort Collins, Colorado. With such a paucity of studies, much remains to be discovered in this biome.

Less common BSC habits within the Great Plains

Badlands

Badlands are characterized as areas of exposed soft rock or soil with little vegetation that has been eroded into a variety of strange shapes. Some of the most recognized and scenic areas of badlands include Makoshika State Park in Montana, Badlands National Park in southwestern South Dakota, and the Theodore Roosevelt National Park in western North Dakota. Other smaller areas of badland habitats are present in Toadstool Geologic Park in the Oglala National Grassland located in northwestern Nebraska; Hell’s Half-Acre in Natrona County, Wyoming; and many other areas dispersed throughout the Great Plains. Given the paucity of vascular plants that would otherwise effectively compete for sunlight, badlands are ideal habitats for BSCs. However, little effort has been made to locate and identify the BSC organisms of the badlands of the United States. Dahal et al. (2017) identified an Actinobacterium of the genus *Streptomyces* in the soils of the badlands of South Dakota. Lichens have been studied in Badlands National Park, and 128 different lichenized and nonlichenized fungal species have been documented (Will-Wolf 1998). Badlands also occur on other continents as well and serve as analogs to the badlands of the Great Plains in the United States. Their associated BSCs have been studied extensively in Spain (Souza-Egipsy et al. 2004; Pintado et al. 2005; Maestre et al. 2011), suggesting that the badlands of North America may be similarly populated.

Prairie dog colonies

Prairie dog colonies occur in parts of the Great Plains, especially where abundant vascular plants do not hinder the ability of prairie dogs to observe approaching predators, and where plant roots do not hinder digging of underground dens. Large areas of barren soil with sparse vascular plant cover can be suitable for BSC formation and establishment. Short mosses such as *Bryum*, *Didymodon*, and *Pterygoneurum* are common BSC organisms that quickly colonize open sites created by burrowing animals (Eldridge et al. 2003; Rosentreter and Root 2019). Occasional fire can assist in the expansion of prairie dog colonies, although the most appropriate season, frequency, and uniformity of fire has yet to be determined, at least in part due to periodic climatic fluctuations (Augustine 2007; Archuleta 2014). Fire may set BSC succession back for up to 30 mo (Ford and Johnson 2006), depending on the season of the fire and despite helping to create and/or restore optimal, more open habitat for BSC colonization. BSC organisms that establish in this habitat may require specific adaptations to occasional disturbance impacts, including survival strategies to cope with occasional burial by soil spread by the animals (Pietrasiak et al. 2014b).

Roadcuts

During the process of constructing or resurfacing paved roads, the topsoil and several horizons of the soil beneath the roads and borrow areas used to create new surfaces may be removed or mixed, thus disturbing or destroying existing soils. Little evaluation of the effects of roadcuts in the Great Plains has been done, although they have been reported on roadcuts elsewhere (Root et al. 2011; Williams et al. 2012; Concostrina-Zubiri et al. 2019). As roadcuts produce considerable bare soil, they serve as an ideal BSC habitat for colonization.

Strip mines, mine tailings, and gas and oil well drill pads

Many areas of the world, including parts of the Great Plains, are increasingly subjected to exploration for and extraction of minerals, coal, natural gas, and oil. Shubert and Starks (1980) reported several species of algae and cyanobacteria that occupy surface mine spoils in North Dakota, assisting in soil stabilization and the fixation of atmospheric nitrogen. Although exploration and extraction occur in some locations in the Great Plains (e.g., Fosher 1976), minimal effort has been made to evaluate BSCs on the areas disturbed by such activities in the region.

