Economic and Ethnic Uses of Bryophytes

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Introduction

A general lack of commercial value, small size, and inconspicuous place in the ecosystem have made the bryophytes appear to be of no use to most people. However, Stone Age people living in what is now Germany once collected the moss *Neckera crispa* (G. Grosse-Brauckmann 1979). Other scattered bits of evidence suggest a variety of uses by various cultures around the world (J. M. Glime and D. Saxena 1991). Now, contemporary plant scientists are considering bryophytes as sources of genes for modifying crop plants to withstand the physiological stresses of the modern world. This is ironic since numerous secondary compounds make bryophytes unpalatable to most discriminating tastes, and their nutritional value is questionable.

Ecological Uses

Indicator Species

Both liverworts and mosses are often good indicators of environmental conditions. In Finland, A. K. Cajander (1926) used terrestrial bryophytes and other plants to characterize forest types. Their value as indicator species was soon supported by A. H. Brinkman (1929) and P. W. Richards (1932). Yet, bryophytes have a somewhat different place in ecosystems than their tracheophyte neighbors.

Several attempts have been made to persuade geologists to use bryophytes for mineral prospecting. R. R. Brooks (1972) recommended bryophytes as guides to mineralization, and D. C. Smith (1976) subsequently found good correlation between metal distribution in mosses and that of stream sediments. Smith felt that bryophytes could solve three difficulties that are often associated with stream sediment sampling: shortage of sediments, shortage of water for wet sieving, and shortage of time for adequate sampling of areas with difficult access. By using bryophytes as mineral concentrators, samples from numerous small streams in an area could be pooled to provide sufficient material for analysis. Subsequently, H. T. Shacklette (1984) suggested using bryophytes for aquatic prospecting. With the exception of copper mosses (K. G. Limpricht [1885–]1890–1903, vol. 3), there is little evidence of there being good species to serve as indicators for specific minerals. Copper mosses grow almost exclusively in areas high in copper, particularly in copper sulfate. O. Mårtensson and A. Berggren (1954) and H. Persson (1956) have reported substrate copper values of 30–770 ppm for some of the copper moss taxa, such as *Mielichhoferia elongata*, *M. mielichhoferi*, and *Scopelophila*.

Although no bryophyte seems to be restricted to substrates containing iron, photosynthesizing bryophytes have the ability to change soluble reduced iron to its insoluble oxidized form and make this molecule visible. A. Taylor (1919) discovered that iron compounds penetrated the tissues of *Brachythecium rivulare* and formed a hard tufa; J. M. Glime and R. E. Keen (1984) found a similar response in *Fontinalis*, where iron oxide completely enveloped the moss in a hard cover. M. Shiikawa (1956, 1959, 1960, 1962) found that the liverwort *Jungermannia vulcanicola* and mosses *Sphagnum* and *Polytrichum* play active roles in deposition of iron ore. Since Japan has few native sources of usable iron, S. Ijiri and M. Minato (1965) suggested producing limonite ore artificially by cultivation of bryophytes in fields near iron-rich springs.

One of the means by which bryophytes sequester both metals and nutrients is to bind them by cation exchange to cell walls of leaves. In this process, *Sphagnum* places hydrogen ions in the water in exchange for cations such as calcium, magnesium, and sodium (R. S. Clymo 1963). Hydrogen ions make the water more acidic, and most peatland ecologists argue that this is the primary means by which bogs and poor fens are made more acidic.

While *Sphagnum* is a reliable indicator of acid conditions, K. Dierssen (1973) found that several other bryophytes successfully indicate other soil conditions. For example, *Ceratodon purpureus* suggests good drainage and high amounts of nitrogen, whereas *Aulacomnium palustre, Pleurozium schreberi*, *Pogonatum alpinum*, and *Pogonatum urnigerum* signal less nitrogen, at least in Iceland. *Funaria hygrometrica, Leptobryum pyriforme,* and *Pohlia cruda* show good base saturation, whereas *Psilopilum laevigatum* indicates poor base saturation and poor physical soil condition.

