Economic and Ethnic Uses of Bryophytes

Janice M. Glime

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

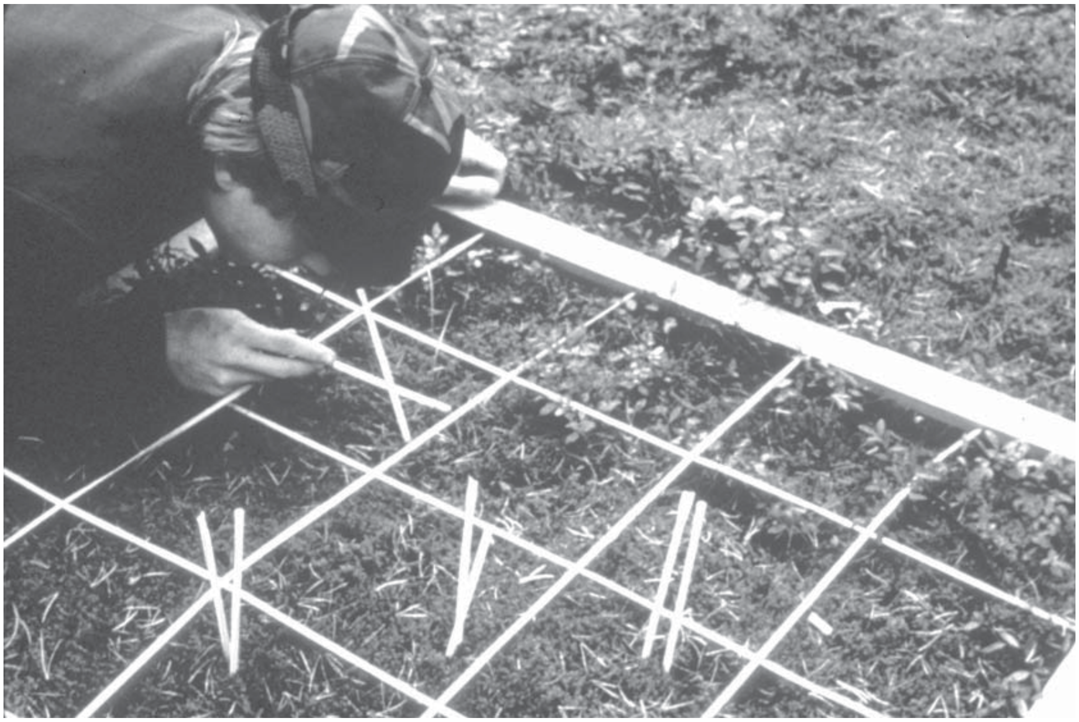

FIGURE 7. *Pleurozium schreberi*, a common component of boreal forests, produces fewer capsules when treated with simulated acid rain (pH 2.5). Photo by Geert Raeymaekers, Ecosystems, Brussels.

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 the least adsorption among these (A. Rühling and G. Tyler 1970). High concentrations of copper may actually block adsorption of manganese and iron to such a degree that mosses can suffer deficiencies of these nutrients.

Bryophytes have a variety of means by which they can sequester substances that are toxic to many higher plants and animals (K. Satake et al. 1989b). These may be bound to cell walls through cation exchange, bound within cells in vesicles that protect the cellular metabolism from interference, located in electron-dense particles in cells or cell walls, or combined with other elements as insoluble compounds, thus rendering them harmless.

For some terrestrial mosses, concentration varies strongly with season. B. Markert and V. Weckert (1989) found that concentrations of cadmium, copper, lead, and zinc in *Polytrichum formosum* decreased in spring due to greater productivity and the dilution effect of growth. The highest concentrations of copper occurred in winter. They recommended September as the best season for measurements.

In Germany, Canada, and other countries, bryophytes have been transplanted from pollution-free areas to areas suspected of pollution damage and observed (F. LeBlanc and D. N. Rao 1973). This method is especially appropriate for epiphytic (L. Rasmussen 1977) and aquatic (J. Martínez-A. et al. 1993) bryophytes. H. C. Greven (1992) espoused retaining a mossy thatch rather than a clean one for similar monitoring purposes.

Other Air Pollutants

Although most of the work on bryophytes has concentrated on heavy metals, sulfur dioxide, and acid rain, bryophytes are useful monitors for other types of air pollution as well. Among these are hydrogen fluoride and ozone. *Orthotrichum obtusifolium* is sensitive to hydrogen fluoride (F. LeBlanc et al. 1971, 1972), whereas *Polytrichum commune*, *Polytrichum strictum*, and *Racomitrium* are tolerant of fluoride fumes (B. A. Roberts et al. 1979).

Few ozone studies have included bryophytes. Recently, however, Z. E. Gagnon and D. F. Karnosky (1992) have shown that *Sphagnum* species are especially susceptible to ozone, having reduced photosynthesis, reduced growth, loss of color, and symptoms of desiccation, but that there are some remarkable reactive differences among species. L. Potter et al. (1996) found that of four *Sphagnum* species studied, only *S. recurvum* suffered damage at 150 ppb, as measured by membrane leakiness and loss of CO_2 assimilation. *Sphagnum angustifolium*, in a separate study, likewise suffered increased membrane permeability, while *Sphagnum magellanicum* showed neither membrane leakage nor pigment loss at concentrations up to 150 ppb (R. Niemi et al. 2002). J. A. Lee et al. (1998) concluded that well-hydrated bryophytes may not be particularly sensitive to ozone at concentrations likely to occur in the atmosphere. Elevated ozone had no effect on germination of *Polytrichum commune* spores at concentrations of 11, 50, 100, and 150 ppb (A. Bosley et al. 1998), but it stimulated protonematal growth at 50 ppb and gametophore area increased to 189, 173, and 125% of the controls at 50, 100, and 150 ppb, respectively, compared to that at ambient concentrations (R. L. Petersen et al. 1999).

UV-B Radiation

The moss *Bryum argenteum* is being used to monitor the thickness of the ozone layer over Antarctica (L. Hedenäs 1991). As the ozone layer decreased, increased exposure to UV-B radiation stimulated production of flavonoids in this species. But, as with ozone exposure, responses vary considerably among species. In *Sphagnum magellanicum* there were no significant differences in chlorophyll or carotenoid concentrations following UV-B exposure; nevertheless, exposure increased its growth in height without a corresponding increase in voltric density, resulting in no effect on biomass (P. S. Searles et al. 2002). Unlike *S. magellanicum*, *Syntrichia ruralis* var. *arenicola* experienced a significant reduction in length increase of both its main and side shoots, but it likewise had no increase in UV-B-absorbing compounds under a UV-B increase equivalent to that occurring with a 15% reduction in ozone (N. V. J. de Bakker et al., unpubl.). Under the same UV-B conditions, *Sphagnum fuscum* experienced a 20% decrease in height increase the first year and 31% the second year, but unlike the previous taxa, it increased its stem dry mass per unit length by 21% and 17%, respectively (C. Gehrke 1998). Interestingly, its dark respiration had a significant decrease of 31%.

S. J. Wilson et al. (1998) reported that, in the presence of adequate water, growth of *Hylocomium splendens* in Norway was strongly stimulated by UV-B equivalent to 15% reduction in ozone, yet C. Gehrke (1999), also working in Norway, found that stem elongation of *H. splendens* became suppressed during the second growing season. In the latter study, *Polytrichum commune* elongation decreases were not apparent until the third growing season. Nevertheless, a decrease in dry mass production was evident all three years in *H. splendens*, while leaf density along the stems of *P. commune* increased, stunting the shoots. *Polytrichum commune* also exhibited a decrease in concentration of UV-B-absorbing compounds after the third year. T. M. Dale et al. (1999) suggested that the genetic variation seen in *Hennediella heimii* in southern Victoria Land, Antarctica, could be a product of genetic mutation as a result of high levels of UV-B radiation.

Radioactivity Indicators

Because of their ability to sequester minerals yet remain unharmed, bryophytes are good indicators of accumulated radioactivity (I. A. Poliakov et al. 1962; G. K. Svensson and K. Liden 1965; N. E. Whitehead and R. R. Brooks 1969; J. Y. Hébrard et al. 1972; P. J. Beckett et al. 1982; T. J. Summerling 1984). N. V. Kulikov et al. (1976) found that the uptake of radioisotopes by epigean mosses occurs not so much from substrates as directly from atmospheric fallout. Because of its cation exchange activity, W. Fischer et al. (1968) suggested that *Sphagnum* could be used to decontaminate water containing radioactive materials.

Aquatic Bioindicators

Bryophytes are particularly useful as monitors in aquatic habitats. Their biggest advantage is an ability to integrate pollution over time and keep a record that cannot be obtained through testing of water chemistry since their contaminant content is more consistent than that of the sediments. J. A. Erdman and P. J. Modreski (1984) found that *Warnstorfia* (*Drepanocladus*) *fluitans* concentrated up to 35,000 µg g^{-1} copper, compared to 1700 µg g^{-1} in the sediment. Furthermore, death is slow, as is release of accumulated substances, permitting bryophytes to retain their toxic load long after death (P. Pakarinen 1977). They are easy to collect and transplant, can be harvested any time of year, and samples can be kept many years for later analysis. Suitable species include *Fontinalis* spp., *Leptodictyum riparium*, *Platyhypnidium riparioides*, and *Scapania undulata*. K. Satake et al. (1989) have identified *S. undulata* surviving at the low pH of 3.9, and it is a very useful accumulator for zinc, lead, and cadmium (H. T. Shacklette 1965, 1965b; R. F. Prigg and G. B. J. Dussart 1980) in nutrient-poor water.

Accumulations differ in different parts of moss plants. M. Soma et al. (1988) found that aluminum, manganese, copper, zinc, and lead were in higher concentrations 1–3 cm below growing stem tips than at tips of *Pohlia ludwigii*, but sodium, phosphorus, calcium, and iron differed little between the 1 cm tip portion and lower parts. The higher concentration of some minerals in older parts may be due to coatings of iron and manganese oxides on leaves and stems, thus increasing adsorption of other metals (G. D. Robinson 1981), to greater exposure time of older leaves, or to greater permeability of older leaves, providing access to interior cell-wall binding sites. Other differences may relate to the ability to transport materials from one part of the plant to another, particularly in *Sphagnum* and in other upright, emergent mosses.

One of the greatest advantages offered by mosses is their ability to aid in the cleanup of some contaminants. At low concentrations of phenol (50 mg phenol dm^{-3}), *Fontinalis antipyretica* can decompose 32–43% of the phenol, and *Platyhypnidium riparioides* 20–27% (A. Samecka-Cymerman 1983). The ability to decompose phenol decreases as concentrations increase, and at 50 mg dm^{-3}, apical growth of the moss is diminished. J.-P. Frahm (1976) found *Fontinalis antipyretica* to be intolerant of four weeks of exposure to 0.02 mg l^{-1} phenol, whereas *Leskea polycarpa*, *Leptodictyum riparium*, and *Fissidens crassipes* were tolerant of 0.08 mg l^{-1} for the same time period, suggesting that these may be even better cleanup organisms. The aquatic bryophyte *Cinclidotus danubicus* is a good accumulator of polychlorinated biphenyls (PCBs) (C. Mouvet et al. 1985).

Bryophytes are not always sensitive to pollutants at levels that would harm other organisms. J. M. Glime and R. E. Keen (1984) found that *Fontinalis* could survive 35 µg cadmium per liter of water, whereas waterfleas and salmonid fish die at 1.2 µg l^{-1}. On the other hand, these aquatic mosses could be used to monitor both cadmium and PCB's because of their high accumulation ability (C. Mouvet et al. 1986).

In some cases, pollution actually increases the cover of bryophytes. N. Takaki (1976, 1977) found that the river bryophytic flora began to appear at a station where the river water quality deteriorated due to pollution from Japanese villages, industries, or mines. In an Alaskan stream, *Hygrohypnum ochraceum* and *H. alpestre* increased extensively in reaches of the stream fertilized with phosphorus (W. B. Bowden et al. 1994).

Treatment of Waste

Bryophytes show great promise for cleaning up toxic waste. Peat mosses (*Sphagnum*) are even more suitable than other kinds of mosses (J. L. Brown and R. S. Farnham 1976; J. A. Taylor and R. T. Smith 1980). Some projects have diverted sewage waste through peatlands, and others have used it to clean up factory effluents containing acid and toxic heavy metal discharge, detergents, and dyes (V. J. P. Poots et al. 1976). B. Coupal and J. M. Lalancette (1976) suggested using it not only to remove unwanted metal, but to retrieve metal for reuse by first bringing peat in contact with metal-containing waste, drying the moss by mechanical pressure, then burning the peat to retrieve the metal. They claimed that this process is economical for developing countries.

Even microorganisms have been cleaned up by *Sphagnum* (A. Rozmej and A. Kwiatkowski 1976), perhaps due to the antibiotic properties of peat. C. K. Lee and K. S. Low (1987) also found the moss *Calymperes delessertii* to be an efficient adsorbent for dye, with the rate being determined by a combination of surface adsorption and diffusion within the moss. Peat is especially effective at removing nitrogen (96%) and phosphorus (97%) applied from eutrophic river water or sewage (H. A. Crum 1988).

Even large oil spills have been contained by floating fences of peat (F. D'Hennezel and B. Coupal 1972); peat has likewise been used to clean waste water containing oil (D. Asplund et al. 1976). In Canada and Finland, researchers are exploring the possibility of using peat as a filter agent for oily waste in vegetable oil factories (M. Ruel et al. 1977). One advantage of using mosses for oil clean up, especially on land, is that at least some mosses are able to live in the presence of oil. J. Belsky (1982) found that in a subalpine meadow, *Racomitrium sudeticum* survived a diesel oil spill and ultimately made the area green again.

The highly toxic pentachlorophenol (PCP) is readily adsorbed by *Sphagnum* peat. Tests show that, at concentrations of 1 mg l^{-1}, 91% of the PCP is removed in five hours at the optimum pH of 3–3.5. The adsorption is essentially irreversible, making peat an effective and inexpensive means of removing such toxicants (T. Virarghavan and S. Tanjore 1994).

In Poland, peat proved to have a favorable effect on recultivation of brown and hard coal ash, resulting from increased microorganisms and nutrient availability, producing a higher crop yield (E. Biernacka 1976). *Sphagnum* is also being sold for reclaiming strip-mined land.

Peat has been considered a possible material for filtering water for reuse in space travel (H. A. Crum, pers. comm.). It could be cultivated so that fully used peat could be replaced by new growth. Although it is capable of growing only a few centimeters per month, its tremendous absorptive abilities may compensate for this slow growth limitation.

Horticultural Uses

Horticulture enjoys a long tradition involving bryophytes (F. Perin 1962; C. B. Arzeni 1963; L. Adderley 1964) as soil additives, ground cover, dwarf plants, greenhouse crops, potted ornamental plants, and for seedling beds (H. Sjors 1980). *Sphagnum* is used in making totem poles to support climbing plants (at the Mossers Lee Plant, horticultural supplier) and moss-filled wreaths, popular in southeastern U.S. Other decorative horticultural uses include making baskets and covering flower pots and containers for floral arrangements (J. H. Thomason 1994), and one company advertises a birch-bark pedestal topped by a moss globe.