Military training areas

Author Warren began his career working 13 yr as a research ecologist for the US Army, followed by a decade as a senior research ecologist and subsequently the director of the Center for Environmental Management of Military Lands at Colorado State University. In that capacity, he visited and/or performed research at the majority of military training and testing areas in the United States, including Fort Bliss, Texas; White Sands Missile Range and Hollomon Air Force Base in New Mexico in the transition zone between the Great Plains and the Chihuahuan Desert; Fort Carson and the Piñon Canyon Maneuver Site in Colorado; Fort Riley in Kansas; Fort Sill in Oklahoma; Fort Hood and Camp Bullis in Texas; and several Wyoming Army National Guard training areas within the Great Plains per se. As the training areas have each experienced intensive soil-disturbing training operations that have reduced vascular plant cover and left large areas of bare soil, BSCs are plentiful there (Warren, personal observation).

Heavily grazed areas

Contemporary domestic livestock grazing has damaged some areas. Where grazing pressure and resulting damage are accentuated surrounding watering holes and salt or mineral licks and then attenuate with increasing distance from the center of disturbance, a piosphere is formed (Andrew and Lange 1986). Vascular plant cover near the center is often severely diminished but increases with distance from the center (Williams et al. 2008; Shahriary et al. 2018). BSC cover is likely accentuated where vascular plant cover is reduced. Such potential habitat for BSC colonization should be explored in future studies.

Burn scars

As noted in a previous section related to the western Great Plains, fire can have a significant negative impact on some BSC organisms where vascular plant cover is adequate to carry the flames. A late-season prescribed burn in the eastern Great Basin had little effect on BSC diversity because, while most organisms growing under sagebrush were killed by the fire, there were many others in the nonvegetated interspaces that were unaffected and served as potential inoculant sources for burned areas (Warren et al. 2015). Burning of a shrub steppe analog in Ukraine had minimal effect on cyanobacterial and green algal species diversity (Shcherbyna et al. 2017). Most fires in the Great Plains and elsewhere tend to burn in a mosaic pattern, leaving some areas unburned (Fuhlendorf and Engle 2001), which can serve as BSC inoculant sources for burned areas.

Challenges in recognizing BSC organisms

Elbert et al. (2009) are among several authors who recognize that BSC organisms may grow on nonsoil surfaces without forming a crust. Some organisms may be recognized for what they are but not their potential role in BSCs. For example, many lichens (Looman 1964; Freebury 2014) and mosses (Smith Merrill 1991; Eckel 1996) occur in the Great Plains without being recognized as BSC components. Other BSC organisms form a crust but may be indistinguishable. Short mosses or crustose lichens may be so small or embedded in the soil that the casual observer may believe it is merely bare soil (see Fig. 1g). Even many rangeland managers seem to have "biocrust blindness" and never note the presence of BSCs (Condon and Pyke 2018). Yet on close examination with a 10x hand lens or under a microscope, or when moist, one discovers that the soil is bound together by a BSC community. Vegetation surveys have often been conducted in the summer when the BSCs are dry and difficult to see. If one uses a water spray bottle as in Hilty et al. (2004), the BSC organisms turn from brown to bright green and are more noticeable. Short mosses of many genera twist or fold up and are more hidden or very much embedded in the soil and go unnoticed. These mosses and the lichen *Collema tenax* Swartz Ach. often occur under the sparse canopy of blue grama *(Bouteloua gracilis)* (Willd. ex Kunth) Lag. ex Griffiths and buffalograss *(Bouteloua dactyloides)* (Nutt.) J. T. Columb. One lichen, *Thrombium epigaeum* (Pers.) Wallr., appears only as discolored soil with the reproductive structures as tiny dark spots (McCune and Rosentreter 2007). This lichen is an early colonizer and is often found along secondary dirt roads. Early colonization by moss spores may be visible only as a thin green layer or filaments that appear similar to green algae until inspection under at least a 50x microscope. McCampbell and Maricle (2018) highlighted BSCs along a transect from the western edge of the Great Plains to the Konza Prairie Biological Station in central Kansas. They illustrated and discussed variations in species composition and stature along the transect.