T. Simon (1975) demonstrated that bryophytes could be used as indicators of soil quality in steppe forests, but their absorption primarily of rain and atmospheric water makes few of them useful as pH indicators. H. A. Crum (1973) considered *Polytrichum* to be a good acid indicator; its ability to live on acid soils may be facilitated by vascular tissue (hydroids and leptoids) in its stem. The rhizoids at its base probably enhance uptake of water and nutrients from soil. *Leucobryum* likewise indicates acid soil, usually combined with dry, infertile, deep humus (T. A. Spies and B. V. Barnes 1985).

Recently, bryophytes have been used as indicators of past climate. Although peatlands and their preserved flora and even their fauna have long revealed the past, we can now use bryophyte assemblages to expose past climatic and hydrologic regimes. Understanding how levels of evaporation and precipitation determine composition of *Sphagnum* communities permits us to use subfossil *Sphagnum* and other moss assemblages to identify past climates (E. A. Romanova 1965; J. A. Janssens 1988). In another example, presence of such drought-tolerant species as *Tortella flavovirens* in subfossils indicates past dry climatic conditions in some areas of the Netherlands (H. Nichols 1969; J. Wiegers and B. Van Geel 1983).

Similarly, our understanding of past vegetation is enhanced by information about past bryophyte assemblages. L. F. Klinger et al. (1990) have suggested that in the Holocene, succession went from woodland to peatland, with peat serving as a wick to draw up water and raise the water level, causing woodland roots to became water-logged. In New England, N. G. Miller (1993) used bryophytes to support conclusions that the flora during 13,500 to 11,500 BP had been tundra-like vegetation similar to that presently in the Arctic.

Erosion Control

Although legumes with their nitrogen-fixing symbionts are usually planted to secure areas devoid of topsoil, H. S. Conard (1935) suggested that sowing spores and vegetative fragments of bryophytes on bare areas could help to prevent erosion. In his home state of Iowa, Conard found that *Barbula, Bryum,* and *Weissia* were important pioneers on new roadbanks, helping to control erosion there before larger plants became established. The protonemata that develop from both fragments and spores form mats that cover and bind exposed substrates (W. H. Welch 1948). In Japan, *Atrichum*, *Pogonatum*, *Pohlia*, *Trematodon, Blasia*, and *Nardia* play a role in preventing erosion of banks (H. Ando 1957). Even areas subject to trampling, such as trails, may be protected from erosion by trample-resistant bryophyte taxa, and by those with high regenerative ability (S. M. Studlar 1980).

On the other hand, when bryophytes such as *Sphagnum* reach water saturation, they can suddenly release a great load of water at unexpected times. Because of its tremendous water-holding capacity, *Sphagnum,* along with *Calliergon sarmentosum,* controls water during spring runoff in the Arctic (W. C. Oechel and B. Sveinbjornsson 1978). When *Sphagnum* is saturated and the layer above the permafrost melts, mosses suddenly permit a vast volume of water to escape all at once, creating problems for road-building engineers.

Nitrogen Fixation

Nitrogen is often a limiting nutrient for plant growth, especially in agriculture. Bryophyte crusts, endowed with nitrogen-fixing Cyanobacteria, can contribute considerable soil nitrogen, particularly to dry rangeland soils. Some of these Cyanobacteria behave symbiotically in *Anthoceros* (D. K. Saxena 1981), taking nitrogen from the atmosphere and converting it to ammonia and amino acids. The excess fixed nitrogen is released to the substrate where it can be used by other organisms. K. T. Harper and J. R. Marble (1988) found that bryophyte crusts not only help protect soil from wind and water erosion, and provide homes for nitrogen-fixing organisms, but they facilitate absorption and retention of water as well.

FIGURE 6. *Polytrichum juniperinum* is an ubiquitous, tall moss that holds soil in place, looks like a small tree in a dish garden, and is strong enough to make brooms, baskets, and door mats. Photo by Janice Glime.

