Chapter 7
Structure, Composition, and Function of Biocrust Lichen Communities

Roger Rosentreter, David J. Eldridge, Martin Westberg, Laura Williams, and Martin Grube

7.1 Introduction

Lichens are symbiotic associations between a fungal partner (mycobiont) and one or more photosynthetic partners, either green algae or cyanobacteria (photobiont), living in a close physiological integration that forms a thallus. The mycobiont provides the basic lichen structure, and the alga provides the nutrition through photosynthesis. Like many other biological components of biological soil crusts (biocrusts), lichens are poikilohydric, meaning that they do not actively regulate water uptake or loss, but gain it from, and lose it to, the environment passively. When desiccated, their metabolic activity ceases and they undergo a transient cryptobiotic phase until metabolism can resume with changing environmental conditions. The particular characteristics of soil as a substrate may include high light intensities, poor water availability, and often an unstable surface to grow

R. Rosentreter (✉)
Biology Department, Boise State University, 1910 University Drive, Boise, ID 83725, USA
e-mail: roger.rosentreter0@gmail.com

D.J. Eldridge
Centre for Ecosystem Science, University of New South Wales, Sydney, NSW 2052, Australia
e-mail: d.eldridge@unsw.edu.au

M. Westberg
Department of Botany, Swedish Museum of Natural History, 104 05 Stockholm, Sweden
e-mail: Martin.Westberg@nrm.se

L. Williams
Faculty of Biology, Plant Ecology and Systematics, University of Kaiserslautern, 67653 Kaiserslautern, Germany
e-mail: williams@rhrk.uni-kl.de

M. Grube
Institute of Plant Sciences, University of Graz, 8010 Graz, Austria
e-mail: martin.grube@uni-graz.at

on. Such a poikilohydric strategy is perfectly suited for life within biocrusts where environmental conditions vary dramatically between the extremes of inundation and drought.

Lichens form a diverse and often colorful part of biocrusts in all parts of the world (see Fig. 7.1 and Chap. 10 by Bowker et al.) and can be the dominant
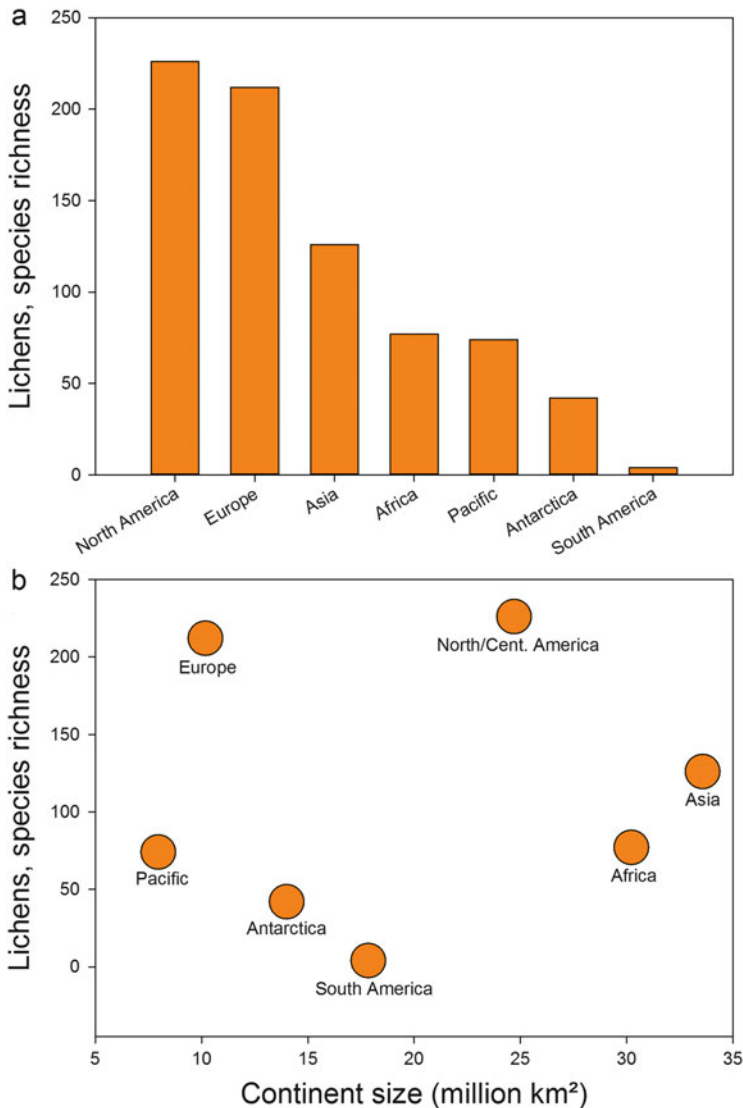

