



Weathering, secondary mineral genesis, and soil formation caused by lichens and mosses growing on granitic gneiss in a boreal forest environment



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ABSTRACT

Lichens and mosses growing on granitic gneiss in a boreal forest environment caused intense chemical weathering of the rock, producing exclusively biogenic secondary minerals and soils and accumulating solubilised rock-forming elements (Si and metals), but weathering in the absence of these organisms was relatively ineffective. Apart from primary biotite, the only phyllosilicates in the rock were sericite and chlorite formed by hydrothermal metamorphism or abiotic weathering, or both, but the biogenic soils contained expandable clay minerals and, in several cases, kaolinite and calcite, together with illite and chlorite. Lichens were especially effective in altering feldspars to clay, but mosses generally produced a greater abundance of expandable clay minerals, and kaolinite was produced *only* by certain species of moss — specifically the ones whose rock-derived element concentrations and Mg/Ca ratios were highest. Rock-derived element concentrations were usually highest in mosses, and element enrichment increased with the charge/radius ratio of the cation of the element, suggesting carrier-mediated transport across cell membranes. Furthermore, lichens and mosses produced different assemblages of expandable clay minerals, and most mosses (but none of the lichens) produced authigenic amphiboles and pyroxenes. Biological weathering is attributable to solubilisation of rock-forming elements by chelating agents and H_2CO_3 , bioaccumulation of the elements, and nucleation of secondary silicates by chelate complexes functioning as templates for epitaxial growth of specific crystal structures. The different weathering and soil-forming processes of lichens and mosses suggest a mutualistic strategy for maximising the release of inorganic nutrients from rocks and retaining them in bioavailable forms in the soil.

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1. Introduction

Chemical weathering is of key importance to life on Earth. Above all, the process releases essential inorganic nutrients, notably phosphate and various metals (K, Ca, Mg, Fe, Cu, Zn, etc.), from rock and soil minerals, solubilising them and making them available for uptake and utilisation by organisms. Another major ecological function of weathering is the production of colloidal secondary minerals (clay minerals and oxides or oxyhydroxides) which, together with humic and non-humic organic matter, form soils and fine-grained sediments, thereby providing organisms not only with habitats but also with supplies of bioavailable nutrients reversibly bound to ligands and other sorption sites of the colloidal minerals and humic matter. Moreover, the weathering action of carbonic acid (H_2CO_3) formed by the reaction of CO_2 with water, plays a pivotal role in the regulation of the Earth's climates by withdrawing CO_2 from the atmosphere, thereby counteracting the heat-trapping effect of atmospheric CO_2 (Schwartzman and Volk, 1989; Berner, 1995; Schwartzman, 1999; Lovelock, 2009; Lenton et al., 2012).

A large body of empirical evidence has established that the activities of organisms greatly intensify and accelerate chemical weathering and mediate the formation of secondary minerals (Schwartzman, 1999). To begin with, the Biosphere as a whole controls the weathering process to a significant degree by regulating atmospheric CO_2 levels (Schwartzman and Volk, 1989; Berner, 1992, 1993, 1995; Berner et al., 2005; Lenton et al., 2012). Thus, biological withdrawal of CO_2 from the air by photosynthesis, carbonate deposition, and the formation of refractory organic substances (notably humic matter), which accumulate as carbon sinks in soils and sediments (Jackson, 1975), is balanced by the emission of respiratory CO_2 ; moreover, the CO_2 emitted by volcanoes is probably for the most part of a product of the thermal decomposition of biogenic sedimentary organic matter by igneous and metamorphic processes. Hence the “abiotic” weathering action of carbonic acid is, in fact, largely, if not wholly, a consequence of biological activities. However, this universal background process is enormously augmented by much more intense weathering processes mediated by various organisms that inhabit rock surfaces and soils.

