Chapter 2
How Biological Soil Crusts Became Recognized as a Functional Unit: A Selective History

Otto L. Lange and Jayne Belnap

2.1 Introduction

It is surprising that despite the worldwide distribution and general importance of biological soil crusts (hereafter referred to as biocrusts), scientific recognition and functional analysis of these communities are a relatively young field of science. In this chapter, we sketch the historical lines that led to the recognition of biocrusts as a community with important ecosystem functions. For earlier treatments of relevant aspects of biocrust history, see Friedman and Galun (1974), Cameron and Blank (1966), and Belnap and Lange (2003).

Biocrusts have had multiple names through time. The term "cryptogamic crust" was first coined by Harper (Kleiner and Harper 1972). At that time, there were only two kingdoms, plants and animals, and the dominant organisms in the crust were all classified as nonflowering plants, or cryptogams. However, later taxonomic changes resulted in cyanobacteria and fungi, including lichens, being placed in different kingdoms. As a result, the name "cryptogamic crust" was no longer accurate, and other names were suggested, including microbial crusts (Loope and Gifford 1972), microphytic crusts (West 1990), microbiotic and cryptobiotic crusts (Belnap 1993), and finally, biological soil crusts (e.g., Lange et al. 1992; Belnap and Lange 2001). The name "biological soil crusts" or "biocrusts" has now become universally accepted, as it is taxonomically correct and inclusive of all organisms in the biocrusts, including microfauna. In addition, it clearly separates biological

O.L. Lange (✉)
Julius-von-Sachs-Institut für Biowissenschaften, Universität Würzburg, Julius-von-Sachs-Platz 3, 97082 Würzburg, Germany
e-mail: ollange@botanik.uni-wuerzburg.de

J. Belnap
Southwest Biological Science Center, U.S. Geological Survey, 2290 S. Resource Blvd., Moab, UT, 84532, USA

B. Weber et al. (eds.), *Biological Soil Crusts: An Organizing Principle in Drylands*,
Ecological Studies 226, DOI 10.1007/978-3-319-30214-0_2

crusts from physical or chemical crusts, which is an important distinction, as biocrusts have very different influences on ecosystem properties than other crust types.

2.2 Two Lines that Lead to the Recognition of Biocrusts

The idea of biocrusts as a functional ecological community has come from two main scientific branches: botany and soil science. Botanists have long recognized that multiple organisms colonize the soil surface in the open and often dry areas occurring between vascular plants. Later, after the initial taxonomic and phytosociological descriptions were made, soil scientists and agronomists observed that these surface organisms interacted with soils in ways that changed the soil structure. Below, we trace these two lines from the distant past until 1990, when biocrusts became well-known to scientists and the public, at least in some parts of the world.

2.2.1 The Floristic, Botanic Approach

2.2.1.1 Lichens

Many lichens common to biocrusts worldwide were among those first described for scientific purposes, including *Psora decipiens*, *Toninia sedifolia*, and *Squamarina lentigera*. In most cases, these species were collected from European dryland habitats where they were found growing on top of the soil. Smith and Sowerby (1803) described *Lichen caeruleonigricans*, the "Black and Blue Lichen" (now *Toninia sedifolia*) (Fig. 2.1), as a lichen that "grows on the ground ... and consists of long branched tufted spongy roots, bearing tufted roundish clustered leaves". Stahl, in 1877, depicted the long multibranched rhizinae of *Endocarpon pusillum* (Fig. 2.2). This biocrust lichen became an important milestone for lichenology when he performed the first laboratory synthesis of a green algal lichen with this species.

In the nineteenth century, there was the general impression that arid habitats were very poor in lichens (von Humboldt 1859; Zukal 1896), despite many early reports of desert soil lichens either from early explorers or specialized lichenologists. For example, Carl Per Thunberg (who named many South African plants) collected *Psora decipiens* in 1774 (see Doidge 1950), which he published as *Lichen incarnatus* (Thunberg 1823). Other early publications of soil crust lichens from desert and semidesert regions include Nylander (1878) and Steiner (1895) from the Sahara, Fink (1909) from Arizona, Tuckerman (1882, 1888) from North America, and Müller (1880) from Egypt.

The steppes, semideserts, and deserts of south Russia, with their rich soil lichen floras, appear to be one of the first areas to attract extensive studies of ground

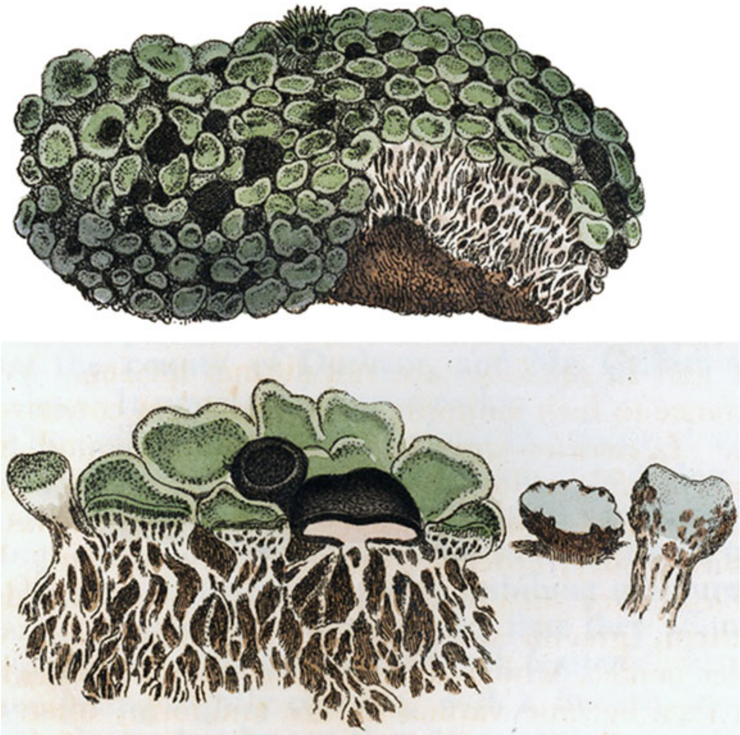

Fig. 2.1 "Black and Blue Lichen", *Toninia sedifolia* [After Smith and Sowerby (1803)]

surface lichens. Peter Simon Pallas (1741–1811), a noted naturalist-explorer who traveled in service of Catherine II of Russia to explore the central Russian provinces, was possibly the first scientist to describe extensive soil lichen covers in the semiarid steppe formation of Kazakhstan (Pallas 1776). He reported that the loamy soil surface was covered by a whitish-gray crust (German "*Rinde*") of *"Lichen tartareum, tinctorium*, *candidum*, *tuberculis*, *atris* Dillenius", most probably a *Diploschistes* sp. He also observed the crust broke into pieces when dry and was growing together with *Tremella terrestris*, a *Collema* sp. These lichens formed a terrestrial community which, without a doubt, we would call a biocrust today. Much later, Tomin (1926) presented possibly the first key for 36 terrestrial lichen species found in the semideserts of southeast Russia. Most of these species had been collected by Keller (1930), who described several types of communities that we today call biocrusts. Keller also published photographs from this site, which was near Pallas' site of 154 years earlier (Fig. 2.3), listing 44 soil lichen species or varieties (e.g., *Collema* sp., *Fulgensia fulgens, Psora decipiens, Squamarina lentigera, Toninia caeruleonigricans,* and *Diploschistes scruposus* var. *terrestris,* which probably is *Diploschistes muscorum* or *Diploschistes diacapsis*. His list also included cyanobacteria (*Microcoleus vaginatus, Scytonema ocellatum, Nostoc commune*) and a moss (*Tortula ruralis*). Keller mentions that growth of these

