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A Review of the Contributions by Lichen to Building Soil

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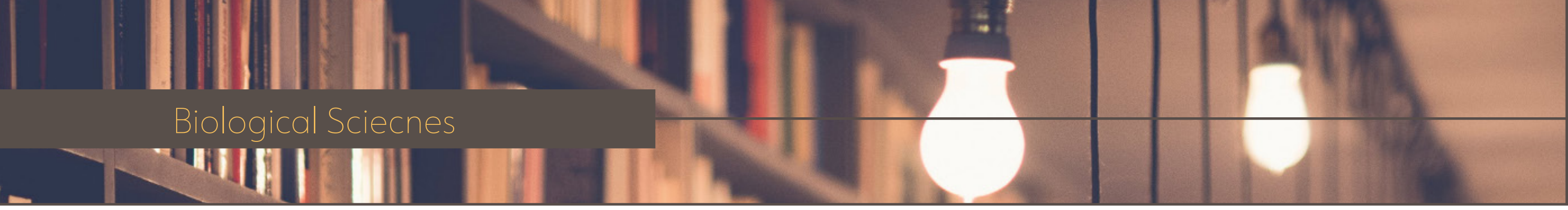
Marie E. Antoine who is the foundation and motivation for my knowledge about lichens.



A Review of the Contributions of Lichen to Building Soil

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Introduction

Lichens have long been implicated as having an important role in the formation of soil and as primary successional pioneers (Plitt, 1927). In fact, lichens are thought to be essential in their role as pioneers, working to make otherwise uninhabitable ground hospitable to tracheophytes and other plants (Cooper, 1953). They are often the first line of biological invasion on bare rock and recent lava flows. This transformation to a landscape habitable by tracheophytes is done primarily through the process of soil formation by lichens. In addition to forming soil, lichens act as intersystem nutrient sinks, contributing to the enrichment of a landscape with minerals and nutrients. Despite lichens' ecologically significant roles, they remain understudied and enigmatic, particularly in comparison to other organisms with similarly important ecological functions. That being the case, this review is intended to organize and present the details that *do* exist in the literature about specific mechanisms and processes relating to soil formation by lichens. Topics covered here include their role in biodeterioration (both physical and chemical), particle entrapment, decomposition, and lichens' broader role as pioneers in the context of soil formation.

Physical Biodeterioration

Perhaps the most intuitive contribution by lichens to soil formation is through physical biodeterioration. Biodeterioration is the process of changing the properties of a material through the action of biological agents—in this case, lichens. Many lichens have rhizines, which are multicellular root-like structures arising mostly from the lower surface of the lichen thallus, or the lichen "body." Rhizines are used to anchor the lichen to a substrate, and they do not play any direct role in nutrient uptake. In the process of anchoring the lichen thallus to its substrate, rhizines probe and explore surfaces of rocks. As lichens go through their normal process of wetting and drying, their rhizines expand and contract with the moisture fluctuation (Adamo and Violante, 2000). This expansion and contraction of their rhizines act like chisels and contribute to the disaggregation and fragmentation of the rock surface below the lichen thallus. Because lichen thalli can expand and contract by up to 300% of their dry weight during wetting, this chisel action can act quite quickly (Creveld, 1981). The disintegrated rock is broken up into smaller fragments, which can either be incorporated into soil or taken up by the lichen thallus (details of which are discussed later in the section about particle entrapment).

Recent lava flows from volcanoes were studied in Mt. Etna in Sicily, Italy and Mt. Vesuvius in Campania, Italy. These lava flows showed that lichens' rhizines do indeed physically weather rocks. At both the Etna and Vesuvius sites, the authors took Scanning Electron Microscope (SEM) and Energy-dispersive X-ray spectroscopy (EDS) images to analyze rock layers beneath lichen thalli. In both cases, the rock substrate was filled with micro-cracks and pores, which were filled with lichen material, suggesting the chisel-like action created the pores in the rocks (Vingiani et al., 2013). This physical weathering by the lichens' rhizines also induces and accelerates other forms of physical and chemical weathering, making the surface more susceptible to erosion and other forms of mechanical weathering (Chen et al., 2000). One example of this is in cold areas, such as the Arctic, where lichens often dominate the biomass of the area. These regions undergo regular freezing-thawing cycles throughout much of the year. Because the rhizines of lichens penetrate relatively deeply in their substrate, water is able to travel down these channels, collecting deep in the rock's surface where it is more difficult to evaporate. Here the water in the perforations will freeze and thaw, and the ice itself will act as an ice-wedge which can chip away at rocks in tandem with the lichen thallus and the rhizines (Creveld, 1981).