Laboratory experiments have demonstrated that bacteria and fungi inhabiting weathered rock surfaces and soils release phosphate and metal cations by solubilising apatite and silicate minerals (Sperber,

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1958; Webley et al., 1963; Duff et al., 1963; Henderson and Duff, 1963; Voigt, 1965; Boyle et al., 1967; Frankel, 1977; Naga et al., 1977; Berthelin, 1983; Robert and Berthelin, 1986; Welch et al., 1999). Similarly, there is evidence that bacteria in groundwater, lake sediments, and mine tailings decompose silicate minerals (Hiebert and Bennett, 1992; Bennett et al., 2001; Bhatti et al., 2011; Jackson et al., 2011) and that bacteria may preferentially colonise particular minerals whose solubilised constituents supply their inorganic nutrient requirements (Bennett et al., 2001; Jones and Bennett, 2014). Among soil microbes, the rhizosphere bacteria associated with the roots of trees and other plants are especially efficient weathering agents, and there are grounds for believing that their relationship with the host plants is mutually beneficial, the plants providing the bacteria with organic nutrients exuded by their roots, whilst the bacteria decompose soil minerals, releasing inorganic nutrients required by the plants (Gerretsen, 1948; Jackson and Voigt, 1971; Ochs et al., 1993; Drever, 1994; Calvaruso et al., 2006; Taylor et al., 2009; Arocena et al., 2012; Parmar and Sindhu, 2013). This raises the possibility that bacteria associated with the pioneer lichens and mosses which inhabit rock surfaces perform comparable functions.

Be that as it may, lichens colonising rock surfaces have been found to enhance enormously the chemical weathering of the rocks on which they grow, and they mediate the formation of distinctive biogenic secondary minerals. Thus, a comprehensive investigation of the chemical weathering and secondary mineral-forming activities of the lichen *Stereocaulon vulcani* growing on basaltic lava flows of known age in wet and dry climatic zones on the Island of Hawaii showed that in regions of high rainfall the lichen [1] accelerated the rate of weathering by orders of magnitude relative to the abiotic weathering of bare rock surfaces, producing conspicuous, relatively thick reddish weathering crusts, and [2] produced copious quantities of an exclusively biogenic form of ferric oxide along with other residual oxides (but no clay minerals, owing to the intensity of the biochemical leaching of silica and metal cations), whereas the ferric oxide produced by abiotic weathering consisted solely of trace quantities of the common mineral hematite which, together with trace quantities of clay minerals, formed an incipient weathering rind that was orders of magnitude thinner than the biogenic weathering crust – so thin, in fact, that it was barely detectable, even under a microscope (Jackson, 1968, 1993; Jackson and Keller, 1970a,b). Detailed analysis employing various techniques established that the biogenic ferric oxide was a mineral previously unknown to science, and its unique crystal structure was attributed to epitaxial growth nucleated by Fe(III) chelate complexes produced by the lichen. This ferric oxide polymorph was subsequently rediscovered elsewhere by others and officially recognised as a new mineral named “ferrihydrite” (Schwertmann and Fischer, 1973; Schwertmann et al., 1986), but the credit for the original discovery of the mineral in nature, the first detailed, systematic investigation of its properties, and appreciation of its biogeochemical significance belongs to T.A. Jackson, as documented elsewhere (Jackson, 1968, 1993; Jackson and Keller, 1970a,b). Subsequent reports by other workers independently confirmed the observation that lichens accelerate chemical weathering and produce biogenic secondary minerals, including ferrihydrite, and corroborated the theory that the weathering action of lichens involves biogenic chelating agents (Jones et al., 1980; Wilson and Jones, 1983; Adamo and Violante, 1991, 2000; Adamo et al., 1993, 1997; Johnston and Vestal, 1993; Hen and Gong, 1995; Chen and Blume, 1999, 2002; Chen et al., 2000; Aghamiri and Schwartzman, 2002; Matthews and Owen, 2008; Zambell et al., 2012). Berner (1992) and Cochran and Berner (1992) put forward the unfounded opinion that the reddish material associated with the Hawaiian lichens consisted of wind-blown dust, but Jackson (1993) proved conclusively that this material was, instead, a weathering crust formed in situ by the lichen, as maintained originally by Jackson (1968) and Jackson and Keller (1970a,b).

