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REVIEW ARTICLE

Biocrust lichen and moss species most suitable for restoration projects

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Reintroducing lichens and mosses to areas slated for restoration or rehabilitation may prove integral to project success by filling the biocrust component (niche) of arid ecosystems. In doing so, it is important to select appropriate species and genetic source material. Some bryophyte and lichen species are early pioneers and are potentially well-suited for restoration projects. Species traits such as high reproductive rates, rapid establishment rates, and large asexual reproductive propagules can be beneficial for restoration. For instance, the large number of spores produced by some mosses are beneficial for reproductive success in arid environments. In addition to identifying the benefit of reproductive strategies, it is important to take habitat needs into consideration; lichen and moss species that are wide-ranging both geographically and ecologically are recommended over geographically and edaphically restricted species that occur only in specific habitats, such as calcareous soils. Biocrusts used in specific restoration areas should have similar genetic source material (local provenance), and harsh environmental conditions should be ameliorated.

Key words: establishment, Great Basin, lichens, mosses, reproductive rate

Implications for Practice

- Biocrusts are a critical component of arid habitats and restorationists are beginning to consider them when preforming restoration activities.
- Determining which of the many arid biocrust species are most likely to be successful for restoration is poorly studied.
- The reproductive rate of individual moss and lichen species, establishment mechanisms, and ecological ranges of those species must be considered in restoration actions.
- This manuscript focuses on a few of those factors—the reproductive rate of the individual species, the establishment mechanism, and the ecological range or tolerance of those species—to answer that question.

Introduction

Reintroducing biocrusts to areas slated for restoration or rehabilitation may prove integral to project success by filling an important niche of arid ecosystems (Belnap et al. 2001; Bu et al. 2018). Identifying biocrust species most suitable for restoration should take into consideration those reproductive traits which facilitate rapid rates of establishment; this may increase restoration success (Chiquoine et al. 2016; Bowker et al. 2017).

Some authors (Warren et al. 2018) suggest that biocrust restoration can be passive in nature, by waiting for propagules to blow into restoration sites. This is one method that occasionally works and has great potential (Condon et al. 2019). The process is known to be episodic and relies on seasonal deposition, in sufficient quantities of the right species composition, and at the right season, for a specific area. Many biocrust species have spores that are present in the wind and can inoculate sites. Many bryophytes, which reproduce by small spores, are stress tolerant, and considered “aggressive,” can colonize a site without active inoculation (Weber et al. 2016). However, for other biocrust species that tend to reproduce locally by vegetative fragmentation or by asexual propagules, active inoculation may be beneficial for enhancing restoration actions. Inoculated mosses and lichens should come from similar habitats and elevations (local provenance) as the restoration site (Chiquoine et al. 2016; Condon & Pyke 2016; Zhao et al. 2016).

Restoration sites are typically ecologically degraded or have burned, so the addition of physical structure is beneficial to colonizing biocrusts by creating a boundary layer from wind and creating some shade (Bu et al. 2018; Antoninka et al. 2019; Faist et al. in press). This physical structure can capture wind-blown propagules (passive restoration) and decrease evaporation, enhancing both inoculated and passive biocrust establishment (Hilty et al. 2004; Weber et al. 2016; Yun et al. 2016). Steppe vegetation includes shrubs and bunchgrasses that create this synergistic structure with biocrusts filling the interspaces (Rosentreter 1999; Rosentreter et al. 2014; Condon & Pyke 2018*b*). This is a basic principle (Palmer et al. 1997) of “build it (the structure) and they (the biocrusts) will come”. Interspaces

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filled with biocrusts help abate invasion by nonnative annual grasses, improve water infiltration, and moderate soil surface temperature extremes (Belnap et al. 2001; Serpe et al. 2012). Biocrusts have also been linked to enhanced establishment of shrubs following rangeland fires (Germino et al. 2018).

