CHAPTER 6
TECHNOLOGICAL AND COMMERCIAL

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Figure 1. Commercial cranberry farm near Black River Falls, Wisconsin, USA. ***Sphagnum*** peatlands are necessary to protect the cranberries and maintain sufficient water for their growth. Photo by Janice Glime.

Sphagnum Peatlands

First, a definition of peat and peatlands is in order. **Peat** is comprised of partly decomposed vegetable matter containing a variety of plants (Figure 2) that may or may not include ***Sphagnum*** (Figure 3). Peat is brown and soil-like and is derived from boggy, acidic ground (Figure 1). **Peat mosses**, on the other hand, are species of ***Sphagnum*** (Figure 3). **Peatlands** are lands consisting largely of peat or peat bogs (Figure 4). They may be dominated by ***Sphagnum*** (Figure 3), but there are also peatlands that have no ***Sphagnum***.

Figure 2. Harvesting peat in Saterland, Germany. Photo by Pyt, through public domain.

Figure 3. ***Sphagnum magellanicum***, one of many species of ***Sphagnum*** from ***Sphagnum*** peatlands and in widespread usage in horticulture, fuel, and other applications. Photo by James K. Lindsey, with permission.

Certainly the best-known and widespread uses for mosses in both modern and ancient times are the uses of ***Sphagnum*** (Figure 3). This is not surprising since it occupies 3% of the Earth's surface, mostly in the northern hemisphere (Clymo 1987). Its abundance, longevity, cation exchange (Clymo 1963; Fischer et al. 1968), and ability to hold water make it ideal for commercial exploitation. Its largest usage in North America is for horticulture and cranberry culture (Figure 1; Figure 5), but in Europe, fuel is an important use as well (Clarke 2008).

Figure 4. Peatlands in Manitoba, Canada. Photo by subarcticmike, MSG Family, Mukhrino FS, through Creative Commons.

Figure 5. Cranberries (*Vaccinium macrocarpon*) growing among ***Sphagnum*** and ***Polytrichum***. Photo by Janice Glime.

Turner (1993) reviewed the human uses of peat. In addition to 100 million tons a year used as fuel in Ireland, peat provides a source of waxes and resins. The by-products provide oily materials for dyes, varnish, and leather treatments. More recent uses include making biofilters.

In the UK, ***Sphagnum*** (Figure 3) has been recommended as a litter for milking cows. Peltola (1986) reported that compared to straw and sawdust, peat provides better absorption of urine and binding of ammonia than the other litters. The spent litter is good for growing plants because it contains more than the average amounts of nitrogen and magnesium in a form readily used by plants.

In Japan, the Technical Academy of Sphagnum and the Marsh Bowz Factory illustrate uses, including peat grown on clay shapes, a restful boardwalk through the green moss (Figure 6), a cover for an aquarium that presumably reduces water loss while still permitting the entry of fresh air, and a peat roof garden with stepping-stones.

Figure 6. Boardwalk on the Fort River Birding and Nature Trail, Hadley, Massachusetts, USA, a restful walk with protection of peatlands and other delicate plants. Photo from USFWS, through public domain.

Heavy Metal Detection and Cleanup

Cleaning up heavy metals from waterways is one of the most important environmental problems facing Americans (and others) today (Trujillo *et al*. 1991). Such methods as chemical precipitation, ion exchange, reverse osmosis, and solvent extract have been widely used, but are less than desirable. Their metal removal is incomplete, they require large quantities of reagents or high amounts of energy, and they generate toxic sludge and waste products that require expensive and dangerous disposal. The U.S. Bureau of Mines is using ***Sphagnum*** (Figure 3) that has been immobilized in porous polysulfone beads. These are able to remove zinc, cadmium, and other metals selectively from zinc mine wastewater, reducing the concentrations to well below the national drinking water standards. Furthermore, the adsorptive capacity of the beads appeared to increase after the first few cycles.

The cation exchange ability of ***Sphagnum*** (Figure 3), with its walls packed with polyuronic acids, gives it unique properties unmatched by its tracheophyte counterparts, and often even by the connivances of humans. It serves well in an electrode for the detection of lead, offering a detectability level of 2 ng ml^{-1} (Ramos *et al*. 1993). The 10% moss electrode is easily regenerated by immersion in 0.05 M perchloric acid for only 60 seconds.

Now that the lead has been detected, one can remove it and other heavy metals with the biomass beads made of dried, ground ***Sphagnum*** (Figure 3) in a porous polysulfone matrix (Spinti *et al*. 1995). However, they seem to have lower capacity than other commercially available ion exchange resins.

Filtration

The ability of peat mosses to bind heavy metals and other substances on their cation exchange sites makes them ideal organisms for cleaning up a variety of heavy metals and organic compounds in liquids. I have used peat mosses to clean up creosote in a very small pond. The peat removed the toxicity and took the toxic substance with the peat when I removed the mosses. Before I used the mosses, the fish all died, even when fresh water sat in the pond for a month. After subsequently letting the mosses soak in the pond water for a month, the new fish survived.

Farmers may use both inorganic and organic (including ***Sphagnum***; Figure 3) amendments to reduce the loss of ammonia from liquid hog manure and to keep the hog pens fresh by controlling odors (Al-Kanani *et al*. 1992a, b)

Other forms of wastewater benefit from peat filtration. A counter-current system is used to purify water, with peat serving to both absorb and adsorb contaminants (Asplund *et al*. 1976; Brown & Farnham 1976; Coupal & Lalancette 1976). Even organic waste such as pentachlorophenol can be removed by using peat as a filter (Viraraghavan & Tanjore 1994). Peat us used to filter out heavy metals, microbes, pesticides, organic acids, oils, and odors (Turner 1993).

Oil Cleanup

Mele, in his book *Polluting for Pleasure* (1993), claims that 420 million gallons of oil from pleasure boating enter our waterways in America each year. This staggering number is equivalent to 40 Exxon Valdez disasters! Peat mosses are among the very best absorbents of the oil and can even be used to rescue birds (Figure 7) and other animals covered in oil. As early as 1972, D'Hennezel and Coupal recognized their utility for cleanup. They are readily available, and bales could be stored near a harbor, ready for small spills. Today, there are also commercial peat moss "fences" available from several sources, especially in Canada, to contain oil spills.

Figure 7. Sea bird covered in oil from Black Sea oil spill. Photo by Pauk, through Creative Commons.

One supplier advertises that Hydro-Weed (Figure 8), made from a blonde ***Sphagnum*** (Figure 3) peat from Newfoundland, is a lightweight, natural hydrocarbon absorbent (Hydro-Weed 2007). The processing sterilizes the plants and kills the insects. Hydro-Weed is currently used by all branches of the United States Navy, Army, National Guard, Marines, and Air Force.

Figure 8. This pile of Hydro-Weed, made with ***Sphagnum***, is a good absorbent of oil while repelling water. Photo from Hydro-Weed 2007.

Hydro-Weed is extremely effective at absorbing oil and other hydrocarbons. One pound will absorb 8-12 times its weight in medium weight oil, fifteen times more than clay absorbers! But it won't absorb water! Anyone knowing the ecology of ***Sphagnum*** (Figure 3) would immediately become skeptical, and I can only conjecture on this water-repelling shift. We know that oil and water don't mix. IF the oil is absorbed preferentially, then the oil would undoubtedly contribute to the loss of water absorption by actually repelling it. Furthermore, if dry peat is used, it would float, and so would the oil, so the oil would be contacted first and make the plants as repellent as a duck's back.

A further advantage of Hydro-Weed is that it will not release the oil. The company suggests putting it along a fencerow where microbes will break down the oil or other absorbed chemical, leaving the peat moss to benefit the soil. And a bird landing on the floating or discarded Hydro-Weed will leave without "a single drop of oil on its feathers."

The saturated Hydro-Weed can be put to even more valuable uses. It can be incinerated as fuel, contributing 7,200 BTU's per pound during incineration (excluding hydrocarbons). It is clean, generating only 0.42% of ash residual per pound after incineration. This makes it a good fuel for cement kilns and coal-generating fossil fuel plants.

Marcus (2002), in a science fair project, compared several materials [Sea Sweep, Spill Magic, saw dust, Enviro-Bond (a polymer that bonds to hydrocarbons), and peat moss] at two temperatures to determine which took the greatest weight of crude oil in salt water. When compared by weight of sorbent, at 6.6ºC the Enviro-Bond worked best, but at 21ºC the peat moss absorbed the most. Most of the sorbents worked best at 6.6ºC.

While this was just a science fair project, use of peat mosses has a sound basis in practice. Hunt (1995-2007, 2000, 2002-2007) reported the use of ***Sphagnum*** (Figure 3) from SpillSorb Canada Inc. to clean up an oil spill at the Dassen and Robben Islands off the coast of South Africa where 41% of the African penguins reside. First, the penguins themselves were dusted with peat dust, rendering them dry and safe to return to the water (Ark Enterprises Inc. 2004). Next, peat-based absorbents were used to clear oil from rocks (Crawford *et al*. 2000). Although the spill occurred on 23 June 2000, the shore was clean by 5 July that year (Hunt 1995-2007, 2000, 2002-2007). The hyaline cells of the ***Sphagnum*** leaves readily absorb the oil, up to

10 or even 20X the oven-dry weight of the moss. The ***Sphagnum*** also aids in the conversion of the oil to safe products. Rich in humic acids, it becomes a natural catalyst to aid in breaking down the hydrocarbon molecules of the oil; with the help of some microbes, it can aid the conversion of the oil to fatty acids, CO_2, and water. Peat Sorb is one such ***Sphagnum*** product (SANCCOB 2006).

Oclansorb Plus from Canada (Hi Point Industries 1991) is an oil-absorbent peat moss designed for application to surface oil and fuel spills in fresh and salt water marshes, wetlands, and any open water environment which cannot be efficiently cleaned by manual techniques. It blends a time-release system of peat moss that begins soaking up the oil within seconds, non-pathogenic bacteria bred specifically to metabolize petroleum hydrocarbons, N, P, trace nutrients, and pH buffers to enhance efficiency of bacterial degradation, and non-toxic gelling agents that facilitate adhesion of Oclansorb Plus to exposed tree roots, aquatic plants, and shoreline rocks.

In New Hampshire, the Department of Environmental Services made a novel use of peat moss. They rehearsed their response to an oil spill in Portsmouth's Great Bay Estuary (Dillon 2003), using peat moss and oranges to simulate the spread of the oil! The peat moss spread across the water like thin oil and the oranges simulated the bobbing tar balls, both without harming the environment.

The terrestrial environment is not immune to oil problems. A diesel oil spill in an Alaskan subalpine meadow had poor recovery after nine years, but the moss ***Racomitrium sudeticum*** (Figure 9) was one of the three species that survived (Belsky 1982). The moss was one of the few plants making the area green.

Figure 9. ***Racomitrium sudeticum***, a species that is able to survive an oil spill. Photo by Hermann Schachner, through Creative Commons.

Leaking crude oil production wells can create contaminated soils that must be cleaned up. For example, in McKean County, Pennsylvania, the use of fertilizers and leaf detritus or peat moss boosts the nitrogen content of the soils. This, combined with aeration by rototilling has been very successful in reducing total petroleum hydrocarbons (TPH) in soils. "Healing" is evident in a few weeks and the area can be replanted with grass seed the same season. The Maryland Department of the Environment (2004) suggests peat moss, among other things, for heating-oil cleanup. In New Zealand, Enviropeat™ is sold for cleanup of service stations, driveways, forecourts, maintenance areas, parking areas, refuelling areas, vehicle repair shops, ports & marinas, shoreline, and open sea oil spills (Enviropeat 2004). Unfortunately, using ***Sphagnum*** (Figure 3) to clean up large oil spills is not practical. Thus, spills like those in the gulf require other methods.

Fuel

The use of mosses for fuel is not just ancient history. Nearly half the world's peat production (Figure 10) is used for fuel (Figure 11-Figure 12), particularly in Scotland (Figure 13) and Ireland, providing the equivalent of 100-200 million tons of oil (UNERG report 1984). In Canada the peat deposits store more energy than do the forests and natural gas reserves combined (Taylor & Smith 1980). Nevertheless, the use of peat as fuel is down in Scotland, from 70,000 tonnes in 1955 to 20,000 tonnes in 1999 (Macleod 2006).

Figure 10. Peat extraction in East Frisia, Germany. Photo by Christian Fischer, through Creative Commons.

Figure 11. Peat mine with peat bricks for fuel. Photo by Paciana, through Creative Commons.

Figure 12. Peat fire. Photo by Cqui, through public domain.

Figure 13. Peat harvested in Lewis, Scotland. Photo by Wojsyl, through Creative Commons.

We might cringe that Ireland burns over 100 million tons of peat each year to generate power (Turner 1993), requiring large peatlands (Figure 14). What a scourge on the landscape! And it certainly does not renew at that rate, if ever. It is also used for waxes, resins, and oily materials for dyes and varnish and in treatment of leather.

Figure 14. Large peatlands like this one at Farwell, Michigan, USA, are rapidly disappearing due to development. Photo by Janice Glime.

At least it doesn't further pollute the environment. For example, in Minnesota it is used to remove chromium from power station wastes (Turner 1993), and it has been important in rescuing penguins in South Africa by cleaning up oil spills (Hunt 2004).

Peat is a promising replacement for our dwindling oil supplies, packing more than 8,000 BTU per dry pound, and is renewable when harvested carefully. It is such a clean-burning fuel that some have attributed the lovely complexions of Irish and Swedish women to use of peat as fuel (Drlica 1982). Its attractive feature as a fuel is that it is low in sulfur content, cleaner burning, and superior in heating value compared to wood, similar to lignite.

No longer restrained in use to the developing countries, liverworts and mosses are important sources of fuel in northern Europe, especially in Finland, Germany, Ireland, Poland, Russia, and Sweden. In Ireland, 25% of the fuel source is mosses (Richardson 1981). It serves not only to produce heat, but also electricity, with the former Soviet Union burning ~70 million tons and Ireland 3.5 million tons of mosses for that purpose in 1975 (Boffey 1975). If Hinrichsen (1981) was correct, the world should have been using peat in the equivalent of 60-70 million tons of oil by the year 2000.

Although peat is often considered to be a clean fuel, such is not the case with CO_2 emissions. Peat burning emits 106 g CO_2 MJ^{-1} whereas coal emits only 94.6 and natural gas only 56.1 g CO_2 MJ^{-1} (VTT 2004).

Peat is currently considered a slow renewable resource. Although peat is renewable, little of it has been harvested with a renewal plan in mind. Hence, many scientific studies are currently focusing on regeneration of various ***Sphagnum*** (Figure 3) species in the hope of restoring some of our lost peatlands. Unfortunately, little of it regenerates at the rate it is being used.

Hence, we need improved methods for harvesting, drying, and conversion to a burnable fuel (Lindstrom 1980). Although harvesting is easy, compared to that for coal, forests, and hunting for oil, we need to find ways that do not destroy the wetlands and convert them to non-peat-producing vegetation.

The Finns, in their attempt to become 40-50% self sufficient (Miller 1981) and provide a cleaner fuel (Johansson & Sipilae 1991), have suggested that placement of processing stations on the peatlands will reduce transport cost (Taylor & Smith 1980). They have introduced a de-watering process that produces dry pellets of partly carbonized peat (Taylor & Smith 1980). Finland is also exporting pulverized peat to northern Sweden, where it is used in industry and municipal heating, power generation, and oil burners of pulp and paper companies (Summerton 1981). However, for heating houses alone, replacement of light fuel oil with peat will require up to 6.2 million tons of peat pellets per year (Kinnunen *et al*. 1982). If this is reduced to only a 5% replacement of fuel oil, that consumption could be reduced to 310,000 tons per yr.

It took a coal miners' strike in 1903 to interest Americans to use peat as a fuel, but the cheaper availability of other fuels has prevented its widespread use (Thieret 1956). Nevertheless, planning for the future, the U. S. Geological Survey and other organizations have mapped North American peat deposits and estimated their extent (Miller 1981). This time it was an energy crisis with the possibility of diminished oil trade that fueled interest in peat fuel in the 1970's. In 1975, First Colony Farm in North Carolina began peat harvest to make methane and to

generate electricity; their land has an estimated 400 million tons of peat, enough to fuel a 400 megawatt power plant for 40 years (Carter 1978). The Minnesota Gas Company planned for its use of methane by applying for a long-term lease on 200,000 acres of peatland (Boffey 1975). Use of peats for production of methane eliminates the chopping that is required for other plants, and peat products can be used to produce ethylene, hydrogen, methanol, synthetic or natural gas, and low and intermediate BTU gas.