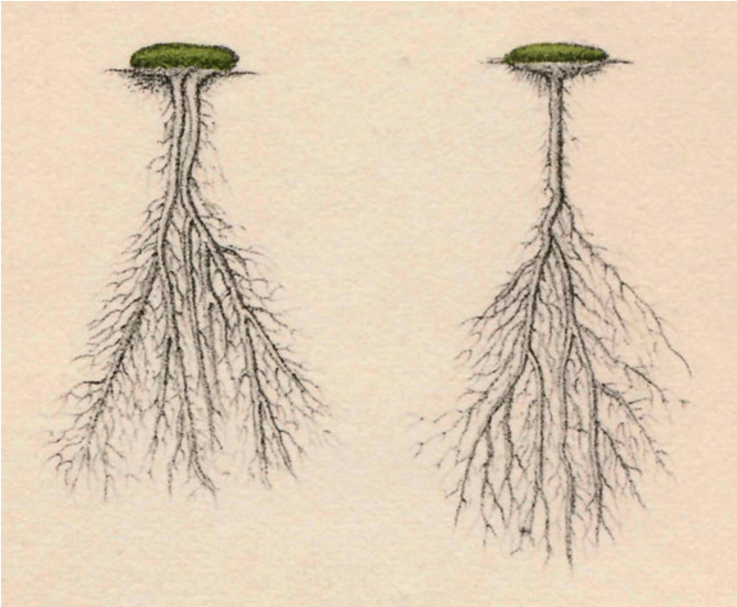

Fig. 2.2 *Endocarpon pusillum* [After Stahl (1877)]

organisms was supported by a dense layer of soil ("*dichte Schicht*"); however, he did not recognize that the organisms themselves were creating this dense layer. Thus, despite having described a true biocrust, Keller thought of this layer as the prerequisite to, rather than the result of, biological activity.

The common coexistence of a group of conspicuous and variously colored terrestrial lichens that included *Psora decipiens*, *Toninia sedifolia*, *Fulgensia* sp., and *Diploschistes* sp., together with *Cladonia* and *Collema* sp. on dry calcareous or gypsum soils, was also recognized early by lichenologists throughout Europe, including Arnold (1868–1897), Tirol; Kaiser (1926) and Gams (1938), Central Germany; and Du Rietz (1925), South Norway. After Braun-Blanquet (1928) had stimulated phytosociological classification of plant communities, lichenologists began defining lichen communities, and the grouping above was named "*Bunte Erdflechten-Gesellschaft*" (i.e., the "colored lichen community"; Reimers 1940, 1950). It is significant that this was one of the very first lichen communities to receive extensive study. For Central Europe, Klement (1955) proposed a general syn-taxonomy of the different types of lichen communities colonizing open soil mainly within local subarid steppe formations within the two main unions of "Toninion coeruleonigricantis" and "Diploschistion terrestris." These lichen communities were often interpreted by him and by others as relicts from late and postglacial times. There continued to be a rich literature in which these or similar lichen communities were described throughout the world [e.g., Europe, Pause (1997); Australia, Rogers (1972); Israel, Galun (1963); Mongolia, Schubert and

Fig. 2.3 Soil vegetation of the lower Ural and Volga Rivers' area [After Keller (1930)]. Dominating "*Diploschistes scruposus* var. *terrestris*" (probably *Diploschistes muscorum* or *Diploschistes diacapsis*)

Klement (1971); Mesopotamia, Schubert (1973)]. Looman (1964) found a striking similarity between the soil lichen communities of the Great Plains in North America and Central Europe with 16 individual species in common.

2.2.1.2 Bryophytes

Similar to lichens, many bryophyte species typically found in biocrusts were taxonomically described in the eighteenth and nineteenth centuries. Several species were included in Linné's *Systema Vegetabilium* (1774), and there are several old reports of bryophytes from dry areas around the word. Examples include the *Conspectus Bryophytorum Orientalum et Arabicorum* by Frey and Kürschner (1991) and Griffith (1849) for Afghanistan, Geheeb (1902) for Syria, and Lorentz (1867) for Egypt and Sinai. Joseph Dalton Hooker collected four Antarctic moss species in 1843–1847 when he participated in James Clark Ross' expedition (Wilson and Hooker 1847), and Skottsberg (1905) was the first to describe moss-dominated tundra of the maritime Antarctic Peninsula.

By the first half of the twentieth century, there were many descriptions and vegetation analyses of habitats with coexisting soil lichens and bryophytes that today would be called biocrusts. In Europe, for example, this includes open patches in local steppe formations where the ground cover was described as communities of "colored soil lichens" growing together with mosses and liverworts on lime or gypsum soil (Du Rietz 1925; Kaiser 1930; Stodiek 1937; Reimers 1940; Bornkamm 1958; Marstaller 1971). There are even phytosociological units defined and named in which bryophytes and lichens are combined, as for instance the "Caloplaca fulgens–Tortella inclinata sinusia" (Zólyomi 1987). In the last decades, our knowledge of bryophytes of arid areas, including their distribution, sociology, and ecology, has considerably improved [e.g., Afghanistan (Frey and Kürschner 2009), Jordan (Frey and Kürschner 1995), and Saudi-Arabia (Frey and Kürschner 1987)]. In the Judean Desert, Frey et al. (1990) and Frey and Kürschner (1990) observed the close connection between bryophyte communities and the colored lichen communities; they also describe cyanobacteria in the loess soil.

Despite the very early taxonomic description of moss and liverwort communities on dry ground, the older literature does not mention these communities as being part of what we today call a biocrust community. There was also no demonstration or observation of these communities consolidating or protecting the soil surface. This may be because in many hot and temperate arid regions, bryophytes, mosses, and liverworts are generally sparse or even absent, whereas cyanobacteria and lichens conspicuously dominate the biocrusts. According to Scott (1982) and many other authors, the earliest stages of biocrust formation in drylands is the stabilization of the soil surface by filamentous cyanobacteria, followed by colonization of lichens and bryophytes. In contrast, cold-polar area biocrusts are often dominated by mosses that can even create continuous carpets. Temporarily wet areas in the continental Antarctic are typically covered by bryophyte flushes, as described by Rudolph (1963) for Cape Hallett in Victoria Land.