Nurserymen typically use wet *Sphagnum* for shipping live plants. A lesser known use of *Sphagnum* in horticulture is that of burning it to produce a smoke screen against frost (J. W. Thieret 1954).

Soil Conditioning

Mosses are often used to condition the soil. Coarse-textured mosses increase water-storage capacity, whereas fine-textured mosses provide air spaces (I. Ishikawa 1974). Mosses improve the nutrient condition by holding nutrients, especially those borne by dust and rainfall, and releasing the nutrients slowly over a much longer period of time than normal nutrient residency near the soil surface (J. M. Stewart 1977; J. O. Rieley et al. 1979). V. R. Timmer (1970) contended that mosses accumulate potassium, magnesium, and calcium from rainfall, but that they do not compete for phosphorus in soil. These trapped nutrients may then be released slowly from mosses to soil. When mosses become dry, their cell membranes suffer damage, so when the moss is rehydrated, it becomes leaky (J. D. Bewley 1974, 1979; R. K. Gupta 1977). It generally takes about a day to repair this damage, and during that time, the moss can leak its more soluble contents (e.g., potassium), thus providing some of these nutrients to plant roots during early stages of rainfall (W. L. Peterson and J. M. Mayo 1975; T. J. K. Dilks and M. C. F. Proctor 1976; Proctor 1981).

N. G. Miller (1981) found that bryophytes increase the buffering capacity of soil, particularly against the changes normally caused by addition of fertilizer. The slow decomposition of many bryophyte taxa makes them suitable for long-lasting mulch. When *Sphagnum* is spread over the ground or mixed with soil, it retains moisture and prevents weed growth; it also discourages damping-off fungi (H. Miller and N. G. Miller 1979). Peat mosses mixed with fish-processing wastes provide a compost superior to sawdust and wood shavings in conserving nitrogen, but it is also more expensive (P. H. Liao et al. 1995).

Culturing

Mosses are especially good for special purposes such as growing ferns (e.g., the moss *Octoblepharum albidum*) (C. B. Arzeni 1963) and orchids (e.g., *Camptothecium arenarium*, *Hypnum imponens*, *Leucobryum* spp., *Rhytidiopsis robusta, Thuidium delicatulum*) (F. Perin 1962; L. Adderley 1964). In the Manila area, *Leucobryum* is substituted for peat moss and induces good root sprouts on orchid cuttings (B. C. Tan 2003). Sungrow, Inc., has had a multi-million-dollar contract with the Campbell (soup) corporation to grow better mushrooms using a *Sphagnum* mix (N. G. Miller 1981; D. H. Vitt, pers. comm.).

Sphagnum seems to be essential in air-layering. The moss is tied or wrapped with plastic around the stems of a plant to retain moisture, encouraging the development of adventitious roots. G. B. Pant (1989) reported the use of such padding for grafting fruit trees. He also contended that *Begonia* and *Fuchsia* bud and flower more profusely if their pot has a layer of moss to separate the humus-rich top and the bottom soil. In Japan, fragments of *Hypnum plumaeforme, Leucobryum bowringii*, *L. neilgherrense*, and occasionally *L. scabrum* are mixed with sand or soil to cultivate *Rhododendron* shrubs (H. Ando 1957).

Seed Beds

Bryophytes as seed beds present both advantages and problems, often promoting seed germination, but inhibiting seedling survival. In Nova Scotia, pioneering white spruce (*Picea glauca*) germinates most prolifically in carpets of *Polytrichum* (G. E. Nichols 1918). On the other hand, a *Polytrichum* and *Cladonia* mat is too dense for aspen (*Populus*) seed penetration; germination is unsuccessful because the moss and lichen mat absorbs water too quickly to allow sufficient soaking of seeds, and frequent wetting and drying of surface soil causes the few successful seedlings to heave (F. C. Gates 1930). In fact, moss has been considered a “pest” when growing in containers of conifer seedlings, where it chokes young seedlings, competes for nutrients, and deprives soil of water (W. A. Haglund et al. 1981). One of the problems seems to be that, in soils with low water content, *Sphagnum* peat has a high affinity for water, providing poor hydraulic conductance for seedlings (P. Y. Bernier et al. 1995); and shoot water potentials are lower than those obtained in sand or sandy loam (Bernier 1992). For trees that develop roots slowly, like *Picea mariana*, roots are too short to reach into soil beyond the moss to obtain water (S. C. Grossnickle and T. J. Blake 1986). On the other hand, in prairie soils, cryptogamic crusts enhance seedling establishment (L. L. St. Clair et al. 1984).

Sphagnum extracts induce germination of Jack pine (*Pinus banksiana*) seeds (R. L. Cox and A. H. Westing 1963) and aqueous extracts of *Polytrichum commune* and *Sphagnum* spp. stimulate growth of *Larix* (tamarack) seedlings. Extracts of these same two mosses, on the other hand, inhibited the growth of other pine (*Pinus*) and spruce (*Picea*) seedlings. Some of this control of germination may be due to the production of indole acetic acid by the moss (Cox and Westing), but under natural conditions it is doubtful if this internal hormone would affect other plants. However, when extracts of ground mosses are supplied, differing effects are found with various plant species.

Most larger mosses, forming deep mats, reduce seedling success. For example, *Pleurozium schreberi* encourages germination of conifer seeds, but the seedlings seldom survive to a second year (R. T. Brown 1967). This seems to be the result of short seedling height that makes it impossible for them to compete with taller mosses for light, or seeds germinate in the mat too far above the soil and are unable to obtain sufficient water and nutrients through their roots. Conversely, P. J. Keizer et al. (1985) found that increased bryophyte cover decreased successful seedling emergence of chalk grassland forbs, but increased seedling survivorship. B. F. van Tooren (1990) suggested that the low red/far red light ratio under bryophyte cover reduced successful emergence, whereas H. J. During (1990) suggested that survivorship may be enhanced by release of nutrients from mosses during summer.

But there are less ambiguous success stories for moss as a seed bed. In the Killarney Oakwoods of Ireland, *Rhododendron ponticum* is spreading, largely due to an increase in bryophyte cover as a result of over-grazing (J. R. Cross 1981). Mosses provide necessary humidity for germination, and seedlings are not eaten because of moss unpalatability and provision of “safe sites” within the moss. Similar protection has been observed in Dutch chalk grasslands (B. F. van Tooren 1988). M. Equihua and M. B. Usher (1993) found that *Calluna vulgaris* grew better and produced more flowers when it occurred in moss beds. However, even in this case, there seemed to be a strong retardation on germination. Mosses have become such a problem for germination in some areas that P. L. Bogdanov (1963) prescribed liming to combat them, a common method for eliminating mosses from lawns.

Although no inhibitory effect could be found using moss extracts on seeds of *Calluna vulgaris,* A. Matsuo et al. (1981b, 1981c; Matsuo and K. Nadaya 1987) have found, in liverworts, several sesquiterpenoids that behave as growth inhibitors.

Moss Gardens

In Japan, mosses are used to create a feeling of serenity in gardens. Instead of the mix of grass and flashes of color typical of western gardens, Japanese moss gardens have an uncluttered look of shades of green. Moss gardens are often associated with Buddhist temples, the most famous of which is Kyoto’s Kokedera, literally translated as “moss temple.” At the Sanboin Temple, Kyoto, three circular and two guitar-shaped patches of mosses symbolize the 1598 cherry blossom banquet of Lord Hideyoshi Toyotomi (J. M. Glime and D. Saxena 1991). *Pogonatum* and *Polytrichum* species are among the most-often used taxa for gardens. Common species in shade are *Dicranum scoparium, Leucobryum bowringii, L. neilgherrense, Rhizogonium dozyanum*, and *Trachycystis microphylla*, which grow in mounds or cushions, creating a gentle, rolling landscape resembling miniature hills.

Japan is not the only place where moss gardens can succeed. In the lichen and moss garden at Chatsworth, Great Britain, 33 moss and 4 liverwort species create a

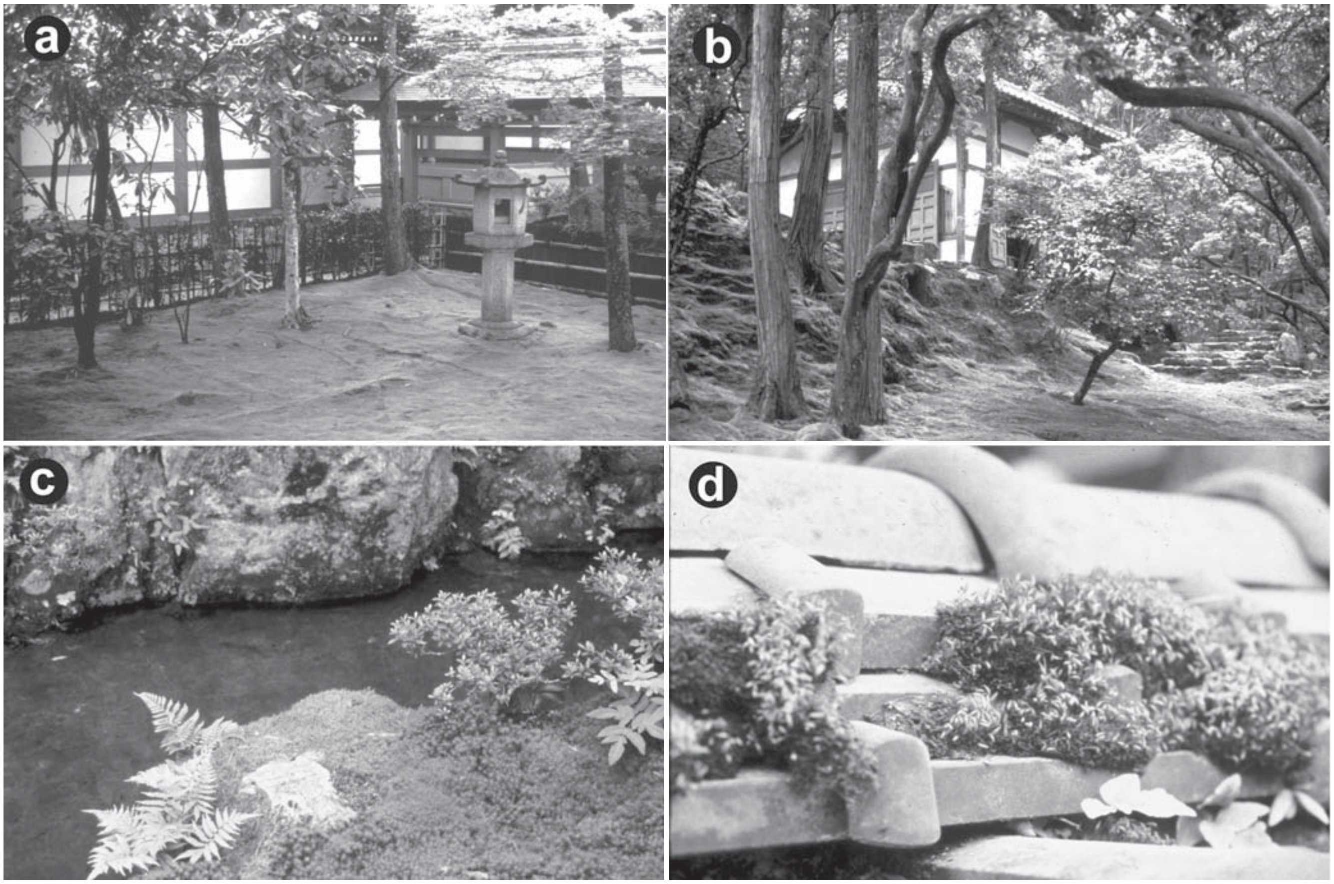

FIGURE 8. Moss gardens in Japan are designed to be restful. **a.** Mosses provide a look of tranquility. **b.** Mosses predominate at Kokedera (temple garden) in Kyoto. **c.** Mosses give small gardens an illusion of distance; stream and ferns provide scale. **d.** Mosses occupy tiles atop a moss garden wall and are being touted in parts of Europe and the USA for making a "green roof." Photos by Janice Glime

peaceful atmosphere. Among the most beautiful of these are *Dicranella heteromalla, Dicranum scoparium*, *Hylocomium splendens, Neckera crispa*, *Plagiomnium undulatum*, *Polytrichum commune, P. piliferum*, *Rhizomnium punctatum*, and *Thamnobryum alopecurum*. The home garden of Poet Laureate W. Wordsworth has cushions of *Polytrichum commune* (H. Ando 1972).

Horticultural magazines are beginning to promote mosses in the garden. H. Massie (1996) considered this move toward moss gardening to be one of capturing the imagination of gardeners seeking new landscape themes. Even wildflower gardeners have added mosses to their repertoire: R. B. Case (1994) argued for *Sphagnum* bog gardens in the Great Lakes area, where maintaining a moss garden of woodland species often requires too much attention. However, in New Jersey, one anthropologist has been able to keep an entire acre of moss garden healthy and pleasing (K. Whiteside 1987).

Moss gardening is not new to the United States. A. J. Grout (1931), considered the moss garden to be an effort by wealthy people to increase the charm of their properties. Even so, despite numerous suggestions for using mosses in horticulture in modern popular horticulture magazines, one interested gardener was forced to write to the editor to ask where supplies could be obtained for growing live mosses (T. Atkinson 1990). The published answer was provided by the Carolina Biological Supply—they sell it! Apparently the proliferation of moss gardens is not a priority for nurserymen in the United States.