Vagrant lichens may not participate in classical BSC functions. However, many grow in association with BSCs, detach easily from the BSC, and are blown around—thus the epithet "vagrant." A large diversity of vagrant lichens can be found in the Great Plains (see Fig. 1a–d). Vagrant lichens, sometimes called "range lichens," of genus *Xanthoparmelia* are common and provide winter forage for wildlife. Pronghorn antelope (*Antilocapra americana* Ord, 1815) commonly occur in the Great Plains and eat vagrant lichens in the winter (Thomas and Rosentreter 1992). These lichens are also eaten by domestic sheep (*Ovis aries* Linnaeus 1758) and wild bighorn sheep (*Ovis canadensis* Shaw 1894) (Rosentreter 1993). McCune et al. (2014) reported six species of vagrant *Xanthoparmelia* species from central Montana. One study of lichens on the Milton Cattle Ranch reported four vagrant *Xanthoparmelia* species as common and co-occurring in well-managed rangelands (Beye 2016). Rosentreter (1993) reported four species of vagrant *Xanthoparmelia* lichens in the shortgrass prairie in Montana and many other species in badlands, alpine areas, or on calcareous sites. As with other BSC organisms, vagrant lichens occur where the vascular vegetation is sparse. Limited vascular plant cover is necessary for the vagrant *Dermatocarpon* lichen species to persist (Rosentreter and McCune 1992). The authors hypothesized that the removal of dead vascular plant litter by wind may be beneficial for vagrant lichens. A study by MacCracken et al. (1983) found that annual variation in species composition of vagrant lichens in Montana was favored by drought conditions and low organic matter content of the soil. They found that moderate summer livestock grazing encouraged vagrant lichen growth. Plant communities that consistently produce little biomass may be essential for their existence.

Other lichens do not attach to the soil, instead attaching to rocks, tree bark, fence posts, gravestones, building façades, and rooftops. Mosses, algae, and cyanobacteria may also colonize such alternative surfaces within the Great Plains and later disperse onto the soil (Karsten et al. 2007; Barberán et al. 2015; McGorum et al. 2015).

Dispersal of BSC organisms to the Great Plains

Given the wide diversity of surfaces colonized, it is reasonable to wonder how BSC organisms get to the Great Plains. Herein lies one of the great mysteries seldom considered or mentioned by BSC aficionados or scientific journals that publish on BSC ecology. Large numbers of BSC organisms have been documented as being present in the air ranging from low to high altitudes above the Earth (Genitsaris et al. 2011; Després et al. 2012; Tesson et al. 2016). Airborne BSC organisms may be deposited almost anywhere in the Great Plains or elsewhere. They have been collected from building rooftops (Tripp et al. 2016) and façades (Samad and Adhikary 2008; Sethi et al. 2012; Barberán 2015), stone monuments (Tomaselli et al. 2000; Macedo et al. 2009), exposed rocks (Danin 1999), plant surfaces (Sethi et al. 2012; Warren personal observation), the backs of grazing animals (McGorum et al. 2015), and on seaborne vessels thousands of kilometers from terrestrial environment (Darwin 1846; Harmata and Olech 1991). Most BSC organisms are dispersed by wind. These include asexual reproductive lichen fragments, soredia, isidia, and/or sexual fungal spores (Bailey 1966; Heinken 1999; Leavitt and Lumbsch 2016), as well as spores, gametophyte fragments, and specialized asexual diaspores of bryophytes (Laaka-Lindberg et al. 2003; Stark 2003). An extensive review of relevant literature revealed a near exclusive dependence on asexual reproduction and a pattern of aerial dispersal over impressive distances up to intercontinentally and interhemispherically (Warren et al. 2019).