2.2.1.3 Cyanobacteria and Green Algae

Ehrenberg (1854) was one of the first to extensively analyze and depict microorganisms in different kinds of soil, and he identified many types of algae. At that time, the term "algae" included both blue–green (cyanobacteria) and green algae. The differentiation between these groups occurred early in the nineteenth century. In 1874, Sachs coined the term "Cyanophyceae" for blue–green algae, and in 1977, Stanier and Cohen-Bazire proposed the term "cyanobacteria" to be used to differentiate between these prokaryote organisms and the eukaryotic green algae. Despite the early separation of these two groups, older studies continued to refer to them collectively as "algae." Whereas most later studies separate them, phycologists still accept the term "algae" when referring to both groups. Therefore, in our discussion below, we use the terms algae, green algae, blue–green algae, or cyanobacteria, depending on the term used in the study being cited.

The terrestrial species of the genus *Nostoc*, typically occurring in most biocrust communities worldwide, were most likely the first cyanobacteria to attract the interest of plant scientists, as well as the public. During the times of Paracelsus (1493–1541), a heavenly, divine, or devilish origin was ascribed to the frightening gelatinous "Nostoch" colonies that suddenly appeared on the surface of wet soil. These colonies were used for medical purposes (Schmid 1951, see monograph by Mollenhauer 1985–1986). More than 280 years ago, the Italian botanist Micheli depicted a *Nostoc* thallus (Fig. 2.4): "*Linckia terrestris, gelatinosa, membranacea, vulgatissima, ex pallida et virescente fulva*" in his 1729 publication. No one less than Johann Wolfgang von Goethe (1892) provided an early description of *Nostoc* growing on soil (see Schmid 1942). He reported in a handwritten journal entry that in 1785 he had found a large amount of gelatinous lobes ("*gallertartige Läppchen*") on the ground in a sandy place after rain. He kept the material in water, and with a magnifying glass he recognized rows of spheres ("*Reihen von Kugeln*"), which he compared with Micheli's *Linckia*. Common English names show the anxiety of people about these strange *Nostoc* colonies on soil, calling them fairies' or witches' butter, star-slime, star jelly, fallen stars, or will-o'-the-wisp. In Goethe's tragedy Faust II (line 11741/42), Mephistopheles alludes to the captured will-o'-the-wisp ("*Irrlicht*") as "disgusting gelatinous dirt" ("*ekler Gallert-Quark*"). Linné ("*Systema Vegetabilium*", 1774) used the name *Tremella Nostoc* within his group "Cryptogamia Algae," and Vaucher (1803) finally defined the genus name *Nostoc*. One hundred years after Micheli, a painting by Turpin (1838) depicts a *Nostoc* colony (Fig. 2.5).

In the article "On a substance known as 'Australian Caoutchouc'", Thiselton Dyer (1872) reports a strange material resembling elastic bitumen that was found on the ground of an open, sandy place in South Australia. It was thought to be the "mineral" coorongite or gamboge, a petroleum or asphalt-type product, some kind of gum, or a plant secretion of some type. However, microscopic analysis showed diatoms as well as cellular structures that were most probably derived from drying gelatinous algae, all intermingled with sand grains (see Fritsch 1907). Thus, this

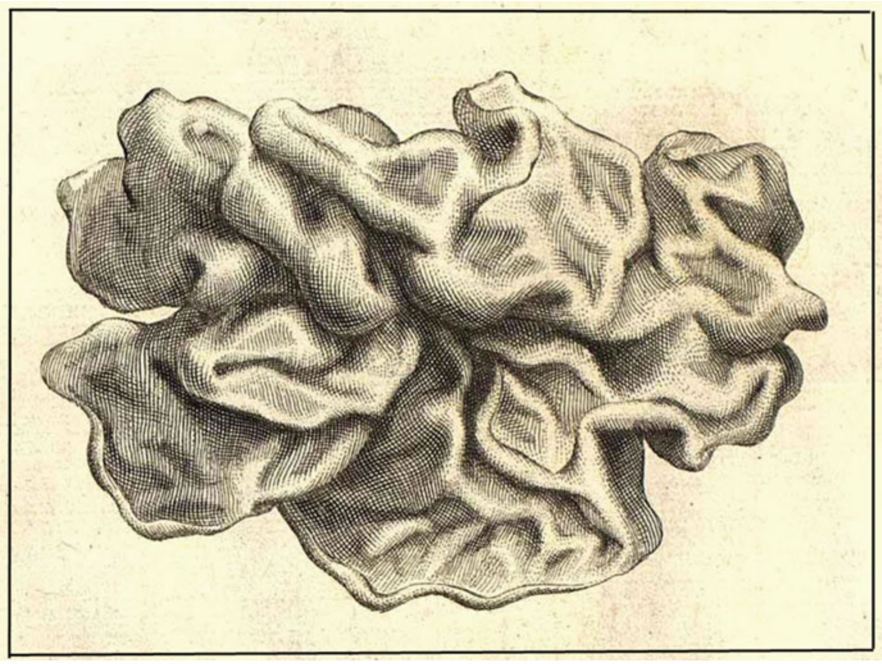

Fig. 2.4 "*Linckia terrestris, gelatinosa,* etc.", *Nostoc* species [After Micheli (1729)]

would be an early recognition of a cyanobacterial soil crust according to our present terminology. Takyr soils were described for deserts and semideserts of Central Asia (Bolyshev and Yevdokimova 1944; Bolyshev 1952). These are formed in flat depressions which are filled with water during heavy rain and dry out during summer. These are often covered and consolidated by soil algae, mainly filamentous cyanobacteria.

There are many reports in the first half of the twentieth century regarding the diversity, life history, and habitat conditions of algae in different soils and locations. These include North America (e.g., Collins 1909; Martin 1939), England (Bristol Roach 1927), Australia (Phillipson 1935), the Sahara (Killian and Fehér 1939), the Negev (Friedmann et al. 1967), and many others. There is a general and extensive treatment "Soil Algae" (in Russian) by Gollerbakh and Shtina (1969), in which more than 800 relevant publications are cited (see also Cameron 1974).

2.2.2 The Soil/Agronomy Scientific Approach

The presence of naturally occurring, nonbiological soil crusts has long been observed by soil scientists and others. In the 1820s in interior Australia, the occurrence of "hard bare soils along the Murrumbidgee River" was documented