Planting Techniques

Many people have tried and failed at transplanting mosses. The problem seems to lie in the tendency of the moss clump to shrink and pull away from soil or substrate as it dries out. J. H. Bland (1971) suggested turning the

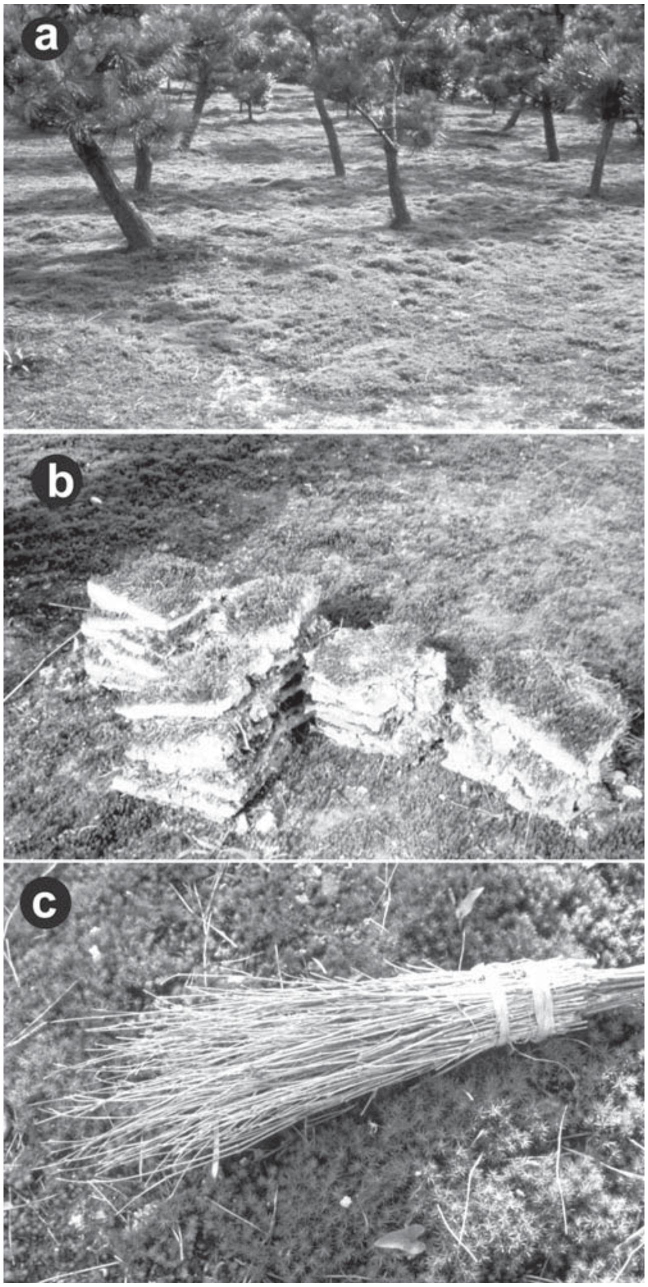

FIGURE 9. Plantations are used to provide mosses for private and public gardens near Nagoya, Japan. **a.** *Pogonatum*, *Polytrichum*, and *Atrichum* grow in shade of pines in a moss plantation. **b.** *Polytrichum* is stacked and ready for transplanting. **c.** A simple broom is used to clean moss gardens, especially for removing deciduous leaves. Photos by Janice Glime.

moss upside down and washing away the soil to prevent the shrinkage that results from drying. Another way to avoid this problem is to pin the mosses to soil with toothpicks or small twigs. Many gardeners apply mosses to loose soil, then trample the mosses once in place.

Many planting techniques take advantage of the ability of bryophytes to grow from vegetative fragments. In experiments with *Atrichum undulatum* and *Bryum argenteum*, many fragments developed shoots, whereas upright stems usually failed to develop from protonemata started with spores (C. J. Miles and R. E. Longton 1990). C. Gillis (1991) explained how to prepare, plant, and maintain a moss garden. She described mixing a handful of moss, a can of beer, and a half teaspoon of sugar in a blender, then spreading the mixture 0.5 cm thick on the ground; it produced moss growth within five weeks. Others have successfully used buttermilk, egg whites, rice water, carrot water, potato water, and even just water as the medium instead of beer (V. L. Ellis 1992). Such mixtures are helpful in assuring that moss fragments adhere to rocks.

In their “Fact sheet for moss gardening,” the American Horticultural Society recommended grinding dried moss and spreading it as powder, cautioning the gardener never to buy moss from a grower unless certain that the moss has been propagated by the seller and not taken from the wild. They recommended keeping the pH below 5.5 by applying sulfur, buttermilk, or aluminum sulfate.

Successful starters can be grown from fragments between two moist sheets of cheesecloth (J. K. Whitner 1992), although spores can be used as well (J. McDowell 1968). Partially dried moss fragments must be spread over cheesecloth that overlies a sand-peatmoss or sawdust mix in a flat. These are covered with a second piece of cheesecloth and kept moist by misting. When the plants are well established (about 4.5 months), it is easy to transplant them by lifting the soil/cheesecloth layer and cutting it into the shape needed. Some gardeners have been successful in growing rock-dwelling taxa this way as well, ultimately draping the cheesecloth over rocks. The mosses grow through the cloth, which eventually rots away. *Brachythecium salebrosum* and *Plagiomnium cuspidatum* are relatively easy to cultivate in this way (H. A. Crum 1973).

In a moss farm near Nagoya, Japan, gardeners dry members of Polytrichaceae (*Atrichum, Pogonatum, Polytrichum*), then fragment them by rubbing them between their hands (pers. obs., with translation by N. Takaki). The resulting pieces are spread on soil of flats by broadcasting as one would grass seed. Mosses grown in these flats are eventually transplanted to an outdoor garden shaded lightly by pines and other trees with evergreen leaves. When a customer wants to buy mosses, clayey soil in the moss plots is cut into squares about 20 cm on a side, lifted, and stacked to dry. The customer then plants the squares in a checkerboard pattern in the garden, again tramples them to break up the squares and dry plants, and begins a daily watering regime. Japan's long rainy season makes it relatively easy to establish a moss garden, but in most of the rest of the world, more extensive care is needed to maintain sufficient humidity. Many parts of Great Britain and the Pacific Northwest in the United States and Canada, however, also have favorable weather.

Most mosses require at least light shade, which must be provided by trees that do not bury the mosses under litter. In Japan, there is a saying that only old men and little boys can care for the moss garden. This is because the garden requires care to remove leaf litter, but it must not look too cared for or it will not look natural. A soft broom made of grasses is usually best to brush away litter. M. Mizutani (1975, 1976) and T. Fukushima (1979, 1979b, 1980) advised preserving the characters of the original habitat, constant weeding, moderate watering, continual care to remove fallen leaves and dung, and elimination of harmful animals such as moles, slugs, crickets, and ants. Z. Iwatsuki and T. Kodama (1961) pointed out that fertilizer should never be used for mosses. In fact, J. Stubbs (1973) recommended the use of fertilizer based on iron sulfate as a means of quickly killing moss. Herbicides such as paraquat, simazine (T. E. T. Bond 1976), 2, 4-D, and atrazine (D. H. Wagner, pers. comm.) will permit moss growth, while eliminating invading tracheophytes (Bond).

Dwarf Plants

Mosses in bonsai and bonkei help to stabilize the soil and retain moisture, providing a warning system when delicate dwarfed bonsai plants need water. Unfortunately, a moist, dense mat inhibits root growth and can result in sudden growths of fungi; bonsai experts advise removing the moss each autumn (J. H. Bland 1971). Useful species include *Atrichum undulatum, Barbula unguiculata, Bryum argenteum*, *Funaria hygrometrica, Leucobryum, Physcomitrium*, and *Weissia controversa* (H. Inoue 1980).

In the Pacific Northwest, *Leptobryum pyriforme*, under the name Kyoto moss, is being sold for bonsai trays (J. Christy, pers. comm.). In Mexico, mosses, especially *Campylopus*, are used for fake bonsai, or dish gardens. Others used are *Dendropogonella rufescens, Hypnum*, and *Thuidium* (C. Delgadillo, pers. comm.).

In Japan, mosses are used to make miniature landscapes in trays (bonkei, bankei, saikei). Mosses provide an appropriate texture and color while withstanding dryness (T. Kawamoto 1980). A variation of the landscape tray served as a daily changing delight for one hospitalized person in the United States (W. Gerritson 1928). "Each day the mosses had changed appearance; so each day added a new joy. The nurses came from time to time to see and admire. Other patients shared its freshness and beauty. Visitors, too were invited to see the charm of a 'platter of mosses.'" Gerritson had arranged sixteen species of mosses, including various stages of maturity of capsules, to insure constant change.

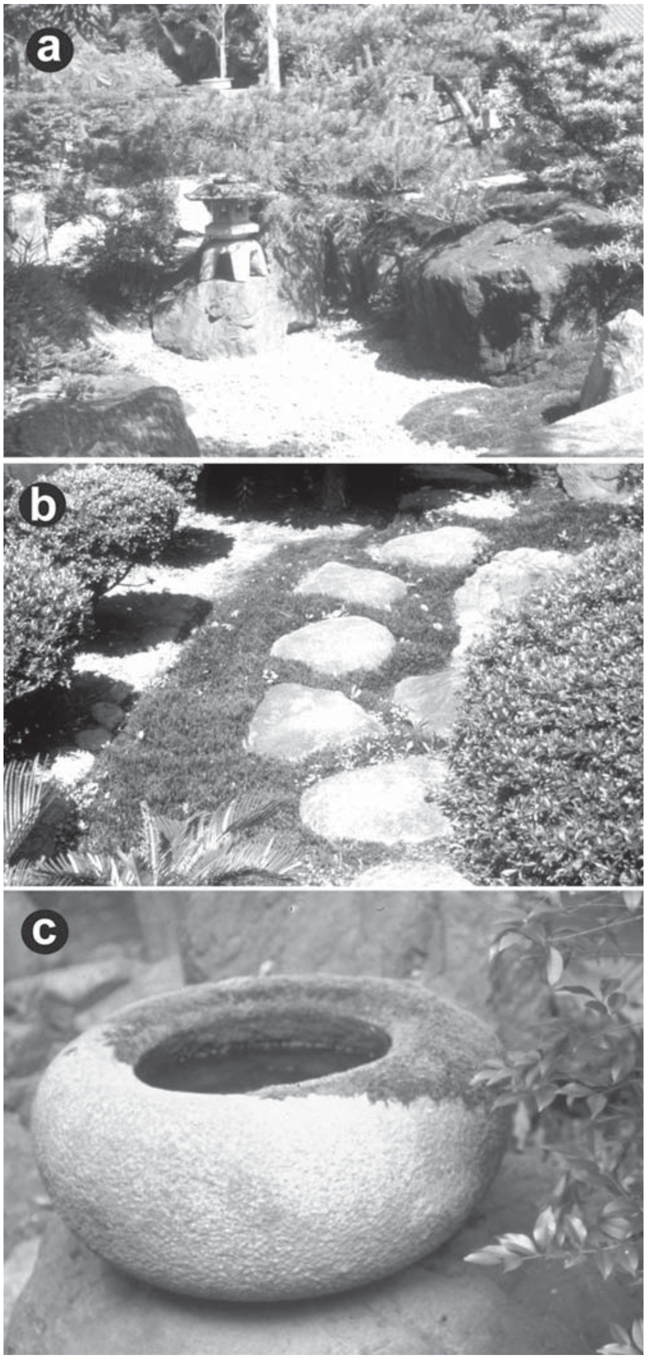

FIGURE 10. Mosses are commonly used in private gardens in Japan. **a.** Moss, boulders, stone lantern, and gravel create effect of distance in this private moss garden. **b.** Mosses border this path in a private moss garden. **c.** Moss have been cultured on this bowl. Photos by Janice Glime.

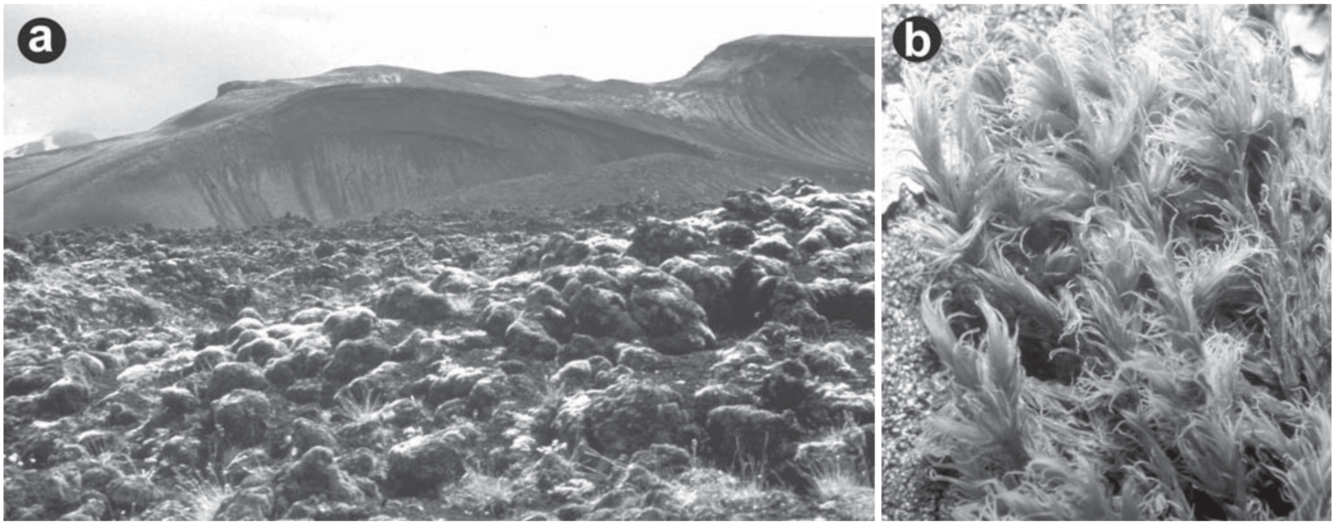

FIGURE 11. *Racomitrium canescens* has a frosted look that is attractive for creating miniature landscapes. **a.** In Iceland it forms large hummocks. **b.** Its white leaf apices are used to give effect of frost or snow on mountain tops in dish and moss gardens. Photo by Janice Glime.

Large mosses such as *Atrichum, Climacium, Dicranum, Polytrichum,* and *Rhodobryum* simulate forests. Grasslands or mountains can be imitated by *Bryum argenteum, Hypnum plumaeforme,* and *Leucobryum*. White-tipped mosses like *Racomitrium canescens* provide a snowy look.

Pesticides

When tracheophytes are stored in an herbarium, moth balls can provide protection from beetle infestation. However, such protection is not necessary for bryophytes because they are apparently not vulnerable. Many authors have suggested that bryophytes may contain natural pesticides (R. B. Yepsen 1984). In fact, the liverwort *Plagiochila* contains the sesquiterpene hemiacetyl plagiochiline A (Y. Asakawa et al. 1980b), a poison extremely potent in mice (A. Matsuo 1983, unpublished data) and it inhibits the feeding of an African army worm (Y. Asakawa et al. 1980).

A. J. Davidson et al. (1989) found that shoots of *Brachythecium rutabulum* and *Mnium hornum* are not grazed by slugs, but that the immature capsules are readily eaten. They isolated ferulic and possibly *m*- or *p*-coumaric acid from a wall-bound fraction of the leafy shoot, suggesting that these compounds served as antifeedants.

C. L. Liao (pers. comm.) has shown that both aquatic and terrestrial isopods devour some mosses readily while avoiding others. L. Russell found that one insect readily devours *Porella navicularis* until it eats a species of *Porella* that has a peppery taste (D. H. Wagner, pers. comm.). After eating the peppery species for a few minutes, it stops eating it and henceforth refuses to eat either *Porella* species. Such evidence, coupled with the fact that many terpenes and other phenolic compounds occur in bryophytes (Y. Asakawa 1982, 1988, 1990, 2001; Asakawa and E. O. Campbell 1982), is sufficient to suggest that exploration of antiherbivory compounds in bryophytes could prove quite profitable.

Moss Industry

Fuel

Nearly half the world's annual peat production is used for fuel, with peat resources worldwide estimated to be equivalent to 100–200 million tons of oil, or about half the known gas reserves (United Nations 1981). In Canada, there appears to be more energy in native peat deposits than in forests and natural gas reserves (J. A. Taylor and R. T. Smith 1980).