Fig. 7.1 Soil crust lichen richness (**a**) at the continent scale and (**b**) in relation to continental area. *S Amer* South America, *Pac* Pacific (Australia, New Zealand), *Ant* Antarctica, *Afr* Africa, *Eur* Europe, and *NC America* North and Central Americas and includes Greenland. *Source*: Büdel (unpublished data)

life-form in many soil surface communities. Their ability to tolerate severe abiotic stresses such as desiccation, extreme temperatures, and high light intensities makes them ideally suited for relatively resource-limited environments that support well-developed biocrust communities: polar regions, high mountains, arid and semiarid deserts, and xerothermic steppe. In temperate regions, lichens also form important biocrust communities. For example, in Europe, lichen-rich biocrust communities can occur where human activity has created or maintained environments and landscapes largely free of vascular plant vegetation through, for example, grazing by cattle or intense mining or military activity. Lichens can also be important as pioneer species in more ephemeral crusts establishing in areas with open soil created by either natural events such as rockslides or human activities such as road cuttings and forest clearings.

Lichens perform many critically important ecological functions such as altering the physicochemical properties of soil, by, for example, enhancing soil stability and altering water infiltration and retention (Eldridge et al. 2010; Chamizo et al. 2012), increasing fertility through nitrogen fixation and carbon sequestration (Maestre et al. 2010; Elbert et al. 2012; Delgado-Baquerizo et al. 2013), and interactions with other organisms (e.g., hosts for parasitic fungi and food for various invertebrates such as snails, mites, and insects but also for larger animals such as reindeer Seaward 1988; Lalley et al. 2006; Li et al. 2006). While lichens are recognized as a key component in many biocrusts, there remain substantial gaps in our understanding of the taxonomy and diversity of the lichens. In this chapter we summarize some important aspects of lichens in biocrusts and highlight the need for taxonomic research on these organisms.

7.2 Structure and Morphology of Lichen Biocrusts

Biocrusts include the full range of lichen types including gelatinous, crustose, squamulose, foliose, and fruticose forms (Eldridge and Rosentreter 1999). The relative importance of these forms can change in relation to average annual rainfall and evaporation (aridity) and substrate type (see Büdel et al. 2009; Chap. 9 by Colesie et al.). A general introduction to the morphology and anatomy of the lichen thallus can be found in Büdel and Scheidegger (2008). Here we will focus on some aspects of lichen morphology that are relevant to their ability to form biocrust communities.

7.2.1 The Importance of Fungal Hyphae

Lichens attach themselves to the substrate by penetrating the soil with their fungal hyphae. These hyphae are generally assumed to be restricted to the surface of their substrate. However, the hyphae of saxicolous lichens have been shown to penetrate

the spaces between mineral particles to a depth of up to 12 mm (Bjelland and Ekman 2005; Chen et al. 2000), suggesting that fungal hyphae of biocrust lichens may be capable of deeper penetration into substrates that are substantially looser than rock. Observations of the dense aggregations of rootlike rhizines and rhizoids (e.g., Poelt and Baumgärtner 1964; see Chap. 3 (Fig. 3.3) by Beraldi-Campesi and Retallack), common in many biocrust communities such as those of the genera *Endocarpon*, *Catapyrenium*, and *Psora*, support this notion. This is also true for some Antarctic soil crust-forming species such as *Acarospora gwynii* (8 mm depth) and *Caloplaca citrina* and *Lecanora expectans* (24 mm depth; Colesie et al. 2013). Indeed, Belnap et al. (2001) demonstrated that hyphae of *Psora cerebriformis* can penetrate to depths of 14 mm. These dense clumps of deeply penetrating rhizines help to aggregate soil microaggregates into macroaggregates, increasing the resistance of biocrusts to wind and water and mechanical deformation (see Chap. 16 by Belnap). They also increase soil surface roughness, which may further improve resistance to wind and water erosion (Eldridge and Rosentreter 1999).

7.2.2   *The Role of the Lichen Photobiont*

Photosynthesis in lichens is performed by either green algae or blue-green algae (cyanobacteria). About 86 % of lichens have green algal photobionts (chlorobionts), creating chlorolichens, and about 10 % have cyanobacterial photobionts (cyanobionts), creating cyanolichens. In addition, about 3–4 % use both cyanobacteria and green algae as their photobionts (Honegger 1991). In the latter case, cyanobacteria are usually found in specific structures called cephalodia, where they are mainly responsible for nitrogen fixation and, consequently, have an elevated frequency of heterocysts (Hyvärinen et al. 2002). Despite the primacy of the photobiont, very little is known about the specificity of fungal–algal association in biocrust lichens. In general, green algae of the genus *Trebouxia* have been found to be the dominant photobiont of biocrust chlorolichens. Very little is known about physiological interactions between lichens and algal colonies outside the thallus structures. Chlorolichens are known to grow in close proximity to cyanobacterial colonies in a wide range of relationships, from facultative to obligate (cyanotrophy, sensu Poelt and Mayrhofer 1988).