Although much attention has been devoted to the weathering of rocks by lichens, hardly any research seems to have been done on the possible weathering action of mosses. However, one study, at least,

produced experimental evidence for enhancement of weathering by a species of moss (Crouch, 2010), and late Ordovician glaciation has been ascribed to a drop in atmospheric CO₂ levels owing to acceleration of chemical weathering due to the evolution of non-vascular plants such as bryophytes (Lenton et al., 2012).

The weathering action of lichens, mosses, fungi, and bacteria is attributable to biological production of weak organic acids as well as carbonic acid. Many of these organic acids solubilise divalent and polyvalent metal cations of minerals by chelation as well as by acid attack. The chelating agents implicated in biologically enhanced weathering include “lichen acids” (an assortment of unique compounds produced by lichens) along with humic and fulvic acids and various common low molecular weight biochemical compounds such as oxalic acid and citric acid; and experimental studies have demonstrated that the effectiveness of these chelators as weathering agents far exceeds that of carbonic acid (Mandl et al., 1953; Schatz et al., 1954; Wright and Schnitzer, 1963; Jackson, 1968, 1975, 1993; Jackson and Keller, 1970a,b; Ong et al., 1970; Huang and Keller, 1970, 1971, 1972; Huang and Kiang, 1972; Schnitzer and Khan, 1972; Jones et al., 1980; Wilson and Jones, 1983; Adamo and Violante, 1991, 2000; Adamo et al., 1993, 1997; Johnston and Vestal, 1993; Chen et al., 2000; Chen and Blume, 2002). Moreover, the theory that biogenic chelate complexes of Fe(III) nucleated the ferrihydrite produced by the lichens that promote the chemical weathering of Hawaiian lava flows (Jackson, 1968, 1993; Jackson and Keller, 1970a,b) has been independently confirmed (Schwertmann et al., 1986). Similarly, experiments have shown that chelate complexes (including fulvic acid complexes) of Al³⁺ may nucleate the formation of kaolinite (Linares and Huertas, 1971; Hem and Lind, 1974).

The purpose of the present study was [1] to investigate and compare the weathering, secondary mineral-synthesising, and soil-forming activities of different species of lichens and mosses which comprised a pioneer community colonising a granitic gneiss outcrop in a boreal forest environment, [2] to compare the effects of weathering and secondary mineral formation in the presence and absence of these organisms, and [3] to assess the ecological implications of the interactions between the organisms and the rock.

2. Field area, materials, and methods

The sampling site was located in the Experimental Lakes Area (ELA) operated by the Canadian government just east of Kenora, Northwestern Ontario, Canada. The ELA is situated on the Canadian Shield within the longitude and latitude ranges 93°30′–94°00′ W and 49°30′–49°45′ N, respectively, at an altitude of 360–380 m above sea level, and it is characterised by cool, humid temperate climatic conditions, boreal forest vegetation, the common occurrence of soils classed as brunisols, an abundance of lakes, Pleistocene till and glacial outwash deposits, and Precambrian bedrock which comprises part of a “pink granodiorite” batholith of Algoman (late Archean) age (Brunskill and Schindler, 1971).

The samples were collected at or near the top of a low, gently sloping outcrop of gneiss located in a clearing surrounded by spruce forest. The gneiss was characterised by pink, predominantly felsic bands alternating with black bands enriched in mafic minerals. Whether it was an outcrop of local bedrock or the exposed top of a large glacial erratic partially buried in finer-grained glacial drift is uncertain, but for the purposes of this paper it makes no difference. The rock had been colonised by different varieties of lichens and mosses underlain by layers of dark brown or black humus-rich soil up to a few centimetres thick. The soil deposits underlying several of the mosses (but none of the lichens) contained abundant sand-sized particles which presumably consisted of quartz and feldspar grains released from the rock by the weathering action of the organisms. In addition, a few scattered clumps of grass and other small vascular plants were growing among the lichens and mosses. The soils occurred solely in association with lichens, mosses, and plants, implying that they owed their existence to biological factors (i.e.,

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