When war and politics threaten access to major oil supplies, peat is a promising substitute for some purposes. Peat is a clean-burning fuel. The lovely complexion of Irish and Swedish women has been attributed to the clean-burning *Sphagnum* peat used in those countries (K. Drlica 1982). With its high caloric value, more than 8,000 BTU per dry pound, peat is receiving unprecedented attention as an alternative fuel source. Mosses, traditionally used as fuel in some devolved and developing countries, now are important sources of fuel in northern Europe, especially in Finland, Germany, Ireland, Poland, Russia, and Sweden. The former Soviet Union burned an estimated 70 million tons and Ireland 3.5 million tons of mosses in one year to produce electricity (P. H. Boffey 1975). According to D. H. S. Richardson (1981), 25% of the fuel in Ireland is moss-based. With at least 50 countries harvesting peat, D. Hinrichsen (1981) estimated that peat equivalent to 60–70 million tons of oil would be in use by the year 2000.

Several technical aspects need improvement before widespread use of peat fuel is feasible. Many peatland ecologists are studying the regeneration capacity of various *Sphagnum* species, and S. Chapman et al. (2003) claimed that limited peat extraction can actually increase biodiversity. Improved methods are needed for harvesting, drying, and conversion to a burnable fuel (O. Lindstrom 1980). Peats are ideal for production of methane, eliminating the chopping that is required in use of water hyacinth, and can be used to produce ethylene, hydrogen, methanol, synthetic or natural gas, and low and intermediate BTU gas. Other advantages include growing with little care, easy harvesting, little maintenance cost, low sulfur content and cleaner-burning, superior heating value compared to that of wood but similar to that of lignite, and ability to renew the resource, although fuel-quality peat does not regenerate at the rate it is being used.

The Finns have solved many of the problems associated with peat fuels in their attempt to become 40–50% self-sufficient through use of indigenous supplies of peat and wood (N. G. Miller 1981). They have developed a dewatering process that results in dry pellets of partly carbonized peat (J. A. Taylor and R. T. Smith 1980). They suggest that sod peat harvesting is likely to be cost effective for local areas, and placement of processing stations on the peatlands reduces cost of transport. Nevertheless, that country has lost 60% of its former active peatland since 1950 due to forestry and agriculture (R. Heikkilä and T. Lindholm 2000).

In addition to its own use of peat, Finland is exporting pulverized peat to northern Sweden, where use in industry and municipal heating, power generation, and oil burners of pulp and paper companies is increasing. The pulp and paper companies have begun full-scale harvesting themselves and expect to enlarge this operation (J. Summerton 1981).

Although, in 1903, a coal miner strike sparked interest in peat as a fuel in the United States, the cost of processing has prevented its widespread use (J. W. Thieret 1956b). Even so, various organizations, including the U. S. Geological Survey, mapped peat deposits and estimated the extent of the resource (N. G. Miller 1981). The energy crisis of the 1970's fueled a strong interest. In 1975, the Minnesota Gas Company applied for a long-term lease on land with an estimated 200,000 acres of peat that the company hoped to use to generate methane (P. H. Boffey 1975). Also in 1975, First Colony Farm in North Carolina began peat harvest for fuel to generate electricity and to produce methane or synthetic gas (L. J. Carter 1978). Their 372,000 acres is believed to have more than 400 million tons of peat, enough to fuel a 400 megawatt power plant for 40 years or an 80-million cubic foot per day gasification plant for nearly 50 years.

Harvesting Peat and Other Mosses

In Ireland, horticulture alone uses nearly one million cubic meters of light, fibrous, recently decomposed peat. Another 7–9 million pounds are exported (D. H. S. Richardson 1981). In the U. S. today, there are about 200 "mossers" (moss growers). Dubbed the "invisible industry," 90% of the world's marketed peat comes from Wisconsin, primarily from Jackson and Monroe counties (B. Epstein 1988), despite the fact that about 3% of the surface of the Earth, almost entirely in the northern hemisphere, is covered with peat (R. S. Clymo 1987).

When this moss industry began in Wisconsin 150 years ago, horses and oxen were used to pull the wagons of moss from wetlands. These animals were replaced by tractors, trains, heavy wooden boats, and finally wooden sleds pulled by tractors with army tank-like wooden treads. The high water content of peat has necessitated these means—before drying, one bale could weigh 180 kg.

With a harvest of 300,000 bales annually (J. M. Glime and D. K. Saxena 1991), it is fortunate that at least some Wisconsin peat harvesters are practicing sustainable yields, at least for horticultural peat. One method in use today to encourage peat regeneration is to hand-rake the peat, load it on a wagon pulled by a tractor with wooden treads, and then permit the harvested area to recover for 10 years before harvesting that area again. Competing grasses and sedges must be removed, and shrubs are eliminated to make harvest easier. In this way, the remaining *Sphagnum* regrows by dichotomously branching heads that fill in the vacated space. The peat is dried on-site out-of-doors, anchored with old tires to prevent dried peat from blowing away.

But for fuel peat, "harvest" is usually a misnomer. Compacted peat desirable for heating will not regenerate quickly. Finnish peatlands have accumulated at the rate of 10–40 cm per thousand years, so that repeatable harvests of deep peat must be discussed in geologic time scales (H. A. Crum 1988). Even more alarming is the loss of 87% of Britain's lowland raised bogs to agriculture and forestry (Crum).

Moss harvesting has become a concern for bryologists and ecologists worldwide. D. Knight (1991) bemoaned the dwindling number of peat bogs and their exploitation

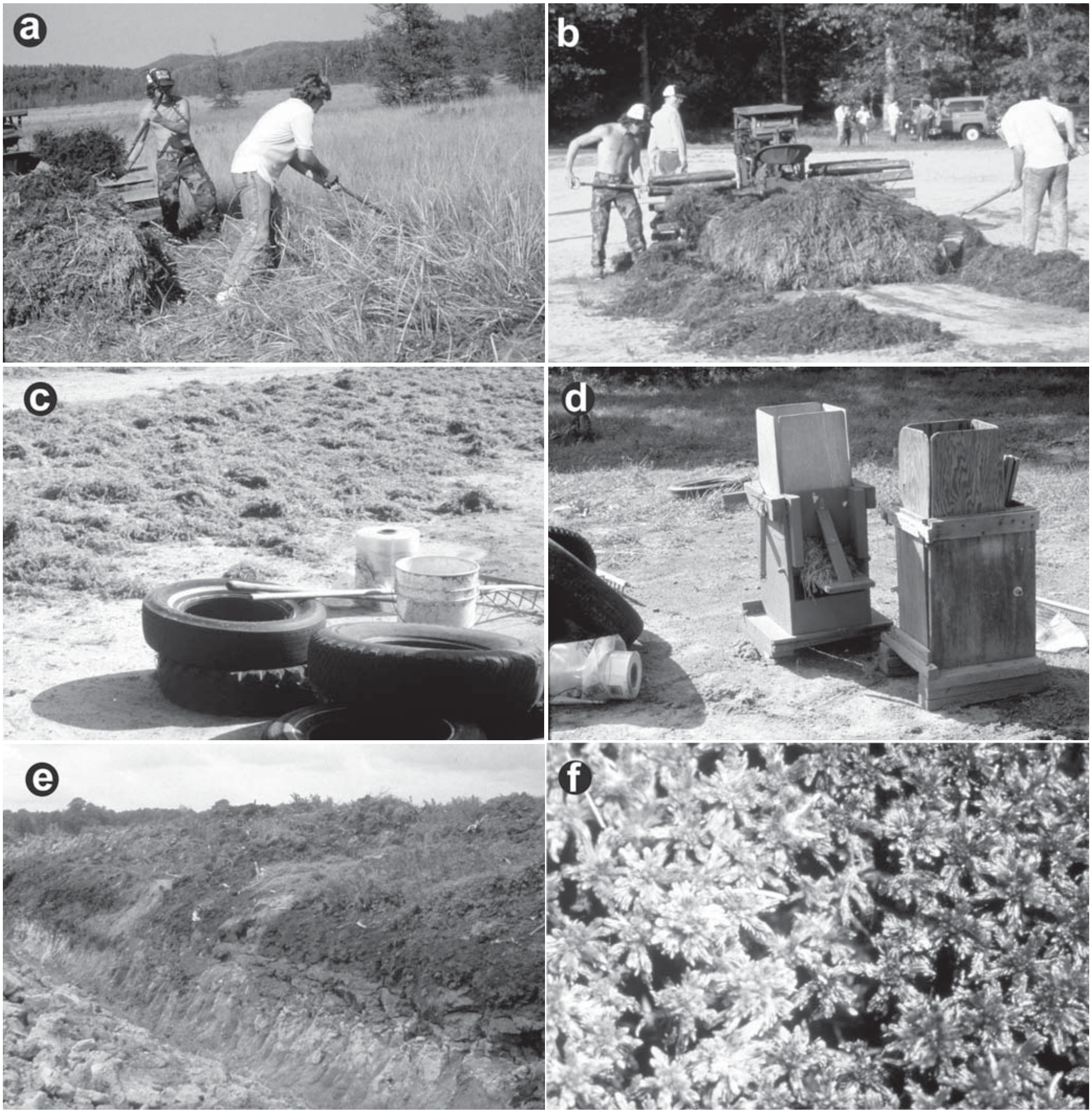

FIGURE 12. Moss harvesting is a major industry in parts of Wisconsin. **a.** Raking peat moss with wooden rakes is labor-intensive; tractor with wooden treads is used to remove peat with the least disturbance. **b.** Peat is spread to dry. **c.** Tires are used to anchor dry peat. **d.** Peat packaged on site is ready for sale. **e.** Compact peat beds (in Maryland) can provide fuel. **f.** Fungus-infected *Sphagnum* is a common threat to peatland moss-gatherers. Photos by Janice Glime.

for plant propagation in British horticulture. Likewise, in Ireland, peat used for fuel is taking a serious toll on the 3 million acres there (K. Drlica 1982). Most of the moss is harvested without propagating new crops, and harvesting seems to be particularly heavy in some areas of the Pacific Northwest in the United States. *Sphagnum* is the most commonly harvested moss, and in countries like Australia, where it is used extensively in horticulture but where there are no extensive peatlands, the peatlands are rapidly disappearing.

Other bryophytes may be in danger of overharvesting as well. In the Pacific Northwest, mosses are sometimes taken from the forest on large, flatbed trucks (P. J. Johnson, pers. comm.). Due to the slow growth of most taxa, it could take decades to replace a single day's collection. In addition to *Sphagnum*, other heavily harvested taxa include *Antitrichia curtipendula, Brachythecium, Hypnum cupressiforme, Isothecium, Metaneckera*, *Rhytidiadelphus,* and *Thuidium* (P. J. Johnson and C. W. Smith, pers. comm.). Fortunately, more and more harvesters are attempting to harvest in a way that will permit the moss to replace itself, and research on regeneration in North America, Europe, and New Zealand continues (A. J. Tilling 1995; L. Rochefort 2000).

Construction

As early as 1903, a Swede extolled the advantage of grinding peat with asphalt to make an enduring street pavement (K. Drlica 1982). In 1920, manufacture of peat-based pasteboard and wrapping paper began near Capac, Michigan (N. G. Miller 1981). In countries where they are common, bryophytes have been important in construction of houses, furnishings, boats, and other items and are still used today, especially in construction of log cabins.

Granite House, built by Scott's last Antarctic Expedition in 1911 at Granite Harbour, Cape Geology, still has remnants of *Bryum argenteum, B. pseudotriquetrum,* and *Hennediella heimii* (= *Pottia heimii*) stuffed in the cracks in the walls (R. Seppelt, pers. comm.). In the Philippines, bryophytes are used as fillers between wooden posts of walls and shingles of roofs (B. C. Tan 2003). Some houses in northern Europe still have *Homalothecium sericeum*, *Isothecium myosuroides*, and *Pleurozium schreberi* between timbers as chinking (D. H. S. Richardson 1981), and Alaskans still use *Hylocomium splendens, Racomitrium canescens, Rhytidiadelphus loreus,* and *Sphagnum* likewise (M. Lewis 1981). In Nordic countries, *Fontinalis antipyretica* has been used as fire insulation between the chimney and walls (J. W. Thieret 1956b). In the Himalayan highlands, shepherds use *Actinothuidium hookeri, Anomodon minor, Entodon, Floribundaria floribunda, Leucodon sciuroides, Macrothamnium submacrocarpum, Philonotis, Thuidium delicatulum, Trachypodopsis crispatula, Herbertus, Plagiochila,* and *Scapania* as chinking in temporary summer homes (G. B. Pant and S. D. Tewari 1989); mosses are pressed between logs with fingers or an instrument and left to dry. There they remain compressed and still green, looking more natural than the fiberglass being used in most log homes in North America today.

Northern Europeans stuffed *Sphagnum* between timbers of houses to deaden sound (J. W. Thieret 1954). Russians have pressed and heated slabs of *Sphagnum* to insulate houses and refrigerators (M. A. Sukhanov 1972; M. Ruel et al. 1977).

Strangely enough, mosses, long considered a nuisance on roofs, are being used throughout Germany as a roofing material (e.g. Behrens Systemtechnik) and are now being touted for debut in the United States. Planted along with grass, the acclaimed advantages include being fireproof, cleaning atmospheric pollution, buffering the temperature, creating a sound barrier, being lighter than slate, and being less expensive (M. A. Posth 1993). When roofs, statues, and walls are adorned with these, however, moisture and organic acids contribute to chemical erosion (D. Perry 1987).

In the Scottish Highlands dried mosses were steeped in tar and used to caulk boats (H. A. Crum 1973); *Eurhynchium striatum* and *Neckera complanata* have been used to seal seams and cracks of boats and canoes (G. B. Pant and S. D. Tewari 1990). *Polytrichum commune* was used to make nautical ropes. In fact, the use of mosses was more than just a casual use of those at hand; mosses were imported from Belgium to Holland after the sixteenth century for caulking carvel-built boats (J. H. Dickson 1973).

The lining of a well in a small Roman villa near Abingdon, Great Britain, had mosses tucked between and behind the stones. Since these mosses were forest species and not likely to have grown in the well, it is presumed that they were placed there (J. H. Dickson 1981). Dickson theorized that they may have served to filter the water.

Hypnum plumaeforme, Loeskeobryum brevirostre, Rhytidiadelphus japonicus, and *Thuidium kanedae* served to stop a leak in a temporary log dam in a Japanese timber harvest operation (H. Ando 1957). In Pennsylvania *Fontinalis* was transplanted intact on rocks to help stabilize new weirs (anonymous forester, pers. comm.).