Despite the diversity of algal species present in biocrusts, lichen mycobionts appear to be highly specific. For example, studies by Ahmadjian et al. (1980) and Ahmadjian and Jacobs (1981) showed that, although the biocrust lichen *Cladonia cristatella* and rock-dwelling *Rhizoplaca chrysoleuca* formed thalli when associated with several photobionts, at least in vitro, development was retarded when distantly related photobionts were used. Similarly, Schaper (2003) demonstrated the extremely photobiont-specific nature of certain lichenized fungi, with a proper lichen thallus developing only when associated with a specific partner. However, the degree of algal specificity of biocrust lichens does not contrast with those lichens growing on other substrates (Wirtz et al. 2003; Pérez-Ortega et al. 2012).

Interestingly, the soil lichen *Psora decipiens* has been shown to be associated with a wide range of chlorobiont species (Ruprecht et al. 2014). We assume that the ability to form associations with a wider range of locally available photobionts may be an important trait that increases the distribution and survival of biocrust lichens growing in environmentally extreme habitats, such as the Antarctic Peninsula (Romeike et al. 2002; Jones et al. 2013). This could account for its widespread global distribution and its ability to tolerate a wide range of environmental conditions ranging from alpine areas to deserts.

Photobiont pools may exist in areas that allow many species to take advantage of locally adapted species or haplotypes, and some species have even evolved to steal their photobionts from other lichen species. A noteworthy example of this is the soil lichen *Diploschistes muscorum*, which parasitizes different *Cladonia* species by developing apothecia in the *Cladonia* squamules and associating with its photobiont *Asterochloris irregularis*. Consequently the *Cladonia* structure breaks down, resulting in free-living *Diploschistes* thalli. In mature thalli of *Diploschistes*, the photobiont is exchanged for *Trebouxia showmanii* (Friedl 1987). *Toninia sedifolia* and *Fulgensia* species are often found growing together and appear to share the same photobiont pool of *Trebouxia* strains (Beck et al. 2002). Indeed, ascospores of *Fulgensia bracteata* have been found to germinate on the thallus of *Toninia sedifolia* and the invading hyphae gain access to the photobiont (Ott et al. 1995).

7.3 Composition of Biocrust Lichens

7.3.1 Distribution of Biocrust Lichens

Biocrust lichens are found on all continents (Fig. 7.2a), although richness seems to be largely independent of continent area (Fig. 7.2b). As with any other organism, the distribution of biocrust lichens ranges from highly localized to globally ubiquitous. Many biocrust species are ubiquitous and have a broad geographic distribution. Species such as *Psora decipiens*, *Toninia sedifolia*, and *Fulgensia bracteata* are often very common components of lichen-dominated biocrusts worldwide (Timdal 1986, 1987). However, morphological variation in *Toninia sedifolia* at different biocrust sites is difficult to interpret and may obscure the presence of different, closely related species. Similarly, *Psora decipiens*, thought to be taxonomically well defined (Schneider 1979; Timdal 1986), is now known to exhibit variation both in morphology and chemistry, and this variation has not been thoroughly studied using molecular techniques. It is likely, therefore, that the considerable variation within this particular lichen taxon could be sufficient to warrant the description of new species. Such variation is also apparent in many other biocrust lichen species and raises the question whether they are also associated with variation in ecophysiological traits of the species. In this context,
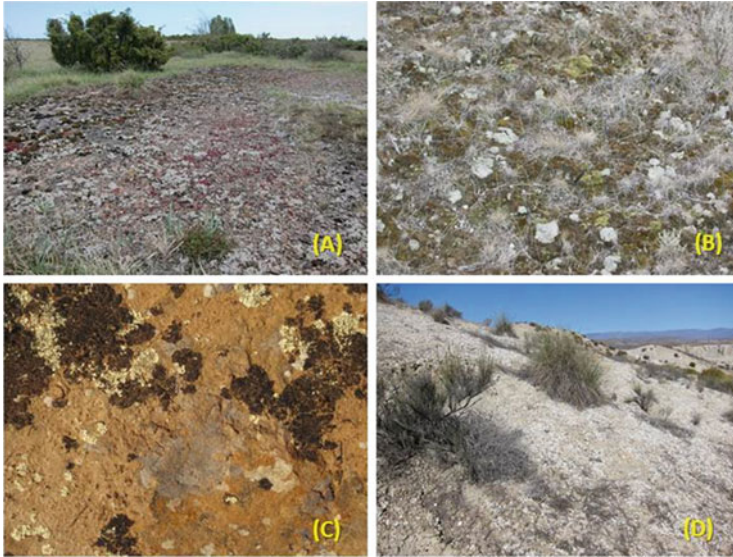
Fig. 7.2 Images of lichen-dominated biocrusts. (**a**) The Great Alvar on Öland, Sweden showing shallow soils on limestone pavement with, e.g., *Diploschistes muscorum*, *Toninia sedifolia*, *Toninia physaroides*, *Psora decipiens*, *Fulgensia bracteata*, and *Collema* spp. (**b**) *Artemisia* shrub-steppe near Boise, Idaho, USA, on deep loess soils with *Diploschistes muscorum*, *Fulgensia bracteata*, and *Psora montana*. (**c**) Crusted loamy soils near Deniliquin, NSW, Australia, with *Xanthoparmelia reptans*, *Neofuscelia pulla*, and *Lecidea ochroleuca*. (**d**) Tabernas badlands near Almeria, Spain, with well-developed biocrusts on gypsum-calcareous soil dominated by *Squamarina lentigera*, *Diploschistes diacapsis*, *Buellia zoharyii*, and *Acarospora nodulosa*