Chemical Biodeterioration

While lichens do play a role in the physical weathering of their substrate, they are even more effective agents of chemical weathering (Jackson, 2015). Oxalic acid, a byproduct of lichen metabolism, is secreted by the mycobiont, or fungal component of a lichen, and is thought to be one of the most active agents of chemical alteration of rocks (Adamo and Violante, 2000). Recently, the magnitude of the effect of both oxalic acid and succinic acid on the deterioration of granite in northeast China was studied. To do this, different concentrations of both chemicals were placed on granite. Both oxalic acid and succinic acid induced the weathering of granite by promoting the release of various ions from the stone and increasing the surface's solubility. Oxalic acid had a stronger effect than succinic acid, and the ions that it released included Na+, K+, Al3+, Fe3+, Mg2+, Mn2+, Ca2+, and SiO2− (Song et al., 2019). While the effects of oxalic acid and succinic acid are significant, they are not the only chemicals secreted by lichens that work to weather rocks.

Carbonic acid has also been shown to increase the rates of substrate weathering. Carbonic acid is generated by respiratory CO_2 reacting with water held by lichen thalli. Carbonic acid increases solubilization processes by lowering the pH of the thallus and surrounding environment (Chen et al., 2000). The lowered pH enhances the dissolution process of the substrate. Carbonic acid and H^+ ions from other organic acids were shown to increase leaching of many metal ions from rocks (Jackson and Keller, 1970). Some researchers even argue that substrate dissolution by respiratory CO_2 may be the most important biogenic weathering mechanism on carbonate substrates (Weber et al., 2011).

In addition to the normal biological byproducts that primarily come from the mycobiont of the lichen thallus, the photobiont also contributes to chemical weathering. Specifically, large biological polymers secreted by the photobiont have been implicated in the chemical weathering of rocks. Instead of directly weathering surfaces, these biological polymers, acidic mucopolysaccharides, act as secondary weathering agents and have been shown to increase dissolution rates of mineral substrates in lab experiments. It is likely that the carboxyl groups in these acidic mucopolysaccharides interact with metals in rocks, thereby increasing the mobility of the metals for easier chelation by the lichen (Barker and Banfield, 1996). These high molecular weight polysaccharides also seem to increase chemical weathering by affecting moisture retention on the surface that can increase disintegration (Banfield et al., 1999).

Before the above modes of weathering were discovered, many researchers in the early and mid-1900's thought that a group of weak, insoluble acids called depsides and depsidones produced by lichens were major players in the chemical degradation of rock substrates (Schatz, 1963). This seemed to be a solid line of reasoning, as lichens produce a unique set of secondary compounds. However, since then, it seems to be the general consensus of researchers that most of these acids play only a very minor role, if any, in the chemical weathering of rock. This is due in part to how weak the acids are, but it is primarily a result of these acids being insoluble in water (Culberson, 1970). The only notable exceptions to this are a number of lichen acids that are slightly soluble in water and therefore available to chelate metal from rocks (Williams and Rudolph, 1974). Even with these slightly soluble acids, however, there is no direct evidence to show that they have any significant and direct effect on weathering of substrates.

A cumulative effect of all the above mentioned modes of chemical weathering leads to long-term dissolution of rocks and other hard substrates into soil. The intensity of disintegration as a result of these characteristics is directly related to physical and chemical properties of the rocks that lichens are deteriorating. Important properties that affect the rate and intensity of degradation are compactness, hardness, lamination, or preexisting surface alteration of the rock. Hard, laminated rocks such as granite are difficult for water and rhizines to penetrate while soft, loose rocks such as limestone are easily broken apart and readily dissolve in weak acids. These factors all affect the accessibility of minerals that lichen need to mobilize in order to degrade rock and convert it to soil. The nature of the lichen thallus is also important, as some lichens secrete more of the chemical weathering elements than others (Adamo and Violante, 2000).