Ralf Pope (pers. comm. 12 July 2012) told me that there in an 860-acre peat mining operation in Deblois, Maine, USA (Figure 15-Figure 16). The Worcester Peat Company harvested peat there until ~2002 and used it to run a 22.8 megawatt peat-fired power plant. When the plant re-opens, they plan to use a mix of peat and septic sludge, billing it as green renewable power.

Figure 15. 860-acre peat mining operation of The Worcester Peat Company in Deblois, Maine, USA. Photo courtesy of Ralph Pope.

Figure 16. 860-acre peat mining operation by The Worcester Peat Company in Deblois, Maine, USA. Note the wood treads that minimize damage to the peatland by distributing the weight. Photo courtesy of Ralph Pope.

Peat in Construction

Whereas other mosses have played minor roles in construction, mostly for chinking, ***Sphagnum*** (Figure 17) has the potential to enter the arena big time (conservation issues aside). As early as 1903, the Swedes ground peat with asphalt to make a durable street pavement (Drlica 1982). Peat Crete, a mixture of peat with light concrete that is hydraulically pressed with Portland cement and water, provides a low-cost material that boasts easy sawing, nailing, casting, and molding, does not need to dry, is inflammable, and of low density (0.7 to 1.2 sp. gr.; 45-70 lb/ft^3) (Ruel *et al*. 1977). Its only negative quality is its low mechanical strength, but this seems more than balanced by its light weight for use in places where transportation is a problem. In dry places, flammability could be a problem.

Figure 17. ***Sphagnum magellanicum*** is a large moss that can be used in making various construction products. Photo by Janice Glime.

In June, 1972, Andrew Gilchrist, Chair of the Highlands and Islands Development Board at Bridge House, Bank Street, Inverness, Scotland, presented to the Right Honourable Gordon T. C. Campbell, Her Majesty's Secretary of State for Scotland, a report in which he referred to the possibility of production of Peat Crete as a means of improving the economy, stating: "We continue to watch over prospects for possible uses of peat, including the Building Research Centre's work on 'peatcrete.'" Unfortunately, or perhaps fortunately, a Google search does not indicate any commercial sources of this commodity.

In 1920, peat-based pasteboard and wrapping paper appeared in Michigan, USA, near Capac (Miller 1981). Peat boards have been used in chicken houses to help insulate them (Moore & Bellamy 1974).

Like many other mosses, ***Sphagnum*** (Figure 3) was used in chinking in log cabins (Lewis 1981), and the northern Europeans, living where peat is abundant to this day, stuffed it between the timbers of their houses to deaden sound (Thieret 1954). To this purpose, the Russians added slabs that they heated and pressed for insulation of refrigerators, and of course their houses (Sukhanov 1972; Ruel *et al*. 1977).

Peat then made its debut in place of particle board, as peatwood (Ruel *et al*. 1977). Dried ***Sphagnum*** (Figure 3) is blended with a phenolic resin and pressed into a heating mold; it offers quick hardening, attractive texture, good strength, easily nailed, screwed, and glued, and light weight (40-60 lb ft^{-3}). Other construction materials include the ultra-light peatfoam (peat moss and foamed resin) and

peatcork (made from the coarse fraction of peat (Ruel *et al*. 1977).

Harvesting Peat and Peatland Destruction

In 1991, a survey of Finnish peatlands revealed that only 26% of the peatlands remained in natural condition (Eurola *et al.* 1991). The majority are drier, less productive, and more forested than just 30 years ago. Most of the loss of peatlands is due to forestry (Finland) and agriculture (France) (Francez & Vasander (1995), although peat harvesting for fuel is a growing concern in northern Europe. In North America, most of the harvest is for horticulture (Ferland & Rochefort 1997). This horticultural loss began early in the 20th century, with the practice of leaving the peatlands to regenerate in their own way when the mining operation was over (Lavoie & Rochefort 1996). Upon examining a typical "regenerating" peatland in Quebec, Lavoie and Rochefort found that although the block-cut trenches had more than 50% cover and were occupied by typical peatland species, ***Sphagnum*** (Figure 17-Figure 19) was much more common in the natural conditions than in the cutover peatland. They concluded that this location was not returning to a functional peatland ecosystem.

Loss of peatlands affects the forestry species that were growing there. For example, in the New Jersey pinelands, *Chamaecyparis* swamps may suffer from loss of ***Sphagnum*** (Figure 3) cover because the tops of hummocks become more prone to drought, making them less suitable for seedling regeneration (Ehrenfeld 1995).

Even large browsers like caribou depend on refuge in peatlands (Dyer *et al.* 2001), but these losses have ramifications far beyond the simple loss of peatlands. Their loss is a contributor to global warming. Reduction in peatlands means that less carbon will be tied up in that carbon sink, instead going to rapidly cycling grasses. Furthermore, it leads to greater decomposition of accumulated peat, releasing yet more greenhouse gases. Ohlson and Økland (1998) found that it can take 40 years of peat accumulation before any significant amounts are lost through decay, resulting in a net carbon sink. In hummocks of ***Sphagnum fuscum*** (Figure 18) and ***S. rubellum*** (Figure 19), carbon accumulation exceeded 2 g dm^{-2} yr^{1} during a 50-year growth period.

Figure 18. ***Sphagnum fuscum***, a hummock species that takes 40 years to recover from harvesting. Photo by Oscar Gran, through Creative Commons.

Figure 19. ***Sphagnum rubellum***, a hummock species that takes 40 years to recover from harvesting. Photo by B. Gliwa, through Creative Commons.

"Harvest" is usually a misnomer for what is more accurately called peatland mining. With a vertical accumulation rate of 10-40 cm per thousand years in Finnish peatlands, repeatable harvests must be discussed in geologic time scales (Crum 1988). Consequently, peatlands the world over are diminishing. Knight (1991) bemoaned the dwindling number of peat bogs in Britain due to exploitation for horticulture.

Others have more encouraging numbers, considering peat formation of ~1-2 mm per year (note, that is not rate of growth). Using this estimate, they consider that harvested (not mined) peat can be replaced in ~20 years. In Ireland, 1 million m^3 of peat is used for horticulture and another 7-9 million pounds are exported yearly (Richardson 1981), not to mention the use for fuel that seriously threatens that country's 3 million acres of peatland (Drlica 1982). Yet 90% of the world's marketed peat comes from Wisconsin, USA, primarily from Jackson and Monroe Counties (Epstein 1988). The series of pictures below shows one company's attempt to maintain a sustainable crop that can be harvested again in about ten years (Figure 20-Figure 27). But this is a labor intensive method that most "miners" would shun.

Figure 20. At this peat harvesting operation in Wisconsin, USA, peat can be reharvested in about a 10-year cycle. The rake being used is wooden and pulls both ***Sphagnum*** and accompanying sedges. Photo by Janice Glime.

Figure 21. A tractor with a wooden tread pulls the wagon on which peat is loaded, minimizing damage to the peatland. Photo by Janice Glime.

Figure 22. A full wagon of peat is ready to be spread for drying. Photo by Janice Glime.

Figure 23. Freshly harvested peat is spread to dry. Photo by Janice Glime.

Figure 24. Spent tires will be used to anchor the mosses. As mosses dry, they become light-weight and can blow away. Photo by Janice Glime.

Figure 25. This packaging equipment is used for bagging the dry mosses ready for sale without need for a building or power. Photo by Janice Glime.

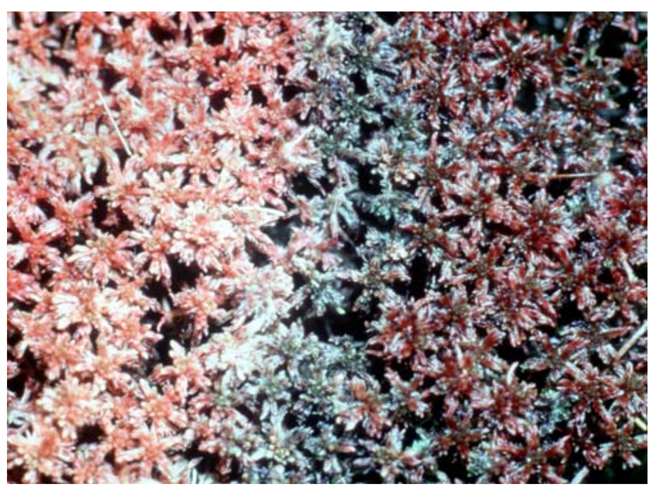


Figure 26. This ***Sphagnum*** is infected with fungus and could cause sporotrichosis. Photo by Janice Glime.

Figure 27. This mined peatland in Maryland, USA, exposes the peat profile. Photo by Janice Glime.

Climate Reconstruction

Peatlands are history books, recording for us what has occurred long before humans considered maintaining a written record (Grosse-Brauckmann 1979; Janssens 1988; Klinger *et al*. 1990). While this often has only heuristic value, it can be invaluable in attempting to interpret our tempestuous climatic variation in the present decades. Whereas fossil and other paleoecological records are scanty and difficult to interpret in other habitats, buried peat can provide us with clear chronosequences of vegetation, giving us indications of alternating dry and wet periods and even of warming and cooling. The pattern of cores can easily be calibrated between locations (Ellis & Tallis 2000). The peat stratigraphy of a blanket mire in Scotland, coupled with radiocarbon dating, indicates eight wet shifts that began about 3250, 2550, 2150, 1400, 1150, 875, 600, and 325 years ago. Seven of these correlate closely with similar indications from peat in Britain and Ireland.

Likewise, in the coastal region of Maine, USA, bryophytes, along with pollen, diatoms, and other plant fossils, have been useful in reconstructing past conditions (Tolonen & Tolonen 1984). In this case, the bryoflora support the other taxa to indicate that the flora is predominately that restricted to calcareous habitats.

Jonsgard and Birks (1995) were able to reconstruct the climate (moisture, temperature, light availability, and *p*H) from partially decomposed fossil mosses at Krakenes, western Norway, by comparing the taxa with bryophyte communities at various present-day altitudes. They found that mosses are able to colonize new habitats as rapidly as their tracheophyte counterparts. The advantage to using mosses for this purpose is that they provide evidence for microhabitats that cannot be obtained from tracheophyte fossils.

Jonsgard and Birks (1995; Birks 1982) also used fossil mosses to characterize late-glacial climate, *p*H, light availability, and continentality of Norway, using the mosses as ecological indicators.

Glaciers are often the site of modern dispersal of moss fragments. This wide, smooth surface also permitted ease of travel of fragments that became fossils in the frozen water, preserving the communities surrounding them. Thus, ice cores serve as historic records of the surrounding communities, much as peatlands do in other areas (Lindskog & Eriksen 1995).

While studying the Quelccaya ice cap in Peru, Ohio State University glaciologist Lonnie Thompson found mosses that had appeared out of ice laid down 5200 years earlier (Rozell 2005). This date of preserving a green moss coincides with the age of the Ice Man found recently in a melting ice field in the Austrian Alps. Thompson used the moss example to demonstrate the rapid response of a sensitive environment. When he returned to the site, he found more of the exposed mosses. Upon sending them to Woods Hole Oceanographic Institute for dating, he learned that one of them was 50,000 years old! In disbelief, Thompson sent the moss to Lawrence Livermore National Laboratory in California. Results were the same. Thompson reasoned that the only way these 5200-year-old mosses and the 50,000-year-old ones could appear together is that the ice field has not been smaller than it is today in the last 50,000 years and that it had to be colder than it is today for the past 50,000 years! Indications are that the ice cap is melting 40 times faster than it was in 1963.

Graves, Burial, and Preservation

Tombstones more than 100 years old typically are encrusted with lichens and mosses (Figure 28). In a recent bryonet discussion, Sean Edwards (Bryonet on 20 April 2005) sought a way to expedite this process (2005). In an old churchyard, strips of marble on a tomb had been replaced and no longer matched the weathered and lichen/moss-covered older marble. He was seeking ways to encourage the mosses and lichens to grow to age the stone.

Figure 28. Moss ***Schistidium apocarpum*** and lichens on cemetery marker, with the moss mostly established in the indentations. Photo by Janice Glime.

Burial ceremonies seem to have been a part of human culture for a long time. Hence, it might be expected that the resourceful human found mosses to be a suitable way to preserve the bodies of loved ones. In the Canary Islands, the Guanche mummy (1380 ± 80 years B.P.) was preserved with the epiphyte ***Neckera intermedia*** (Figure 29) in its abdominal cavity (Horne & Ireland 1991). However, an earlier report of a frozen Eskimo woman with moss in her lungs seems instead to have been the result of inhalation of the moss as she was being accidentally buried alive (Zimmerman & Smith 1975; Horne & Ireland 1991).

Figure 29. ***Neckera intermedia***, the moss used in the abdominal cavity to preserve the Guanche mummy. Photo by Jan-Peter Frahm, with permission.

In one case, a strange coincidence got a man to confess to the murder of his wife (Dente 1997). Police in Macclesfield, England, had investigated reports that Peter Reyn-Bardt had boasted of murdering his wife 23 years earlier and buried her dismembered body in his backyard. But the police could find no such evidence. However, the backyard bordered a peat excavation site where only a short time later an excavation uncovered a well preserved skull of a 30-50-year-old female. After the man confessed to the murder of his wife, the Oxford University Research Laboratory for Archaeology determined that the skull was actually 1660-1820 years old!

More recently, it appears that mosses have been used to clothe the last resting place. In Siberia 2,500 years ago, large mosses like ***Pleurozium schreberi*** (Figure 30), ***Ptilium crista-castrensis*** (Figure 31), and ***Rhytidium rugosum*** (Figure 32) were used with sheets of bark to line the roofs of tombs (Rudenko 1970). In Alaska and Japan, they have provided a burial bed (Bland 1971; Ando & Matsuo 1984) with larger mosses such as the pendant ***Aerobryopsis subdivergens*** (Figure 33) (Iwatsuki & Inoue 1971).

Figure 30. ***Pleurozium schreberi***, a moss once used in Siberia with sheets of bark to line the roofs of tombs. Photo by Janice Glime.

Figure 31. ***Ptilium crista-castrensis***, a moss once used in Siberia with sheets of bark to line the roofs of tombs. Photo by Janice Glime.

Figure 32. ***Rhytidium rugosum*** is a pleurocarpous moss that has been used to line the last resting place of humans in Siberia. Photo by Michael Lüth, with permission.

Figure 33. ***Aerobryopsis subdivergens***, one of the large mosses that has been used as a burial bed in Japan. Photo through Creative Commons.

The expansive peatlands of northern Europe seem to have provided a grave for hundreds of men, taking us back to the days of Roman rule – The Iron Age (Glob 1969). At first, these men were assumed to be peat cutters who had in recent years been trapped in the muck (Robinson 2002). But with 1500 bodies (Robinson 2002), speculation about the reasons for the early demise of these "bogmen" soon abounded (Painter 1991). Sanders (2002) relates that the Nazis used them as propaganda, claiming that two men found together in a Dutch peatland had been executed for their crime of homosexuality, whereas Heinrich Himmler was more cautious in a 1937 speech, stating that the deaths had been "not a punishment, but simply the termination of such an abnormal life."

In 1835, a well preserved woman in a Danish moor was identified as Queen Gunhild, a monarch in a Norse legend (Sanders 2002). When the Danish King, Frederick VI, learned of this find, he prepared her for a royal burial beside Danish royalty in a churchyard. However, carbon dating belies the royalty theory, placing the lady in a much earlier time.

In Tollund Fen in Bjaeldskor Dale in Denmark, two brothers (peat cutters) were surprised in 1952 by a body that surely was a recent victim of an onerous crime (The Discovery of Tollund Man). On closer inspection, the man had a twisted leather noose about his neck, but his face bespoke peace, as if death was his salvation (Figure 34-Figure 35). Police work turned to archaeologists who determined the "crime" to be 2000 years old. That look and the grains in his stomach have led many to conclude that he was a holy man sacrificed and preserved in the peat.

Figure 34. Tollund Man who lived in the 4th century BC. This "bogman" was perfectly preserved for centuries by the tannic acid in the peatland. Photo by Seamus Heaney, through Creative Commons.

Figure 35. Tollund Man head with rope around his neck. Photo by Seamus Heaney, through Creative Commons.

The Tollund Man

Seamus Heaney

I

Some day I will go to Aarhus
To see his peat-brown head,
The mild pods of his eye-lids,
His pointed skin cap.