U. Granhall and T. Lindberg (1978) reported high nitrogen fixation rates (0.8–3.8 g m^{-2} y^{-1}) in *Sphagnum* communities in a mixed pine and spruce forest in central Sweden; thus bryophytes, as substrate for nitrogen-fixing organisms, are important to the forestry industry. In *Sphagnum*, and probably other taxa as well, three types of nitrogen-fixing associations exist: epiphytic Cyanobacteria, intracellular Cyanobacteria, and nitrogen-fixing bacteria (U. Granhall and H. Selander 1973; U. Granhall and A. V. Hofston 1976). Nitrogen-fixing Cyanobacteria of bryophyte species also provide growth enhancement for oil-seed rape, the supply plant for canola oil (D. L. N. Rao and R. G. Burns 1990).

Pollution Studies

Bryophytes have played a major role in monitoring changes in the Earth's atmosphere. Working in Japan, H. Taoda (1973, 1975, 1976) developed a *bryometer*, a bag of mosses that respond in predictable ways to various levels of air pollution. By exposing a variety of mosses to various levels of SO_2, he determined that most species are injured by 10–40 hours of exposure at 0.8 ppm SO_2, or at 0.4 ppm after 20–80 hours. Since that time, use of the bryometer has spread around the world, but has been of especial value in Europe, where it has also been known as a moss bag. In Finland, A. Makinen (unpubl.) used *Hylocomium splendens* moss bags to monitor heavy metals around a coal-fired plant. D. R. Crump and P. J. Barlow (1980) have likewise used the method to assess lead uptake.

SO_2 and Acid Rain

While North Americans have apparently not adopted the bryometer per se, they began using bryophytes for monitoring relatively early. In 1963, A. G. Gordon and E. Gorham published what seems to be the first North American study on the effects of pollutants on mosses, examining a site suffering from SO_2 emissions at about 100,000 tons per year from 1949 to 1960. Using transects radiating from the source, they found that the first mosses to appear with increasing distance from the source, namely the tolerant *Dicranella heteromalla* and *Pohlia nutans*, were at the bases of trees.

Appreciation of mosses as reliable indicators has grown (T. H. Nash and E. H. Nash 1974; O. L. Gilbert 1989). Gilbert (1967, 1968) found that SO_2 could limit distribution, reproductive success, and capsule formation in mosses. In 1969, he published the successful use of *Grimmia pulvinata* as an SO_2 indicator in England. Others followed with similar applications of other bryophytes in Europe (S. Winkler 1976) and North America (M. B. Stefan and E. D. Rudolph 1979).

As monitoring studies continued, researchers developed a list of tolerant and intolerant species that could be used as indicators. In Japan, H. Taoda (1972) used epiphytic species to assess pollution impact in the city of Tokyo. He divided the city into five zones, based on pollution intensity, and listed four groups of bryophytes (both mosses and liverworts) in order of increasing sensitivity to SO_2: (1) *Glyphomitrium humillium*, *Hypnum yokohamae*; (2) *Entodon compressus*, *H. plumaeforme*, *Sematophyllum subhumile*, *Lejeunea punctiformis*; (3) *Aulacopilum japonicum*, *Bryum argenteum*, *Fabronia matsumurae*, *Venturiella sinensis*; (4) *Haplohymenium sieboldii*, *Herpetineuron tocceae*, *Trocholejeunea sandvicensis*, *Frullania muscicola*. Later, Taoda (1980) used three liverworts (*Conocephalum supradecompositum*, *Lunularia cruciata*, *Marchantia polymorpha*) to assess the degree of urbanization in Chiba city near Tokyo. In Europe, K. Tamm (1984) used epiphytes, and these natural assemblages became quite popular as a means of assessing air pollution.

Mosses exposed to SO_2 fumigation exhibit reductions in coverage. However, it is difficult to determine if the damage is due directly to the sulfur dioxide or if it is the result of the ultimate formation of sulfuric acid. When SO_2 dissolves in water, it ultimately forms sulfuric acid, which dissociates to form free hydrogen ions, making the water acid. In the cell, these hydrogen ions can replace the magnesium of the chlorophyll molecule, destroying it. Mosses that are tolerant of an acid environment must have a means of protecting their chlorophyll from that degradation or of preventing the dissociation. For example, some mosses (e.g. *Dicranoweisia*) change SO_3^{-2} into a harmless sulfate (SO_4^{-2}) salt (W. J. Syratt and P. J. Wanstall 1969). High chlorophyll concentration seems also to help protect this moss.