Creating a pattern of clumped perennials with small gaps among them provides greater site resistance to cheatgrass (Condon & Pyke 2018*a*) and space for sagebrush-associated wildlife to travel freely (Connelly et al. 2016). Maintaining shrub and bunchgrass habitats is critical for biocrusts and associated and coevolved wildlife. Agencies, at times, have planted tall rhizomatous grasses in an attempt to restore wildlife habitat, but these grasses have little wildlife value (Connelly et al. 2016) and inhibit biocrust persistence. Rhizomatous grasses do not provide space for biocrusts to colonize, and tall rhizomatous grasses such as intermediate wheatgrass compete with biocrusts for moisture and light (Serpe et al. 2012). Disking short-statured but native Sandberg bluegrass (*Poa secunda*) to plant these larger nonnative grasses is counter-productive for wildlife values and for promoting biocrusts (Pyke et al. 2013; Connelly et al. 2016).

Biocrusts can reestablish following a burn or rangeland restoration efforts, but they are easily damaged by trampling when small, new, and still weakly attached to the soil. When bunchgrasses are planted post-fire and the seeding is successful, it is often grazed after two growing seasons (1.5 years post-burn). In arid habitats, this is not enough time for biocrusts to establish and mature (Hilty et al. 2004). South of Boise, near Kuna Butte (178–305 mm precipitation), Hilty et al. (2004; Hilty et al. 2003) studied a site rested from livestock grazing for 9 years post-seeding. The site grew into a perennial bunchgrass community with continuous short moss biocrusts in the interspaces and very little cheatgrass (<1%) (Hilty et al. 2004).

Small-scale biocrust restoration has utilized road-cut areas for source material (Chiquoine et al. 2016). The source material can be spread on the restoration site as plugs, or as broken-up soil, or mixed in water for broader dispersal. Some restorationists have added mineral soil or tackifier and even kitty litter to the mix to achieve broader more even dispersal (L. Lass 2019, retired University of Idaho, personal communication).

The diversity of morphology and functions found in biocrusts offers different features that make them useful for various restoration situations. Sites with highly variable moisture conditions might rely on vegetation propagation rather than growth from spores due to the harshness of the site (Ott et al. 2019). Highly degraded sites that are semi-arid might be suitable for mosses that start from spores if there are seasonal periods of cool moist weather in the winter or spring such as in the Great Basin deserts of North America (Rosentreter 1986, Eldridge et al. 2003). Less degraded sites may just need some biocrust species incorporated to enhance site biodiversity.

Basic biology is the backbone for understanding how a species reproduces and colonizes a site. For many organisms, this information can be found in one place in the literature, but for biocrust species, ecological and reproductive data are rarely available (Bowker et al. 2018).

The relative composition of biocrusts changes from location to location (Rosentreter & Belnap 2001). Here, I deal exclusively with lichens and mosses which can be the dominant biocrust in arid habitats worldwide (Rosentreter et al. 2016), especially cool and cold deserts. Thus, my main conclusions may not apply in regions in which cyanobacteria are the dominant component of the biocrust.

Lichens

Sexual

Lichens reproduce sexually by producing fungal spores rather than the composite organism (Brodo et al. 2001), making it challenging for lichens to disperse. A fungal spore, in theory, finds a compatible algal cell living free in nature and then germinates. This appears to be a difficult task since most free-living algal cells are not compatible with lichen fungi. Many lichenologists believe that the spores land on other more common cosmopolitan lichen species and then capture those algal cells to form a new composite organism. This has been documented for species in the genus *Diploschistes* (Friedl 1987), but for most lichen species it is unknown exactly how they reproduce. Therefore, asexual reproduction by lichen fragments or specialized asexual structures such as soredia and isidia are a more likely means of site colonization.

It has been assumed that colonization by sexual spores is a slower mechanism for successful lichen establishment (Brodo et al. 2001) than asexual fragmentation, but this assumption is yet to be tested, since the details for lichen reproduction are still somewhat theoretical.

Lichens consist of fungal threads and microscopic algae living together and functioning as a single organism. Lichens with no roots, stems, or leaves receive their nutrients directly from the atmosphere and dust. The fungus provides the structure that protects the algae from ultraviolet light and from drying under harsh conditions. A sexually reproducing lichen only produces a sexual spore from the fungal partner. A more in-depth treatment of the biology of lichens can be found in Brodo et al. (2001), and in McCune and Rosentreter (2007).