In the flat country near by
Where they dug him out,
His last gruel of winter seeds
Caked in his stomach,

Naked except for
The cap, noose and girdle,
I will stand a long time.
Bridegroom to the goddess,

She tightened her torc on him
And opened her fen,
Those dark juices working
Him to a saint's kept body,

Trove of the turfcutters'
Honeycombed workings.
Now his stained face
Reposes at Aarhus.

II

I could risk blasphemy,
Consecrate the cauldron bog
Our holy ground and pray
Him to make germinate

The scattered, ambushed
Flesh of labourers,
Stockinged corpses
Laid out in the farmyards,

Tell-tale skin and teeth
Flecking the sleepers
Of four young brothers, trailed
For miles along the lines.

III

Something of his sad freedom
As he rode the tumbril
Should come to me, driving,
Saying the names

Tollund, Grauballe, Nebelgard,
Watching the pointing hands
Of country people,
Not knowing their tongue.

Out here in Jutland
In the old man-killing parishes
I will feel lost,
Unhappy and at home.

In the same year, 1952, Grauballe Man (Figure 36) was found in a similar manner by peat cutters (Grauballe Man 2002). His body was dated to about 210-410 AD. His stomach was full of porridge of 63 different grains, but no fruits or leafy green material, no meats, suggesting a winter meal or a poor harvest? A gruel with that recipe tastes horrible (Lienhard 1988). Unlike the Tollund Man, his face expressed terror and pain (Grauballe Man 2002). His throat had been cut and his skull was fractured. Later, in 1984, Lindow Man was found under similar circumstances in England (Lindow Man 2002). Like the Grauballe Man, his skin betrayed a man of high rank, not one who labored. He was at least 2000 years old, yet preserved well by the peat. He had died a violent death, with two blows to the head, his throat cut, and a thong for hanging. Was he a human sacrifice, or victim of a brutal murder?

Figure 36. Grauballe Man as he was discovered. Photo through public domain.

As history unfolds and great minds conjecture, it seems that Druid priests, important in the Celtic tribes, may have died in this manner, chosen as a sacrifice to the Earth Goddess (Robinson 2002). The Lindow Man had a last meal consisting only of a small cake containing bits of charred flour that would have required 400°C – much hotter than one would ever consider for baking. Archaeologists Ann Ross and Don Robbins speculate that this cake was used in a lottery to determine who should be sacrificed – perhaps explaining the look of pain and terror! Parts of such a ceremony still existed in England in the 20th century, but without the ultimate sacrifice.

Peatlands have a number of qualities that make them ideal preservation sites (Robinson 2002). Although the low oxygen and high acidity discourage most bacteria, it is the peat itself that imparts the preservation. The **Sphagnan** resulting from phenolic breakdown binds the sparse minerals in the water. Lacking their essential minerals, bacteria are unable to grow. Much like the tanning of cowhide to leather, the body is turned to leather by the tannins from the ***Sphagnum*** (Figure 3), preserving wool and leather garments along with the skin. The calcified bone, however, loses its calcium in the acid water, becoming rubbery and crumpled under the weight of the peat. And linen, faring less well than wool, disappears due to decay, accounting for the Tollund Man wearing nothing but his leather belt and hat when he re-appeared in the 20th century.

Sphagnum (Figure 3) even has a modern use in commemoration of the dead. In Wisconsin, USA, thousands of cemetery wreaths are made. These usually have various decorations and flowers attached to them, with the ***Sphagnum*** peat retaining water to keep them fresh.

Anthropology and Archaeology

An archaeologist investigating Paleolithic settlements reported finding animal and human bones in cave sediments (Patxi Heras & Marta Infante, Bryonet, 5 April 2006). These are often eroded with shallow depressions and holes. The zoologist she consulted disclaimed the marks, suggesting they were created by plant growth. Since there is typically abundant moss growth in the cave entrances, the archaeologist considered that they could make the marks. While no one could confirm that mosses make such marks on bones, we do know that mosses in the **Splachnaceae** (Figure 37), among others, can grow on bones.

Figure 37. ***Tetraplodon angustatus*** on caribou skull, Jasper, Canada. Photo by Janice Glime.

Peat mosses (***Sphagnum*** species; Figure 3) are well known for their ability to preserve the dead (Folger 1992). When a giant mastodon (Figure 38) was found in Ohio, USA, it likewise had been preserved in ***Sphagnum*** for 11,000 years. It was so well preserved that its last meal remained.

Figure 38. Burning Tree Mastodon excavation, Heath, east-central Ohio, USA, where that animal was preserved in peat. Photo by James St. John, through Creative Commons.

Hawes *et al*. (2002) attempted to use bryophyte growth markers to hindcast ice melt patterns in Arctic lakes, but they were unable to establish any correlation, concluding that the relationship was more complex.

Forensics

I have always loved mystery books, but I never dreamed I could be part of a criminal investigation, especially not a likely murder. But one day I opened my email and found a plea for help from a detective from one of the Michigan police departments. He introduced me to the case in which a father had left with his baby daughter and she had never been seen again. He had been convicted for unlawful imprisonment, but the police were seeking evidence that would help them find the child and convict him of murder. His missing daughter was believed to be discarded in a swamp. This belief was based on items adhering to the shoes of the father. These included the sedge *Carex*, a 2-needle pine, a fern, and moss, all of which are known from a wet conifer environment. I wasn't able to participate in the search, but I referred them to Matt von Konrat, who was able to identify ***Sphagnum affine*** (Figure 39), ***Warnstorfia fluitans*** (Figure 40), and ***Plagiomnium rostratum*** (Figure 41) from the clothing. This enabled the botanists to narrow the search to one location. A search, including von Konrat on the team, ensued in wetlands that matched the known plants from the shoes, but the baby was never found.

Figure 39. ***Sphagnum affine***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

Figure 40. ***Warnstorfia fluitans***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

Figure 41. ***Plagiomnium rostratum***, a moss that provided forensic evidence in the case of a missing child. Photo by Michael Lüth, with permission.

In Finland, a man disappeared and his body was later found in a woodland (Korpelainen & Virtanen 2003b). Three suspects were arrested, but there was no direct evidence to connect them. However, the bryophytes ***Brachythecium albicans*** (Figure 42), ***Calliergonella lindbergii*** (Figure 43), and ***Ceratodon purpureus*** (Figure 68, Figure 95) were identified from their shoes, clothes, and also in their car. Using DNA fingerprinting analyses on the two pleurocarpous species (***B. albicans***, ***C. lindbergii***) that primarily reproduce clonally, they were able to determine that these two species were likely to have originated from populations of the same two species found near the body (Korpelainen & Virtanen 2003a, b). Based largely on the moss evidence, the three suspects were convicted.

Figure 42. ***Brachythecium albicans***. This moss species adhered to clothing of three murderers and helped to convict them. Photo by Janice Glime.

Figure 43. ***Calliergonella lindbergii***. This moss species adhered to clothing of three murderers and helped to convict them. Photo by Bob Klips, with permission.

Figure 45. ***Climacium dendroides*** from Beppo Japan, a species tested for its genetic variability among locations. Photo by Janice Glime.

Following that court case, Virtanen and Korpelainen were able to obtain a grant to design species-specific microsatellite markers for a group of bryophytes that are globally common so that they can be used in forensic applications (Virtanen *et al*. 2004). They selected 12 species for which they obtained 20 specimens to represent the entire distribution area of each species, thus representing the range of genetic variation. The selected species were the mosses ***Aulacomnium palustre*** (Figure 44), ***Brachythecium albicans*** (Figure 42), ***Climacium dendroides*** (Figure 45), ***Dicranum polysetum*** (Figure 46), ***Hylocomium splendens*** (Figure 47), ***Plagiomnium cuspidatum*** (Figure 48), ***Pleurozium schreberi*** (Figure 30), ***Racomitrium microcarpon*** (Figure 49), ***Rhytidiadelphus squarrosus*** (Figure 50), and ***Sphagnum fuscum*** (Figure 18), and the leafy liverworts ***Plagiochila asplenioides*** (Figure 51) and ***Ptilidium ciliare*** (Figure 52).

Figure 46. ***Dicranum polysetum*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 44. ***Aulacomnium palustre***, a species tested for its genetic variability among locations. Photo by Tim Waters, through Creative Commons.

Figure 47. ***Hylocomium splendens*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 48. ***Plagiomnium cuspidatum*** from Europe, a species tested for its genetic variability among locations. Photo by Michael Lüth, with permission.

Figure 49. ***Racomitrium microcarpum*** with capsules, from Europe, a species tested for its genetic variability among locations. Photo by Michael Lüth, with permission.

Figure 50. ***Rhytidiadelphus squarrosus*** near Swallow Falls, Wales, a species tested for its genetic variability among locations. Photo by Janice Glime.

Figure 51. ***Plagiochila asplenioides***, a leafy liverwort species tested for its genetic variability among locations. Photo by Tim Waters, through Creative Commons.

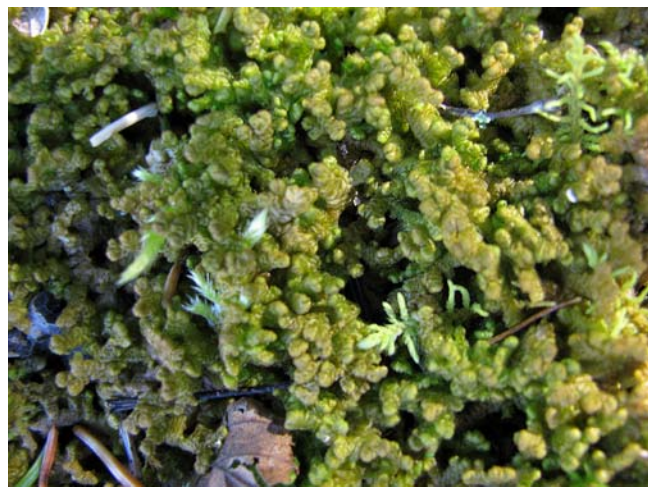
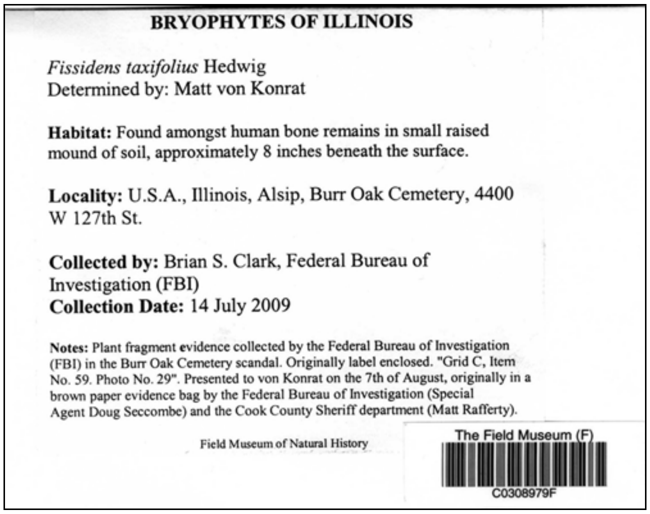


Figure 52. ***Ptilidium ciliare*** from Michigan, USA, a species tested for its genetic variability among locations. Photo by Janice Glime.

In another case, the FBI was interested in bryophytes in the soil covering a number of bodies that had been relocated from their graves. More than 200 bodies were discovered in shallow graves outside the cemetery. The FBI alleged that the cemetery workers had dug up the bodies and relocated the remains so that they could resell the graves at an historic African-American cemetery. However, some of the defendants claimed that the bodies had been moved before they began working there. Thus, it was important to determine when the relocation occurred. The anthropologist Anne Grauer discovered something green on some of the bodies ~20 cm beneath the surface and determined it to be a moss. The FBI then delivered the moss to bryologist Matt von Konrat at the Chicago Field Museum (Figure 53). He was able to identify it as ***Fissidens taxifolius*** (compare Figure 54 to Figure 55), but the important question was how long the buried mosses had been there. How long does a buried moss stay green? With the help of a physiologist, von Konrat experimented with the moss and also compared it to herbarium specimens of various ages (Figure 56). Ultimately he determined the moss to have been buried alive between six months and two years earlier, refuting the claim that the bodies had been moved after employment began for the accused.

Furthermore, no ***Fissidens taxifolius*** could be found growing near the bodies, but it did grow in the main cemetery. Matt von Konrat (Figure 56) was declared an expert witness by the court and the moss evidence led to convictions.



BRYOPHYTES OF ILLINOIS

Fissidens taxifolius Hedwig
Determined by: Matt von Konrat

Habitat: Found amongst human bone remains in small raised mound of soil, approximately 8 inches beneath the surface.

Locality: U.S.A., Illinois, Alsip, Burr Oak Cemetery, 4400 W 127th St.

Collected by: Brian S. Clark, Federal Bureau of Investigation (FBI)
Collection Date: 14 July 2009

Notes: Plant fragment evidence collected by the Federal Bureau of Investigation (FBI) in the Burr Oak Cemetery scandal. Originally label enclosed. "Grid C, Item No. 59. Photo No. 29". Presented to von Konrat on the 7th of August, originally in a brown paper evidence bag by the Federal Bureau of Investigation (Special Agent Doug Seccombe) and the Cook County Sheriff department (Matt Rafferty).

Field Museum of Natural History

The Field Museum (F)
C0308979F

Figure 53. ***Fissidens taxifolius*** forensic label in material delivered by FBI to the Field Museum. Photo courtesy of Matt von Konrat.

Figure 54. ***Fissidens taxifolius*** found with buried bodies that had been illegally relocated from the cemetery. Photo courtesy of Matt von Konrat.

Figure 55. ***Fissidens taxifolius*** in fresh condition such at that found in the cemetery. Photo by David Holyoak, with permission.

Figure 56. Matt von Konrat looking for comparison specimens of ***Fissidens taxifolius*** in the Herbarium at the Chicago Field Museum. Photo courtesy of Matt von Konrat.

One of the uses of plants in forensics is to establish the "post mortem interval (PMI)." Cardoso *et al*. (2009) found bryophytes to be useful in determining the time of death of an adult male in Portugal in an advanced state of skeletonization. The skeleton had green algae, bryophytes, and shrub roots in, around, and through the remains. The bryophytes and shrub roots were aged at three years, making the remains at least three years old. Time to colonization and state of decomposition of the remains put death at six years earlier, coinciding with the time the person went missing.

In another case, the aquatic moss ***Leptodictyum riparium*** (Figure 57) was used to estimate the PMI of skeletal remains in a wooded area in Central Italy (Lancia *et al*. 2013). Lacking specific growth rates for ***L. riparium***, the authors used the known rate for ***Hypnum cupressiforme*** (Figure 58), a moss with similar structure and growth habit. By counting the annual segments of the stem, they determined the moss to be 24-30 months old, narrowing the search for missing person records to those known to be missing for at least 2.5 years.

Figure 57. ***Leptodictyum riparium***, a moss used to help identify the body of a missing person. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>.

Figure 58. ***Hypnum cupressiforme*** var. cupressiforme, a moss with a growth rate assumed to be similar to that of ***Leptodictyum riparium***. Photo by David Holyoak, with permission.

Bryophytes can accomplish their own form of DNA fingerprinting (Korpelainen & Virtanen 2003a). Mosses can be used in much the same way as tracheophytes in crime investigation. Virtanen and coworkers (2004) are developing protocol for linking patches of bryophytes from the crime scene with fragments found on a suspect. Their approach is to find specific microsatellites to identify globally common bryophytes. Many species fragment easily and stick to clothing, making DNA analysis possible long after the event of fragmentation. Such evidence can tie the suspect to the scene of a crime.

Bryophytes could be useful forensic tools, but do we know enough about them, or is there still much work to do? Ann Mills (Bryonet 17 August 2011) reports identifying ***Brachythecium rutabulum*** (Figure 59) growing "in profusion" around an area where a human skeleton was discovered. To be useful forensically, we need to know how fast this moss might grow over the skeleton in this red spruce (*Picea rubens*) forest. In this case, Furness and Grime (1982) give us some information on growth rate of ***B. rutabulum***. Rod Seppelt (Bryonet 17 August 2011) adds that this species is an opportunist that propagates easily from fragments. To this, Steve Newmaster (Bryonet 18 August 2011) added observations from the long-term biodiversity research plot in Ontario, Canada. There ***Brachythecium rutabulum*** colonizes disturbed areas on organic soil, remaining there for several years. The mean increase per year is ~15% in southern Ontario (285 plots).