taxonomists often stress the concept of cryptic species (i.e., species that are not characterized by distinct phenotypic characteristics). This, however, may reflect merely an ignorance of subtle phenotypic traits that have been overlooked or inadequately studied.

The abundance of some biocrust taxa may exhibit skewed distributions across their geographic range due to differences in their ecological response to idiosyncratic environmental cues. One species with a skewed distribution is *Solorinella asteriscus*, a xerothermic continental species that typically occurs on loess soils. Its sporadic occurrence in continental valleys in Norway and dry valleys in the Canadian Alps and Italy does not reflect a global rareness, because it is relatively common in semiarid steppe grasslands in Asia, and also occurs in isolated pockets in moderate continental climates in urban and peri-urban environments in Europe (e.g., Bratislava, Slovakia). It is likely that populations of this species, which were isolated during the Late Glacial and Holocene periods, are also genetically distinct, although their scarcity in Central Europe may also be related to the loss of available habitats due to human activity (Farkas and Lökös 1994).

Other biocrust species have very limited geographic distributions and, to date, are known only from the locations where they were first described. For example, the

squamulose coralloid lichen *Protopannaria alcicornis* (Jorgensen 2001) is an endemic biocrust lichen known from only two specimens from the subantarctic Kerguelen Islands. It is difficult to establish the realized niche of this species because comparable habitats on other subantarctic islands are difficult to survey and therefore have been poorly sampled. The high number of currently endemic lichens worldwide probably reflects the poor state of floristic research rather than true endemism per se. For some species, local or regional endemism has been adequately established through substantial regional collections. For example, *Tephromela siphulodes* is a species with a distinct, three-dimensional growth form and has only been found on soils in high-altitude alpine areas in Nepal (Poelt and Grube 1993a). Similarly, *Lecanora himalayae* and *Lecanora chondroderma* are well-described species from the same area, but are absent from other alpine habitats (Poelt and Grube 1993b). In Mediterranean habitats, some white-colored *Buellia* species, known as the *Buellia epigaea* group, have a wide distribution in the Northern Hemisphere, but three species of the group (*Buellia dijiana*, *Buellia georgei*, and *Buellia lobata*) are only known from Australia (Trinkaus et al. 2001). The preceding discussion about lichen distribution and endemism indicates that considerable work is required to determine the true distribution of many of our biocrust-forming lichen taxa.

While many scientists acknowledge the close links between biocrusts and the condition or health of dryland ecosystems (Klopatek 1993; Rosentreter and Eldridge 2002), biocrusts and their component lichens and bryophytes are rarely recorded during field-based assessment (West 1990). In the mid- to late 1980s, Australian rangeland scientists pioneered a range of techniques to determine the health of landscapes that placed more emphasis on soil and landscape function rather than relying, as previously, on the status and condition of the vascular plant community (Tongway and Smith 1989). The resulting "soil surface classification system" used biocrust cover as an important measure of the capacity of the soil to carry out two functions: resist deformation and cycle nutrients.

7.3.2 Richness and Abundance of Biocrust Lichens

A global assessment of biocrust lichen richness is difficult to conduct. Part of the reason for this lies in the difficulties associated with the term "biocrust." Although this term and its synonyms (biological soil crust, cryptogamic crust, cryptobiotic crust, microphytic crust) are widely used by ecologists, its application for a well-described group of lichens is problematic. Biocrusts have been defined as a community of organisms that are an intimate part of binding soil surface particles into a crust. However, fruticose (shrubby) lichens (e.g., *Chondropsis semiviridis*) do not form true crusts (Eldridge and Greene 1994), and it is doubtful whether vagrant (*syn*. vagrant) lichens (e.g., *Xanthoparmelia chlorochroa*), that are associated with soils and biocrusts, have a role in crust formation or whether the thallus itself represents a biocrust without the underlying soil. Here we avoid this ontological

issue by adopting a wider concept of biocrusts, which also includes lichen taxa that develop more complex thallus forms when growing on soils (i.e., terricolous lichens). A key of terricolous species in Italy includes 439 species (Nimis and Martellos 2004). Extrapolating globally, we expect that the worldwide number of species may be beyond 1000. Unpublished data on lichen richness (Büdel et al. 2014, pers. comm.) indicates a described lichen richness of about 550 taxa (Fig. 7.2a).