Asexual

Lichens can also produce asexual spores of the fungal partner called pycnidia. The spores can detach from these black dot, flask-shaped features which are much smaller than a sexual apothecium or perithecium. Pycnidial spores have the same challenges as sexual spores. Some of the relatively early-colonizing *Placidium* (Verrucariaceae) species produce pycnidia that are imbedded in the thallus of the lichen and disperse algal cells with those fungal spores. When spores discharge from perithecia of all lichens in the Verrucariaceae family, they carry along groups of hymenial algal cells (Ahmadjian & Heikkilä 1970). In this way, the fungus has the algae necessary for re-association nearby. Common biocrust genera in this family include *Catapyrenium*, *Endocarpon*, *Heteroplacidium*, and *Placidium*, all of which have some documented examples of carrying the necessary algae for re-association (Ahmadjian & Heikkilä 1970). Many of these genera are relatively early colonizers. However, these lichens occur as very small (0.5–2 mm) scattered individuals rather than colonial populations and are probably not ideal for restoration projects. Small scattered individuals are not as effective as soil binders as more continuous, larger colony-forming biocrusts. Biocrusts that form larger more continuous colonies, such as the mosses and *Cladonia* spp., are better suited for active restoration because they are larger and function to bind and stabilize the soil.

Many biocrust lichens produce soredia which are powdery clumps of algal cells wrapped with fungal hyphae. Soredia disperse these packages of algae and fungal hyphae to new locations by wind or by insects and animals. There are few biocrust lichens that disperse by isidia, which are specialized finger-like asexual structures with an outer cortex of thickened fungal hyphae with a few algae cells included within. Other biocrust lichens disperse by mere fragmentation. The thalli break off and disperse, forming a new lichen colony. Some of the larger, arid land vagrant lichens disperse and reproduce predominantly by fragmentation (McCune & Rosentreter 2007).

Mosses and Liverworts

Sexual

Mosses are bryophytes and are classified as plants that consist of small, slender stalks and leaves with no vascular tissue or true roots. Mosses have structures that resemble roots, stems, and leaves, but they lack true water- and food-conducting tissues. Most mosses sexually reproduce by spores. Information on the basic biology of arid land mosses is even more difficult to find at the species level, since many of the mosses and liverworts are wide-ranging and species-level information is based solely on sexual reproduction. Arid land mosses only produce sexual structures under moist conditions that rarely occur in many arid habitats. The mechanism of reproduction and even the sex ratio of bryophytes might be very different in arid habitats (Bowker et al. 2000; Stark et al. 2005). This requires some basic anatomical investigation and an understanding of how spores and asexual structures interact with the environment. The life history of mosses includes several stages. In sexually reproducing moss species, these stages include spore, protonema, buds and full-grown gametophyte, gametangia, and sporophyte. Moss sperm are microscopic and have flagella that require moisture to swim to the female structure (archegonium), which limits sexual reproduction in arid habitats (Glime 1993). Bryophytes in which both sexes are found on the same individual (monoicous) can more easily reproduce sexually than species which bear male and female sex organs on different individuals (dioicous). This may require a larger population size and longer time period, with liquid moisture available for sexual reproduction to occur, than arid mosses commonly receive.

Asexual

As early as 1901, bryophytes were well known for their ability to reproduce by vegetative means (Best 1901). In general, arid land ecologists have not focused on bryophytes, despite their role as a major component of biocrust communities (Belnap et al. 2001), and the fact that mosses are more disturbance tolerant than lichens (Eldridge & Rosentreter 1999; Ponzetti & McCune 2001; Condon & Pyke 2018*b*).

The asexual cycle includes only diaspore, protonema, and then the "full-grown" gametophyte. The gametophyte stage is what most biologists can recognize as a moss or liverwort (During 1979). Bryophyte diaspores can be in the form of gemmae (from either the gametophyte, rhizoid, or protonema), lamellae (filaments branching off a leaf), or buds (often axillary buds with multiple small leaves and a stub of a stem) (During 1979). Bryophytes can also reproduce by mere fragmentation of their leaves or other tissue, similar to fragmentation in lichens. Some moss genera such as *Dicranum* specialize in this mode of reproduction, and insects, birds, and small animals facilitate this vegetative reproduction by breaking off the tips of the leaves (Glime 1993).