If we are to use bryophytes as a regular forensic tool, we need to determine how well they adhere to clothing, especially footwear, and how long the DNA can remain before breakdown destroys it. Virtanen *et al*. (2007) set out to contribute to answering these questions. Sixteen persons walked outdoors wearing rubber boots or hiking boots to determine what would adhere to the footwear. All plant fragments were collected after 24 hours of wear. In a second experiment, fresh bryophyte material from nine species was stored in a shed in adverse conditions for 18 months, and then DNA was extracted and subjected to genotyping. Both experiments supported the usability of bryophytes for forensics. Footwear did indeed collect bryophytes, and the bryophytes remained despite the wearer walking on dry ground and roads after walking on the bryophytes. And the DNA was still in good condition after 18 months of unfavorable storage conditions.

Figure 59. ***Brachythecium rutabulum***, a moss used to determine how long a corpse had been at that location. Photo by Michael Lüth, with permission.

Fuselier *et al*. (2011) used a forensic theme to make an investigative lab for Fuselier's students. The students had to pose the question, evaluate the evidence, and report the results. She based the study on Virtanen *et al*. (2007) and Korpelainen and Virtanen (2003a). The students learned how to use bryophytes in forensics and developed proficiency in DNA isolation, polymerase chain reaction, gel electrophoresis, capillary electrophoresis, and genotyping. The students paid more attention to accuracy in their methods than in standard labs. The researchers found that the students who participated in the bryophyte forensic lab performed well on content-based assessment (Figure 60) and exhibited positive attitudes toward the experience, indicative of engaged learning.

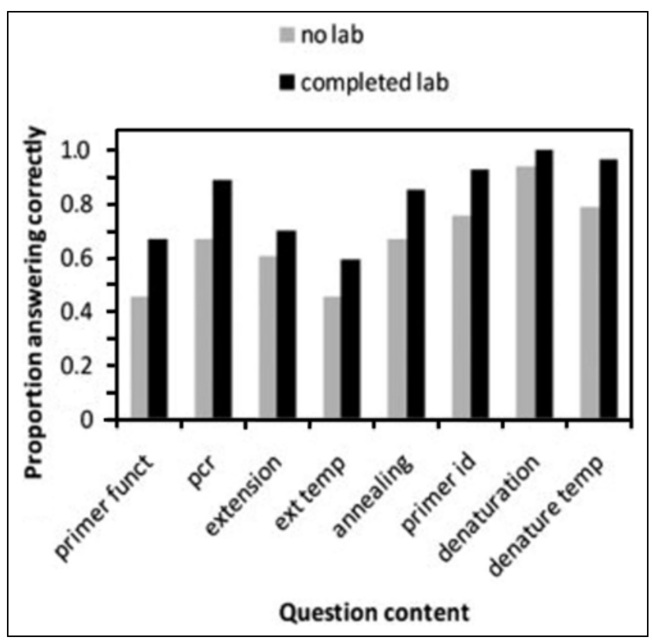


Figure 60. Student performance after bryophyte forensic lab, compared to performance of students who did not have the lab. Modified from Fuselier *et al*. 2011.

Archaeological Preservation

A recent recommendation for the use of ***Sphagnum*** (Figure 3) extracts is in the preservation of artwork (Zaitseva 2009). Extracts of polysaccharides (**Sphagnan**) were tested first on 17 fungal species and several bacteria species that could be found on ethnographic museum objects and archaeological objects from Arctic excavations. The bacteria ***Escherichia coli*** (Figure 61) and ***Pseudomonas aeruginosa*** (Figure 62) were negatively affected, whereas ***Staphylococcus aureus*** (Figure 63) was unaffected.

Twelve of the fungal species were inhibited (Zaitseva 2009). In one experiment, 1 ml of the nutritious broth with 40µl of 3% solution of polysaccharides in water killed 10,000 fungal spores in 6 hours. The Sphagnan was then added to conservation waxes as a preservative. With three weeks of exposure, the wax alone experienced a 44% consumption by the fungus *Aspergillus* (Figure 64). But when ~0.1% Sphagnan was included in the wax mix, the weight loss from the wax was only 4%. Zaitseva recommended using Sphagnan in art conservation. Additional discussion on the antibiotic properties of bryophytes are in the Chapter on Medicine in this volume.

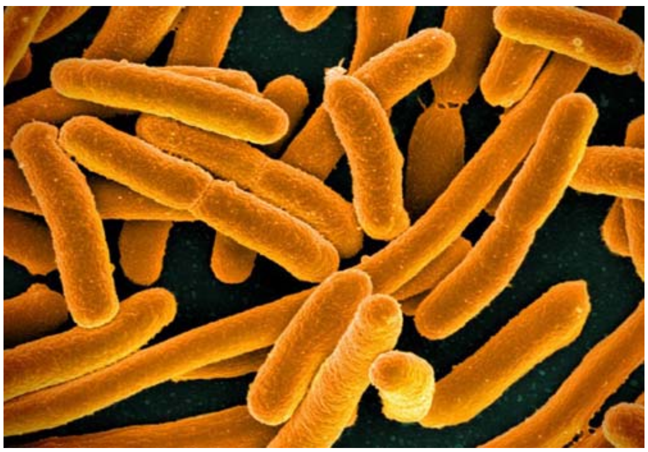


Figure 61. ***Escherichia coli***, a bacterium that is negatively affected by ***Sphagnum*** extracts, thus permitting preservation of archaeological artifacts with these extracts. Photo by NIAID, through Creative Commons.

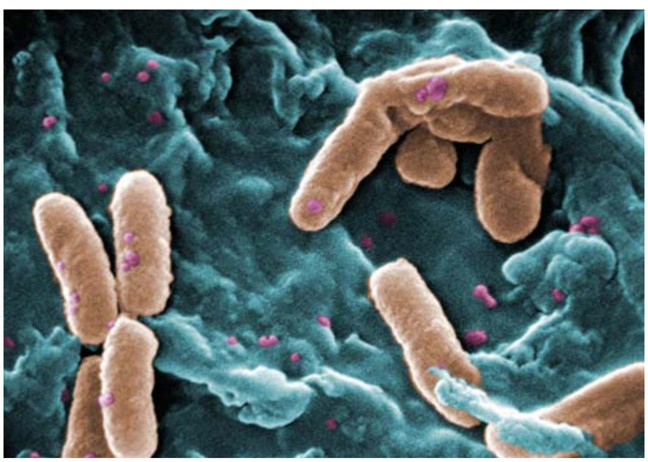


Figure 62. ***Pseudomonas aeruginosa***, a bacterium that is negatively affected by ***Sphagnum*** extracts, thus permitting preservation of archaeological artifacts with these extracts. Photo by Janice Haney Carr, through public domain.

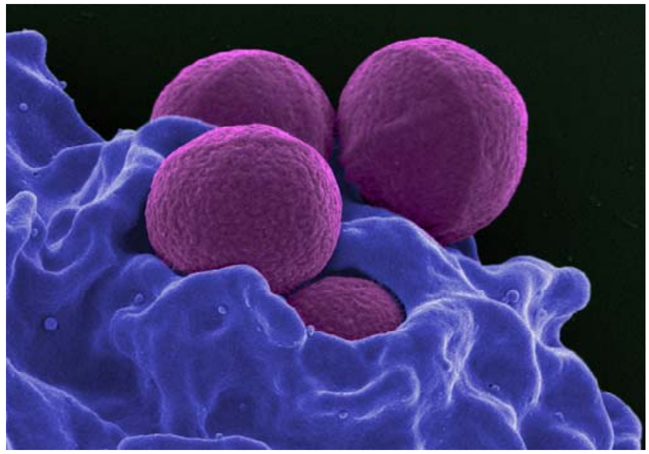


Figure 63. ***Staphylococcus aureus***, a bacterium that is not affected by peat extracts. Photo by NIAID, through Creative Commons.

Figure 64. ***Aspergillus fumigatus***. The genus ***Aspergillus*** was inhibited by Sphagnan and helps to preserve the waxes in art conservation. Photo through Creative Commons.

Erosion Control

The role of bryophytes in erosion control is well known (Figure 65), and several people have considered their commercial use along roadsides and other steep slopes through transplantation or propagation from fragments.

Figure 65. Erosion control on steep streamsides is an important use for bryophytes, both naturally, and on manmade slopes along canals or roads. Here, naturally occurring ***Polytrichum*** does the job. Photo by Janice Glime.

On dunes, seaside bluffs, and other areas where tourists often disturb the clinging vegetation, few plants, commercial or natural, survive the unstable conditions. Nevertheless, certain mosses may cling there when most other plants have been destroyed. Michel Chiaffredo and coworkers have a patent for Procédé BRYOTEC (BRYOTEC Process) that uses bryophytes instead of tracheophytes to stabilize such fragile sites (Chiaffredo 2007). The company MCK Environnement, using the BRYOTEC Process, has managed to restore, in only five years, the indigenous vegetation of a cliff top in a maritime setting in the Vendée region of France (Figure 66), where the tourist trampling had completely eradicated the original vegetation. This restoration involved the introduction of bryophytes with a small number of seeds from the native vegetation.

Figure 66. Restoration of a trampled cliff using a mix of bryophytes and other naturally occurring plants. Photo courtesy of Michel Chiaffredo.

The association ***Ceratodonto-Polytrichetea piliferi*** (Figure 67-Figure 68) (Dierßen 2001) is one that has proved particularly successful in helping to restore lost vegetation on a disturbed site.

Figure 67. Dry ***Ceratodon purpureus*** with ***Polytrichum piliferum*** (mostly at lower left), an association that has helped to restore vegetation on a disturbed site. Photo by Janice Glime.

Figure 68. Wet ***Ceratodon purpureus*** with capsules at left and ***Polytrichum piliferum*** at middle right. Photo by Michael Lüth, with permission.

In France, one may observe granitic embankments along a highway with the grass *Festuca ovina duriuscula* enduring the summer sun, but only in crevasses where mosses share the space. Perhaps the moss is necessary to provide sufficient moisture for seed germination of the grass (see Figure 69).

Figure 69. *Festuca ovina guestfalica* established in a crevice. The subspecies *Festuca ovina duriuscula* invades crevices in granitic embankments where it shares space with mosses. Photo by Andrea Moro, through Creative Commons.

One approach to rehabilitation has been to accelerate the establishment and growth of mosses by introducing mosses to the damaged area. However, the technique has used fragmented or chopped mosses and has met only limited success, despite the humid climate (rain on 80% of days). Furthermore, it has required collection of great quantities of samples from nature, which is contrary to the objectives of such a project. The BRYOTEC Process, on the other hand, produces large quantities of pioneer mosses from small samples of several cm^2. It therefore enjoys the status of a non-destructive biotechnology.

In addition to controlling erosion, mosses may help to stabilize and build soil on mine spoil. Peat mosses have been used for recultivation of ash dumps from brown and hard coal, a difficult substrate to colonize (Biernacka 1976).

Revegetation

Occasionally mosses are used to revegetate mining spoils. In a discussion on Bryonet in August 2007, several people suggested ***Polytrichum*** species (Figure 70), measuring some degree of success in the United States and Canada, as pointed out by Jean Faubert. Justin Wynns reports that in Boone, NC, USA, large carpets of ***Polytrichum*** have been planted in full sun, covered with large pieces of cloth to stabilize and retain moisture. Steve Timme suggested that naturally appearing mosses on mine tailings of one South Kansas site included ***Ceratodon purpureus*** (Figure 68), ***Bryum argenteum*** (Figure 71), and ***Bryum pseudotriquetrum*** (Figure 72), making those good choices to start. Shana Gross has found that she can get ***Ceratodon purpureus*** and ***Bryum argenteum*** to grow easily from fragments in the greenhouse, but they do not easily form thick mats. It is even more difficult to get such mats in the field.

Figure 70. ***Polytrichum piliferum***, a species tolerant of full sun and drying habitats such as mine tailings. Photo by Thomas Brown, through Creative Commons.

Figure 71. ***Bryum argenteum***, a cosmopolitan species tolerant of full sun and drying habitats such as mine tailings. Photo by Janice Glime.

Figure 72. ***Bryum pseudotriquetrum***, a species that colonizes mine tailings. Photo by Michael Lüth, with permission.

Road cuts, construction, and other forms of "progress" often leave huge scars on the landscape that do not quickly heal and soon become unstable detractants from the landscape around them. Thus, it is desirable to solve both the technical stabilization problem and to create an attractive replacement for the former vegetation. To this end, the Bryotec Corporation has introduced mosses as a solution to both problems. They have found that such bare terrain can be stabilized in a few months with a bed of bryophytes combined with other vegetation to form a pre-sod. The mat is both stable and attractive and helps to prepare the landscape for larger plant species (Michel Chiaffredo, Bryotec Corp., Pers. Comm.)

Recreation

Bryophyte forays have been part of many cultures for a long time (Glime 1982). These have been organized groups that included beginners through top experts who gathered to catalog bryophytes in an area, to learn new species, and to share interests with fellow bryologists.

But in Japan, a new trend has begun. These are excursions, led by an expert, for recreation of non-bryologists, and usually many non-bryologists (Pfanner 2015). In 2013, the Hoshino Resorts Oirase Keiryu Hotel in Aomori Prefecture initiated a one-night stay that included a moss tour on a riverside in the forest region (Matsumoto 2015). Most of the participants are women who find the tours a relaxing way to escape the normal stresses and competition of daily life. But they are shy about sharing their interest in mosses to friends and family.

It is not surprising to me that this interest in mosses by non-biologists has arisen in Japan. Japan is the land of famous moss gardens. It is the land where women traditionally have learned the finer things in life. And as pointed out by Nozu and Thompson (2015), it is a culture that values age and history. And mosses themselves are a thing of beauty with vibrant colors that vary from brown to bright green to red. And mosses make a soft and inviting surface. The slow growth and longevity give the mosses an inherent virtue. There is even a moss reserve around lake Shirakoma that has been designated by the Bryological Society of Japan and is known as a "precious moss-covered forest."

Pesticides and Antifeedants

Frahm (2004) extolled the virtues of bryophytes as anti-snail and anti-fungal sources. He reported that bryophyte extracts only spoil the appetite of the slug ***Arion lusitanicus*** (Figure 73) without killing it (Figure 74). The tested extracts came from the rock-dwelling moss ***Neckera crispa*** (Figure 75) and the leafy liverwort ***Porella obtusata*** (Figure 76) (Frahm & Kirchhoff 2002).

Figure 73. ***Arion lusitanicus*** mating, a species that is discouraged from consuming lettuce that has extracts from the moss ***Neckera crispa*** or leafy liverwort ***Porella obtusata***. Photo from Biopix, through Creative Commons.

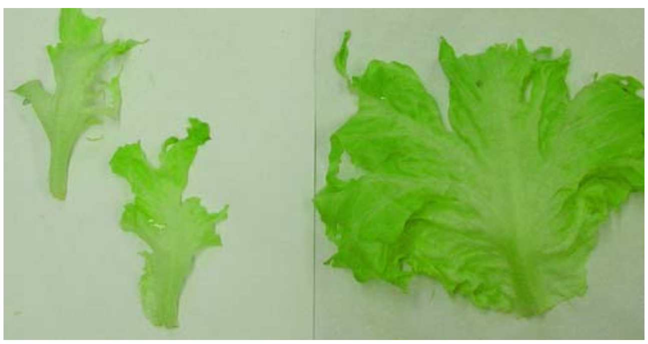


Figure 74. Slugs (***Arion lusitanicus***) can devour garden vegetables, especially soft tissues such as those of lettuce. Here the untreated control on the **left** has been almost completely eaten whereas the liverwort-treated leaf on the **right** remains unharmed. Photos by Jan-Peter Frahm, with permission.

Figure 75. ***Neckera crispa***, the source of a slug antifeedant. Photo by David T. Holyoak, with permission.

Figure 76. ***Porella obtusata***, a leafy liverwort source of a slug antifeedant. Photo by Kristian Hassel, through Creative Commons.

When fungal spores fall on bryophyte leaves, the bryophyte releases phenolic compounds when the surface becomes wet, inhibiting spore germination. To support the anti-fungal use, Frahm encouraged the head of the Department of Phytopathology at the University of Bonn to test their properties in greenhouse experiments. Crop plants such as green peppers, tomatoes, and wheat were infected with such fungal plant pathogens as *Phytophthora infestans* (Figure 77, Figure 78), *Botrytis cinerea* (Figure 79), and *Blumeria graminis* (Figure 80). These infected plants were treated with alcoholic extracts from 20 European species of bryophytes (*e.g.* Figure 78). The extracts had various effects, with liverworts (Figure 76) being most effective (Figure 81), followed by ***Sphagnum*** (Figure 3), then other mosses (Tadesse 2002). Two of the liverworts caused systemic effects. Plants that were sprayed prior to their inoculation were not affected at all by the fungi; the leaves that developed after the application of the extract were resistant, suggesting that the antibiotic substance was translocated within the plant. The ability of moss extracts to inhibit fungal growth is easily demonstrated by saturated disks on inoculated Petri plates (Figure 82).