The composition of the lichen flora in biocrusts varies considerably with differences in soil physical and chemical properties, climate, and vegetation community (see Chap. 10 by Bowker et al.). Although lichens are often a prominent or even dominant component of biocrusts, it is often difficult to compare species richness between different areas because the taxonomic status of some ubiquitous species is under revision (e.g., *Buellia* spp., Trinkaus et al. 2001). Advances in the molecular taxonomic techniques and improved DNA sequencing could result in range extensions for some species or the splitting of globally distributed taxa into different species or subspecies.

In general, biocrust lichen richness tends to be higher in environments such as deserts, arctic, and alpine areas, where competition from vascular plants is low. Cool habitats, in particular, seem to support a large diversity and biomass of lichen taxa (Eversman 1995), possibly because the balance of photosynthesis and respiration between the symbiotic partners maximizes the opportunity to form complex thallus structures. Several studies have shown that large-seeded grass species, such as cheatgrass, *Bromus tectorum*, are inhibited by biocrusts (Serpe et al. 2006, 2008). In arid and semiarid environments, competition from vascular plants is generally low, either because the distribution of vascular plants is also low or lichen crusts inhibit vascular seed germination (Prasse and Bornkamm 2008; Serpe et al. 2006). In more mesic environments that support larger populations of herbivores, there is often positive feedback between increased soil moisture, fluctuations in vascular plant cover, and the response of biocrusts to these altered levels of bare soil (see Chap. 19 by Zhang et al.).

7.3.3 Taxonomy and Identification of Biocrust Lichens

Biocrust lichen taxonomy is still in its relative infancy compared with vascular plant taxonomy. For example, in a study of lichen species richness by a number of lichen experts at four sites in Europe (Austria, Germany, Spain, and Sweden, Büdel et al. 2014), about 9 % of all lichens collected remained unidentified at the species level even though these areas have previously been studied intensively. Given this uncertainty in identification, we would expect that even more remote and poorly studied biocrust communities would yield many new lichen species.

Similar to many other organisms associated with biocrusts, lichens are also often difficult to identify. In contrast to most prokaryotes and many other microscopic eukaryotes, however, lichens have macroscopic structures with characters that

allow the recognition of species or at least their classification to higher (taxonomic) ranks. Many terricolous macrolichens found in biocrusts are characterized by large, leaflike thalli. These biocrusts are easily recognizable but include "difficult" genera that are hard to identify at species level because they are morphologically variable and have few external characteristics. Genera typical of this group are found in the families of Aspiciliaceae, Acarosporaceae, Lichinaceae, and Verrucariaceae. In addition, the high substrate specificity typical for many lichens may not be strictly maintained on soil substrates. Some species normally found on rocks may occasionally be found on compacted or gypsiferous soils, and in alpine environments, corticolous (bark-inhabiting) species are sometimes found on soil (e.g., *Evernia divaricata*). The taxonomic significance of such substrate shifts is relatively unknown, but a reasonable hypothesis is that the variable composition of soils could facilitate the adaptation of species to alternative substrate types.

The accurate identification of biocrust lichens generally requires expert knowledge that goes beyond the information presented in formal lichen texts. Specific problems of identification arise when biocrust lichens lack reproductive structures needed for determination. Molecular techniques and DNA sequencing of individual thalli may help to improve the identification of species. Such a DNA bar-coding approach to the identification of lichenized fungi, however, will only be useful after basic data on the genetic variation of species have been collected (e.g., Del-Prado et al. 2010; Kelly et al. 2011; Pino-Bodas et al. 2013). Unfortunately, such information is virtually unknown for the majority of biocrust lichens. Moreover, microlichens often occur mixed together in a rich tapestry rather than occurring as discrete individuals. Without knowledge of the species, it is difficult to recognize which structures belong to separate species, and molecular approaches that do not consider these problems will undoubtedly lead to confusing results.