Recently, "peatcrete" and "peatwood," using *Sphagnum* with binders for solidification and strengthening, have served as construction materials (M. Ruel et al. 1977). To make peatcrete, *Sphagnum* is mixed with light concrete and hydraulically pressed with Portland cement and water. Its low mechanical strength is balanced by the advantages of low cost, easy sawing, nailing, casting, and molding, lack of the need for drying, nonflammability, and low density (0.7–1.2 sp. gr.; 45–70 lb/ft^3) (Ruel et al.). Because of their light weight, peat construction products are especially useful in places where transportation is a problem. Peatwood, dried *Sphagnum* blended with a phenolic resin and pressed into a heating mold, has advantages for construction (Ruel et al.). These

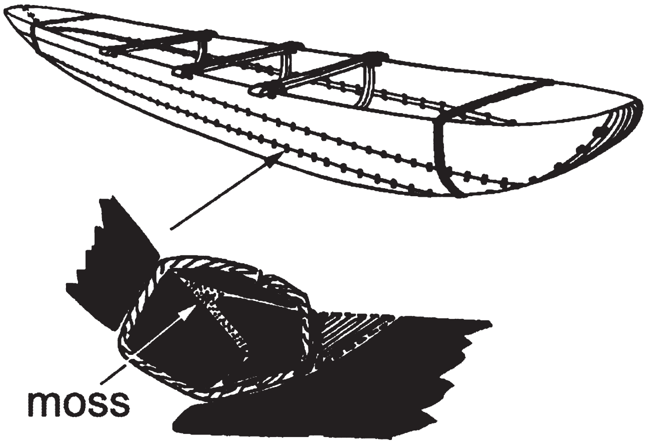

FIGURE 13. Views of old boat (upper) and joints of boat (lower) showing mosses used to permit flexibility of the boat, thus giving it strength. Redrawn from diagram in J. H. Dickson (1973).

include quick hardening, attractive texture, good strength, easily nailed, screwed, or glued, and light weight (40–60 lb ft^{-3}). Peatfoam is an ultra-light construction material based on peatmoss and foamed resin. Peatcork is made from the coarse fraction of peat (Ruel et al.).

Household Uses

Mosses are widely used for decoration in store windows and displays, Christmas tree and toy train yards, floral arrangements, and Christmas ornaments. For Christmas tree yards and nativity scenes, mosses are collected in sheets (H. A. Miller in H. A. Crum 1973). In Mexico, *Hypnum* and *Thuidium* are used as carpets for nativity scenes; in the U.S.A., *Hypnum cupressiforme* and *Ptilium crista-castrensis* are common choices. Sheet moss is collected at any time, but preferably in summer. A single wholesaler supplies the decorative industry with about 14,000 pounds of dry moss per year (T. C. Nelson and I. W. Carpenter 1965).

Climacium americanum is used to make wreaths and crosses, and *Hylocomium splendens* to make moss roses (W. H. Welch 1948; J. W. Thieret 1956b). In Japan, dried *Climacium japonicum* is used to make ornamental water flowers that expand in a glass of water (M. Mizutani 1963), and pressed, dried bryophytes are often used in framed artwork (K. Saito 1973b). Even sporophytes are used in Japan to make decorative arrangements (T. Manzoku 1963). In Missouri, *Bryum* is collected for floral arrangements.

Hypnum cupressiforme, Isothecium myosuroides, Pleurozium schreberi, and *Pseudoscleropodium purum* adorned a shop window in Rambouillet near Paris, during a May festival in 1970 (H. Ando 1972), and I have recently seen *Rhytidiadelphus* used in a craft display in a hotel in Montana. At Rennes, France, Ando found cushions of *Leucobryum glaucum* arranged decoratively in a tailor's shop window. *Dicranum scoparium* is popular for shop windows because it forms large banks of green, and *Hylocomium splendens, Rhytidiadelphus loreus*, and *R. triquetrus* are popular as green carpets for floral exhibitions (W. H. Welch 1948; J. W. Thieret 1956b).

Bryophytes in aquaria provide oxygen, hiding places, and egg-laying substrates for fish (G. Benl 1958), and they are usually more delicate and graceful-looking than aquatic higher plants. Many taxa can be used, provided the water is not too warm for them: *Bryum pseudotriquetrum, Fontinalis antipyretica, Glossadelphus zollingeri, Leptodictyum riparium, Platyhypnidium riparioides, Rhacopilum aristatum, Taxiphyllum barbieri, Vesicularia dubyana, V. ferriei, Chiloscyphus polyanthos, Riccia fluitans,* and *Ricciocarpus natans* (Benl; C. D. K. Cook et al. 1974; N. Takaki et al. 1982).

In 1990, a species of *Polytrichum* decorated one side of the Finnish 50 penny coin, with the national animal, a brown bear, on the other side (J. Hyvönen 1990). There is a linguistic association between the bear and moss in the Finnish language (karhunsammal). This association may be due to the fact that bears sometimes bury their food in wet forests under carpets of *Polytrichum commune*, or to their habit of using tufts of *Hylocomium splendens, Pleurozium schreberi*, and *Polytrichum* to line winter hibernation sites.

Clothing

In Germany, *Sphagnum* is used to line hiking boots (L. Hedenäs 1991), where it absorbs moisture and odor. Several cultures have used *Sphagnum* and *Dicranum scoparium* for lining diapers. Michigan's Chippewa Indians used *Sphagnum* for this purpose to keep babies clean and warm (H. A. Crum 1973). Even modern diapers in the U.S.A. and Canada can have *Sphagnum* liners (J. H. Bland 1971). Today, the Johnson & Johnson Company uses *Sphagnum* in diapers and sanitary napkins (L. M. Johnson Gottesfeld and D. H. Vitt 1996). They have learned from indigenous people to avoid short, yellow-green and red Sphagna, presumably because they, like red *Sphagnum capillifolium* (= *S. nemoreum*), cause irritation, whereas the long, pink, but non-red *Sphagnum magellanicum* is preferred

B. O. van Zanten (1973) pictured a native of New Guinea wearing *Dawsonia grandis* in his hair and bracelet. *Dawsonia grandis* is stripped of its leaves, put

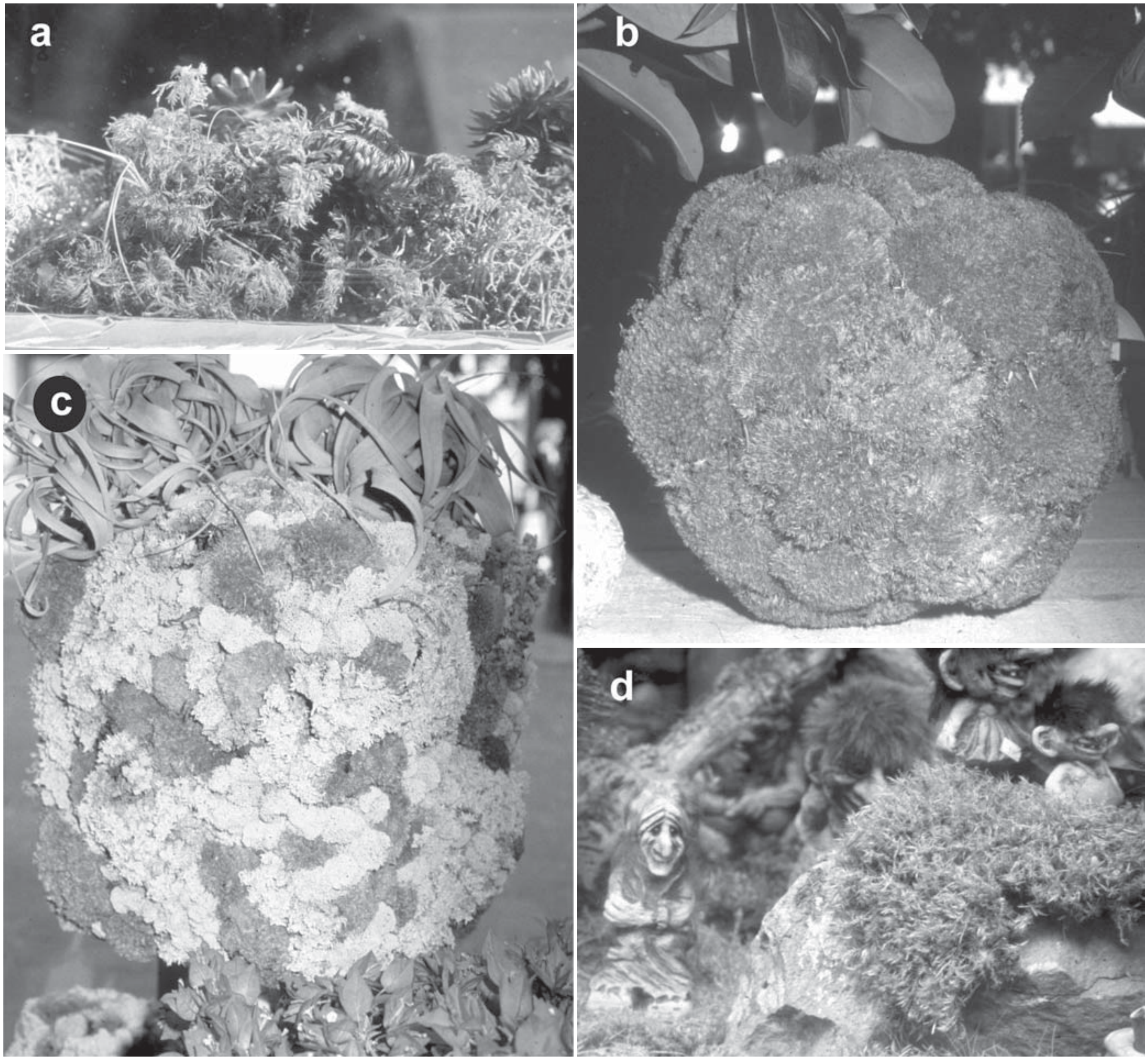

FIGURE 14. Bryophytes are often used decoratively. **a.** Bryophytes decorate shop window in Trosa, Sweden. **b.** Manmade moss ball adorns window of a value shop at Paradeplatz in Zürich, Switzerland. **c.** Tree made of bryophytes and lichens, decorate window of flower shop at Paradeplatz in Zürich, Switzerland. **d.** Mosses provide backdrop for trolls in shop in Helsingborg, Sweden. Photos by Irene Bisang, Universität Zürich.

over a glowing fire, stripped of its outer layers, then split in two and plaited into a rope that is used to make red decoration in net bags and other objects (van Zanten). Women also wear these stems in their hair and as decorations in bracelets. D. H. S. Richardson (1981) reported that New Guinea natives also use mosses to decorate ceremonial masks. In the Philippines, natives use mosses to decorate headware and clothing (B. C. Tan 2003).

J. E. Beever and J. E. Gresson (1995) recently discovered shoots and leaves of *Polytrichum commune* and *Polytrichadelphus magellanicus* used in two New Zealand Maori cloaks; presumably clusters of 3–5 leafy moss stems originally completely covered the flax backing

FIGURE 15. *Ricciocarpus natans* is sometimes floated in aquaria to provide oxygen. Photo by Janice Glime.

of the cloak, and alternating colors of brown and black served as decoration. Not only were mosses decorative, but they also served as an added layer of insulation. In some parts of Germany, wool was woven with *Sphagnum* to make a good, cheap cloth (J. W. Hotson 1921). In Mexico, wool is sometimes colored dark by extracts from a rupestral moss (C. Delgadillo, pers. comm.). In England, *Climacium dendroides* was artificially colored and sold in the market (C. H. Clarke 1902) or used to decorate a lady's hat (F. Tripp 1888). In Boston, braids were constructed of *Pseudoscleropodium purum* and cords made of *Neckera crispa* and *Dicranum* to decorate ladies' hats and bonnets (Clarke).

Women in the villages of Kumaun, India, stuff mosses (*Hylocomium, Hypnum, Trachypodopsis*) into cloth sacks to make head cushions (sirona) that also absorb leaking water as they carry water vessels (G. B. Pant and S. D. Tewari 1989). Soft mosses, including *Hylocomium brevirostre*, were used in Europe to pad Mesolithic flint blades to protect the user's hand (J. H. Dickson 1973).

Household Goods and Furnishings

The absorbent properties of *Sphagnum* make it the most used moss of all the bryophytes. It serves as an insulator, pillow, mattress, and furniture stuffing, to keep milk warm or cool, to stuff into footmats to clean shoes, to weave welcome mats, and in Lapland to line baby cradles, keeping the infant clean, dry, and warm (R. M. Stark 1860). The durability and elasticity of mosses may well have contributed to Japanese stuffing balls and dolls with *Hypnum* (G. B. Pant and S. D. Tewari 1990). Romans, living near what is now Glasgow, used mosses for toilet paper (H. J. B. Birks 1982). Some mosses make ideal lamp wicks: *Dicranum elongatum* by the Cree Indians, *Racomitrium lanuginosum* by Labrador Eskimos (J. H. Bland 1971), and *Sphagnum* by others (H. A. Crum 1988). In India, mosses are used for door covers and

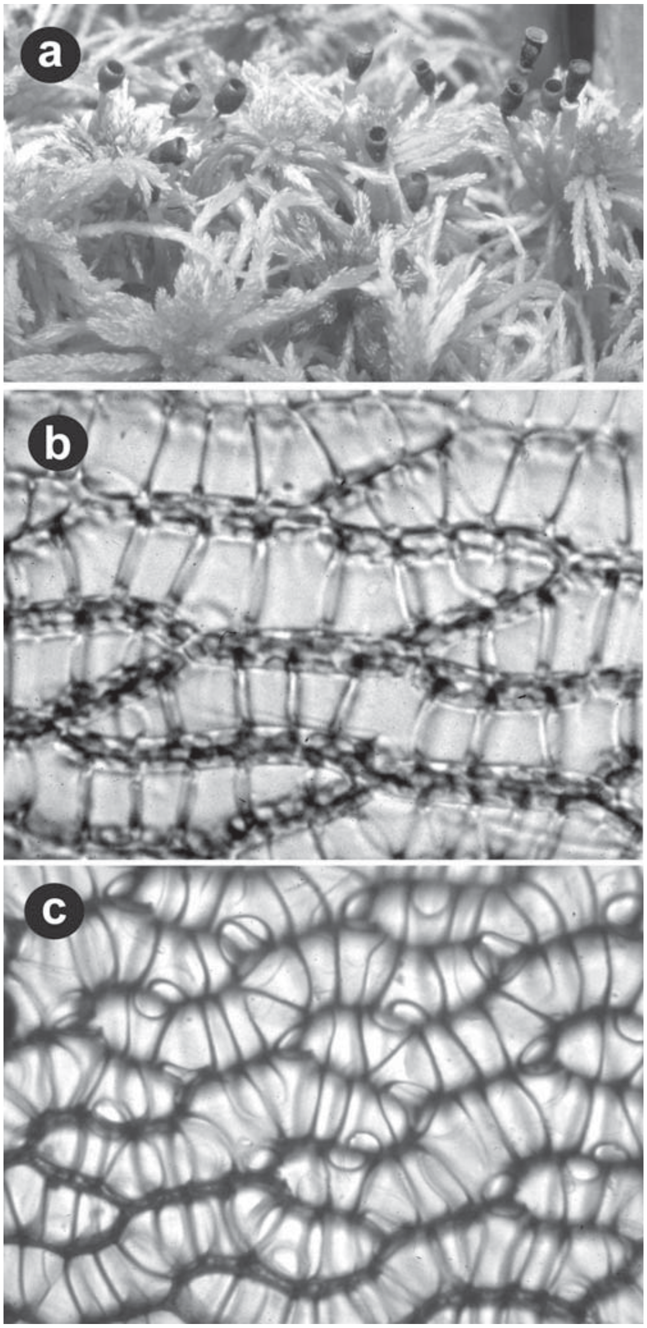

FIGURE 16. *Sphagnum* has numerous uses because of its absorptive capacity and antibiotic properties. **a.** *Sphagnum* forms capsules in its natural habitat. **b.** Living *Sphagnum* has green photosynthetic cells forming a network around hyaline cells. **c.** Staining makes pores and hyaline cells more visible. Photos by Janice Glime.