Figure 77. *Phytophthora infestans* blight on tomatoes. Photo by Scot Nelson, through Creative Commons.

Figure 78. Extracts of 20 species of bryophytes inhibit the growth of fungal pathogens on vegetable crops such as these tomatoes. The plant on the **left** is the control and is infected with the fungus *Phytophthora infestans*. The other two have been treated with two concentrations of alcohol extract from bryophytes. Photo by Jan-Peter Frahm, with permission.

Figure 79. *Botrytis cinerea* on grapes. Photo by John Yesberg, through public domain.

Figure 80. *Blumeria graminis* on Kentucky bluegrass, *Poa pratensis*. Photo by Rasbak, through Creative Commons.

Figure 81. The healthy tomato plant on the **left** has been treated with liverwort extract, whereas the untreated plant on the **right** is infected with *Phytophthora infestans*. Photo by Jan-Peter Frahm, with permission.

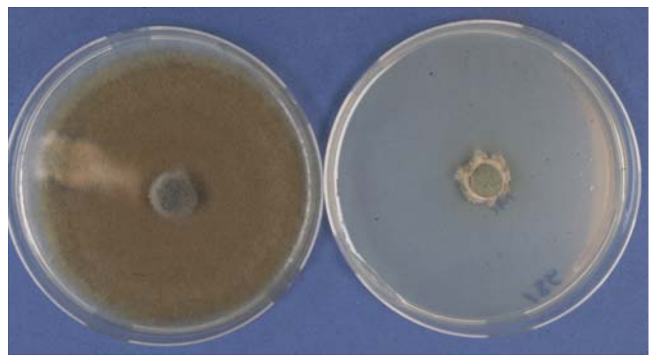


Figure 82. Rampant fungal growth occurs on the plate lacking bryophyte extract (**left**) while growth is inhibited on a plate with a bryophyte extract disk (**right**). Photo by Jan-Peter Frahm.

Once the news of this antifungal activity was distributed to the news media, there was a huge response, indicating a great need for such an alternative product. The moss extracts are a safer alternative to the copper sulfate and other heavy metal salts currently being used. The heavy metals accumulate in the soil, whereas the bryophyte extracts quickly degrade in the soil. Furthermore, it is easy to produce and farmers in third world countries could even produce it themselves. Are these anti-herbivore compounds safe for our consumption?

A private German development company, Red de Accio´n en Alternativas al uso de Agroquı´micos (RAAA) persuaded the Universidad Nacional de San Martin in Peru to test extracts of local bryophytes on coffee and tomatoes as protection against tropical plant diseases in the field. Unfortunately, they tried only mosses and not the more potent liverworts, but they still achieved positive results. Sadly, the high cost of the alcohol prevented wide-scale use in Peru.

In Bolivia, the Unidad de Investigacio´n y Desarollo FAN made extracts of ***Frullania brasiliensis*** (Figure 83) and ***Sphagnum*** sp. (Figure 3) and applied them to tomatoes and potatoes. While controls were infected, the treated plants exhibited no visible bacterial or fungal infections (Figure 78; Figure 81).

Figure 83. ***Frullania brasiliensis***, a species that prevented infections on tomatoes and potatoes. Photo by Jan-Peter Frahm, with permission.

Frahm, failing to persuade any German company to produce the product, took the product to a company that produces herb liquors. It was sold by a chain of drugstores(!) as an alternative to fungicides. Finally, a new commercial company received permission from Biologische Bundesanstalt to produce the product commercially. Several thousand liters of bryophyte extract were sold during the first 8 months. This product is diluted 1:100 for use. A major limitation is obtaining enough plant material in the field. Although the moss used is abundant in silvicultural fir forests, the quantities needed for agriculture is enormous.

Frahm's group is conducting further testing to produce the moss horticulturally and hopefully to find clones with higher biological activity. Such commercial production would also eliminate the need for cleaning, reducing costs and time.

Rearing Fish

The Nashua National Salmon Hatchery has considered using the aquatic moss ***Fontinalis*** (Figure 84) in the salmon raceways (Abigail Walker, Intern, Nashua National Fish Hatchery, 19 April 2005). It grows there on the cement and they hope to use it as both a nutrient sink and a natural cover for young fry in the rearing tank.

Figure 84. ***Fontinalis antipyretica*** is a moss used in fish hatcheries today, but formerly used for chimney chinking with the belief it would insulate against fire or heat. Photo by Michael Lüth.

As described in the Aquarium subchapter, Bohlen (1999) reported the use of aquaria equipped with a thick moss tuft for spawning of the spined loach *Cobitis taenia* (Figure 85). The moss was placed on top of a gauze-covered plastic box. The fish laid their eggs in the most dense vegetation available. The dead eggs fell through the gauze and collected in the box.

Figure 85. ***Cobitis taenia***, a species that benefits from mosses in aquaria for spawning. Photo by Ron Offermans, through Creative Commons.

The bryophytes may well be protected from herbivory by the fish at the same time. Asakawa *et al*. (1985) has shown that at least one liverwort (***Riccardia lobata*** var. ***yakushimensis***), although not itself aquatic, has piscicidal secondary compounds (diterpenedial).

Toxicity Testing

Numerous studies have used bryophytes as indicators of pollution, with symptoms indicating, in many cases, the type of pollution. These are so numerous as to warrant several chapters, if not an entire volume. It is almost predictable that one of the organisms that has been studied for this potential is the bryological lab rat, ***Physcomitrella patens*** (Figure 86). Morgan *et al*. (1990) used cultures of this moss to examine effects of various salt solutions (aluminium sulfate, barium chloride, boric acid, cadmium chloride, cobalt chloride, as well as lead nitrate, mineralized-acidic leachate, and coal combustion fly ash leachate) on various life cycle stages (Figure 86). Aberrations such as altered morphology, loss of regeneration ability, reduced dry weight, and altered chlorophyll contents indicated damage by the salts. Surprisingly, the spore and gametophore cultures differed little in their responses. Cadmium chloride and aluminum sulfate caused the greatest reduction in chlorophyll concentration and dry weight, whereas boric acid and barium chloride were least toxic. Fly ash likewise seemed to cause no harm to the plants.

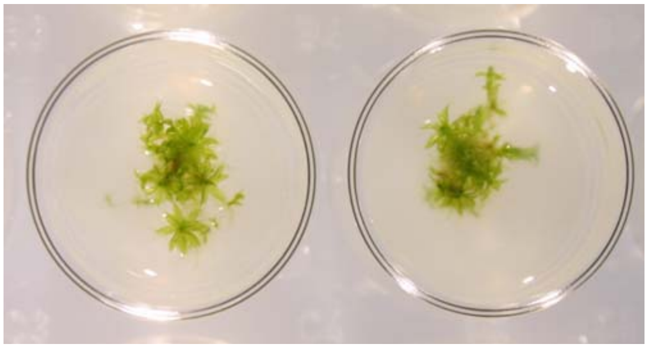


Figure 86. Mosses such as ***Physcomitrella patens*** can be used to test effects of salt concentrations, acidic leachates, heavy metals, and fly ash on morphological alterations and changes in chlorophyll concentrations. Photo by Ralf Reski, with permission.

Kenneth Adams (pers. comm. 1 November 2013) used balls of acid-washed ***Sphagnum*** (Figure 3) in bun hair nets in the 1970's to accumulate airborne heavy metals in locations of interest. These were placed in concentric survey locations around smelters in the U. K. and assayed with flame photometry. This was used routinely to assay for petrol lead levels along roadsides. He even found a zinc source from burned car tires in east London.

There is considerable literature on the use of bryophytes for biomonitoring, including moss bags and *in situ* assessment in concentric rings or distances along a transect starting from a pollution source. These have been useful in both aquatic and terrestrial studies. Several reviews and books (*e.g.* Leblanc & Rao 1974; Nash & Wirth 1988; Tyler 1990; Bates & Farmer 1992; Greven 1992; Onianwa 2001; Zechmeister *et al*. 2003; Tuba *et al*. 2011; Harmens *et al*. 2013) have been written on these studies, so I will not elaborate here. Hopefully I will write a volume on this after other volumes are completed.

Filters

Copper is toxic to plants except in small quantities. Itouga *et al*. (2006) tested the copper mosses ***Scopelophila cataractae*** (Figure 87) and ***S. ligulata*** (Figure 88) for their effect in removing the copper toxicity in copper-polluted water used for growing rice. Using bryophyte columns packed with each of these two species, the researchers determined that ***S. cataractae*** was superior at copper toxicity removal. Furthermore, ***S. cataractae*** filtrate was no longer toxic to the rice. We still need to know the practicality of this method – how much moss would be required and how long would the column be effective. Nevertheless, this could be a practical solution for small applications such as home aquaria and pools.

Many studies exist on the sorption of metal ions by mosses. These have been reviewed in several books on bryophytes and pollution. However, their use as filters has received much less attention. Al-Asheh and Duvnjak (1997) discussed the adsorption of metal ions by mosses. Such publications led to the exploration of bryophytes as filters against metal ions. Abdel-Jabbar *et al*. (2001) successfully modelled the copper adsorption of a moss-packed bed. This model accounted for differences such as axial dispersion, external film, and within-particle diffusion. In a different study, Ho and McKay (2000) developed a sorption model for copper using ***Sphagnum*** (Figure 3). They determined that sorption through chemical bonding might be rate limiting. Nevertheless, they were able to develop a model that could predict the sorption capacity of metal ions sorbed.

Figure 87. ***Scopelophila cataractae***, a moss that successfully removes copper from water used in rice culture and that is superior for this purpose compared to ***S. ligulata***. Photo by Blanka Shaw, with permission.

Figure 88. ***Scopelophila ligulata***, a copper moss that is less effective than ***S. cataractae*** in removing copper toxicity from water used to culture rice. Photo by Michael Lüth, with permission.

Electricity

Using mosses to produce electricity might be a pipe dream, but it has at least limited possibilities. Mosses are able to produce enough energy through photosynthesis to power a clock, but the same amount would only keep a laptop alive for about 20 seconds (Chandler 2012).

In another example, mosses have been placed in a glasstop table (University of Cambridge 2011). They are able to power the lamp through photosynthesis (Inhabitat 2017). Mosses photosynthesize and release organic compounds into their substrate. Bacteria in that soil break down these organic compounds, liberating by-products, including electrons. The table is designed to capture these electrons and use them to produce an electrical current. This research is led jointly by Dr. Adrian Fisher, Professor Christopher Howe, and Professor Alison Smith at Cambridge, and Dr. Petra Cameron at Bath.

Scientific Use

Today, bryophytes are receiving considerable attention from the scientific world. ***Marchantia polymorpha*** (Figure 89) has long been a subject of physiological studies. ***Funaria hygrometrica*** (Figure 90) and ***Physcomitrella patens*** (Figure 91) are everyday names to the plant physiologists. And ***Syntrichia*** (syn.=***Tortula***; Figure 92) is being studied by the Department of Agriculture (Comis 1992; Hoffman 1992)! What is it that has caused this sudden agricultural interest in bryophytes?

Figure 89. ***Marchantia polymorpha***, a common liverwort, is used for teaching and scientific research. Photo by Michael Lüth, with permission.

Figure 90. ***Funaria hygrometrica***, a moss that has often been used in plant physiological studies. Photo by Michael Lüth, with permission.

Figure 91. ***Physcomitrella patens***, a moss with a fully mapped genome and that has often been used in plant physiological studies. Photo by Michael Lüth, with permission.

Figure 92. ***Syntrichia ruralis***, a desiccation-tolerant moss that has been used in many physiological studies. Photo by Michael Lüth, with permission.

The ability to grow bryophytes from spores and fragments has made some kinds of physiological studies easy. Much of what we know about tropisms has been learned from studies on moss protonemata, which respond to gravity and demonstrate what occurs inside the cell. With only one cell in thickness, and an easily observable and measurable linear structure, the moss protonema provides an ideal study organism for this purpose. But agriculture? It seems that mosses have characteristics that are desirable for crop plants. They tolerate desiccation better than almost any crop plant and can withstand freezing while still in a state of hydration, yet recover almost instantly (Rütten & Santarius 1992). Furthermore, they seem seldom to be eaten, especially by insects. With our new tools for moving genes around almost anywhere we want with the help of bacteria and bryophytes, the genes of mosses suddenly became an attractive commodity.

The bryophytes, and especially ***Physcomitrella patens*** (Figure 91), and to a lesser extent ***Ceratodon purpureus*** (Figure 68), have been a true boon to unravelling the genetic control of physiology and development by identifying which genes control which actions (Cove & Cuming 2014). With only one set of chromosomes, inserting a new gene so that it is expressed is a much simpler task in bryophytes than doing the same thing in a flowering plant with two sets of chromosomes. Furthermore, it is easy to grow large quantities of these mosses in culture. And both species experience a high frequency in gene targetting, permitting researchers to knock out a gene to determine its function (*e.g.* Brücher *et al*. 2005). ***Physcomitrella patens*** has been completely sequenced and much of the genome of ***C. purpureus*** is likewise known (Cove & Cuming 2014).

Model Systems

It seems fitting, yet ironic, that these plants of ancient use may reach the forefront of technology. But this time, their uses are much less obvious and much more sophisticated.

In the early part of the last century, bryophytes led the arena of genetic research (Wettstein 1932). Mutagenic effects of X-rays [on ***Sphaerocarpos donnellii*** (Figure 93; Knapp 1935, Schieder 1973); on ***Marchantia polymorpha***

(Figure 89; Miller *et al*. 1962a, b); on ***Physcomitrium pyriforme*** (Figure 94; Barthelmess 1941a); and on ***Physcomitrella patens*** (Figure 91; Engel 1968)], α particles on ***Physcomitrium pyriforme*** (Barthelmess 1938), and γ-rays on ***Brachythecium rutabulum*** (Figure 59; Moutschen 1954), and chemical mutagenesis on ***Physcomitrium pyriforme***, and ***Physcomitrella patens***, among others, Barthelmess 1941a, b, 1953) were more easily studied on these haploid organisms, and their multi-year life exposed to the atmosphere made them ideal for integrating effects over time. Both morphological and physiological effects were manifest (Cove 1983).

Figure 93. ***Sphaerocarpos donnellii***, a species used to determine mutagenic effects of X-rays. Photo by Belinda Lo, through Creative Commons.

Figure 94. ***Physcomitrium pyriforme***, a moss used to test the mutagenic effects of α particles. Photo by Janice Glime.

Although bryophytes seldom reach the headlines, they have served as model systems in many branches of biology for a long time. The first sex chromosomes in plants were described from a liverwort, then the continuity of chromosomes during mitosis, then the discovery of non-Mendelian inheritance (Reski 1998). Mutagenesis, using UV, was first demonstrated in mosses (Reski 2005).

Many aspects of plant physiology have been elucidated using mosses as model systems. It seems that photorespiration was first recognized in ***Fontinalis*** (Figure 84) (Buch 1945), although Buch is not given credit in modern literature. And it is much easier to study tropisms, amyloplasts, and statoliths in the one-cell-wide protonema (Walker & Sack 1990; Young & Sack 1992; Sack 1993; Chaban *et al*. 1998; Kern *et al*. 2001). This system likewise is ideal for trying to understand the early developmental pathways and their hormonal controls (Bopp 1974). The moss provides a simple plant system in which to understand mechanisms of Ca regulation and signal transduction in plants (Schumaker & Gizinski 1995).

Thus, in recent years bryophytes have become established as model plants for the study of many physiological aspects of plants, especially in linking genes to function, including developmental processes [cell polarity and plastid development (Jenkins & Cove 1983)], homologous recombination, and cellular (calcium signaling) processes. Expression of characters in the haploid state makes it much easier to understand gene expression (*e.g.* Wood *et al*. 2004 on GAPN enzyme effects), and isolation of mutants has facilitated the breakdown of developmental and biochemical pathways. Now, the ability to transplant genes or target knockout genes in mosses, especially in ***Physcomitrella patens*** (Figure 91), permits us to understand gene/pathway/phenotypic response relationships through the use of reverse genetics (Reski 2005).

Sineshchekov *et al*. (2000) transplanted the moss ***Ceratodon purpureus*** (Figure 95) CP2 gene to the yeast *Saccharomyces cerevisiae* (Figure 96) to reconstitute **phycocyanobilin**. This permitted examination of emission spectra of the pigment in isolation from the influence of other pigments. Studies such as this are being used to understand a variety of gene functions in plants, with bryophytes expressing transplanted genes more easily than do other plants. Hence, they have been invaluable in advancing our understanding of plant functions.