7.3.4 A Morphospecies Approach to Biocrust Lichen Identification

The notion that similar morphology reflects similar functions (or susceptibilities) in ecosystems could improve our understanding of biocrust function, leaving taxonomic intricacies aside. Ecological studies are often conducted by assessing "morphological groups" (sensu Eldridge and Rosentreter 1999), rather than fully resolving diversity at the species level. Morphological groups are groups of superficially similar species that are difficult to differentiate in the field, but which possess similar morphologies (e.g., "green leafy lichens" or "gelatinous lichens") and often function similarly (Eldridge and Rosentreter 1999). In many cases, morphological groups are surrogates for functional groups (Pike 1978; Rosentreter 1995). For example, the gelatinous lichen genera *Collema*, *Leptogium*, and *Leptochidium* of shrub-steppe communities in the western USA all fix nitrogen

and provide a similar degree of protection from surface soil erosion (Anderson et al. 1982; Brotherson et al. 1983).

The concept of functional groups is well illustrated by the susceptibility of biocrusts to trampling, which is seen as a major factor threatening soil crust communities worldwide. Some lichen species appear more tolerant of trampling than others (Rogers and Lange 1971). This is probably due to differences in their morphologies, as foliose or fruticose forms seem to be more susceptible than crustose and squamulose forms (Eldridge and Rosentreter 1999). Morphological groups of lichens can also provide valuable insights into the health and recovery of ecosystems. For example, in a study across more than 0.6 million km^2 of eastern Australia, Eldridge and Koen (1998) found that the presence of the "yellow foliose" morphological group, which was comprised of foliose lichens of the genera *Heterodea*, *Xanthoparmelia*, and *Chondropsis*, was consistently correlated with stable, productive landscapes with little evidence of accelerated erosion.

Biocrust color has been shown to be a useful morphological trait to indicate the role of biocrusts in nitrogen cycling. For example, the later successional, dark cyanobacteria-dominated biocrust is known to be more closely involved in nitrification and denitrification than the earlier successional light forms (Barger et al. 2013; Rosentreter et al. 2007). While light cyanobacterial crusts are generally dominated by cyanobacteria of the genus *Microcoleus*, dark biocrusts contain nitrogen-fixing cyanobacteria (e.g., *Nostoc*, *Scytonema*) and often the nitrogen-fixing lichens *Collema tenax* and *Collema coccophorum*. Some lichen morphologies may be indicative of moisture type and inundation conditions. Gel-like cyanolichens (e.g., *Collema*) depend on liquid water for activity. Some chlorolichens may be activated by humidity alone. Thus, they are likely to be relatively intolerant of inundation and found therefore in exposed situations (Lange et al. 2001). Water vapor alone, however, is insufficient to activate some chlorolichens such as *Acarospora gwynii*. The ability of chlorolichens to be activated by water vapor may be an adaptation to very low liquid water availability (Colesie et al. 2014). Moderately cool habitats with high levels of humidity are often dominated by fruticose lichens. Their productivity under such conditions seems to be the result of high photosynthetic rates compared to respiration. The markedly different response of lichens to environmental conditions thus provides useful information on environmental quality.

7.4 Functional Roles of Biocrust Lichens

The important functional roles of biocrust lichens related to the physiological or chemical properties are already highlighted in several chapters of this book, including soil stabilization (see Chap. 16 by Belnap), weed abatement, lowering or raising of the albedo of the soil (see Chap. 12 by Weber and Hill, and Chap. 22 by Reed et al.), provision of microhabitats for invertebrates (see Chap. 8 by Darby and Neher), and nitrogen fixation (see Chap. 14 by Barger et al.). However, the

assignment of particular species or morphological groups to such categories is an important task if we are to be able to assess the ecosystem value of particular soil crust communities.

Different photobionts influence the capacity of biocrust lichens to undertake different functions. For example, cyanolichens fix nitrogen which makes them efficient pioneers on degraded soils (Eldridge 1998). They preferably grow at sites of lower potential radiation (Pinho et al. 2010) and tend to have a lower photosynthetic efficiency compared to chlorolichens (Wu et al. 2013). But the soil crust lichen *Collema tenax* has been shown to reach higher values than most soil crust chlorolichens and to be saturated at light intensities as high as 1500 μmol photons m^{-2} s^{-1} (Lange et al. 1998; Lange 2003). Soil biocrusts may also help to maintain resistance of ecosystems to invasion. In the western USA, lichen-dominated biocrust communities have been shown to reduce the invasibility of shrublands by large-seeded Eurasian weeds such as *Bromus tectorum* (Deines et al. 2007; Serpe et al. 2008; Reisner et al. 2013, see Chap. 19 by Zhang et al.). Before the introduction of European livestock, a combination of low levels of disturbance in dry times and the presence of a stable lichen-dominated biocrust have kept weedy flammable grass species at low levels. With an increase in human- and livestock-induced soil disturbance, European annual grasses have proliferated, increasing the extent and intensity of wildfire in areas which had not coevolved with frequent fire.