Fragmented leaf tissue generally grows a filamentous protonema (which microscopically looks like algal threads or filaments), followed by production of a bud that grows into a full-grown gametophyte. Only *Bryum argenteum* leaf and bud fragments can establish new colonies without first going through a protonema growth stage (Clare & Terry 1960). In bryophytes, as in other plants, reproduction is closely allied to dispersal. For bryophytes, asexual reproduction often plays a more important role than sexual reproduction (During 1979), particularly in arid environments, where temperature and moisture fluctuations can be extreme and unpredictable (Patiño et al. 2013).

In summary, biocrusts, whether they are lichens, mosses, or liverworts, disperse by a large variety of sexual or asexual methods.

Synthesis and Analysis

A list of common regional and globalbiocrust-forming species that could be used for restoration and rehabilitation projects was developed and discussed with regional and international ecologists and taxonomic specialists (Table 1). Experts were asked to comment on the ratings based on the below definitions and add or subtract species. Their opinions were documented and were used to develop Tables 2 and 3. Expert opinions are used in both medical and biological fields and most lists of rare, palatable, or old-growth associated species are developed or refined by expert opinion or by a similar panel method (FEMAT 1993; Rosentreter 2005; Rosenthal et al. 2012).

To systematically evaluate biocrust species most suitable for use in the restoration of arid environments, I gathered data from the taxonomic and ecological literature on the (1) rate and (2) establishment mechanism, for the most common biocrusts. The experts were asked to comment and add to the list that was sent to them and to comment on the definitions of rate of reproduction for lichens and bryophytes.

The defined reproductive rating or ease of reproducing is a cumulative rating:

Table 1. The rate and mechanism of reproduction by some common biocrusts with an emphasis on North American species.

Genus and Species	*Reproductive Rate: Fast, Medium, Slow*	*Establishment Mechanism*
Lichens		
Acarospora schleicheri	Slow	spores (small)
Acarospora terricola	Slow	spores (small)
Arthonia glebosa	Slow	spores
Aspicilia aspera	Slow	unknown, fragmentation
Aspicilia filiformis	Slow	unknown, fragmentation
Aspicilia hispida	Slow	unknown, fragmentation
Aspicilia mansourii	Slow	unknown, fragmentation
Aspicilia reptans	Slow	unknown, fragmentation
Aspicilia rogeri	Slow	unknown, fragmentation
Buellia elegans	Slow	spores
Buellia punctata (syn = *Amandinea*)	Slow	spores
Caloplaca atroalba	Slow	spores
Caloplaca jungermanniae	Med	spores and legacy
Caloplaca lactea	Slow	spores
Caloplaca tominii	Fast	soredia and spores, legacy
Candelariella aggregata	Med	spores and legacy
Candelariella rosulans	Slow	spores
Cladonia fimbriata	Fast	soredia and fragmentation, legacy
Cladonia pocillum	Fast	fragmentation of thalli, asexual squamules in the cups, legacy
Collema coccophorum	Med	fragmentation of thalli and spores
Collema tenax	Med-Fast	fragmentation of thalli and spores and legacy
Diploschistes muscorum	Slow	spores
Endocarpon loscosii	Slow	spores
Endocarpon pusillum	Med	large muriform spores
Heppia lutosa	Med	large muriform spores
Heteroplacidium congestum	Slow	spores
Lecanora epibryon	Slow	spores
Lecanora flowersiana	Slow	spores
Lecanora muralis	Slow	spores
Lecidea laboriosa	Slow	spores
Lepraria spp.	Med	soredia
Leptochidium albociliatum	Med	fragmentation of thalli and spores
Leptogium lichenoides	Med	fragmentation of thalli and spores
Massalongia carnosa	Slow	spores
Peltigera rufescens	Med	spores
Peltula patellata	Med	large muriform spores
Peltula richardsii	Slow	large muriform spores
Physconia enteroxantha	Med	soredia
Physconia muscigena	Slow	spores
Placidium lachneum	Med	pycnidia and spores
Placidium squamulosum	Med	pycnidia and spores
Placidium	Med	pycnidia and spores
Placynthiella icmalea	Med	isidia
Psora cerebriformis	Slow	spores
Psora decipiens	Slow	spores
Psora icterica	Slow	spores
Psora montana	Slow	spores
Psora tuckermanii	Med	spores and pycnidia
Squamarina lentigera	Slow	spores
Sarcogyne mitziae	Slow	spores
Texosporium sancti-jacobi	Slow	spores
Thelenella muscorum var. *octospora*	Slow	spores
Thrombium epigaeum	Med	fragmentation of thalli and spores
Toninia sedifolia	Slow	spores
Trapeliopsis bisorediata	Slow	spores and soredia
Trapeliopsis steppica	Slow	spores and soredia
Xanthoparmelia spp.	Slow	fragmentation