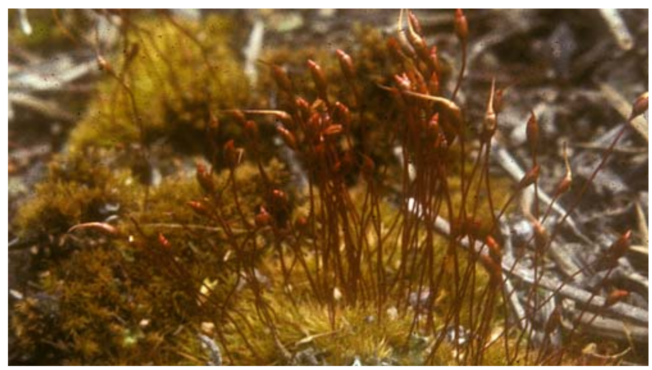


Figure 95. The moss ***Ceratodon purpureus***, used for transplanting genes to yeast in order to identify pigment emission spectra. Photo by Janice Glime.

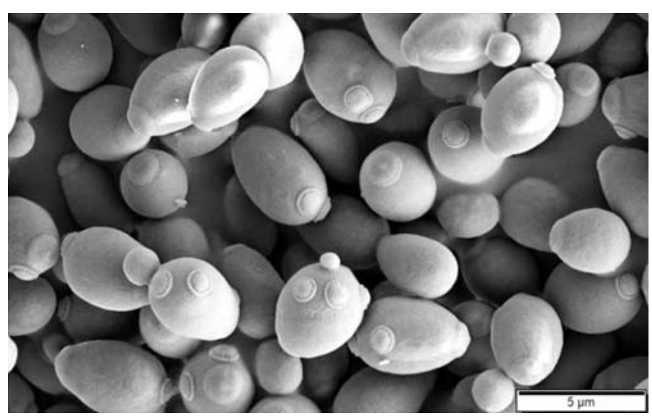


Figure 96. *Saccharomyces cerevisiae* SEM, a yeast that received genes for phycocyanobilin from the moss ***Ceratodon purpureus*** so that the emission spectrum could be isolated and analyzed. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

Genetic Engineering

While genetic engineers are making the headlines with marketable fruits, vegetables, and even modified animals, the genetic engineers of bryophytes remain quietly in the background figuring out "what makes things tick." Although few people have any interest in how a moss functions, the ability of using mosses to figure out how a tracheophyte, especially a crop plant, goes about its daily life is of enormous importance to the agriculture industry.

Cove and coworkers (1997) have suggested that mosses "hold many attractions" as model organisms, arguing that position as the simplest of land plants permitted them to shed light on the development of terrestrial plants from formerly aquatic ancestors. But this simple evolutionary approach soon blossomed into a new and strategic use of bryophytes in understanding not only evolution, but in understanding the functioning of plants in general (Reski & Frank 2005).

To quote Reski (1998), "due to the simplicity of the plants, development can be pinpointed to the differentiation of a single cell and be analyzed in living tissues, making mosses ideal candidates for analysis of development in an integrated approach of cell and molecular biology." In fact, it is the humble moss ***Physcomitrella patens*** (Figure 91) that is proving to be an appropriate model for studying the molecular development of not just mosses, but plants in general. The nuclear genes of this moss can be targeted for homologous recombination, making reverse genetics a viable tool for plant physiologists.

In the past, we have studied gene function by identifying the gene product, then trying to identify the gene involved. With reverse genetics, we instead identify the gene on the basis of its position. We can then remove it or insert it in another organism to determine the effect that gene has on phenotypic expression. As haploid organisms, mosses are ideal for this approach because the gene is not masked by a second allele that may alter or prevent its expression. It is as easy in this moss to target nuclear genes for recombination as it is in yeast, providing a powerful tool for understanding plant gene function (Reski & Frank 2005). Using ***Physcomitrella patens*** (Figure 91) to confirm the transgene in chloroplast transformation, Cho and coworkers (1999) were able to demonstrate the applicability of this moss as a model system for basic biological research.

The model moss ***Physcomitrella patens*** (Figure 91) not only is useful for expressing genes transferred from other plants, but it also has genes of its own to contribute. Its high tolerance against drought, osmotic stress, and salt (Frank *et al*. 2005) suggest that it has genes that could be useful in other plants. Because it is easier to identify specific genes and link them to their functions in haploid plants, it could serve as a source for genes that could be moved into crop plants to endow them with these desirable traits.

One advantage of using mosses to understand physiology is their ability to exhibit conditional lethal genes (King 1986). Such mutants permit physiologists to understand processes because the gene is lethal until the problem is corrected.

Beike *et al*. (2010) discussed the use of bryophytes in biotechnology, known as bryotechnology. Many of these uses have been discussed earlier in this chapter or in the chapter on medicine. Beike noted some of the potential uses in agriculture. For example, the leafy liverwort ***Porella platyphylla*** (Figure 97) inhibits the growth of radish seedlings, whereas an extract from the moss ***Brachythecium rutabulum*** (Figure 59) promotes the growth. Stress tolerance is more common among bryophytes and genes effecting that ability have potential for introduction into flowering plants, including food plants. But there are tradeoffs we must not ignore. If a plant puts its energy into making the products of those new genes, what other aspects of the plant might be sacrificed? Will the plant still be safe to eat? Will it still have the same nutritional value? Will it become allergenic?

Figure 97. ***Porella platyphylla***, a species that can inhibit the growth of radish seedlings. Photo by Janice Glime.

One such stress-responsive gene is ALDH21A1 from ***Syntrichia ruralis*** (Figure 92) (Chen *et al*. 2002). This appears to be a unique stress tolerance gene not present in tracheophytes. It is important in the detoxification of aldehydes that are created in response to desiccation and salinity stress.

Modification of non-food crop plants poses fewer risks. Yang *et al*. (2012, 2016) have isolated the ScALDH21 gene from the very drought-tolerant ***Syntrichia caninervis*** (Figure 98) that grows in deserts of Central Asia and North America. This gene was effectively transplanted into cotton (*Gossypium hirsutum*; Figure 99). Testing indicated that the gene was expressed, and under drought stress the cotton with the new gene accumulated ~11.8-304% more of the amino acid proline than did the unmodified cotton. It furthermore produced a lower concentration of lipid peroxidation-derived reactive aldehydes than untreated plants, and it had a higher peroxidase activity under oxidative stress. These modified plants exhibited greater plant height, larger bolls, and greater cotton fiber yield, while losing nothing in fiber quality.

Figure 98. ***Syntrichia caninervis***, a drought-tolerant species whose genes have been successfully transplanted into cotton and expressed. Photo by John Game, through Creative Commons.

Figure 99. Cotton (*Gossypium hirsutum*), a species that benefits from drought tolerance genes from ***Syntrichia caninervis***. Photo by Forest & Kim Starr, through Creative Commons.

Manufacturing Human Protein

Most recently, the mosses, and especially ***Physcomitrella patens*** (Figure 91), are being used to culture needed human proteins because they are much easier systems than tracheophytes for gene manipulation (Figure 100) (Reski 1998; Baur *et al*. 2005). And mosses are much cheaper and easier to culture than human cell systems.

Reski and Frank (2005) have identified three public demands in modern plant biotechnology:

1. More people in the population require more food, but they also reduce the area of arable land, constraining the food production.
2. The mean age of the population is increasing, requiring a higher quality of food to prevent typical "diseases of civilization" such as cardiovascular diseases and cancer.
3. Medical science is experiencing a paradigm shift from broad-based treatments to very patient-specific treatments, requiring safe and cost-effective production of complex pharmaceuticals.

Reski and Frank (2005) suggest that ***Physcomitrella patens*** (Figure 91) can contribute in all three of these needs. "Virtually every gene can be knocked out by targeted ... approaches in attempts to establish saturated mutant collections." And the phenotypes can be screened within weeks! Gene targeting in this moss is about five orders of magnitude more efficient than in any seed plant and about two orders of magnitude more than in embryonic mice stem cells.

Figure 100. ***Physcomitrella patens*** is cultured for gene manipulation and proteomics. Photo courtesy of Ralf Reski.

It appears that there are already over 200,000 expressed sequence tags in ***Physcomitrella patens*** (Figure 91) (Reski & Frank 2005). There are about 6000 protein-encoding genes which are not identifiable in the public databases, most likely representing novel genes, out of the 30,000 protein-encoding genes present in the moss. It is interesting that about 100 genes in this moss can be matched only to non-plant organisms, including humans!

One advantage to working with a moss such as ***Physcomitrella patens*** (Figure 91) is the ability to culture it in a bioreactor (Figure 101), thus eliminating the problems of contamination from soil or other growth media (Reski & Frank 2005). This makes the study of proteomics (examination of the protein complement of a genome) much easier.

Figure 101. Moss bioreactors provide sterile cultures of ***Physcomitrella patens***, avoiding the contamination problem prevalent with soil-grown plants. Photo by Ralf Reski, with permission.

Mosses may help us to address needs in the human diet that are not available from other plants. For example, eicosapentaenoic acid (EPA) and arachidonic acid (AA) are only produced by non-seed plants, including bryophytes. Yet these acids play a role in human eicosanoid metabolism. Furthermore, polyunsaturated acids are most abundant in non-seed plants, including mosses, and likewise are beneficial for human growth and continued good health. As our fish (also large sources of polyunsaturated acids) dwindle and become contaminated with metal pollutants, these plants may become an essential source of these important fatty acids. Genes from ***Physcomitrella patens*** (Figure 91), identified to have this function of producing polyunsaturated fatty acids, have already been planted and expressed in tobacco (*Nicotiana tabacum*; Figure 102) and linseed (*Linum usitatissimum*; Figure 103) (Abbadi *et al.* 2004).

One problem with many plant cell culture systems is genetic instability (Reski & Frank 2005). The ***Physcomitrella patens*** (Figure 91) bioreactor, on the other hand, maintains well-differentiated and genetically stable cell types. The culture conditions are much simpler than those required for mammalian cells.

Figure 102. Tobacco, *Nicotiana tabacum*, a species that is able to express genes for producing polyunsaturated fatty acids, transplanted from the moss ***Physcomitrella patens***. Photo by Magnus Manske, through Creative Commons.

Figure 103. *Linum usitatissimum*, a species that is able to express genes for producing polyunsaturated fatty acids, transplanted from the moss ***Physcomitrella patens***. Photo through Creative Commons.

Targetted gene removal or transfer can render the moss products safe for humans, avoiding production of allergenic products that are unsafe for humans (Reski & Frank 2005). For example, xylose and fucose form allergenic residues of plant glycoproteins in most plants, but in the mosses, a targetted double knockout provides moss plants with no fucose or xylose residues attached to their proteins. This modified moss was still able to produce the same level of recombinant human growth factor, serving as a living reservoir for this purpose.

A New Carbohydrate

A research team at the University of Adelaide (Roberts *et al.* 2018) discovered that mosses can produce a new complex carbohydrate. While exploring the evolutionary history of beta glucan, a dietary fiber that has many health benefits, they found that the mosses they examined had similar genes, so they set out to determine their function. They found that it coded for a new polysaccharide made of glucose and arabinose, and thus named it **arabinoglucan**.

While they don't advocate eating mosses, they suggest that the compound could become medically important. Of course the moss in the analysis was the well-known ***Physcomitrella patens*** (Figure 86, Figure 91, Figure 94).

Model for Pipettes

Plants have been used as models in engineering, but use of a bryophyte for this purpose is unusual. Nakamura *et al*. (2018) used ***Marchantia polymorpha*** (Figure 104) to understand the mechanism of fertilization in its archegonial head. This study not only challenges some of our traditional concepts about fertilization in this species, but also provides a model for a very effective small pipette.

Figure 104. ***Marchantia polymorpha*** archegoniophores at the stage used in experiments by Nakamura and coworkers. Photo by Janice Glime.

This liverwort has an archegoniophore shaped like a parasol, but with finger-like apppendages radiating from its head (Nakamura *et al*. 2018). When it is young, the fingers of the archegonial head tend to hang downward and provide an ideal water-trapping device through the cohesive and adhesive properties of water. This collection of water droplets provides a suitable medium for sperm to swim to the archegonia on the lower surfaces of the fingers. Nakamura and coworkers developed a similar parasol-like object to grab, transport, and release water droplets up to about 1 cm in diameter. Their simulated "archegoniophore," like the plant that serves as its model, is "largely insensitive" to such properties of water as surface tension and viscosity. This permits bubble-free capture and drop of liquids that is useful in laboratories and in soft robotics.

Goodyear Tires

Thank you to my alert former graduate student, Geert Raeymaekers, I am reporting to you on the use of "moss" in Goodyear tires (Figure 105). The "mosses" are packed into the sidewalls of the tires, where they can photosynthesize, absorb CO_2, and put O_2 into the atmosphere (Leary 2018). The tires are made of recycled tires and can't go flat, thus requiring fewer needs for new tires. Goodyear estimates that in a city about the size of Paris, the tires could absorb more than 4,000 tons of CO_2 and release ~3,000 tons of O_2 per year.

Figure 105. Goodyear Oxygene tire, showing "moss in sidewall. Photo from Goodyear, through Creative Commons at Futurism.

I have several concerns about this innovation. First, they look more like an ***Evernia***-type lichen, or perhaps reindeer "moss" – also a lichen. But more importantly, whether a true moss or a lichen, to work they must be alive. I would think that the heat created in a tire, the salt on winter roads, mud puddles, and rapid drying on a revolving wheel would make an unsuitable habitat for either.

After I questioned the identity of the tire material as a moss, Geert Raeymaekers contacted the company about our concerns. It turns out that the "moss" in the picture is indeed Icelandic moss, the lichen *Cetraria islandica*. The experiments had been done with the moss ***Hypnum cupressiforme*** (Figure 58), but because the tires would sit in the display for long periods of time, they substituted the lichen because it would retain its color without further care.

Summary

Sphagnum is the most widely used moss, including uses for bandages, diapers, boot liners, sanitary napkins, horticultural soil mixes, cranberry farms, orchid and mushroom culture, green roofs, flower arrangements, fuel, peatwood, peatcrete, litter for animals, lead detection electrodes, filtration, and oil spill cleanup. Products such as Hydro-Weed, SpillSorb, Oclansorb Plus, and Peat Sorb are peat products designed for hydrocarbon cleanup projects. These properties also make it an effective filter for removing heavy metals and other pollutants. Sphagnan makes a good preservative and is probably responsible for the preservation of the Tollund man.

Peat is a renewable fuel and horticultural source, but it must be harvested with sustainability in mind. Hand raking and light-weight wagons travelling on restricted paths can leave sufficient live plant material that harvesting may be repeated in 10-20 years. Lack of care about renewability has caused mass destruction of peatlands, along with destruction caused by development of industry, business, and housing land.

In addition to burning the peat, peatlands can be used to generate methane for fuel. Peat has been used in construction to make asphalt, peatcrete (light concrete), peatfoam, peatcork, and peatwood. Their natural role to control erosion has recently been copied in road construction.

Peatlands harbor a rich history and because of their antiquity can be used for aging and determining past vegetation and climate. And bryophytes on Ötzi and other icemen can tell us about their origins and suggest some of their uses of bryophytes.

The Japanese have capitalized on the beauty of bryophytes to lead excursions for people who have become interested in the natural world.

Bryophytes produce a wide range of antibiotics that have been used against fungi, slugs, and other invertebrate herbivores. The antibiotic and absorbent capabilities make bryophytes good agents of preservation, as seen in ancient tombs, stuffed mummies, and the preservation of bogmen. Photosynthesis of bryophytes has been used indirectly to power small users such as lights and clocks.

Because of their 1*n* state, bryophytes are useful in unravelling the roles of individual genes in plant physiology. And subsequently, adaptive genes are being moved into crop plants to increase drought tolerance (cotton) or lower targeted fatty acids. In other cases, genes are moved into bryophytes to make them create a needed human protein without causing an immune response in the human recipient.

Modern science is now using bryophytes in forensics to put suspects at the scene of a crime, using the techniques of DNA fingerprinting to match fragments on clothing to a particular location. They can also help to determine the post mortem interval.