Dust and accompanying BSC organisms may be transported by air on scales ranging from centimeters to thousands of kilometers, a process that has been ongoing for at least a millennium (He et al. 2015). Primary sources of dust arriving in the Great Plains are the Taklamakan and Gobi Deserts of China and Mongolia, restrictively (Guo et al. 2017), via the "Pacific Dust Express," so named by the National Aeronautics and Space Administration (Barry 2001). Prevailing trade winds between 30 and 60 degrees in the northern and southern hemispheres tend to blow from west to east, such that dust and accompanying microorganisms from China and Mongolia blow onto the northwest coast of the continental United States, then to the Great Basin and on to the Great Plains (Creamean et al. 2013). With the advent of satellite imaging technology, such clouds of dust are now recognized as common events (Husar et al. 2001) that occur mainly in the springtime in the western and southwestern United States (Fischer et al. 2009; Achakulwisut et al. 2017) and in the summertime in the Great Plains (Pu and Ginoux 2018), and they typically carry BSC microorganisms (Griffin 2007; Behzad et al. 2018). The mass of dust and bioaerosols from overseas sources rivals all domestic sources in North America (Yu et al. 2012). Dust and microorganisms form condensation nuclei that are essential for the formation of raindrops and snowflakes (Hoose and Möhler 2012; Creamean et al. 2013). Evidence of cyclic dust deposition in Nebraska has been shown by analysis of loess deposits there (Rousseau et al. 2007).

Management and monitoring recommendations for BSCs in the Great Plains

The most effective tool to limit damage to BSCs is to limit unnecessary physical disturbances, such as excessive trampling by livestock, when the soils are dry (Belnap et al. 2001). The extent of damage is related to seasonality and can have significant effects on BSC stability. Management and maintenance of roads, powerlines, etc. should be scheduled for a time of year when the soils are stable due to being frozen or moist but not saturated (Belnap et al. 2001). Although the simplest management tool would be to limit disturbance during the dry season, that may not always be feasible. Grazing and other activities during the dry season may be more detrimental to BSCs than activities during the moist season (Anderson et al. 1982; Marble and Harper 1989; Eldridge and Kinnell 1997), presumably because BSCs are more brittle during the dry season and slower to recover. Memmott et al. (1998) found that winter use by livestock resulted in a BSC cover similar to rested pastures. They recommended that BSCs needed 4–6 wk of moisture to recover from the trampling by the livestock. In ecosystems where burning is used, burning during the winter when vegetation is dry may be a worthwhile strategy, as late-season fires when vascular plants are dormant but the soil is moist may limit the burn intensity, thus leaving a vegetative mosaic and their BSC understory unscathed (Warren et al. 2015).

Future directions and research priorities

Throughout this manuscript, we have noted where potential exists to conduct meaningful research that can add to the knowledge related to the BSCs of the Great Plains. Specifically, areas needing additional research include 1) refined taxonomy of organisms that participate in the formation of BSCs; 2) improved understanding of ancillary ecological roles played by organisms involved in the formation of BSCs; 3) improved understanding of the universality of BSC organisms, even where their presence remains hidden or disguised by other organisms; and 4) techniques to study airborne organisms (aerobiology), including seasonality of their presence and abundance.

Conclusions

Biological soil crusts, composed of a variety of small to microscopic organisms living at and stabilizing the soil surface, are a common feature of rangelands where aridity and/or disturbance have left patches of bare soil readily available for colonization. Such patches are of variable size and continuity, such that they may be scarcely noticeable in biomes such as the Great Plains. They are, nonetheless, vitally important, contributing to soil stability and the acquisition and cycling of important soil nutrients and moisture. This review is intended to highlight their presence and ecological importance in the Great Plains, as well as to highlight the way they arrive via natural aerobiological processes. It is hoped that this review will help remove BSCs of the Great Plains from their scholarly "blind spot" and foster increased study and understanding of this important but seemingly overlooked ecological feature. Some potential research directions resulting from this review may include refined taxonomy and ecology of BSC organisms in underexplored areas, particularly those previously less or not recognized as BSC habitat, and incorporation of techniques to sample airborne organisms.

Declaration of Competing Interest

None.

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