Table 1. continued

Genus and species	Reproductive rate: fast, medium, slow	Establishment mechanism
Bryophytes		
Aloina bifrons	Med	monoicous and lamellae on the upper leaf surface, but a small thallus
Athalamia hyalina (liverwort)	Slow	large spores
Bryoerythrophyllum columbianum	Slow	spores, dioicous
Bryum argenteum	Fast	axillary buds, spores and rhizoidal, and protonemal gemmae
Bryum lanatum	Med	spores only
Bryum caespiticium (syn = *Gemmabryum*)	Fast	spores mostly, and fragmentation
Cephaloziella divaricata (associated with rock and thin soils)	Slow	spores and fragmentation
Ceratodon purpureus	Fast	many spores and limited asexual fragmentation
Didymodon brachyphyllus	Med	multicellular axillary gemmae and spores
Didymodon vinealis	Med	spores
Encalypta vulgaris	Med	lots of spores, monoicous
Funaria hygrometrica	Fast (fastest growing taxa)	many spores, monoicous, more or less a true annual species
Grimmia tenerrima	Fast	spores, monoicous
Pterygoneurum ovatum	Fast	many spores, monoicous
Riccia sorocarpa (liverwort)	Slow	large spores
Syntrichia caninervis	Slow	spores, dioicous
Syntrichia ruralis	Med	spores, dioicous
Tortula brevipes (more common in rock crevices but sometimes on soil)	Fast	spores, monoicous and lots of protonemal gemmae

Table 2. Biocrust species determined to be the most suitable for active restoration projects in many arid habitats, including harsh sites. Common names follow Brodo et al. (2001) for lichens and Rosentreter et al. (2007) for mosses.

Genus and Species	Common Names
Lichens	
Caloplaca tominii	Powdered fire dot lichen
Cladonia fimbriata	Trumpet lichen
Cladonia pocillum	Carpet pixie-cup
Collema tenax (complex)	Soil jelly lichen
Bryophytes	
Bryum argenteum	Silver-tipped moss
Ceratodon purpureus	Red-roof moss, or puzzling moss
Funaria hygrometrica	Fire moss, or cord moss
Pterygoneurum ovatum	Onion moss

Table 3. Biocrust species for increased biodiversity in many arid and semi-arid habitats. These species might require inoculation.

Genus and Species	Common Names
Bryum caespiticium	Tufted bryum
Syntrichia ruralis	Twisted moss
Syntrichia caninervis	Small twisted moss
Diploschistes muscorum	Cowpie lichen
Leptogium lichenoides	Tattered jelly lichen
Placidium spp.	Scale lichens (various species)
Psora spp.	Scale lichens (various species)

For Lichens

- Fast = specialized asexual soredia or isidia, or readily fragments;
- Medium = nonspecialized asexual fragmentation, large spores, pycnidia (asexual spores), legacy (tends to remain at a site even with moderate soil disturbance);
- Slow = spores that must find compatible algal partner, or unknown reproductive method.

For Bryophytes

- Fast = specialized asexual features such as axillary buds, bulbils, gemmae, brood bodies; lots of spores, monoicous. These are considered aggressive species and many of them may occur without active inoculation and are stress tolerant.
- Medium = nonspecialized asexual features, fragmentation, fewer spores, monoicous;
- Slow = spores only, no specialized asexual reproduction, or dioicous reproduction.