Bryophytes are good organisms for testing the toxicity of various substances, using the bryological "lab rat" ***Physcomitrella patens***. Other scientific uses include unravelling the mysteries of gene function and plant physiology by studies with knock-out genes and gene transplants. Mosses are ideal for this because of their dominant 1*n* generation. This same advantage permits us to put genes for producing human substances such as blood protein into a moss and produce it in culture, avoiding any animal rights violations. Recently researchers found a new carbohydrate, an **arabinoglucan**, that mmay be a potential pharmaceutical.

Marchantia polymorpha archegoniophores serve as a good model for a laboratory pipette. Goodyear is experimenting with using "mosses" in the sidewalls of tires to clean the air of CO_2 and replenish it with O_2.

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Literature Cited

Abbadi, A., Domergue, F., Bauer, J., Napier, J. A., Welti, R., Zähringer, U., Cirpus, P., and Heinz, E. 2004. Biosynthesis of very-long-chain polyunsaturated fatty acids in transgenic oilseeds: Constraints on their accumulation. Plant Cell 16: 2734-2748.

Abdel-Jabbar, N., Al-Asheh, S., and Hader, B. 2001. Modeling, parametric estimation, and sensitivity analysis for copper adsorption with moss packed-bed. Separ. Sci. Technol. 36: 2811-2833.

Al-Asheh, S. and Duvnjak, Z. 1997. Adsorption of metal ions by moss. Adv. Environ. Res. 1: 194-210.

Al-Kanani, T., Akochi, E., MacKenzie, A. F., Alli, I., and Barrington, S. 1992a. Organic and inorganic amendments to reduce ammonia losses from liquid hog manure. J. Environ. Qual. 21: 709-715.

Al-Kanani, T., Akochi, E., MacKenzie, A. F., Alli, I., and Barrington, S. 1992b. Odor control in liquid hog manure by added amendments and aeration. J. Environ. Qual. 21: 704-708.

Ando, H. and Matsuo, A. 1984. Applied bryology. In: Schultze-Motel, W. (ed.). Advances in Bryology, Vol. 2, pp. 133-224.

Ark Enterprises Inc. 2004. Coastal oil spills benefit from the use of peat absorbents. Oils spills on water are devastating to the environment. Accessed 11 December 2004 at <http://www.arkent.com/coastal_spills/coastal_spills.html>.

Asakawa, Y., Harrison, L. J., and Toyota, M. 1985. Occurrence of a potent piscicidal diterpenedial in the liverwort *Riccardia lobata* var. *yakishimensis*. Phytochemistry 24: 261-262.

Asplund, D., Ekman, E., and Thun, R. 1976. Counter-current peat filtration of waste water. In: Proc. 5th Internat. Peat Congr., Poznabn, Poland, Vol. 1. Peat and Peatlands in the Natural Environment Protection, pp. 358-371.

Barthelmess, A. 1938. Mutationsversuche mit einem Laubmoos *Physcomitrium pyriforme*. I. Phänoanalyse der Mutanten. Zeit. Indukt. Abst. Vereb. 74: 479-581.

Barthelmess, A. 1941a. Mutationsversuche mit einem Laubmoos *Physcomitrium pyriforme*. II. Morphologische und Physiologische Analyse der univalenten und bivalenten Protonemen einiger Mutatenten. Zeit. Indukt. Abst. Vereb. 79: 153-170.

Barthelmess, A. 1941b. Über Beziehungen zwischen Genetik, Systematik, Morphologie und Entwicklungs-physiologie und die Möglichkeit einer Zusammenarbeit. Zeit. ges. Naturwiss. H3/4: 84-92.

Barthelmess, A. 1953. Mutationsauslösung mit Chemikalien. Naturwissenschaften 22: 583-584.

Bates, J. W. and Farmer, A. M. 1992. Bryophytes and Lichens in a Changing Environment. Oxford Science Publications, Clarendon Press, Oxford, UK, 404 pp.

Baur, A., Reski, R., and Gorr, G. 2005. Enhanced recovery of a secreted recombinant human growth factor using stabilizing additives and by co-expression of human serum albumin in the moss *Physcomitrella patens*. Plant Biotech. J. 3: 331-340.

Beike, A. K., Decker, E. L., Frank, W., Lang, D., VervlietScheebaum, M., Zimmer, A. D., and Reski, R. 2010. Applied Bryology – Bryotechnology. Trop. Bryol. 31: 22-32.

Belsky, J. 1982. Diesel oil spill in a subalpine meadow: 9 years of recovery. Can. J. Bot. 60: 906-910.

Biernacka, E. 1976. Peat effect on the recultivation of ash dumps from brown and hard coal. In: Proc. 5th Internat. Peat

Congr., Poznabn, Poland, Vol. 1. Peat and Peatlands in the Natural Environment Protection, pp. 397-412.

Birks, H. J. B. 1982. Quaternary bryophyte palaeo-ecology. In: Smith, A. J. E. (ed.). Bryophyte Ecology. Chapman and Hall, New York, pp. 473-490.

Bland, J. 1971. Forests of Lilliput. Prentice-Hall, Inc., Englewood Cliffs, 210 pp.

Boffey, P. H. 1975. Energy: Plan to use peat as fuel stirs concern in Minnesota. Science 190: 1066-1070.

Bohlen, M. C. 1999. Reproduction of spined loach. *Cobitis taenia*, (Cypriniformes; Cobitidae) under laboratory conditions. J. Appl. Ichthyol. 15(2): 49-53.

Bopp, M. 1974. Action mechanism of cytokinins in mosses (a model for the effects of cytokinins). In: Proc. 8th Int. Conf. Plant Growth Subst., Plant Growth Substances 1973, Hirokawa Publ. Co., Inc., Tokyo, pp. 934-944.

Brown, J. L. and Farnham, R. S. 1976. Use of peat for wastewater filtration – Principles and methods. In: Proc. 5th Internat. Peat Congr., Poznabn, Poland, Vol. 1. Peat and Peatlands in the Natural Environment Protection.

Brücker, G., Mittmann, F., Hartmann, E., and Lamparter, T. 2005. Targeted site-directed mutagenesis of a heme oxygenase locus by gene replacement in the moss *Ceratodon purpureus*. Planta 220: 864-874.

Buch, H. 1945. Über die Wasser- und Mineralstoffversorgung der Moose. I. Soc. Sci. Fenn. Comment. Biol. 9(16): 1-44.

Cardoso, H. F. V., Santos, A., Dias, R., Garcia, C., Pinto, M., Sérgio, C., and Magalhães, T. 2009. Establishing a minimum postmortem interval of human remains in an advanced state of skeletonization using the growth rate of bryophytes and plant roots. Internat. J. Legal Med. 124:451-456.

Carter, L. J. 1978. Peat for fuel: Development pushed by big corporate farm in Carolina. Science 199: 33-34.

Chaban, C. I., Kern, V. D., Ripetskyj, R. T., Demkiv, O. T., and Sack, F. D. 1998. Gravitropism in caulonemata of the moss *Pottia intermedia*. J. Bryol. 20: 287-299.

Chandler, B. 2012. Mossy posse. Evening Standard, London, Monday 30 April 2012, pp. 30-31.

Chen, X., Zeng, Q., and Wood, A. J. 2002. The stress-responsive *Tortula ruralis* gene ALDH21A1 describes a novel eukaryotic aldehyde dehydrogenase protein family. J. Plant Physiol. 159: 677-684.

Chiaffredo, M. 2007. Bryotec. Accessed on 20 August 2007 at <http://www.greenroofs.com/premium.php?sid=54>.

Cho, S. H., Chung, Y. S., Cho, S. K., Rim, Y. W., and Shin, J. S. 1999. Particle bombardment mediated transformation and GFP expression in the moss *Physcomitrella patens*. Molec. Cells 9: 14-19.

Clarke, D. 2008. The origins and development of the peat industry in Ireland. Peatlands Internat. 2008/1:1 2-15.

Clymo, R. S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. Ann. Bot. (London), New Ser. 27: 309-324.

Clymo, R. S. 1987. The ecology of peatlands. Sci. Prog. Oxford 71: 593-614.

Comis, D. 1992. Miracle moss: Add water and watch it grow. Agricultural Research, June: 10-11.

Coupal, B. and Lalancette, J. M. 1976. The treatment of waste water with peat moss. Water Res. 10: 1071-1076.

Cove, D. J. 1983. Genetics of bryophytes. In: Schuster, R. M. 1983. New Manual of Bryology I. Hattori Botanical Laboratory, pp. 222-231.

Cove, D. J. and Cuming, A. C. 2014. Genetics and genomics of moss models: Physiology enters the twenty-first century. In: Hanson, D. T. and Rice, S. K. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Adv. Photosyn. Resp. 37: 187-199.

Cove, D. J., Knight, C. D., and Lamparter, T. 1997. Mosses as model systems. Trends Plant Sci. 2(3): 99-105.

Crawford, R. J. M., Davis, S. A., Harding, R., Jackson, L. F., Leshoro, T. M., Meÿer, M. A., Randall, R. M., Underhill, L. G., Upfold, L., Dalsen, A. P. Van, Merwe, E. Van Der, Whittington, P. A., Williams, A. J., and Wolfaardt, A. C. 2000. Initial effects of the Treasure oil spill on seabirds off Western South Africa. Avian Demography Unit Department of Statistical Sciences University of Cape Town. Accessed on 11 December 2004 at <http://web.uct.ac.za/depts/stats/adu/oilspill/oilspill.htm>.

Crum, H. 1988. A Focus on Peatlands and Peat mosses. University of Michigan Press, Ann Arbor, 306 pp.

Dente, J. 1997. Reluctant Time Travelers: the Bog Bodies of Europe. Accessed on 26 May 2007 at <http://www.utexas.edu/courses/wilson/ant304/projects/projects97/dentep/dentep.html>.

D'Hennezel, F. and Coupal, B. 1972. Peat moss: A natural absorbant for oil spills. CIM Bull. 65(717): 51-53.

Dierßen K. 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. In: Cramer, J. (ed.). Bryophytorum Bibliotheca 56, Stuttgart, 289 pp.

Dillon, R. M. 2003. A Spill Drill. NHPR News. 15 May 2003. Accessed 11 December 2004 at <http://nhpr.org/view_content/4777/>.

Drlica, K. 1982. A burning question. Garden 6(6): 26-29.

Dyer, S. J., O'Neill, J. P., Wasel, S. M., and Boutin, S. 2001. Avoidance of industrial development by woodland caribou. J. Wildlf. Mgmt. 65: 531-542.

Ehrenfeld, J. G. 1995. Microsite differences in surface substrate characteristics in *Chamaecyparis* swamps of the New Jersey pinelands. Wetlands 15: 183-189.

Ellis, C. J. and Tallis, J. H. 2000. Climatic control of blanket mire development at Kentra Moss, north-west Scotland. J. Ecol. 88: 869-889.

Engel, P. P. 1968. The induction of biochemical and morphological mutants in the moss *Physcomitrella patens*. Amer. J. Bot. 55: 438-446.

Enviropeat. 2004. Accessed on 11 December 2004 at <http://www.ravensdown.co.nz/growingmedia/products/pdf/Enviropeat_Leaflet.pdf>.

Epstein, B. 1988. Inside the invisible moss industry. Milwaukee Journal, 4 Jan. 1988.

Eurola, S., Aapala, K., Kokko, A., and Nironen, M. 1991. Mire type statistics in the bog and southern aapa mire areas of Finland (60-66°N). Ann. Bot. Fenn. 28: 15-36.

Ferland, C. and Rochefort, L. 1997. Restoration techniques for *Sphagnum*-dominated peatlands. Can. J. Bot. 75: 1110-1118.

Fischer, W., Schlungbaum, G., and Kadner, R. 1968. Cation exchange capacities of peat investigated by means of *p*H titrations, KI/KIO_3, $CuSO_4$ and methylene blue. In: Robertson, R. A. (ed.). Trans. Second International Peat Congress, Leningrad, 1963. Her Majesty's Stationery Office. Edinburgh, pp. 985-997.

Folger, T. 1992. Oldest living bacteria tell all. Discover 13(1): 30-31.

Frahm, J.-P. 2004. Recent developments of commercial products from bryophytes. Bryologist 107: 277-283.

Frahm, J.-P. and Kirchhoff, K. 2002. Antifeedant effects of bryophyte extracts from *Neckera crispa* and *Porella obtusata*

against the slug *Arion lusitanicus*. Cryptog. Bryol. 23: 271-275.

Francez, A.-J. and Vasander, H. 1995. Peat accumulation and peat decomposition after human disturbance in French and Finnish mires. Acta Oecol. 16: 599-608.

Frank, W., Ratnadewi, D., and Reski, R. 2005. *Physcomitrella patens* is highly tolerant against drought, salt and osmotic stress. Planta 220: 384-394.

Furness, S. B. and Grime, J. P. 1982. Growth rate and temperature responses in bryophytes. I. An investigation of *Brachythecium rutabulum*. J. Ecol. 70: 513-523.

Fuselier, L., Bougary, A., and Malott, M. 2011. From trace evidence to bioinformatics: Putting bryophytes into molecular biology education. Biochem. Molec. Biol. Ed. 39: 38-46.

Glime, J. M. 1982. Bryological excursions: A comparison. Bryol. Times 17: 1-2.

Glob, P. V. 1969. The Bog People: Iron-Age Man Preserved. (Tr. R. Bruce-Mitford). Cornell University Press, New York. In: Lienhard, J. H. The Engines of Our Ingenuity. Copyright © 1988-1997, University of Houston. Accessed 7 July 2002 at <http://www.uh.edu/engines/epi487.htm>.

Grauballe Man. 2002. Accessed 9 July 2002 at <http://www.plc.vic.edu.au/Curriculum/History/tollundweb/Evidence/grauballe.html>.

Greven, H. C. 1992. Changes in the Dutch Bryophyte Flora and Air Pollution. Dissertationes Botanicae, Vol. 194: 237 pp, 43 figs, 39 tables, 15 tab. as app.

Grosse-Brauckmann, G. 1979. Major plant remains of moor profiles from the area of a stone-age lakeshore settlement on Lake Duemmer, West Germany. Phytocoenologia 6: 106-117.

Harmens, H., Foan, L., Simon, V., and Mills, G. 2013. Terrestrial mosses as biomonitors of atmospheric POPs pollution: A review. Environ. Pollut. 173: 245-254.

Hawes, I., Andersen, D. T., and Pollard, W. H. 2002. Submerged aquatic bryophytes in Colour Lake, a naturally acidic polar lake with occasional year-round ice-cover. Arctic 55: 380-388.

Hi Point Industries. 1991. Accessed on 11 December 2004 at <http://www.oclansorb.com/plus.htm>.

Hinrichsen, D. 1981. Peat power: Back to bogs. Ambio 10: 240-242.

Ho, Y. S. and McKay, G. 2000. The kinetics of sorption of divalent metal ions onto *Sphagnum* moss peat. Water Res. 34: 735-742.

Hoffman, P. (ed.). 1992. Born-again moss. Discover 13(9): 12.

Horne, P. and Ireland, R. R. 1991. Moss and a Guanche mummy: An unusual utilization. Bryologist 94: 407-408.

Hunt, Steven. 1995-2007. Spill-Sorb. Accessed on 19 August 2007 at <http://www.spillsorb.com/>.

Hunt, Steven. 2000. Mopping Up Oil with Nature's Help. Animal Tracks. Accessed 11 December 2004 at <http://www.exn.ca/AnimalTracks/Penguins/Story2.cfm>.

Hunt, Steven. 2002-2007. Article from Discovery Channel: Mopping up Oil with Nature's Help. Accessed 19 August 2007 at <http://www.arkent.com/coastal_spills.html>.

Hunt, Steven. 2004. Mopping up Oil with Nature's Help. Animal Tracks. Accessed 11 December 2004 at <http://www.exn.ca/AnimalTracks/Penguins/Story2.cfm>.

Hydro-Weed. 2007. Accessed on 11 July 2007 at <http://www.befreetech.com/hydroweed.htm>.

Inhabitat. 2017. Biophotovoltaic Moss Table Generates Electricity Through Photosynthesis. Accessed 13 September 2017 at <http://inhabitat.com/moss-table-by-biophotovoltaics-generates-electricity-through-photosynthesis/>.

Itouga, M., Ono, Y., Sakakibara, H., Sudo, E., and Yoshida, K. 2006. Mitigation of Cu-toxicity through "bryo-filtration": An evaluation with rice leaf photosynthesis and gene expression profile. Hikobia 14: 419-429.

Iwatsuki, Z. and Inoue, H. 1971. Dare nimo wakaru koke no subete. [All about bryophytes.]. Nat. Sci. Mus. Tokyo, 143 pp.