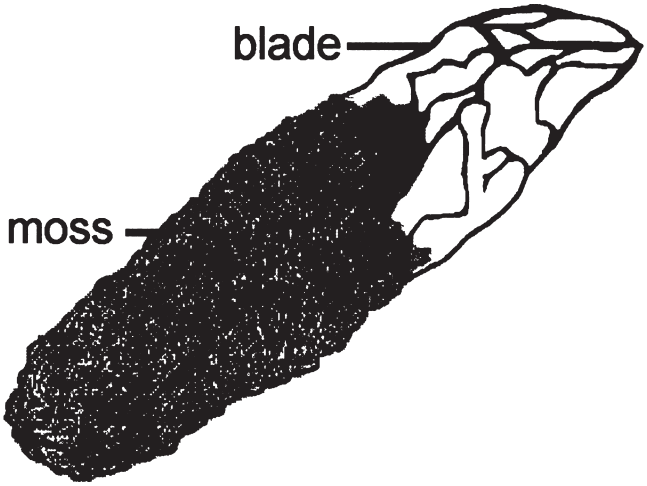

FIGURE 17. Mesolithic knife handles in Europe were sometimes wrapped with moss. Drawing based on photograph by Dickson (1981).

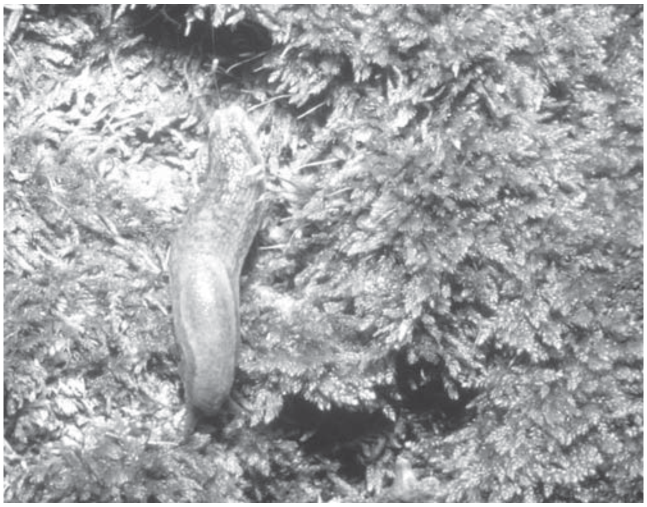

FIGURE 18. Slugs eat *Hypnum*, so-named because it was thought to induce sleep; it was used to stuff pillows. Photo by Janice Glime.

smoke filters (Pant 1989). In Germany, *Sphagnum* was used in hospitals as neck and head rests, to support hips and backs, and to elevate the legs of wounded people (J. W. Hotson 1921). Himalayan villagers use mosses, shrubs, grasses, and bamboo to make a pharki (door mat) (J. M. Glime and D. K. Saxena 1991) and southern Swedes use *Polytrichum commune* to make door mats and brushes (L. Hedenäs 1991). Because of its long, stiff stems, *Polytrichum* makes good brooms for dusting curtains and carpets (H. A. Crum 1973). Stems are stripped of their leaves to make a broom 12–18 inches in length (J. W. Thieret 1954). Early Romans apparently used *Polytrichum* for making baskets (Bland). In the Azores, *Thuidium tamariscinum, Pseudoscleropodium purum*, and *Hypnum cupressiforme* were used to stuff pillows and mattresses (P. Allorge 1937). In fact, J. J. Dillenius (1741) named the genus *Hypnum* because of its widespread use in stuffing pillows and therefore inducing sleep. Linnaeus himself used *Polytrichum commune* for bedding material (Crum), stating that if a quilt were to be made of this moss, nothing could be more warm and comfortable (C. Linnaeus 1979). In Northumberland, England, archeological evidence suggests that both man and domestic animals were bedded on mosses, which contributed not only something soft, but also could absorb liquids (H. Ando and A. Matsuo 1984). The most commonly used taxa were *Hylocomium splendens* (55%), *Rhytidiadelphus squarrosus* (33%), and *Pseudoscleropodium purum* (6%). Mosses, including *Brachythecium, Dicranum, Hypnum, Neckera, Papillaria,* and *Thuidium,* add the advantages of being insect-repellent and resistant to rot (Pant and Tewari 1989).

Sphagnum is particularly good for absorbing urine from livestock and pets. It is used in the laboratory to prevent red-leg in frogs. The absorptive property is useful for cleaning pots when camping (A. Gould, pers. comm.), and any remaining mosses can be used to keep the fishing worms alive. In India, villagers clean household utensils with a mixture of mosses and ashes (G. B. Pant 1989).

H. J. During (pers. comm.) was asked by the archaeological group in Leiden to identify mosses found in French Stone Age pottery. These early potters had used *Neckera crispa*, *Tortula*, and other mosses, apparently for the same purpose people now use sand, to make the pottery less “fat,” improving the quality of the pottery.

Mosses seem to be useful in maintaining structural integrity of a variety of materials. In Siberia, the Eskimos roll up skins and freeze them into shape as a sled runner. Then they cover these with a moss and water mixture to protect the skins. The moss and water mixture is smoothed as it is shaped onto the skin runners (R. Seppelt, from ABC-TV series “Man on the Rim”).

Packing

Long before the discovery of secondary compounds in bryophytes, Himalayans used them as insect repellents when storing food (G. B. Pant and S. D. Tewari 1989). They were dried, made into a coarse powder, and sprinkled over grains and other containerized goods. A wad of bryophytes also plugged the container. The light-

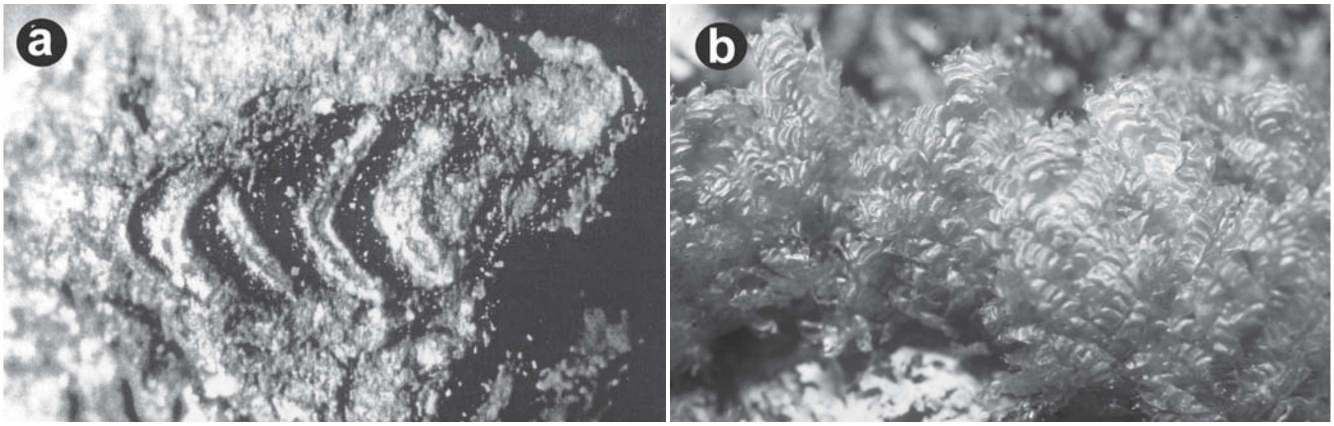

FIGURE 19. *Neckera* species were used as early as the Stone Age. **a.** Piece of ancient pottery with impression of *Neckera crispa* that has been used as a mordant. Photo courtesy of Heinjo During of Universiteit Utrecht and Wim Kuijper of Leiden University. **b.** *Neckera pennata*, showing the undulations represented in the pottery. Photo by Janice Glime.

weight bryophytes could be easily blown off before using the grain.

In some western U.S. states, *Antitrichia californica, Dendroalsia abietina,* and *Neckera menziesii* were used to pack vegetables, serving to retain moisture as well (A. J. Grout 1902; T. C. Frye 1920), and even today *Antitrichia curtipendula, Isothecium*, and *Metaneckera* are used to pack mushrooms in the Pacific Northwest (C. W. Smith, pers. comm.). In India *Sphagnum* is frequently used for packing apples, and in the Himalayas, apples and plums are still wrapped in *Brachythecium salebrosum, Cryptoleptodon flexuosus, Hypnum cupressiforme, Macrothamnium submacrocarpum, Neckera crenulata, Trachypodopsis crispatula*, and *Thuidium tamariscellum* (G. B. Pant and S. D. Tewari 1989). In the tropics, leafy liverworts are used because of their abundance (J. H. Bland 1971). Biological supply houses use mosses for packing live plants and animals, taking advantage of their retention of moisture and antibiotic properties. In Great Britain, mosses were used as temporary stuffing for mammalian skins at the British Museum (A. J. Harrington 1985). Throughout history, bryophytes have been used to protect fragile articles. During World War II, the Defense Department used *Sphagnum* to pack bomb sights (K. Parejko, pers. comm.). In Japan, *Aerobryopsis subdivergens, Barbella determisii, Meteorium helmintocladulum,* and *Neckera calcicola* have been found in boxes holding ancient silk clothes (A. Noguchi 1952); these pendant mosses have the advantage of having no soil attached. *Rhytidiadelphus triquetrus* has been used to protect fragile articles such as China (J. H. Dickson 1973). Vikings used mosses to pack soft leather slippers. Elsewhere in Europe, *Hypnum, Plagiomnium undulatum,* and *Sphagnum* were used to protect the blades of daggers and scrapers (Dickson 1967).

Pseudoscleropodium purum (J. H. Dickson 1967), *Hylocomium splendens*, and *Rhytidiadelphus squarrosus* have been dispersed around the world because of their widespread use in packing (M. R. D. Seaward and D. Williams (1976). B. H. Allen and M. R. Crosby (1987) referred to the worldwide travel and establishment of *Pseudoscleropodium purum* as legendary, and its use as packing material in boxes of young trees currently being shipped to Tristan da Cuñha seems destined to introduce it there as well.

Graves

The preservation in bogs of men with their associated hats and hanging ropes is well known (T. J. Painter 1991). The action of peaty waters in tanning hides preserved these bodies for centuries. Both Alaskans and Japanese have been known to use a bed of moss for burial of the dead (J. H. Bland 1971; H. Ando and A. Matsuo 1984), and a wooden coffin about 1300 years old was found to contain *Aerobryopsis subdivergens* and other mosses at Ohira-cho, Tochigi-ken, Japan (Z. Iwatsuki and H. Inoue 1971). Siberians used mosses, including *Pleurozium schreberi, Ptilium crista-castrensis,* and *Rhytidium rugosum*, to help fit together sheets of bark in lining the roofs of tombs, now 2,500 years old (S. I. Rudenko 1970).

The Guanche mummy, from the Canary Islands, had *Neckera intermedia* (an epiphyte) in the abdominal cavity for mummification; the body was carbon dated to 1380 ± 80 years BP (P. Horne and R. R. Ireland 1991). Previously there was a report of a frozen Eskimo woman with moss in her lungs, but this has been considered to be accidental, with the moss inhaled when the woman

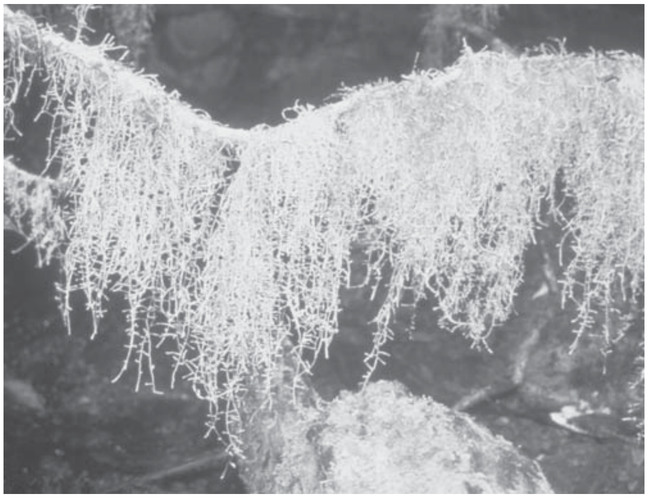

FIGURE 20. Meteoriaceae form large, pendant growths on trees in Japan and many tropical areas, providing clean packing material. Photo by Janice Glime.

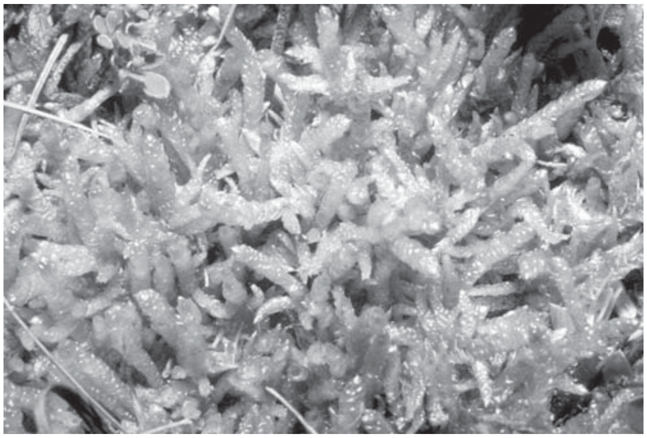

FIGURE 21. *Pseudoscleropodium purum*, used for packing, has consequently been introduced into ecosystems throughout the world. Photo by Janice Glime.

was accidentally buried alive (M. R. Zimmerman and G. S. Smith 1975; Horne and Ireland).

Medical Uses

Surgical

Early in the twentieth century, several authors published accounts of the use of *Sphagnum* as a surgical dressing (J. B. Porter 1917; J. W. Hotson 1918, 1919, 1921; G. E. Nichols 1918, 1918b, 1918c, 1918d, 1920), saving precious cotton for use in gunpowder during World War I. According to Nichols (1918c, 1920), *Sphagnum* dressings were used extensively by the British Army, reaching ca. one million pounds of dressings per month, saving about US $200,000 (J. H. Bland 1971), by the Canadian Red Cross of ca. 200,000 pounds per month, and by the United States of ca. 500,000 pounds, during the last six months of that war (Bland). Although the use of *Sphagnum* as a dressing all but ceased after World War I, the Chinese have continued to use it for this purpose (Ting H. S. 1982).

Sphagnum is superior to cotton dressings in a number of ways (J. B. Porter 1917). It absorbs three to four times as much liquid at a rate about three times as fast, necessitating less frequent change. It is also cooler, softer, less irritating, retards bacterial growth (R. D. Banerjee 1974), and is economical. Recently, S. J. Varley and S. E. Barnett (1987) cited evidence from controlled testing that indicated that the amount of wound area covered by new epidermis doubled with use of *Sphagnum* dressing compared to none.