Since different species have different sensitivities to contaminants, a change in species composition can be indicative of changes in atmospheric conditions. In some areas, the acidification of bark from acid rain has resulted in the growth on bark of species that are normally confined to acid rocks (A. J. Sharp, pers. comm.).

Acid rain, resulting from SO_2 emissions, can actually improve conditions for *Pleurozium schreberi* in some Jack pine (*Pinus banksiana*) forests (G. Raeymaekers 1987). *Pleurozium schreberi* grew faster and increased in cover when sprayed with water acidified to pH 4.5. In fact, habitats of *P. schreberi* in nature tend to be rather acid. However, at pH 3.5, its growth and chlorophyll content were reduced and capsule production decreased. Similarly, in boreal forests *Hylocomium splendens* and *Ptilium crista-castrensis* can replace the somewhat pollution-sensitive *Pleurozium schreberi* when SO_2 stress increases, but closer to the pollution source these species disappear as well (W. E. Winner and J. D. Bewley 1978).

A pH as low as 3.5 is not uncommon in acid fog. While acid rain may favor some bryophytes, acid fog can be more damaging. In areas like the California coast, Isle Royale National Park, or most parts of Great Britain, severe damage can occur during the frequent fogs because tiny droplets of water may have a high sulfur content, often resulting in very low pH. When these droplets rest on one-cell-thick bryophyte leaves, the high acid content can readily affect the cell's interior.

Not only can bryophytes serve as warning systems, but they can protect the nutrients and roots beneath them. By intercepting sulfate ions, they prevent formation of sulfuric acid that contributes to leaching valuable nutrients from soil (W. E. Winner et al. 1978). This benefits not only mosses, but tracheopytes that depend on soil nutrients.

During atmospheric precipitation episodes, bryophytes serve as filters before water reaches the soil, trapping dissolved pollutants washed from trees. Mosses exposed to long, dry periods usually are not damaged by SO_2 during those dry periods, but SO_2 dissolved in rain or fog will readily damage rehydrating bryophytes. This is due to damaged membranes that now readily admit acidic water (resulting from dissolved SO_2), which in turn easily dissolves the more soluble cell contents and leaches them out of the leaf. Loss of very soluble potassium and magnesium quickly occurs, and the moss becomes pale, an easily observed symptom of damage. Without magnesium, the damaged chlorophyll cannot be repaired.

Bioindicators of Heavy Metals in Air Pollution

The First European Congress on the Influence of Air Pollution on Plants and Animals strongly recommended the use of cryptogamic epiphytes as biological pollution indicators (O. L. Gilbert 1969). The Europeans were among the first to practice this recommendation. There, bryophytes have been used to monitor airborne pollution caused by emissions from factories. In 1981, J. Maschke cited countries throughout the industrialized world where bryophytes were used as indicator species. Further evidence supports the contention that absence of epiphytic