Recent research in the Orchard Combat Training Center south of Boise, Idaho, USA, has focused on the role of biocrust diversity on ecosystem functions, particularly the capacity of different biocrust taxa, including lichens, to withstand disturbance from livestock trampling and military vehicles (Table 7.1). Sites with a high richness of biocrust taxa have been shown to support only a sparse cover of flammable grasses whereas low-richness sites are dominated by flammable grasses (Rosentreter, unpublished report to the Idaho Army National Guard, Nov. 2014). Apart from their suppressive effect on large-seeded, annual plants, biocrusts may also facilitate the succession of other plant communities by, for example, fixing nitrogen, providing a niche for specialized microbes, or stabilizing the soil by trapping resources such as organic matter and water (Maestre et al. 2008). They also moderate the flow of water into the soil (see Chap. 17 by Chamizo et al.).

In order to convince land managers, practitioners, farmers, politicians, and the general public of the ecosystem role provided by biocrust lichens, it may be more useful to consider a functional group approach to lichen identification rather than one based on a traditional species approach. This emphasizes the extent to which they are critical for providing ecosystem goods and services rather than merely how many individual species they support. These roles and functions include, but are not limited to, erosion prevention and soil stabilization, which are of increasing concern in relation to environmental change and global warming (see Chap. 22 by Reed et al.). In some ecosystems, soil lichens form food for ungulates as well as invertebrates, and absorption of environmental pollutants by lichens can result in transfer into the food chain (Skuterud et al. 2005).

Table 7.1 Biological soil crust taxa recorded in the Orchard Training Center, Idaho, their life-form, functional role, and tolerance to disturbance

Species and authorities	Life-form	Functional role	Disturbance rating
Bryum argenteum Hedw.	Bryophyte	Soil stabilizer	H
Bryum argenteum Hedw. var. *lanatum* (P. Beauv.) Hampe	Bryophyte	Soil stabilizer	H
Caloplaca cerina (Ehrh. ex Hedwig) Th. Fr.	Bryophyte	Detritus binder	M
Ceratodon purpureus (Hedw.) Brid.	Bryophyte	Soil stabilizer	H
Crossidium sp.	Bryophyte	Soil stabilizer	H
Didymodon vinealis (Bridel) Zander	Bryophyte	Soil stabilizer	H
Pterygoneurum ovatum (Hedw.) Dix.	Bryophyte	Soil stabilizer	H
Riccia frostii Aust.	Bryophyte	Soil stabilizer	M
Syntrichia caninervis Mitten	Bryophyte	Soil stabilizer	H
Syntrichia ruralis (Hedwig) F. Weber & D. Mohr	Bryophyte	Soil stabilizer	H
Microcoleus sp.	Cyanobacterium	N fixer, soil stabilizer	H
Acarospora schleicheri (Ach.) A. Massal.	Lichen	Soil stabilizer	L
Buellia punctata (Hoffm.) Coppins & Scheid.	Lichen	Detritus binder	M
Arthonia glebosa Tuck.	Lichen	Soil stabilizer	M
Aspicilia aspera (Mereschk.) Tomin	Lichen	Soil stabilizer	L
Aspicilia filiformis Rosentreter	Lichen	Soil stabilizer	VL
Aspicilia mansourii Sohrabi	Lichen	Soil stabilizer	L
Aspicilia sp.	Lichen	Soil stabilizer	L
Caloplaca jungermanniae (Vahl) Th.Fr.	Lichen	Detritus binder	M
Caloplaca tominii Savicz.	Lichen	Soil stabilizer	H
Caloplaca sp.	Lichen	Detritus binder	M
Candelariella aggregata M. Westb.	Lichen	Detritus binder	M
Candelariella rosulans (Müll. Arg.) Zahlbr.	Lichen	Soil stabilizer	M
Candelariella vitellina (Hoffm.) Müll. Arg.	Lichen	Soil stabilizer	M
Candelariella sp.	Lichen	Soil stabilizer	M
Cladonia pocillum (Ach.) Grognot	Lichen	Soil stabilizer	M
Cladonia pyxidata (L.) Hoffm.	Lichen	Soil stabilizer	M
Collema tenax (Sw.) Ach.	Lichen	N fixer	M
Collema coccophorum Tuck.	Lichen	N fixer	M
Diploschistes muscorum (Scop.) R. Sant.	Lichen	Soil stabilizer	L
Endocarpon pusillum Hedwig	Lichen	Soil stabilizer	H
Lecanora flowersiana H. Magn.	Lichen	Detritus binder	M
Lecanora muralis (Schreber) Rabenh.	Lichen	Soil stabilizer	M
Lecidea laboriosa Mull. Arg.	Lichen	Soil stabilizer	L
Lepraria sp.	Lichen	Soil stabilizer	H
Leptochidium albociliatum (Desm.) M. Choisy	Lichen	N fixer	L