Any contact of *Sphagnum* with the human body requires being alert to the presence of fungi among these plants. Fungal-caused sporotrichosis is a hazard to nursery workers and harvesters of *Sphagnum* (D. J. D'Alessio et al. 1965; S. E. Tamblyn 1981), and in one case a horticultural worker contracted sporotrichosis of the abdomen (E. H. Frankel and D. F. Frankel 1982). The American Orchid Society warns its members of this occupational hazard (A. A. Padhye and L. Ajello 1990). Perhaps more dangerous is pulmonary sporotrichosis, an infection of the lung resulting from breathing the causative fungi (W. H. McCain and W. F. Buell 1968). Even forestry workers can contract the disease when working in peatlands (K. E. Powell et al. 1978), and sporotrichosis reached sufficient proportions in 1988 for the Milwaukee Journal to report *Sphagnum* as the culprit (N. Rosenberg 1988). The Macauley Institute in Aberdeen, England, is investigating the use of hydroponics to produce *Sphagnum* free of micro-organisms and other contaminants.

Medicines

The Doctrine of Signatures (where medicinal employment of plants is suggested by their shape) has played a major role in the use of bryophytes, especially liverworts, in herbal medicine. For example, because *Polytrichum commune* has long hairs on its calyptra, covering the capsule, the ladies in the time of Dillenius used an oil extract from the calyptra to strengthen and beautify their hair (J. J. Dillenius 1741; J. H. Bland 1971; H. A. Crum 1973).

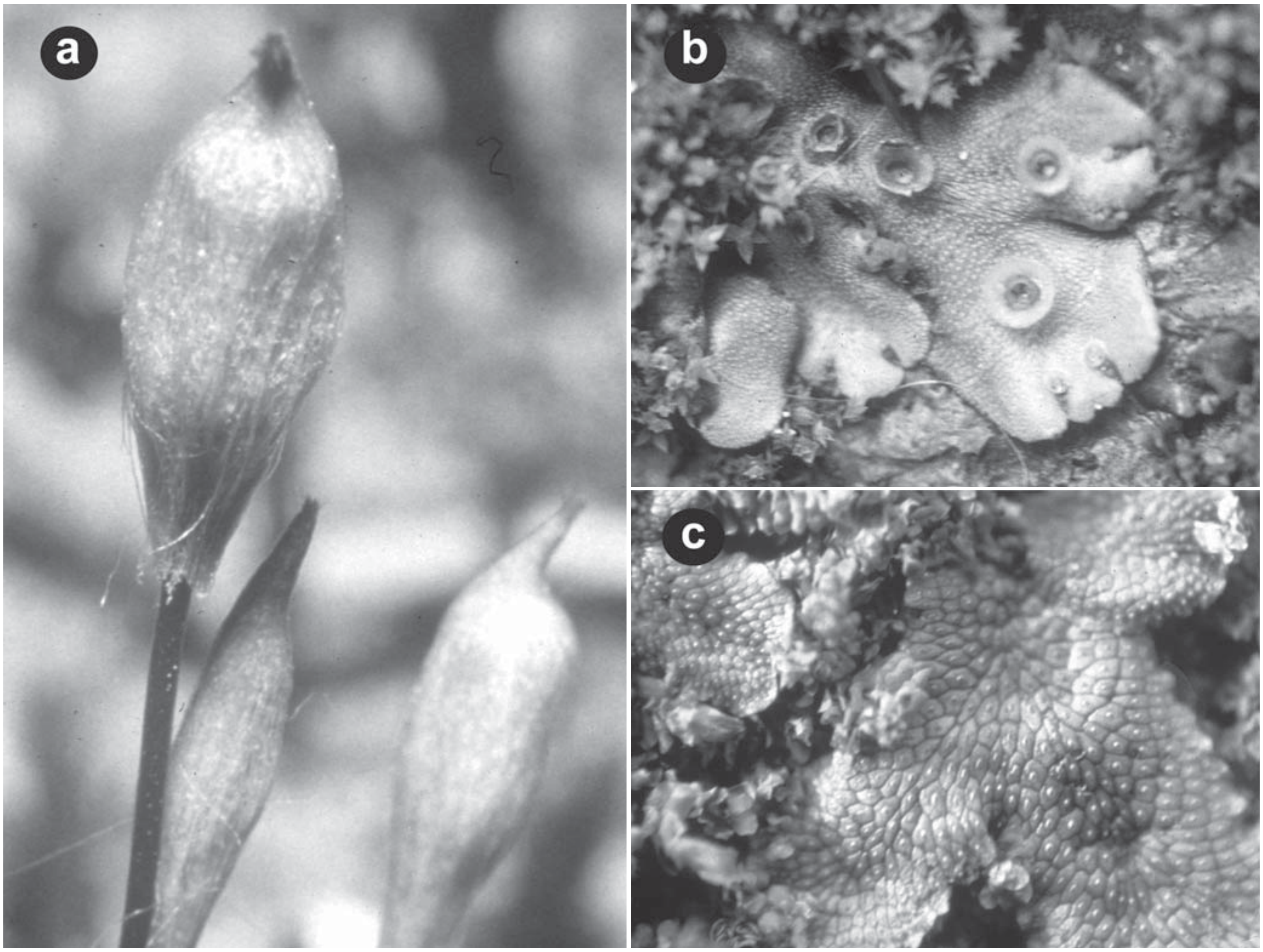

FIGURE 22. Many bryophytes have been used for medical purposes, mostly based on appearance according to the Doctrine of Signatures. **a.** The hairy calyptra of *Polytrichum* was used to strengthen and beautify hair. **b.** *Marchantia polymorpha*, shaped like a liver and identifiable by its gemmae cups, has been used to treat liver ailments, pulmonary ailments, and boils. As a source of Marchantin A, it may have true medicinal properties against the KB cells involved in leukemia. **c.** The snakelike appearance of *Conocephalum conicum*, a common liverwort used medicinally along with *Marchantia polymorpha* and vegetable oils as a salve for burns, boils, bites, cuts, eczema, and wounds, is known to inhibit micro-organisms. Photos by Janice Glime.

The use of bryophytes in herbal medicines has been common in China, India, and among Native Americans since ancient times. Numerous compounds, including oligosaccharides, polysaccharides, sugar alcohols, amino acids, fatty acids, aliphatic compounds, prenylquinones, and aromatic and phenolic compounds occur in bryophytes, but few links have been made between any medical effects and specific bryophyte species or compounds (G. B. Pant and S. D. Tewari 1990).

Perhaps the most widely known example of the Doctrine of Signatures is the use of *Marchantia polymorpha* to treat liver ailments; the surface suggests a cross section of liver (H. Miller and N. G. Miller 1979); it reputedly will cool and cleanse the liver, remove yellow jaundice, and remove inflammation (J. H. Bland 1971). In China, it is still used to treat the jaundice of hepatitis and as an external salve to reduce inflammation (Hu R. L. 1987). Himalayan Indians use *Marchantia polymorpha* or *M. palmata* to treat boils and abscesses because the young archegoniophore resembles a boil as it emerges from the thallus (G. B. Pant and S. D. Tewari 1989). Its similarity to the texture of lung tissue caused Europeans to use *M. polymorpha* to treat pulmonary tuberculosis (Bland). *Riccia* species were used in the Himalayas to treat ringworm because of the resemblance of that liverwort to the rings made by this fungal infection.

Recent tests on *Riccia fluitans* from Florida indicated no ability to inhibit growth of bacteria (*Pseudomonas aeruginosa, Staphylococcus aureus*) or yeast (*Candida albicans*) (A. L. Pates and G. C. Madsen 1955), and it is unlikely that this liverwort does any better with ringworm.

In China, 30–40 species of bryophytes have been considered to be medicinally effective (Ting H. S. 1982). Dried *Sphagnum* is sold to treat hemorrhages (J. H. Bland 1971), and *S. teres* is used to treat eye diseases (Ting), but J. C. Mitchell and A. Rook (1979) cautioned against the possible allergenic effects of *Sphagnum*, probably because it may harbor the fungus causing sporotrichosis (J. E. Adams et al. 1982). *Rhodobryum giganteum* and *R. roseum* are used to treat cardiovascular diseases and nervous prostration, *Polytrichum commune* to reduce inflammation and fever, as a detergent diuretic, laxative, and hemostatic agent (Hu R. L. 1987), and *Haplocladium microphyllum* to treat cystitis, bronchitis, tonsillitis, and tympanitis. A mixture of *Conocephalum conicum* and *Marchantia polymorpha* with vegetable oils is used on bites, boils, burns, cuts, eczema, and wounds (Wu P. C. 1977; Ting; H. Ando 1983). *Fissidens* is used as an antibacterial agent for swollen throats and other symptoms of bacterial infection. Presumably on the same rationale, *Polytrichum commune* is boiled to make a tea for treating the common cold. This species also reputedly helps dissolve stones of kidney and gall bladder (A. Gulabani 1974). Surprisingly, some ancient treatments in China now have clinical support (Ting). In 1976 the staff of the Laboratory of the Fourth Medical School in China went to eastern Sezchuan, where they studied mosses used by peasants (Wu 1982). Clinical research showed that an ether extract of *Rhodobryum giganteum*, used by peasants to cure angina, contains volatile oils, lactones, and amino acids. When given to white mice, the extract actually reduced oxygen resistance by increasing the rate of flow in the aorta by over 30%.

In Montana, the Cheyenne use *Polytrichum juniperinum* in medicines (J. A. Hart 1981). In Utah, the Gasuite Indians used *Bryum, Mnium, Philonotis,* and various matted hypnaceous forms, crushing them into a paste and applying the poultice to reduce the pain of burns (S. Flowers 1957). They used similar poultices for bruises and wounds or as padding under splints to set broken bones.

In the Himalayas, Indians use a mixture of moss ashes with fat and honey as a soothing and healing ointment for cuts, burns, and wounds (G. B. Pant et al. 1986). They claim it has a soothing effect and heals wounds more quickly (Pant and S. D. Tewari 1989). The antibiotic properties of *Sphagnum* have been discovered throughout the Northern Hemisphere. In Alaska, the Indians mix it with fat to make a salve (W. B. Schofield 1969; H. Miller and N. G. Miller 1979); in Britain it was used to treat boils (J. H. Bland 1971); the derivative sphagnol relieves the itch of a mosquito bite (H. A. Crum 1988); and it has been used for medicinal baths (Crum 1973; K. Weber and G. Ploetner 1976), but the small amounts of active substances put into an average bath are not likely to have any effect.

FIGURE 23. *Rhodobryum ontariense* is a member of a genus used to treat cancer in China. Photo by Janice Glime.

Antibiotics and Other Biologically Active Substances

In addition to the many medicinal uses by ancient cultures, one of the factors that has led to pharmaceutical investigation of bryophytes is the presence in many taxa, particularly in liverworts, of unique odors. For example, *Conocephalum conicum* smells like mushrooms and species of *Leptolejeunea* and *Moerckia* are distinctly aromatic (R. M. Schuster 1966–1992, vol. 1). *Lophozia bicrenata* has a pleasant fragrance, species of *Solenostoma* smell like carrots, and *Geocalyx graveolens* has a turpentine-like odor.

Isotachis japonica has at least three aromatic esters: benzyl benzoate, benzyl cinnamate, and ß-phenylethyl cinnamate (A. Matsuo et al. 1971). S. Hayashi et al. (1977) have found monoterpene hydrocarbons such as a-pinene, ß-pinene, camphene, sabinene, myrcene, a-terpinene, limonene, fatty acids, and methyl esters of low molecular weight and contend that unique odors are the result of a mixture of many compounds.

Since mosses and liverworts seldom show signs of infection in nature, it is not surprising that G. C. Madsen and A. L. Pates (1952) found inhibition of microorganisms in products of bryophytes, including *Sphagnum portoricense*, *S. strictum*, *Conocephalum*

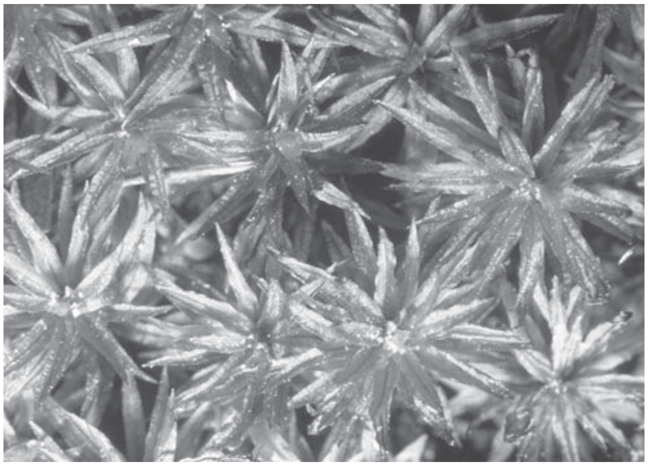

FIGURE 24. *Atrichum* species, in addition to having antibacterial properties, are commonly used in moss gardening because of their ease of propagation by fragments. Photo by Janice Glime.

conicum, and *Dumortiera hirsuta*. J. A. McCleary et al. (1960) suggested mosses as a source for antibiotics. Later, F. P. Belcik and N. Wiegner (1980) found antimicrobial activity in extracts of the liverworts *Pallavicinia* and *Reboulia*, and S. Isoe (1983) reported this from *Porella*. McCleary and D. L. Walkington (1966) suggested that non-ionized organic acids and polyphenolic compounds might contribute to the antibiotic properties of bryophytes; they found eighteen mosses, the most active being *Atrichum, Dicranum, Mnium, Polytrichum*, and *Sphagnum*, that strongly inhibited either or both gram-positive and gram-negative bacteria. *Atrichum undulatum* effectively inhibited growth of all bacteria tested except *Aerobacter aerogenes* and *Escherichia coli*. Z. Pavletic and B. Stilinovic (1963) found that *Dicranum scoparium* strongly inhibited all bacteria they tested but (gram-negative) *Escherichia coli*. K. G. Gupta and B. Singh (1971) found high occurrence of antibacterial activity in the extract of *Barbula* species, reaching as high as 36.2%, whereas in *Timmiella* species it was only 18.8%.

Even virus and fungal diseases may some day be cured by extracts of mosses. Although L. van Hoof et al. (1981) found no effect of 20 species of moss extracts on the herpes virus, R. Klöcking et al. (1976) found that at least some peat humic acids possess antiviral activity against herpes simplex virus types 1 and 2, with the most sensitive phase being during the adsorption of viruses to the host cells. J. Witthauer et al. (1976) characterized several antivirally active humic acids in *Sphagnum*, and *Camptothecium* extracts that can inhibit growth of polio virus. Some fungi are inhibited by some bryophytes. We know of important antifungal activities of many moss extracts against tested dermatophytes (van Hoof et al.). *Hypnum cupressiforme* has marked antibacterial and antifungal effects.