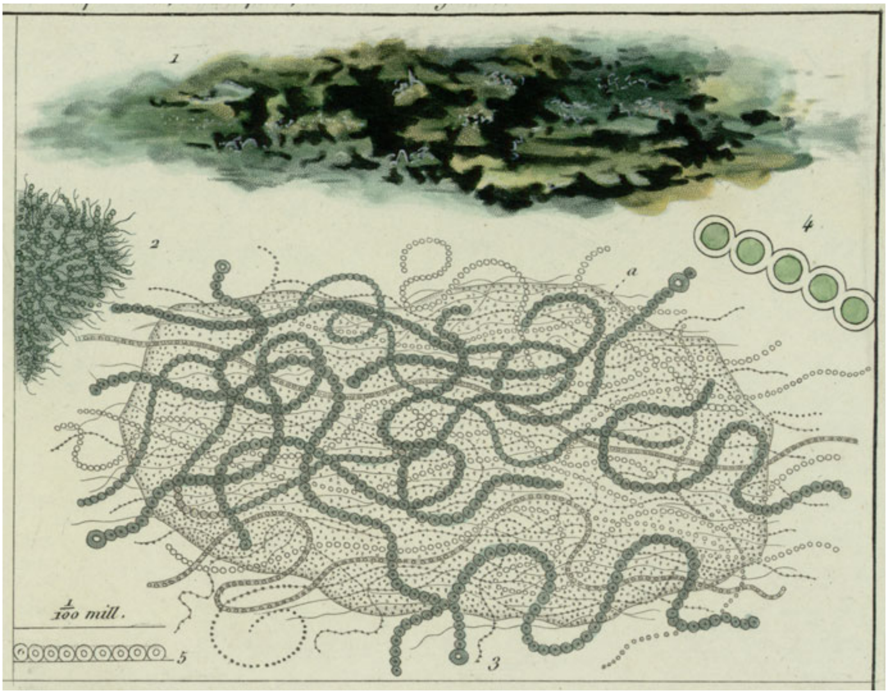

Fig. 2.5 *Nostoc thermalis* [After Turpin (1838)]

by Charles Sturt, an explorer [cited in Chartres (1992)]. Studies of these hardened surfaces in semiarid and arid landscapes began in earnest during the 1900s, and it was determined they were mostly physical and/or chemical crusts. Physical crusts are formed by the disruption of soil aggregates by raindrop or compressional forces (e.g., hoof action). When water pools on the soil surface, the fine soil particles are suspended and upon drying, adhere together to form a hard physical crust. Chemical crusts are formed by the deposition of salts or other compounds on the soil surface when soils dry (e.g., Blanck et al. 1926; Schiff and Yoder 1941). Both physical and chemical crusts increase runoff and erosion (Dudley and Kelly 1939). Early in the study of physical and chemical crusts, some soil scientists noted that algae often grew on top of, inside of, or in place of these nonbiological crusts (e.g., Booth 1941; Fletcher and Martin 1948). These authors noted that after rains, soil surfaces often turn green, which alerted them to the presence of the algae. Fletcher and Martin also observed that if one picked up a piece of these crusts (Fig. 2.6), the soil held together and the underside of "these algae-impregnated crusts had a fuzzy appearance with sand grains adhering to what proved to be fungus mycelium". Both Booth (1941) and Fletcher and Martin (1948) went on to test how the presence of the algae affected local hydrology, and Fletcher and Martin also measured their influence on soil texture, organic matter, and nitrogen. In contrast to physical and chemical crusts, they found the algae decreased runoff and soil erosion and increased the silt,

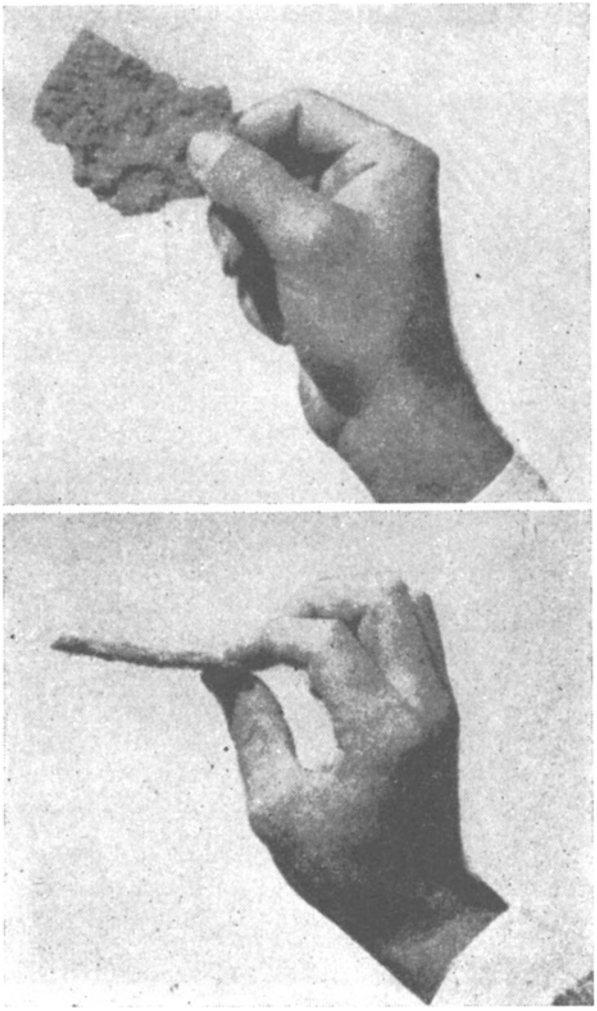

Fig. 2.6 A piece of rain crust from the soil's surface, Arizona [After Fletcher and Martin (1948)]

clay, carbon, and nitrogen in the soil. This was, therefore, probably the first instance of soil scientists publishing on the presence of algal soil crusts and their influence on ecological processes.

Around the same time as the research into physical and chemical crusts began, agronomists noticed that soil algae could stimulate the growth of vascular plants by increasing soil N (therefore, it was actually cyanobacteria they were investigating). Breazeale (1929) was one of the first agronomists to intentionally introduce cyanobacteria onto the surface of a crop soil; in this case, he inoculated pots in which Valencia oranges were growing. He found this inoculation increased plant height, plant leaf length, and healthy plant color. Other early work showed the value of cyanobacteria in stimulating rice production (De 1939) and other crops. Since this time, many studies have been conducted on this topic.

2.3 Biological Soil Crusts as a Functional Ecological Unit

Perhaps one of the earliest conceptualizations of the ability of biocrusts to consolidate soil was reported in 1861 by E.F. Klinsmann, a medical doctor. Earlier in this publication, he notes that in 1828, and again at later times, he observed a thick carpet of mixed lichen and algal threads on top and throughout the surface sands of dunes at the Baltic Sea near Gdansk, Poland. His material was sent to F.T. Kützing, who identified the dominant organism as an alga *Stereonema chthonoblastes* A. Br. (Kützing 1849), which was later determined to be a lichen (Kupffer 1924). Its name was changed to *Lecidea uliginosa* var. *chthonoblastes* (A. Braun) Erichsen and then again to *Placynthiella uliginosa* (Schrad.) Coppins & James. However, the description of threads being present in the samples of Klinsmann (1861) makes it likely that cyanobacteria and soil fungi were also present in the material collected. He noted this carpet stabilized blowing sand and facilitated the colonization of other species, starting first with the moss *Ceratodon purpureus* and other lichens and then later followed by vascular plants. The author even discussed the possibility of propagating and spreading this "alga" for dune stabilization, noting it was cheaper than planting grasses which was done at that time.