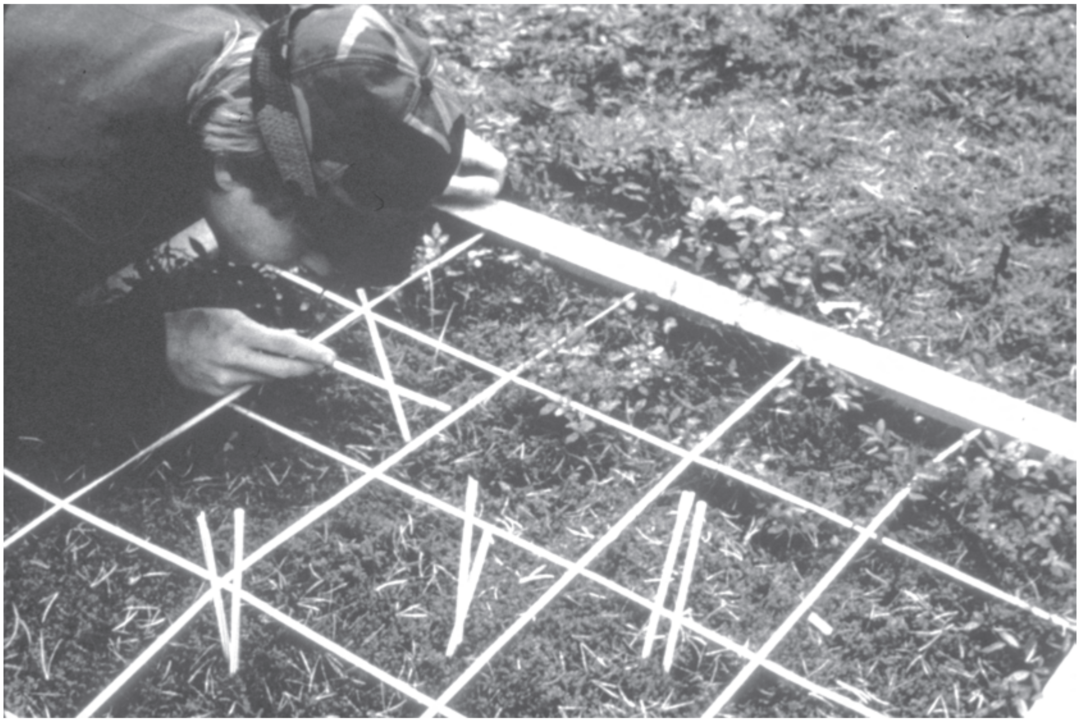

FIGURE 7. *Pleurozium schreberi*, a common component of boreal forests, produces fewer capsules when treated with simulated acid rain (pH 2.5). Photo by Geert Raeymaekers, Ecosystems, Brussels.

mosses, lichens, and most liverworts from urban areas is strongly correlated with air pollution (J. J. Barkman 1958; E. Skye 1965; Gilbert 1967, 1968; H. Lundstrom 1968; D. L. Hawksworth and F. Rose 1970; F. Arnold 1891–1901). For example, Barkman (1969) found that 15% of the bryophyte flora of the Netherlands had been lost by the time of his publication. Further investigations made in cities in Europe and North America showed that air pollutants affect growth and reproduction of bryophytes and lichens (D. N. Rao and F. LeBlanc 1967; Lundstrom; LeBlanc 1969; Hawksworth and Rose; U. Kirschbaum et al. 1971; LeBlanc et al. 1971; S. Winkler 1976; Rao et al. 1977; W. E. Winner and J. D. Bewley 1978; Winner et al. 1978; P. Ferguson and J. A. Lee 1978; Rao 1982).

Lack of significant cuticle or epidermis and leaves being only one cell thick make mosses and liverworts particularly well suited as bioindicators and biomonitors. Because of this construction and lack of a well-developed conduction system, most bryophytes absorb both nutrients and pollutants directly from the atmosphere. Thus, effects are not ameliorated by the soil as they are in tracheophytes. Furthermore, the perennial habit of most bryophyte taxa permits accumulation while most tracheophyte taxa are inactive.

Bryophytes readily absorb heavy metals without the regulation characteristic of their nutrient absorption. The ability of many bryophytes to sequester heavy metals while remaining unharmed makes them good biomonitors. For example, *Marchantia polymorpha* accumulates lead (D. Briggs 1972) and *Calymperes delessertii* is a good monitor for aerial lead and to a less extent copper (K. S. Low et al. 1985). *Pottia truncata*, *Polytrichum ohioense*, *Dicranella heteromalla*, and *Bryum argenteum* are very tolerant of high tissue levels of cadmium (610 ppm), copper (2,700 ppm), and zinc (55,000 ppm) (E. H. Nash 1972). *Hypnum cupressiforme* accumulates three times as much zinc, copper, and cadmium as do lichens or seed plants (W. Thomas 1983). One advantage of using bryophytes over other analytic methods is that bryophytes can easily be stored in an herbarium and analyzed later; in fact, historic records can be obtained by using old herbarium specimens because of the habit of most herbarium curators to store bryophytes in packets that protect them from additional pollution that might be present in the herbarium.

Differences in metal uptake by mosses between sites will depend upon the array of metals present and reflect differences in adsorption affinities: adsorption of copper and lead is greater than that of nickel, which is greater than that of cobalt, with zinc and manganese experiencing