(continued)

Table 7.1 (continued)

Species and authorities	Life-form	Functional role	Disturbance rating
Massalongia carnosa (Dickson) Körber	Lichen	N fixer, soil stabilizer	L
Physconia enteroxantha (Nyl.) Poelt	Lichen	Soil stabilizer	L
Physconia muscigena (Nyl.) Poelt	Lichen	Soil stabilizer	L
Placidium squamulosum (Ach.) Breuss	Lichen	Soil stabilizer	H
Placynthiella icmalea (Ach.) Coppins & P. James	Lichen	Detritus binder	H
Psora montana Timdal	Lichen	Soil stabilizer	M
Psora tuckermanii R. A. Anderson ex Timdal	Lichen	Soil stabilizer	L
Texosporium sancti-jacobi (Tuck.) Nadv.	Lichen	Soil stabilizer	L
Thelenella muscorum var. *octospora* (Nyl.) Coppins & Fryday	Lichen	Soil stabilizer	L
Trapeliopsis bisorediata McCune & Camacho	Lichen	Soil stabilizer	L
Trapeliopsis steppica McCune & Camacho	Lichen	Soil stabilizer	L
Toninia ruginosa (Tuck.) Herre	Lichen	Detritus binder	L

N fixer: fixes nitrogen; soil stabilizer: binds surface sediments using a range of mechanisms, generally hyphae or physical protection; detritus binder: stabilizes organic material. *VL* very low, *L* low, *H* high, and *VH* very high. Disturbance rating based on a soil crust index (Rosentreter and Eldridge 2004)

7.4.1 Sampling Biocrust Lichen Communities

Qualitative studies of lichen diversity often involve the collection of specimens in a somewhat haphazard sequence, over landscapes that are often of ill defined, or with no specific number, size, or extent of plots. The landscapes sampled are often of variable complexity and sampling is conducted with variable effort (Nash and Sigal 1981; Will-Wolf 1998). This opportunistic sampling, however, has resulted in the collection of data from ecologically interesting sites such as within ecotones, undisturbed areas excluded from grazing, or biodiversity hot spots (Wetmore 1985; Neitlich and McCune 1997). Consequently, there may appear to be some bias in the collection of these data (McCune et al. 2000).

Biocrust lichen research has advanced considerably in the past two decades with a greater attention to systematic sampling. Intensive sampling of different patch types within landscapes is now standard practice, with stratification of sampling sites in relation to vascular plant community composition, soils, and climate. For example, Root and McCune (2012) recorded 99 biocrust lichen species within fifty nine 0.4-ha plots. Of these, one-third were observed only once. The use of morphological, functional, or taxonomic group approaches has also improved field-based assessment of biocrust communities, allowing researchers to increase the consistency and statistical power by lumping taxa that are morphologically similar into groups (Ponzetti et al. 1998; Ponzetti and McCune 2001; Eldridge and

Rosentreter 1999). The use of morphological groups for biocrust lichens minimizes the errors associated with overlooking small or otherwise inconspicuous species or species which are frequently intertwined and decreases the sampling variance by increasing statistical power. It also increases the repeatability of cover or abundance estimates (Ponzetti et al. 1998). Using morphological groups in the field will, however, invariably underestimate true alpha diversity (Ponzetti and McCune 2001).

7.5 Lichens in Biocrusts: Concluding Remarks

A number of knowledge gaps compromise our ability to fully understand how lichens function and how they affect their environment. First, biocrust lichens are still poorly studied, resulting in an underestimation not only of their abundance and diversity, but a lack of understanding of how they interact with their environment and the extent to which they influence the provision of ecosystem goods and services. Some disciplines have developed lists of key indicator species that are useful for assessing the health of ecosystems (e.g., aquatic algae; McCormick and Cairns 1997). Extending this concept to biocrust lichen (and bryophyte) taxa would be a valuable contribution to the field of biocrust ecology. Second, any studies of biocrust lichens must take into account the physicochemical differences in substrates that are likely to affect their diversity and functionality. Third, a more comprehensive understanding of biocrust lichens must consider the degree to which they interact with associated microbiota. Only recently, for example, have bacterial communities associated with biocrust lichens been examined in detail using relatively modern techniques (see Chap. 5 by Maier et al.). Fourth, little is known about functional redundancy in biocrust lichen taxa and the physiological responses of different taxa to a range of perturbations. This can only be solved when taxonomic work has advanced to the stage where the majority of taxa are readily identified and can be studied in situ or where techniques are available for studying ex situ communities (e.g., Maestre et al. 2012). Finally, the study of biocrust lichens is hampered by the lack of consistent, rigorous methodologies, which are exacerbated due to the small size of the target organisms.

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