Subsequent early research showed soil algal growth was an important first step in increasing the fertility and stability of the soils, thus likely enhancing the recolonization of other organisms. One of the first places this was observed was following the volcanic eruption of Mount Krakatoa (Treub 1888), where the disturbed ground was first covered by a layer of blue–green algae before other species colonized the site. Fritsch (1907, 1922) developed an early conceptual model of terrestrial algae and their ecological relevance. He distinguished between subterranean and surface communities, describing the species composition and site morphology for different climatic regimes. His conclusion is very similar to a modern interpretation of algal soil crusts: "The . . . consideration will have shown that the terrestrial Alga possess an equipment which suits it admirably to be a coloniser of inhospitable substrates. Here its small moisture-requirements can probably often be better met than those of any other group of plants. As colonisers these Algae are of importance in three ways: they play a rôle in the erosion of exposed surfaces, by their decay they afford the first available supplies of humus, and especially the more mucilaginous forms afford a moisture-retaining substratum... On mobile substrata the filamentous forms are also often of great importance in binding the loose particles together" (Fritsch 1922, p. 232). In later publications (e.g., Fritsch and Haines 1923), the authors conducted field and laboratory experiments to examine the moisture relations of these organisms.

Use of lichens and mosses for sand stabilization was also reported later for several different areas of the world. Possibly one of the first examples of mosses affecting soil function was noted by Moore (1931), when he observed them, along with lichens, consolidating moving sand on the British Isle of Man (Irish Sea) and preparing the way for the subsequent colonizers. Leach (1931) studied the ability of mosses like *Polytrichum piliferum* and *Polytrichum juniperinum* to act as pioneers on sand habitats in England, analyzing their soil-binding qualities with laboratory experiments. In the USA, Martin and Waksman (1940) showed that soil algae increased soil aggregation and decreased erosion.

In 1955, Vogel provided the decisive insight that the condensed layer at the soil surface, which he observed in South African deserts and which we today call biocrusts, was created by organisms such as lichens and algae. He published what was possibly the first vertical profile of a biocrust, describing it in German as "*Bodenkruste*" or soil crust (Fig. 2.7). In his illustration, a dust film is shown at the surface, below which lies a layer with *Schizothrix* sp. (cyanobacteria), followed by a layer of fungal hyphae mainly belonging to soil lichens. He provided a description of how these organisms are interwoven with the soil particles, gluing them together into compact layers. The text notes that when broken, fibers with soil particles can be seen dangling from the biocrust pieces. The nitrogen-fixing ability of the soil cyanobacteria is discussed as well. Vogel also posited that these "*Bodenkrusten*" are of geological importance by preventing soil erosion over the hundreds of square kilometers where he observed them. Thus, with this study, Vogel described 60 years ago most of the important ecological roles we ascribe to biocrusts today.

Studies of the ecological roles of biocrusts began intensifying in the late 1950s and 1960s. For instance, Shields et al. (1957), Tchan (1959), Shields and Durrell (1964), Bond and Harris (1964), Avnimelech and Nevo (1964), Rogers and Lange (1966), Mayland et al. (1966), and Granhall and Henriksson (1969) showed that biocrusts stabilize soils, affect hydrological cycles, and enhance soil nitrogen content. A very early photograph of typical biocrusts from Arizona Upland Desert (Fig. 2.8) was published by R. E. Cameron (1958) in his M.S. thesis. Prompted by finding ways to detect life in extraterrestrial environments, he and others conducted extensive investigations in the distribution and abundance of biocrusts in deserts throughout the world (e.g., Cameron and Blank 1966; Cameron 1969). Cameron and Devaney (1970) also described the successional sequence of soil surface organisms in the Antarctic dry valleys, starting with cyanobacteria and algae, followed by lichens and ending with mosses. Ugolini (1966) observed that initial soil formation exposed after the retreat of an Alaskan glacier occurred under a "mossy crust". Worley (1973) found three types of "Black Crust" in the Upper Glacier Bay, Alaska, that covered and penetrated into the recently deglaciated soils, observing they protected the soil from erosion. These mats contained the leafy liverwort *Lophozia badensis*, mosses, lichens, and cyanobacteria in differing proportions.

A great deal of work was done on biocrusts in the western USA in the 1970s by scientists working independently or with the International Biome Program. They documented the controls on distribution and many ecological roles of biocrusts, including an influence on nitrogen cycling, soil aggregation, and soil moisture

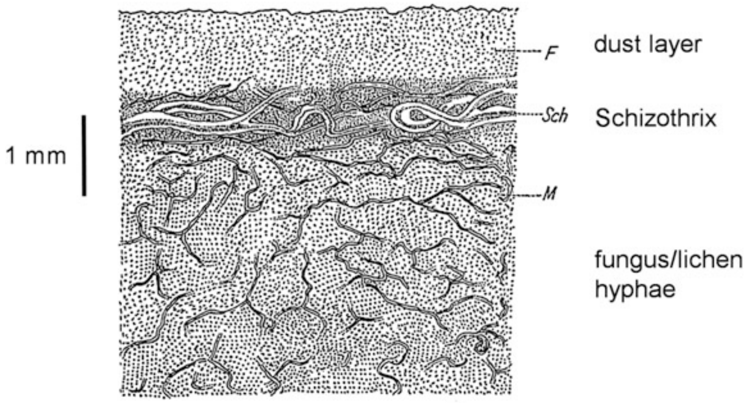

Fig. 2.7 Profile of the uppermost millimeters of soil crust, Knersvlakte, South Africa [After Vogel (1955)]

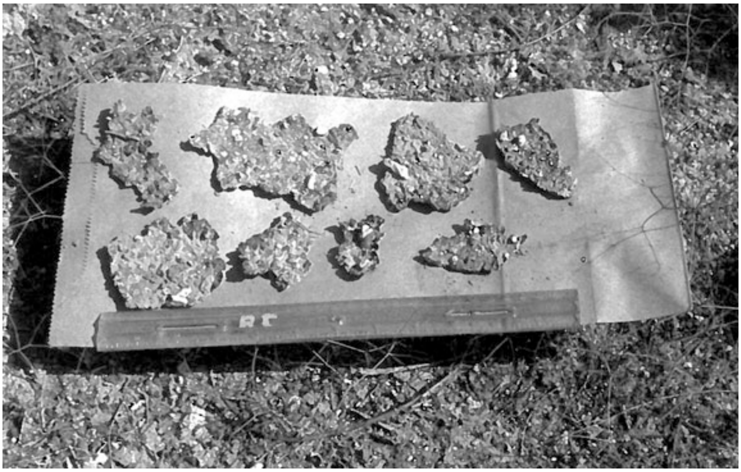

Fig. 2.8 Soil algal and lichen crusts, Arizona [After Cameron (1959), by courtesy of University of Arizona]. See also Cameron and Blank (1966)

(e.g., Faust 1971; Kleiner and Harper 1972, 1977; Bailey et al. 1973; Marathe 1972; Loope and Gifford 1972; West and Skujins 1977; Rychert et al. 1978).