Decomposition

Lichens contribute to soil formation by decomposition as well. There are two primary types of decomposition that contribute to the formation of soil: in-situ decomposition and litterfall. In litterfall, lichens fall to the ground where their thalli are decomposed and incorporated into the soil beneath their epiphytic habitat or downstream to where they are carried. In-situ decomposition is when a lichen dies and decomposes where it initially grew. In this case, like a lichen that has colonized a recent lava flow, the thallus may provide the only source of organic material for decomposition. This mode of soil formation is particularly important, ecologically, for a pioneer ecosystem in which not many other organisms can live.

The amount of organic material that lichens can contribute to soil through decomposition is significant. In California it was found that if canopy cover is 100%, then the amount of thallus tissue decomposing and falling to the ground is 1,020 kilograms per hectare (Knops et al., 1996). In addition to contributing organic matter for decomposition, lichen thalli also slow the rate of decomposition of other litterfall. When lichens and *Quercus* leaves decomposed together, leaves decomposed more thoroughly and more slowly than if they were left to compose on their own (Knops et al., 1996). This effect was particularly pronounced in regards to the retention of nitrogen in the soil. Ultimately, lichens not only contribute a significant amount of organic matter themselves, but they also make the products of decomposition of other matter more valuable to the immediate ecosystem.

Additionally, lichens leach chemicals that affect the decomposition process of other organic matter. Laccases and other chemicals that are important in lichen physiology are also likely to play a significant role in humification (Beckett et al., 2013). Humification is the natural process of transforming organic matter into humic substances that are essential biotic components of soil. Part of this process is the production of a number of enzymes including phenol oxidases, peroxidases, and cellulases that are directly involved in organic matter turnover in free-living saprophytic fungi (Laufer et al., 2009; Liers et al., 2011; Yagüe and Estévez, 1988). These same enzymes are also leached by lichenized fungi, and they most likely function in the same way as those leached by their free-living counterparts. Overall, lichens contribute to soil formation through decomposition in a number of ways, including contributing their thalli as biomass to be decomposed, affecting decomposition rates of other organic matter, and by altering the process of decomposition by leaching enzymes involved in decomposition.

Particle Entrapment

In addition to contributing to organic matter through decomposition, lichens also act as a net for particles in the air and from the substrate that eventually get cycled into the ecosystem as usable matter. As lichens break down rocks, they can incorporate minerals from rocks they are deteriorating into their thallus. This phenomenon of capturing particles and incorporating it into the soil is known as particle entrapment. While particle entrapment occurs as a transfer of particulate matter from rock to lichen thallus, it also occurs as entrapment from the air to lichen thallus. This, along with gaseous uptake of various elements, is one of the primary ways lichens contribute to intersystem inputs via soil building and nutrient enrichment. The different modes of particle entrapment (via air versus substrate) are expressed differently and can be measured by comparing mineral concentrations found in the upper versus the lower portion of the lichen thallus. Mineral compositions of the upper and lower cortex of lichen thalli vary quite drastically: the lower cortex particles match elements commonly found in the substrate, while the upper thallus of lichen have a very different composition that likely came from the air (Clark et al., 2001).

Particle entrapment on the upper cortex of lichens was studied in Italy using a number of species native to the area. Mineral composition between coastal and inland lichen was compared. Lichens living near the Mediterranean Sea had higher concentrations of sodium, potassium, and calcium than normally found in their counterparts farther inland (Vingiani et al., 2013). This increase in nutrient concentration is attributed to the wind-blown sea salts off the Mediterranean being incorporated into the lichen thalli. In fact, the composition of sea-salt particles from the Mediterranean matched those being incorporated into the lichen. The bulk of sea-salt crystals in the Mediterranean Sea are composed of halite (the mineral form of $NaCl$) and Mg-K sulphate (Benitez-Nelson, 2006). These crystals alone, then, could explain the source of the majority of the nutrient enrichment seen in the seaside lichens and makes a strong case for this being a result of particle entrapment from the air.

