Flora of North America, Volume 27, 2007

1981c, 1981d, 1984) added *Lepidozia vitrea* and *Plagiochila semidecurrens*. These substances have demonstrated activity against carcinoma of the nasopharynx, at least in cell culture.

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

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

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

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

Food Sources

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

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

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

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

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

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

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

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

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

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

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

Genetic Engineering

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

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

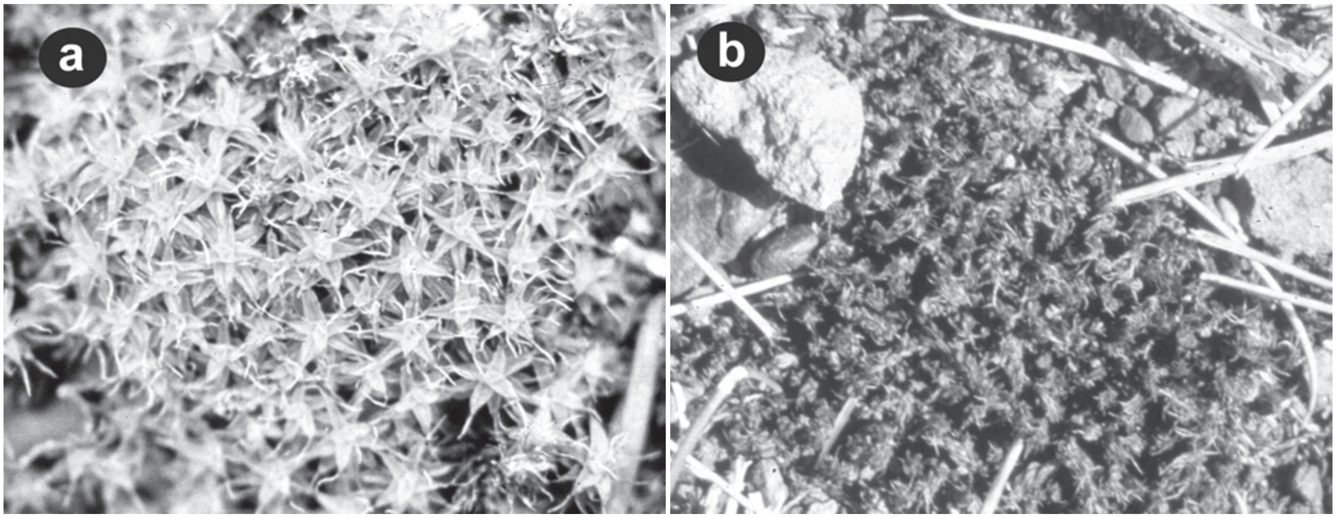

FIGURE 26. Wet (**a**) and dry (**b**) *Syntrichia ruralis*, a moss used for genetic engineering of other plants for drought resistance. Photo by Janice Glime.

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

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

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

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

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