The pace of studies increased even more rapidly during the 1980s and early 1990s, especially in Australia, Israel, and the western USA (e.g., Shachak and Steinberger 1980; Graetz and Tongway 1986; Rogers 1989). Research addressed all aspects of the ecological functions of biocrusts, ranging from their contributions to soil fertility, including carbon and nitrogen fixation, their ability to stabilize soils, their response to and recovery from fire and surface disturbance, and their effects on vascular plant establishment and growth. Sufficient research was done to produce at least six review articles within 6 years (Harper and Marble 1988; Dunne 1989;

Isichei 1990; West 1990a, b; Metting 1991; Johansen 1993). These efforts culminated in the first symposium on biocrusts held at the joint American Bryological and Lichenological and Ecological Society of America meetings in San Antonio, Texas, in 1991 (St. Clair and Johansen 1993). This marked a turning point in the acceptance by biologists and ecologists alike of the importance of the biocrust communities in the structure and function of dryland ecosystems. The first compendium volume on biocrust research, "Biological Soil Crusts: Structure, Function and Management," was published in 2001 and reprinted in 2003 (Belnap and Lange 2001, 2003). Since then, there have been two international symposia on Biological Soil Crusts (in Germany and Spain), and the number of researchers involved in this field and the number of papers published have increased exponentially.

Acknowledgments The authors are very grateful to the following colleagues for their valuable information and for help with historical hints: Burkhard Büdel (Kaiserslautern), Allan Green (Hamilton/Madrid), Thorsten Lumbsch (Chicago), Rolf Marstaller (Jena), Thomas Peer (Salzburg), Regine Stordeur (Halle), Stefan Vogel (Wien), and Gerhard Wagenitz (Göttingen). Special thanks are to Wilma Kreßmann (Würzburg): our work would not have been possible without her adept and resourceful literature search. Ulrike Lange is thanked for her help with Russian translations. JB was supported by the US Geological Survey Ecosystems and Climate and Land Use programs. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

References

Arnold F (1868–1897) Lichenologische Ausflüge in Tirol. Part I–XXX. Verh Zool Bot Ges Wien 18–48

Avnimelech Y, Nevo Z (1964) Biological clogging of sands. Soil Sci 98:222–226

Bailey D, Mazurak AP, Rosowski JR (1973) Aggregation of soil particles by algae. J Phycol 9:99–101

Belnap J (1993) Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. Great Basin Nat 53:89–95

Belnap J, Lange OL (2001) Biological soil crusts: structure, function, and management, vol 150, 1st edn, Ecological studies. Springer, Heidelberg, 503 p

Belnap J, Lange OL (2003) Biological soil crusts: structure, function, and management, vol 150, 2nd edn, Ecological studies. Springer, Heidelberg, 503 p

Blanck E, Passarge S, Rieser A (1926) Über Krustenböden und Krustenbildung wie auch Roterden, insbesondere ein Beitrag zur Kenntnis der Bodenbildung Palästinas. Chem Erde 2:348–395

Bolyshev NN (1952) The origin and evolution of takyr soils (in Russian). Pochvovedeniye 5:403–417

Bolyshev NN, Yevdokimova TH (1944) On the nature of the crust of takyrs (in Russian). Pochvovedeniye 7–8

Bond RD, Harris JR (1964) The influence of the microflora on physical properties of soils. I. Effects associated with filamentous algae and fungi. Aust J Soil Res 2:111–122

Booth WE (1941) Algae as pioneers in plant succession and their importance in erosion control. Ecology 22:38–46

Bornkamm R (1958) Die Bunte-Erdflechten-Gesellschaft im südwestlichen Harzvorlande. Ber Deut Bot Ges 71:253–270

Braun-Blanquet J (1928) Pflanzensoziologie. Springer, Berlin
Breazeale JM (1929) Algae and their effect upon the growth of citrus seedlings. Master thesis, University of Arizona, pp 41
Bristol Roach BM (1927) On the algae of some normal English soils. J Agric Sci 17:563–588
Cameron RE (1958) Fixation of nitrogen by algae and associated organisms in semi-arid soils: identification and characterization of soil organisms. M.S. thesis, University of Arizon, Tucson
Cameron RE (1969) Abundance of microflora in soils of desert regions. Calif. Institute of Technology, National Aeronautics and Space Administration, Jet Propulsion Laboratory. Pasadena Technical Report 32-7378, pp 1–16
Cameron RE (1974) A review of the Russian book 'Soil Algae' by M. M. Gollerbakh and E. A. Shtina, including a translation of the bibliography. Phycologia 13:109–120
Cameron RE, Blank GB (1966) Desert algae: soil crusts and diaphanous substrata as algal habitats. Pasadena, California, Jet Propulsion Laboratory, California Institute of Technology, Technical report no. 32–971
Cameron RE, Devaney JR (1970) Antarctic soil algal crusts: scanning electron and optical microscope study. Trans Am Microsc Soc 89:264–273
Chartres CJ (1992) Soil crusting in Australia. In: Summer ME, Stewart BA (eds) Soil crusting: chemical and physical processes. Lewis Publishers, Boca Raton, pp 339–365
Collins FS (1909) The green algae of North America. Tufts college studies, vol II. Tufts College Press, Mass
De PK (1939) The role of blue-green algae in nitrogen-fixing in rice fields. Proc R Soc London Ser B 127:121–139
Doidge EM (1950) The South African fungi and lichens to the end of 1945. Bothalia 5:1–1094
Du Rietz GE (1925) Zur Kenntnis der flechtenreichen Zwergstrauchheiden im kontinentalen Südnorwegen. In: Svenska Växtsociologiska Sällskapets Handlingar IV. Lundequist, Uppsala, pp 1–80
Dudley FL, Kelly LL (1939) Effect of soil type, slope, and surface conditions on intake of water. Nebr Agric Exp Stn Res Bull 112:1–15
Dunne J (1989) Cryptogamic soil crusts in arid ecosystems. Rangelands 11:180–182
Ehrenberg CG (1854) Zur Mikrogeologie. Leopold Voss, Leipzig
Faust WF (1971) Blue-green algal effects on some hydrologic processes at the soil surface. Hydrology and water resources in Arizona and the Southwest. Proceedings of the 1971 meetings, Arizona Section. American Water Resources Association, and the Hydrology Section, Tempe, Arizona Academy Science, pp 99–105
Fink B (1909) The composition of a desert lichen flora. Mycologia 1:87–103
Fletcher JE, Martin WP (1948) Some effects of algae and molds in the rain-crust of desert soils. Ecology 29:95–100
Frey W, Kürschner H (1987) A desert bryophyte synusia from the Jabal Tuwayq mountain systems (Central Saudi Arabia) with the description of two new Crossidium species (Pottiaceae). Nova Hedwigia 45:119–136
Frey W, Kürschner H (1990) Das Fossobronio-Gigaspermetum mouretii ass. nov. in der Judäischen Wüste. 1. Verbreitung und Soziologie. Cryptogamic Bot 2:56–63
Frey W, Kürschner H (1991) Conspectus bryophytorum orientalum et arabicorum. An annotated catalogue of the bryophyes of southwest Asia, vol 39, Bryophytorum bibliotheca. Cramer, Berlin, pp 1–181
Frey W, Kürschner H (1995) Bryosoziologische Untersuchungen in Jordanien. 3. Lebensstrategieanalyse der terrestrischen und epilithischen Mossgesellschften. Fragm Flor Geobot 40:491–511
Frey W, Kürschner H (2009) New records of brophytes from Afghanistan—with a note on the bryological exploration of the country. Nova Hedwigia 88:503–511
Frey W, Herrnstadt I, Kürschner H (1990) Verberitung und Soziologie terrestrischer Bryophytengesellschaften in der Judäischen Wüste. Phytocoenologia 19:233–256