Janssens, J. A. 1988. Fossil bryophytes and paleoenvironmental reconstruction of peatlands. In: Glime, J. M. (ed.). Methods in Bryology. Hattori Botanical Laboratory. Nichinan, Miyazaki, Japan, pp. 299-306.

Jenkins, G. I. and Cove, D. J. 1983. Light requirements for regeneration of protoplasts of the moss *Physcomitrella patens*. Planta 157: 39-45.

Johansson, A. and Sipilae, K. 1991. New ecologically acceptable methods for fuel and power production from biomass and peat. International Symposium on Energy Options for the Year 2000, Wilmington, DE, USA.

Jonsgard, B. and Birks, H. H. 1995. Late-glacial mosses and environmental reconstructions at Krakenes, western Norway. Lindbergia 20: 64-82.

Kern, V. D., Smith, J. D., Schwuchow, J. M., and Sack, F. D. 2001. Amyloplasts that sediment in protonemata of the moss *Ceratodon purpureus* are nonrandomly distributed in microgravity. Plant Physiol. 125: 2085-2094.

King, J. 1986. Plant cells and the isolation of conditional lethal variants. Enzyme Microbial Technol. 8: 514-522.

Kinnunen, A., Niittylae, H., Orjala, M., and Oravainen, H. 1982. Turvepellettien jakelun, kaesittelyn ja polton kehittaeminen. [Development of delivery, handling and combustion in peat pellets.]. Tech. Res. Cent. Finland (VTT), Vuormiehentie 5, Sf 02150 Espoo 15, Finland, 1982, 159+ pp.

Klinger, L. F., Elias, S. A., Behan-Pelletier, V. M., and Williams, N. E. 1990. The bog climax hypothesis: Fossil arthropod and stratigraphic evidence in peat sections from southeast Alaska, USA. Holarct. Ecol. 13: 72-80.

Knapp, E. 1935. Untersuchungen über die Wirkung von Roentgenstrahlen an dem Lebermoos *Sphaerocarpus*, mit Hilfe der Tetraden-analyse I. Zeits. Indukt. Abstam. Vererb. 70: 309-350.

Knight, D. 1991. Growing threats to peat. New Sci. 1780: 27-32.

Korpelainen, H. and Virtanen, V. 2003a. DNA fingerprinting of mosses. J. Forensic Sci. 48: 804-807.

Korpelainen, H. and Virtanen, V. 2003b. Bryophytes witness in a homicide investigation. Bryol. Times 109: 6.

Leary, Kyree. 2018. Goodyear's Moss-Filled Tires Are Here to Save the Environment. 8 March 2018. Accessed 16 March 2018 at <https://futurism.com/goodyears-moss-filled-tires-here-save-environment/>.

Lancia, M., Conforti, F., Aleffi, M., Caccianiga, M., Bacci, M., and Rossi, R. 2013. The use of *Leptodyctium* (*sic*) *riparium* (Hedw.) Warnst in the estimation of minimum postmortem interval. J. Forensic Sci. 58: 239-242.

Lavoie, C. and Rochefort, L. 1996. The natural revegetation of a harvested peatland in southern Quebec: A spatial and dendroecological analysis. Ecoscience 3: 101-111.

Leblanc, F. and Rao, D. N. 1974. A review of the literature on bryophytes with respect to air pollution. Bull. Soc. Bot. France 121(suppl. 2): 237-255.

Lewis, M. 1981. Human uses of bryophytes. I. Use of mosses for chinking log structures in Alaska. Bryologist 84: 571-572.

Lienhard, J. 1988. The Bog Men. The Engines of Our Ingenuity. Copyright © 1988-1997 by John H. Lienhard, University of Houston. Accessed 7 July 2002 at <http://www.uh.edu/engines/epi487.htm>.

Lindow Man. 2002. Accessed 9 July 2002 at <http://www.plc.vic.edu.au/Curriculum/History/tollundweb/Evidence/linfeld.html>.

Lindskog, A. and Eriksen, B. 1995. Identifiering av fossila vaextfragment i glaciaerer. [The identification of fossil plant fragments in glaciers.]. Svensk Bot. Tidskr. 89: 83-88.

Lindstrom, O. 1980. The technology of peat. Ambio 9: 309-313.

Macleod, M. 2006. Keep the flame alive for peat's sake. Scotland on Sunday, 20 Aug 2006. Accessed on 20 August 2007 at <http://scotlandonsunday.scotsman.com/index.cfm?id=1221192006>.

Marcus, R. H. 2002. Does Temperature Affect Oil Spill Cleanup? California State Science Fair 2002 Project Summary. Accessed 11 December 2004 at <http://www.usc.edu/CSSF/History/2002/Projects/J0815.pdf>.

Maryland Department of the Environment. 2004. Fact Sheet. Heating Oil Release. Maryland Department of the Environment, Baltimore, MD. Accessed on 11 December 2004 at <http://www.mde.state.md.us/assets/document/factsheets/Heating%20Oil%20Release.pdf>.

Matsumoto, Satoe. 2015. Moss-viewing trips catching on among women. Japan Times 27 July 2015 <www.japantimes.co.jp/news/2015/07/27/national/moss-viewing-trips-catching-on-among-women/#.WbrYSMiGM2w>.

Mele, A. 1993. Polluting for Pleasure. WW Norton & Company, New York & London, 229 pp.

Miller, M. W., Gauber, E. D., and Voth, P. D. 1962a. Nutritionally deficient mutants of *Marchantia polymorpha* induced by X-rays. Bot. Gaz. 124: 94-102.

Miller, M. E., Gauber, E. D., and Voth, P. D. 1962b. Biosynthetic pathways in nutritionally deficient mutants of *Marchantia polymorpha* L. Nature (London) 195: 1220-1221.

Miller, N. G. 1981. Bogs, bales, and BTU's: A primer on peat. Horticulture 59(4): 38-45.

Mills, Robyn. 2018. Could eating moss be good for your gut? <https://phys.org/news/2018-04-moss-good-gut.html#jCp>.

Moore, P. D. and Bellamy, D. J. 1974. Peatlands. Springer Verlag, New York, 221 pp.

Morgan, E. L., Wu, Y.-C. A., and Young, R. C. 1990. Plant toxicity test with the moss *Physcomitrella patens* (Hedw.) B.S.G. ASTM Spec. Tech. Publ., ASTM, Philadelphia, Pa. 1091: 267-279.

Moutschen, J. 1954. Contribution a l'étude de la génétique des mousses. Action des rayons X et des rayons gamma. Le Cellule 46: 181-210.

Nakamura, K., Hisanaga, T., Fujimoto, K., Nakajima, K., and Wada, H. 2018. Plant-inspired pipettes. J. Royal Soc. Interface 15: 20170868. <http://rsif.royalsocietypublishing.org/>.

Nash, T. H. III and Wirth, V. (eds.). 1988. Lichens, bryophytes and air quality. Biblio. Lichenol. 30. J. Cramer, Johannesstrasse 3 A, D-7000 Stuttgart, West Germany, 297 pp.

Nozu, Mako and Thompson, Brian. 2015. What's behind Japan's moss obsession? The Conversation 10 December 2015, 6:18 am EST. <http://theconversation.com/whats-behind-japans-moss-obsession-50500>.

Ohlson, M. and Økland, R. H. 1998. Spatial variation in rates of carbon and nitrogen accumulation in a boreal bog. Ecology 79: 2745-2758.

Onianwa, P. C. 2001. Monitoring atmospheric metal pollution: A review of the use of mosses as indicators. Environ. Monitor. Assess. 71: 13-50.

Painter, T. J. 1991. Lindow Man, Tollund Man and other peat-bog bodies: The preservative and antimicrobial action of Sphagnan, a reactive glycuronoglycan and tanning and sequestering properties. Carbohydrate Polymers 15: 123-142.

Peltola, I. 1986. Use of peat as litter for milking cows. In: Nielsen, V. C., Voorburg, J. H., and L'Hermite, P. (eds.). Seminar on Odour Prevention and Control of Organic Sludge and Livestock Farming Silsoe (UK), 15-19 Apr 1985, pp. 181-187.

Pfanner, E. 2015. In Japan, moss gathers new fans. Wall Street Journal 2 November 2015.

Ramos, J. A., Bermejo, E., Zapardiel, A., Perez, J. A., and Hernandez, L. 1993. Direct determination of lead by bioaccumulation at a moss-modified carbon paste electrode. Analyt. Chim. Acta 273: 219-227.

Reski, R. 1998. Development, genetics and molecular biology of mosses. Bot. Acta 111: 1-15.

Reski, R. 2005. Do we need another model plant? Plant Biol. 7: 219.

Reski, R. and Frank, W. 2005. Moss (*Physcomitrella patens*) functional genomics – Gene discovery and tool development, with implications for crop plants and human health. Brief. Func. Genomics Proteomics 4: 49-57.

Richardson, D. H. S. 1981. The Biology of Mosses. Blackwell Sci. Publ., Oxford, xii + 220 pp.

Roberts, A. W., Lahnstein, J., Hsieh, Y. S. Y., Xin, Xiaohui, Yap, K., Chaves, A. M., Scavuzzo-Duggan, T. R., Dimitroff, G., Lonsdale, A., Roberts, E. M., Bulone, V., Fincher, G. B., Doblin, M. S., Bacic, A., and Burton, R. A. 2018. Functional characterization of a glycosyltransferase from the moss *Physcomitrella patens* involved in the biosynthesis of a novel cell wall arabinoglucan. Plant Cell (2018). DOI: 10.1105/tpc.18.00082.

Robinson, Richard. 2002. Murder Preserved: Tales of the bogmen. Created by Richard Robinson, Science Writer. Accessed 9 July 2002 at <http://www.whfreeman.com/RAVEN/content/rv18/rv18pe01.htm>.

Rozell, N. 2005. The message within the moss. Article #1732. Alaska Science Forum, Geophysical Institute, University of Alaska, Fairbanks, 2 pp.

Rudenko, S. I. 1970. Frozen tombs of Siberia: The Pazyryk burials of Iron-Age Horsemen. In Horne, P. and Ireland, R. R. 1991. Moss and a Guanche mummy: An unusual utilization. Bryologist 94: 407-408.

Ruel, M., Chornet, S., Coupal, B., Aitcin, P., and Cossette, M. 1977. Industrial utilization of peat moss. In: Radforth, N. W. and Brawner, C. O. (eds.). Muskeg and the Northern Environment of Canada. Toronto, pp. 221-246.

Rütten, D. and Santarius, K. A. 1992. Relationship between frost tolerance and sugar concentration of various bryophytes in summer and winter. Oecologia 91: 260-265.

Sack, F. D. 1993. Gravitropism in protonema of the moss *Ceratodon*. Mem. Torrey Bot. Club 25: 36-44.

SANCCOB. 2006. South African Foundation for the Conservation of Coastal Birds. Accessed 11 July 2007 at <http://www.sanccob.co.za/news.htm#news8>.

Sanders, K. 2002. Tales from the Bog. Accessed on 9 July 2002 at <http://ls.berkeley.edu/divisions/art-hum/framing/sanders.html>.

Schieder, O. 1973. Untersuchungen an Nicotinsaüre-auxotrophen Stämmen von *Sphaerocarpus donnellii*. Aust. Zeit. Pflanzenzpysiol. 70: 185-189.

Schumaker, K. S. and Gizinski, M. J. 1995. 1,4-dihydropyridine binding sites in moss plasma membranes. Properties of receptors for a calcium channel antagonist. J. Biol. Chem. 270: 23461-23467.

Sineshchekov, V., Koppel, L., Hughes, J., Lamparter, T., and Zeidler, M. 2000. Recombinant phytochrome of the moss *Ceratodon purpureus* (CP2): Fluorescence spectroscopy and photochemistry. J. Photochem. Photobiol. B: Biol. 56: 145-153.

Spinti, M., Zhuang, H., and Trujillo, E. M. 1995. Evaluation of immobilized biomass beads for removing heavy metals from wastewaters. Water Resources Res. 67: 943-952.

Sukhanov, M. A. 1972. The use of peat as a thermal-insulating material in large panel building. Proc. 4th Int. Peat Congr., Otaniemi, Finland, pp. 319-332.

Summerton, J. 1981. Energy in Sweden. Gearing up for renewable energy. Ambio 10: 219-224.

Tadesse, M. 2002. Characterisation and mode of action of natural plant products against leaf fungal pathogens. Shaker, Aachen.

Taylor, J. A. and Smith, R. T. 1980. Peat – a resource reassessed. Nature 288: 319-320.

The Discovery of Tollund Man. 2002. Accessed on 9 July 2002 at <http://www.plc.vic.edu.au/Curriculum/History/tollundweb/home/discovery.html>.

Thieret, J. W. 1954. Mosses and liverworts: Old and new uses. Chicago Nat. Hist. Mus. Bull. 1954: 4, 8.

Thieret, J. W. 1956. Bryophytes as economic plants. Econ. Bot. 10: 75-91.

Tolonen, K. and Tolonen, M. 1984. Late-glacial vegetational succession at four coastal sites in Northeastern New England: Ecological and phytogeographical aspects. Ann. Bot. Fenn. 21: 59-77.

Trujillo, E. M., Jeffers, T. H., Ferguson, C., and Stevenson, H. Q. 1991. Mathematically modeling the removal of heavy metals from a wastewater; using immobilized biomass. Environ. Sci. Technol. 25: 1559-1565.

Tuba, Z., Slack, N. G., and Stark, L. R. (eds.). 2011. Bryophyte Ecology and Climate Change. Cambridge University Press, Cambridge, UK, 505 pp.

Turner, R. G. 1993. Peat and people: A review. Adv. Bryol. 5: 315-328.

Tyler, G. 1990. Bryophytes and heavy metals: a literature review. Bot. J. Linn. Soc. 104: 231-253.

UNERG Report. 1984. (source lost).

University of Cambridge. 2011. The hidden power of moss. September 22, 2011. PhysOrg. Accessed 23 March 2013 at <http://phys.org/news/2011-09-hidden-power-moss.html>.

Viraraghavan, T. and Tanjore, S. 1994. Removal of pentachlorophenol from wastewater using peat. Hazardous Waste Hazardous Materials 11: 423-433.

Virtanen, V., Korpelainen, H., Kostamo-Liusvaara, K., and Pohjamo, M. 2004. Utilizing bryophytes in criminal investigations – a research project in Finland...and a request for collaboration. Bryol. Times 112: 8-9.

Virtanen, V., Korpelainen, H., and Kostamo, K. 2007. Forensic Botany: Usability of bryophyte material in forensic studies. Forensic Sci. Internat. 172: 161-163.

VTT. 2004. Wood in peat fuel – impact on the reporting of greenhouse gas emissions according to IPCC guidelines.

Walker, L. M. and Sack, F. D. 1990. Amyloplasts as possible statoliths in gravitropic protonemata of the moss *Ceratodon purpureus*. Planta 181: 71-77.

Wettstein, Fr. von. 1932. Genetik. In: Verdoorn, F. (ed.). Manual of Bryology. Martinus Nijhoff, The Hague, pp. 233-272.

Wood, A. J., Reski, R., and Frank, W. 2004. Isolation and Characterization of ALDH11A5, a novel non-phosphorylating GAPDH cDNA from *Physcomitrella patens*. Bryologist 107: 385-387.

Yang, H., Zhang, D., Wang, J., Wood, A. J., and Zhang, Y. 2012. Molecular cloning of a stress-responsive aldehyde dehydrogenase gene ScALDH21 from the desiccation-tolerant moss *Syntrichia caninervis* and its responses to different stresses. Molec. Biol. Rep. 39: 2645-2652.

Yang, H., Zhang, D., Li, X., Li, H., Zhang, D., Lan, H., Wood, A. J., and Wang, J. C. 2016. Overexpression of ScALDH21 gene in cotton improves drought tolerance and growth in greenhouse and field conditions. Molec. Breed. 36(34): 1-13.

Young, J. C. and Sack, F. D. 1992. Time-lapse analysis of gravitropism in *Ceratodon* protonemata. Amer. J. Bot. 79: 1348-1358.

Zaitseva, N. 2009. A polysaccharide extracted from *Sphagnum* moss as antifungal agent in archaeological conservation. Master's Thesis, Queen's University, Kingston, Ontario, Canada.

Zechmeister, H. G., Grodzińska, K., and Szarek-Łukaszewska, G. 2003. Bryophytes, Chapt. 10. Trace Metals and other Contaminants in the Environment 6: 329-375.

Zimmerman, M. R. and Smith, G. S. 1975. A probable case of accidental inhumation of 1,600 years ago. Bull. N. Y. Acad. Med. Ser. 2, 51: 828-837.