On the other side, particle entrapment by lichens' lower thallus comes from their substrate (Banfield et al., 1999). Particle uptake by the lichen thallus is often the result of chemical and physical weathering of their substrate, as discussed in a previous section. The action of the freeze-thaw cycles, chiseling of the rhizines, and chemical weathering via the byproducts of lichen metabolic processes act to free up minerals from their substrates that are then incorporated into the lichen thallus. In one example of this, many lichens are considered "pruinose," which refers to a white dusting of calcium oxalate on the surface of the lichen cortex and throughout the thallus. This trait is considered diagnostic for many lichen genera, and is caused by lichens breaking down rocks that contain calcium carbonate, such as limestone, and incorporating the products into their thalli (Heiđmarsson and Heidmarsson, 1996).

Researchers have even captured the process of mineral uptake from lichens' substrate through microscopy (Barker and Banfield, 1996). As lichens incorporate minerals into their thallus, the minerals themselves are transformed. Mineral transformation is the process of altering the physical and/or chemical structure of minerals. The exact mechanisms of this process, however, are unknown because they were occurring at a scale beyond the resolution of the microscope used in the study (Barker and Banfield, 1996). So, not only do lichens uptake particulate matter in the form of elements from their substrate, they are also potentially converting it into different forms, which might be more usable by living organisms. This phenomenon of nutrient transformation was also observed in Ontario, Canada. Here, lichens were shown to effectively weather their rock substrate Feldspar, which is a rock-forming tectosilicate group of minerals that make up almost half of the Earth's continental crust. In the process of weathering the stone, lichens transformed the elements from Feldspar to clay minerals and they did so at a much higher rate than bryophytes, which was the other study system (Jackson, 2015). This mineral transformation is one of the key reasons why lichens are so important in ecosystems beyond simple soil building. Lichens are able to transform substances and nutrients from unusable consolidated forms to nutritious bioavailable forms, often in the form of chelated metals (Vingiani et al., 2013).

Ecological Succession

Although all of the evidence above is compelling on its own, taken together they form a clear picture of how ecologically important lichens are as pioneer species that enable succession by "higher plants." To summarize, lichens play a role in building soil via a number of mechanisms including physical and chemical biodeterioration, decomposition (litterfall and in-situ), and particle entrapment. We know, too, that in addition to creating soil, they are able to make nutrients more bioavailable, through the chelation and breakdown of metals in rocks, for example. With all this in mind, it is easy to see how lichens enable succession.

In terms of what succession actually looks like, here is an example from Charles Plitt in *The Bryologist*: bare rock is colonized by microlichens who are nutritionally supported by the air and use the rock simply as a substrate. The microlichens begin to break down the rock ever so slightly, and when they die they decay and leave behind a thin organic layer. This layer is substantial enough that foliose lichens can dig their rhizines in, and they start to physically and chemically weather the rock even further. After a few successive generations of these larger lichens, there is a substantial layer of humus laid down through in-situ decomposition, which becomes suitable for colonization by bryophytes. Bryophytes go through a few successional stages and live for quite a while until their decay and breakdown of the substrate create even more soil, allowing for small herbaceous plants to thrive (Plitt, 1927). By this time, the ecosystem is starting to resemble a more typical terrestrial system, and small shrubs start to pop up and they are eventually replaced by larger, longer-lived tracheophytes. In many cases, lichens and bryophytes will start to grow epiphytically on the larger tracheophytes such as trees. Although this is an idealized, typical model of succession from lichens to tracheophytes, the way this happens varies with the specific environmental conditions of a location. Differences in lichen composition, rate of succession, and whether succession occurs at all, is dependent on many variables including altitude, temperature, moisture, sunlight, and more. In deserts, succession will be much different than in alpine environments. And in some ecosystems, such as the harsh Arctic, succession beyond lichens and some bryophytes may not occur at all unless induced by global climate change (Nascimbene et al., 2017).

That said, there are some scientists who claim that lichens' role in ecological succession is greatly exaggerated, particularly on recent lava flows (Williams and Rudolph, 1974). For example, after the explosion of a volcano (which is what would render new lava flows) there is enough dust and debris from the explosion that lichens are unnecessary for the creation of soil. Surveys taken after a recent explosion found enough debris to be considered soil hidden even deep in the nooks and crannies of lava rock. This soil is hypothesized to be suitable for plant roots and bryophytes (Williams and Rudolph, 1974). Overall, though, particularly in more modern literature, there seems to be a general consensus that lichens *do* play a crucial role in soil formation and succession.

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