Friedman EI, Galun M (1974) Desert algae, lichens, and fungi. In: Brown GW Jr (ed) Desert biology, vol 2. Academic Press, New York, pp 165–212
Friedmann I, Lipkin Y, Ocampo-Paus R (1967) Desert algae of the Negev (Israel). Phycologia 6:185–195
Fritsch FE (1907) The rôle of algae growth in the colonization of new ground and in the determination of scenery. Geogr J 30:531–548
Fritsch FE (1922) The terrestrial algae. J Ecol 10:220–237
Fritsch FE, Haines FM (1923) The moisture-relations of terrestrial algae II. Ann Bot 37:684–728
Galun M (1963) Autecological and synecological observations on lichens of the Negev, Israel. Isr J Bot 12:179–187
Gams H (1938) Über einige flechtenreiche Trockenrasen Mitteldeutschlands. Hercynia 1 Heft 2:277–284
Geheeb A (1902) Beitrag zur Moosflora von Syrien. Allg Bot Zeitschr 8:42–44
Goethe JW (1892) Einige Bemerkungen über sogenannte Tremella ("Some remarks about so-called Tremella"). In: Großherzogin Sophie von Sachsen (ed) Goethes Werke. II. Abt., 7. Band, Hermann Bölau, Weimar, pp 355–356
Gollerbakh MM, Shtina EA (1969) Soil algae (Russian). Nauka Publishing House, Leningrad, 228 pp
Graetz RD, Tongway DJ (1986) Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semi-arid chenopod shrubland. Aust J Ecol 11:347–360
Granhall U, Henriksson E (1969) Nitrogen-fixing blue-green algae in Swedish soils. Oikos 20:175–178
Griffith W (1849) Notulae ad planta asiaticas, part II. In: On the higher cryptogamous plants. C. A. Serrao, Calcutta
Harper KT, Marble JR (1988) A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller PT (ed) Vegetation science applications for rangeland analysis and management. Kluwer Academic Publishers, Dordrecht, pp 135–169
Isichei AO (1990) The role of algae and cyanobacteria in arid lands. A review. Arid Soil Res Rehabil 4:1–17
Johansen JR (1993) Cryptogamic crusts of semiarid and arid lands of North America. J Phycol 29:140–147
Kaiser E (1926) Die Pflanzenwelt des Hennebergisch-Fränkischen Muschelkalkgebietes. Fedde Rep Spec Nov Regni Veg Beih 44:1–280
Kaiser E (1930) Die Steppenheiden in Thüringen und Franken zwishen Saale und Main. Sonderschriften der Akademie gemeinnütziger Wiss. zu Erfurt. Carl Villaret, Erfurt
Keller B (1930) Die Erdflechten und Cyanophyceen am unteren Lauf der Wolga und des Ural. In: Karsten G (ed) Vegetationsbilder, Reihe 20, Heft 8. Fischer, Jena
Killian C, Fehér D (1939) Recherches sur la microbiologie des sols désertiques. Paul Lechevallier, Paris
Kleiner EF, Harper KT (1972) Environment and community organization in grasslands of Canyonlands National Park. Ecology 53:299–309
Kleiner EF, Harper KT (1977) Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. J Range Manag 30:202–205
Klement O (1955) Prodromus der mitteleuropäischen Flechtengesellschaften. Fedde Rep Spec Nov Regni Veg Beih 135:5–194
Klinsmann EF (1861) Ueber Bildung und Entstehung von Humus and Festlegung des fliegenden Dünensandes durch Stereonema Chthonoblastus Al. Br. Schrifen Physik.-Oekon. Ges. Koenigsberg Preussen 2:127–130
Kupffer KR (1924) Steronema chthonoblastes, eine lebende Urflechte. Korrespondenzbl. Naturf Ver Riga 58:111–112
Kützing FT (1849) Species algarum. F.A. Brockhaus, Leipzig

Lange OL, Kidron GJ, Büdel B, Meyer A, Kilian E, Abeliovich A (1992) Taxonomic composition and photosynthetic characteristics of the "biological soil crusts" covering sand dunes in the western Negev Desert. Funct Ecol 6:519–527
Leach W (1931) On the importance of some mosses as pioneers on unstable soils. J Ecol 19:98–102
Linné C (1774) Systema vegetabilium—secundum—classes ordines—genera species—cum characteribus et differentiis. Adornata Murray JA. Jo. Crist. Dieterich, Gottingae, Gothae
Looman J (1964) The distribution of some lichen communities in the prairie provinces and adjacent parts of the great plains. Bryologist 67:209–224
Loope WL, Gifford GF (1972) Influence of a soil microfloral crust on select properties of soils under pinyon-juniper in southeastern Utah. J Soil Water Conserv 27:164–167
Lorentz PG (1867) Über die Moose, die Hr. Ehrenberg in den Jahren 1820–1826 in Aegypten, der Sinaihalbinsel und Syrien gesammelt. Abh Königl Akad Wiss 1867:1–57
Marathe KV (1972) Role of some blue-green algae in soil aggregation. In: Desikachary TV (ed) Taxonomy and biology of blue-green algae. Bangalore Press, Bangalore, pp 328–331
Marstaller R (1971) Zur Kenntnis der Gesellschaften des Toninion-Verbandes im Unstruttal zwischen Nebra und Artern sowie im Kyffhäusergebirge. Hercynia 8:34–51
Martin TL (1939) The occurrence of algae in some virgin Utah soils. Soil Sci Soc Am Proc 4:249–250
Martin JP, Waksman SA (1940) Influence of microorganisms on soil aggregation and erosion. Soil Sci 150:29–47
Mayland HF, MacIntosh TH, Fuller WH (1966) Fixation of isotopic nitrogen on a semiarid soil by algal crust organisms. Soil Sci Soc Am Proc 30:56–60
Metting B (1991) Biological surface features of semiarid lands and deserts. In: Skujins J (ed) Semiarid lands and deserts: soil resource and reclamation. Marcel Dekker, New York, pp 257–293
Micheli PA (1729) Nova plantarum genera—iuxta Tournefortii methodum disposita. Paperini, Florenz (Reprint 1976, The Richmond Publishing Co. Ltd., Richmond, Surrey)
Mollenhauer D (1985–1986) Blaualgen der Gattung Nostoc—ihre Rolle in Forschung und Wissenschaftsgeschichte I–IV. Natur und Museum 115:305–334, 369–379, 116:43–59, 104–120
Moore EJ (1931) The ecology of the Ayreland of Bride, Isle of Man. J Ecol 19:115–136
Müller (Argoviensis) J (1880) Les lichens d'Egypte. Revue Mycologique. Toulouse 1879:6–21
Nylander W (1878) Symbolae quaedam ad lichenographiam Sahariensem. Flora 61:337–345
Pallas PS (1776) Reise durch verschiedene Provinzen des Russischen Reiches in einem ausführlichen Auszuge. Johann Georg Fleischer, Frankfurt, Leipzig
Pause SM (1997) Die Erdflechtenvegetation Nordwestdeutschlands und einiger Randgebiete. Bibl Lichenol 66:1–222
Phillipson J (1935) Some algae of Victorian soils. Proc Roy Soc Victoria 47:262–287
Reimers H (1940) Bemerkenswerte Moos- und Flechtengesellschaften auf Zechstein-Gips am Südrand des Kyffhäuser und des Harzes. Hedwigia 79:61–174
Reimers H (1950) Beiträge zur Kenntis der Bunten Erdflechten-Gesellschaft. I. Zur Systematik und Verbreitung der Charakterflechten der Gesellschaft besonders im Harzvorland. Ber Deut Bot Ges 68:147–156
Rogers RW (1972) Soil surface lichens in arid and subarid south-eastern Australia III. Aust J Bot 20:301–316
Rogers RW (1989) Blue-green algae in southern Australian rangeland soils. Aust Range J 11:67–73
Rogers RW, Lange RT (1966) Nitrogen fixation by lichens of arid soil crusts. Nature 209:96–97
Rudolph ED (1963) Vegetation of Hallett station area, Victoria Land, Antarctica. Ecology 44:585–586