Establishment mechanism refers to the plant's life history, size, and abundance of the spores and the chance of legacy or species retention despite disturbance. Cumulative ratings are presented in Table 1. I used this summary of reproductive traits, from Table 1, and the cumulative influence of biological factors, to present to experts for their opinions, to select species for use in restoration (Tables 2 & 3). Biocrust species that grow relatively quickly post-disturbance are identified in Table 1. Asexual reproduction is often faster and less moisture dependent than growing from a small sexual spore. Spores need to be moist for several days before growth starts and may require a filamentous growth stage (protonema) before forming a mature growth form. It is not always a one-to-one relationship, but likely a synergy of factors as well as physiological adaptations that make certain species superior candidates for restoration. The comments from the experts as well as the form and function of each biocrust growth form were also considered.

Table 2 lists the biocrust species rated as the most suitable for use in restoration projects by the author and several taxonomic experts. It includes four lichen species and four moss species. Some of these species have been tested in the lab, but only a few have been field tested (Blankenship et al. 2019; Jones & Rosentreter 2006; Condon & Pyke 2016). Increasing the testing of these species as restoration and rehabilitation species appears to be the most promising for practical application.

Biocrust species that form large colonies and reproduce quickly (Table 2) were chosen over species that occur as small individuals scattered across the landscape, since the goal is for a more continuous carpet of biocrusts between vascular plant interspaces. These species stabilize the soil surface making the soil suitable for colonization by other biocrust species. Therefore, some species were not chosen due to their small size and distribution on the landscape. However, some biologists believe that using both early and later successional species might be appropriate. Table 3 lists biocrust species recommended for increased biodiversity which might not arrive by passive means in arid habitats. These species may need to be actively inoculated, even in semi-arid habitats.

Discussion

Local or regional restorationists can use the species recommended in Table 2 as the core biocrust species for restoration projects. They can also refer to Table 1, and to Table 3, to find other locally occurring biocrust species with medium to fast reproduction to use in their restoration efforts. Knowing what local species are abundant or occur as the dominant biocrust in each region is helpful (Miller et al. 2011). Species rated as slow in their reproduction rate and ease of establishment might be avoided for restoration efforts.

Recommending site-appropriate biocrust restoration species is difficult due to vast differences in geography and climates (Rosentreter et al. 2007; Root & McCune 2012; Mallen-Cooper et al. 2018). Environments vary due to factors such as shade and aspect, timing and amount of precipitation, snow versus rain, soil texture and compaction, all which influence establishment and growth of biocrust species (Rosentreter & Belnap 2001; Ponzetti et al. 2007; Rosentreter et al. 2016). Biocrusts that are actively inoculated must be retained on site and not allowed to blow away, defeating the restoration's purpose. Breaking the boundary layer (wind) of bare ground is critical to improve establishment success. Condon and Pyke (2016) found that merely placing jute netting over the ground increased the establishment and growth of inoculated mosses. Likewise, in natural habitats, vascular plants create windbreaks and shade, greatly influencing moisture retention (Belnap et al. 2001; Rosentreter & Root 2019). Vascular plants also trap leaf litter, keeping the interspaces between the plants free of this organic litter (Rosentreter & McCune 1992). The interaction of biocrusts and clumped vascular vegetation is likely synergistic for their coexistence (Rosentreter et al. 2014; Rosentreter & Root 2019).

Choosing the right species for any given restoration project is a challenge, but consideration of both the reproductive and establishment rates of biocrust species will lead to more successful restoration efforts in the future.

In arid habitats worldwide, biocrust communities are diminishing due to human development, livestock trampling, and increased fire (Mallen-Cooper et al. 2018; Condon & Pyke 2018*a*). With this biocrust decline, their wind-blown propagules also decline, while nonnative plant cover expands. Using biocrusts for restoration and rehabilitation can counteract these challenges (Zhao et al. 2016). However, it is important to select the appropriate species, with rapid and abundant reproduction, and establishment rates, and to ameliorate the environmental conditions for successful biocrust establishment (Condon & Pyke 2016).

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