Out of more than 80 species of mosses tested, T. Ichikawa (1982) and Ichikawa et al. (1983) found antimicrobial activity in nearly all of them. Acyclic acetylenic fatty acid and cyclophentenonyl fatty acid extracts from the mosses completely inhibited the growth of the rice blast fungus *Pyricularia oryzae*.

R. D. Banerjee and S. P. Sen (1979) found that degree of antibiotic activity in a given species may depend on age of the gametophyte, and A. Matsuo et al. (1982, 1982b, 1983) demonstrated that antifungal activity of the liverwort *Herbertus aduncaus* was age-dependent. In their study, its extracts inhibited the fungi *Botrytis cinerea, Pythium debaryanum,* and *Rhizoctonia solani.* They subsequently isolated three aging substances: (-)-a-herbertenol; (-)-ß-herbertenol, and (-)-a-formylherbertenol from it. The absence of fungal diseases in liverworts led R. J. Pryce (1972) to suggest that lunularic acid, an aging hormone found in liverworts but not in mosses, might be responsible for liverwort antifungal activity. However, aging substances are not the only antimicrobial agents in liverworts; Y. Asakawa et al. (1982) isolated three prenyl bibenzyls from *Radula* spp. and demonstrated that they could inhibit growth of *Staphylococcus aureus* at concentrations of 20.3 µg ml^{-1}.

Use of bryophytic extracts is not yet a fact. The possibilities of using bryophytes in control of disease and malfunction are exciting, but exploratory work has just begun. Twenty-five years ago, virtually nothing was known of bryophyte biochemistry, but now it is sure that the variety of chemicals produced by these morphologically simple organisms is phenomenal. Unfortunately, biologically active substances so far obtained from bryophytes have not proved economical in practice. While their pharmaceutical worth seems promising, we lack any understanding of potential harmful side effects.

Anti-tumor Properties

M. Belkin et al. (1952) found that extracts of *Polytrichum juniperinum* had anticancer activity against Sarcoma 37 in mice. Y. Ohta et al. (1977) isolated *ent*-eudesmanolide, diplophylline, from *Diplophyllum albicans* and *D. taxifolium*. Diplophyllin showed significant activity (ED50 4–16 µg/ml) against human epidermoid carcinoma (KB cell culture). Y. Asakawa (1981, 1982b) isolated the sesquiterpenoids costunolide and tulipinolide, tumor growth-inhibiting substances also known from higher plants, from *Conocephalum supradecompositum, Frullania monocera, F. tamarisci, Marchantia polymorpha, Porella japonica,* and *Wiesnerella denudata,* to which A. Matsuo et al. (1980, 1981, 1981b, 1981c, 1981d, 1984) added *Lepidozia vitrea* and *Plagiochila semidecurrens*. These substances have demonstrated activity against carcinoma of the nasopharynx, at least in cell culture.

Bryophytes subsequently aroused the interest of the U.S. National Cancer Institute, where R. W. Spjut et al. (1986) tested 184 species of mosses and 23 species of liverworts for antitumor activity. They found that extracts of 43 species were active, while those of 75 species were toxic to the test mice. The most activity was found in Brachytheciaceae, Dicranaceae, Grimmiaceae, Hypnaceae, Mniaceae, Neckeraceae, Polytrichaceae, and Thuidiaceae. However, in 1988, this team reported that the antitumor activity of the moss *Claopodium crispifolium* was greatest in samples with the Cyanobacterium *Nostoc* cf. *microscopicum*, and they suggested that the *Nostoc* could be the direct source of the activity or that the activity could be the result of interaction between the species (Spjut et al. 1988). Interaction could result from the transfer of a precursor from the *Nostoc* to the moss and subsequent alteration to the active substance by the moss, or it might result from an allelopathic response of the moss to the presence of the *Nostoc*. In any event, this raises important and intriguing questions, both medically and ecologically.

Several compounds from leafy liverworts exhibit antileukemic activity (Y. Asakawa 1981). Marchantin A from *Marchantia palacea, M. polymorpha*, and *M. tosana*, riccardin from *Riccardia multifida*, and perrottetin E from *Radula perrottetii* all show cytotoxicity against the KB cells (Asakawa et al. 1982). Peat preparations hold some promise against some types of human cancer (W. Adamek 1976).

Caution is in order regarding medicinal use of bryophytes, particularly liverworts, because of potential allergic reactions. *Frullania* is well known for its ability to cause contact dermatitis, especially in forest workers (J. C. Mitchell et al. 1969), and in southern Europe, in olive pickers (J. Curnow, pers. comm.). The active component is a sesquiterpene lactone (Y. Asakawa 1981). D. H. Wagner (pers. comm.) reports that this reaction can be caused by other liverworts as well, including *Chiloscyphus polyanthos*; this is especially a problem when it is squeezed to remove excess water. By 1981, Asakawa and others had identified 24 liverwort species with potential allergenic sesquiterpene lactones.

For some reason, work has concentrated on the liverworts, perhaps because of their distinctive aromas, but mosses also have phenolic compounds and their potential utility for medical purposes has largely been ignored.

Food Sources

Most ecologists consider bryophytes to be unimportant as food sources for animals. On Mount Washington in New Hampshire, mosses had the lowest caloric values of any plants analyzed (R. T. T. Forman 1968). Absence of herbivory on bryophytic herbarium specimens lends further support to this contention. The same compounds that may make bryophytes medicinal usually endow them with a nasty taste. M. Mizutani (1961) complained that it was necessary to gargle to get rid of the bitter liverwort taste, hardly surprising in view of the number of phenolic compounds in a single species. Y. Asakawa et al. (1979) identified and described the source of pungency in *Porella arboris-vitae* as the sesquiterpene polygodial. Nevertheless, J. J. LaCroix (1996) has shown that the aquatic pillbug *Asellus militaris* will eat *Fontinalis antipyretica* despite its typically high phenolic content, finding shaded populations with lower phenolic content.

Occasionally ungulates ingest mosses. For example, Alaskan reindeer occasionally graze on *Aulacomnium turgidum*, *Hylocomium splendens*, and *Polytrichum* (J. H. Bland 1971). Mosses are known from the alimentary tract of Mylakhchinsk bison (V. V. Ukraintseva et al. 1978), and one prehistoric woolly mammoth died and was preserved in ice with *Hypnum* and *Polytrichum* in his rumen (Bland). In the Canadian Arctic archipelago, rumens of Peary caribou can contain up to 58% mosses (D. C. Thomas and J. Edmonds 1983), but digestibility in summer is only 11–35% and in winter only 3–11% (Thomas and P. Kroeger 1980). It is thus unlikely that they are being consumed for nourishment.

O. E. Jennings (1926) concluded that mosses could not be infected by fungi because the fungi had no enzyme to break down the cell membrane and extract cell contents; he used this argument to suggest that it was therefore unlikely that a cow could do any better, since fungi are specialists at such activities. However, we now know that there are fungi that do infect bryophytes (P. Doebbeler 1997; M. R. Khan et al. 1997; E. Brouwer 1999).

Bryophytes may be the source of specific needs of animals at a time when fresh food is scarce. For example, *Barbella pendula* has a high content of vitamin B_{12}, a vitamin that is difficult to obtain on a strictly vegetarian diet. When fed to puppies and chickens, it causes no noticeable side effects (S. Sugawa 1960). Hog farms take advantage of unique properties of *Sphagnum* to administer vitamins. Piglets are often anemic, and milled peat moss, used as a binder for iron and vitamins, is fed to them.

Given this, it is not surprising that moss predation increases in northern climates. One benefit there may be the presence of large quantities of arachidonic acid in bryophytes, especially at cooler temperatures (R. H. Al-Hasan et al. 1989). This fatty acid has greater pliability at low temperatures (melting point -49.5°C) than other fatty acids and can be used to replace the fatty

FIGURE 25. *Herbertus*, a leafy liverwort used for chinking, forms “muffs” on trunks of trees on the Queen Charlotte Islands in British Columbia. Photo by Janice Glime.

acids of cell membranes in winter to keep them pliable. H. H. T. Prins (1981) suggested that it might keep the foot pads of arctic mice and lemmings from freezing.

One would not expect a group of plants with insecticidal properties to be a common product in the marketplace. The Chinese consider mosses to be a famine food (J. H. Bland 1971). Otherwise, the only direct use of bryophytes for human food seems to be that of the Laplanders who once used *Sphagnum* as an ingredient in bread (Bland). Although the moss itself is not eaten, *Sphagnum* contributes to the flavor of Scotch whisky. Peat and coke are burned in kilns under screens holding barley malt sprouts, and this pungent flavor persists through the subsequent distillation process (N. G. Miller 1981).

In the Himalayas, Kumaun Indians use slender bryophytes such as *Anomodon, Entodon, Hypnum, Meteoriopsis, Herbertus,* and *Scapania*, wrapped in a cone of *Rhododendron campanulatum* leaves, to serve as a filter for smoking tobacco (G. B. Pant and S. D. Tewari 1989).

In China, bryophytes are critical to the important gallnut industry. Gallnuts are not only a delicacy, but are important in medicine as pain killers, antiseptic and antidiarrheal agents, expectorants, astringents, and preservatives (Min L. Y. and R. E. Longton 1993), and in industry as a source of tannic acid. The gall aphids, *Schlechtendalia chinensis*, overwinter on mosses, especially species of *Plagiomnium*, before migrating to leaves of *Rhus javanica* to make their galls (Y. Horikawa 1947; Wu P. C. 1982). In Japan, G. Takagi (1937) advised an increase of suitable mosses to increase gallnut production. Now the Chinese rear the aphids agriculturally on mosses (Tang C. 1976). But in Yunnan, the host tree does not grow well in the same places as the most common host moss, *P. maximoviczii*, so the Chinese are trying to find ways to increase growth of this moss near the trees. In some areas, bowls of moss are placed under *Rhus* trees for several weeks while autumn-migrant aphids return and locate them, then kept in sheds for winter (Min and Longton). In April, the moss is taken from the bowls and replaced under the trees. Meanwhile, the bowls are supplied with fresh soil and remaining moss fragments regenerate moss plants sufficiently to be used again in October. The aphid depends on the moss as food for young larvae.

Such delicate ecological interactions as these pervade the world, involving human medicines and critical emergency foods for wild mammals and birds, and providing nesting and safe sites for countless insects, frogs, and other creatures. Surely many interesting surprises await science as we only now begin to understand the role of the bryophyte in this complex world.

Genetic Engineering

Some of the most exciting uses for mosses are just beginning to emerge. With the capabilities of modern genetic engineering, it is now theoretically possible to manipulate the genomes of plants to endow them with desirable traits for human use. While bryophytes themselves have had limited application, their ability to survive drought and become functional again within 24 hours has aroused the imagination of agriculturalists (D. Comis 1992; P. Hoffman 1992). Furthermore, current research reveals how bryophytes can withstand freezing while still in a state of hydration, yet recover almost instantly (D. Rütten and K. A. Santarius 1992).

M. J. Oliver and colleagues, working at the United States Department of Agriculture in Lubbock, Texas, have isolated several genes specific for recovery of desiccated gametophytes of mosses (H. B. Scott and M. J. Oliver 1994). His group is hopeful that leaves of crop plants can be given ability to withstand drought, or more particularly, to recover from desiccation damage. The best candidate for this is the drought-tolerant moss *Syntrichia ruralis*, and the most likely experimental recipient is tobacco (Comis).

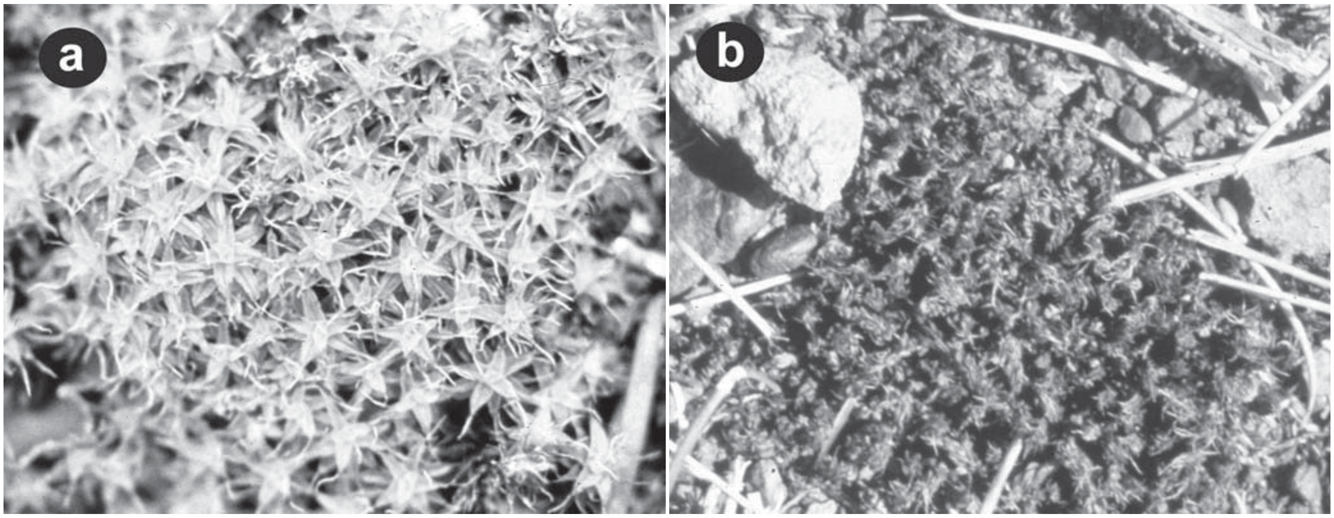

FIGURE 26. Wet (**a**) and dry (**b**) *Syntrichia ruralis*, a moss used for genetic engineering of other plants for drought resistance. Photo by Janice Glime.

Even more exciting is the use of the tiny moss *Physcomitrella patens* to produce human proteins (A. Hohe et al. 2002). Mosses, and particularly this moss, have a high frequency of homologous recombination. Thus there is a stable integration of inserted genes. *Physcomitrella patens* is the only plant being used to produce the blood-clotting factor IX for pharmaceutical purposes (http://www.greenovation.com/). The mosses are grown in a bioreactor where only water and minerals, along with with light and CO_2, are needed to keep the system active. The moss offers an advantage of requiring no antibiotics during culture, thus avoiding contamination of the final product. Its small size permits lab culturing, reducing the possibility of escape of transgenic plants.

Through their long evolutionary history bryophytes have acquired an array of biochemicals that may one day prove to be a substantial source of human medicines or provide a gene bank for making proteins, enzymes, sugars, or fatty acids permitting crop plants to survive drought, cold, or infestations. While their economic value to date has been limited, there are indications of exciting new uses for bryophytes in the near future.

Table 1. Weight gain measured as the ratio of wet to dry weight of selected bryophytes (Horikawa 1952).

Atrichum	6.9
Barbula	8.3
Bazzania pompeana	4.0
Haplomitrium mnioides	12.0
Hylocomium cavifolium	9.8
Plagiomnium maximoviczii	6.7
Rhodobryum	10.0
Sphagnum	12.4
Trachycystis microphylla	3.2

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