Rychert R, Skujins J, Sorenson D, Porcella D (1978) Nitrogen fixation by lichens and free-living microorganisms in deserts. In: West NE, Skujins J (eds) Nitrogen in desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg, pp 20–30

Sachs J (1874) Lehrbuch der Botanik. Wilhelm Engelmann, Leipzig

Schiff L, Yoder R (1941) Dynamics of water erosion on land surfaces. Trans Am Geophys Union 1941(2):287–298

Schmid G (1942) Goethe über Tremella. Werkst. Burg Giebichenstein, Halle

Schmid G (1951) Irrlicht und Sternschnuppen. Viermonatsschr NF Jb Goethe-Ges 13:268–289

Schubert R (1973) Notizen zur Flechtenflora des nördlichen Mesopotamien (Irak). Feddes Repertorium 83:585–589

Schubert R, Klement O (1971) Beitrag zur Flechtenflora der Mongolischen Volksrepublik. Feddes Repertorium 82:187

Scott GM (1982) Desert bryophytes. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 105–122

Shachak M, Steinberger Y (1980) An algae-desert snail food chain: energy flow and soil turnover. Oecologia 46:402–411

Shields LM, Durrell LW (1964) Algae in relation to soil fertility. Bot Rev 30:92–128

Shields LM, Mitchell C, Drouet F (1957) Alga- and lichen-stabilized surface crusts as soil nitrogen sources. Am J Bot 44:489–498

Skottsberg C (1905) Some remarks upon the geographical distribution of vegetation in the colder southern hemisphere. Ymer 25:402–427

Smith JE, Sowerby J (1803) English botany; or, coloured figures of British plants, vol 16, no. 1139, London

St. Clair LL, Johansen JR (1993) Introduction to the symposium on soil crust communities. Great Basin Nat 53:1–4

Stahl E (1877) Beiträge zur Entwicklungsgeschichte der Flechten II, Über die Bedeutung der Hymenialgonidien. Arthur Felix, Leipzig

Stanier RY, Cohen-Bazire G (1977) Phototrophic prokaryotes: the cyanobacteria. Ann Rev Microbiol 31:225–274

Steiner J (1895) Ein Beitrag zur Flechtenflora der Sahara. Sitzungsber Kaiserl Akad Wiss Wien Math-naturwiss Kl 104:382–393

Stodiek E (1937) Soziologische und ökologische Untersuchungen an den xerotopen Moosen und Flechten des Muschelkalkes in der Umgebung von Jena. Fedde Rep Spec Nov Regni Veg Beih 99:1–46

Tchan YT (1959) Study of soil algae III. Bioassay of soil fertility by algae. Plant Soil 10:220–232

Thiselton Dyer WT (1872) On a substance known as “Australian caoutchouc”. J Bot 1:103–106, New Series

Thunberg CP (1823) Flora capensis. Cotta, Stuttgard

Tomin, MP (1926) Über die Bodenflechten aus den Halbwüsten von Süd-Ost-Russland (translated from Russia). In: Keller BA (ed) Die Pflanzenwelt der russischen Steppen, Halbwüsten und Wüsten (translated from Russia), vol 2. Voronezh, pp 19–31

Treub M (1888) Notice sur la nouvelle flora de Krakatau. Ann Jard Bot Buitenzorg 7:35–38

Tuckerman E (1882) A synopsis of the North American lichens 1. Cassino, Boston

Tuckerman E (1888) A synopsis of the North American lichens 2. Anthony & Sons, New Bedford, Mass

Turpin PJF (1838) Étude microscopique, comparée, de la Barégine de M. Longchamp, observée dans les eaux thermales sulfureuses de Barége, et de la Barégine recueillie dans les eaux thermales sulfureuses de Néris, par M. Robiquet. Mém Acad Sci Paris 15:355–382

Ugolini FC (1966) Soils. In: Soil development and ecological succession in a deglaciated area of Muir Inlet, Southeast Alaska. Institute of Polar Studies, Report 20. Ohio State University, Columbus, Ohio, pp 29–72

Vaucher JP (1803) Histoire des Conferves d’eau douce. J.J. Paschoud, Genève

Vogel S (1955) Niedere "Fensterpflanzen" in der südafrikanischen Wüste. Eine ökologische Schilderung. Beitr Biol Pfl 31:45–135

von Humboldt A (1859) Ansichten der Natur mit wissenschaftlichen Erläuterungen, 2nd edn. Cotta'scher Verlag, Stuttgart

West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Adv Ecol Res 20:179–223

West NE, Skujins J (1977) The nitrogen cycle in North American cold winter semi-desert ecosystems. Oecol Plant 12:45–53

Wilson W, Hooker JD (1847) Musci. In: Hooker JD (ed) The botany of the Antarctic voyage of H. M. Discovery ships Erebus and Terror in the years 1839–43, under the command of Captain Sir James Clark Ross, 1. Flora Antarctica, Part II. Reeve Brothers, London, pp 395–423, 550–551

Worley IA (1973) The "black crust" phenomenon in Upper Glacier Bay, Alaska. Northwest Sci 47:20–29

Zólyomi B (1987) Buntflechten-Moos und Lebermoos Synusien. In: Pócs T, Simon T, Tuba Z, Pondani J (eds) Proceedings of the IAB Conference of Bryology. Symposia Biologica Hungarica 35:375–378

Zukal H (1896) Morphologische und biologische Untersuchungen über die Flechten, 3. Abh. Sitzungsber Kaiserl Akad Wiss Wien, Mathem-naturw Cl 15:197–264

http://www.springer.com/978-3-319-30212-6

Biological Soil Crusts: An Organizing Principle in Drylands

Weber, B.; Büdel, B.; Belnap, J. (Eds.)

2016, IX, 549 p. 130 illus., 81 illus. in color., Hardcover
ISBN: 978-3-319-30212-6