Advances in Bryology 2

**Applied Bryology**

by

Hisatsugu Ando

Botanical Institute, Faculty of Science, Hiroshima University,
Higashisenda-machi, Naka-ku, Hiroshima, 730 Japan

and

Akihiko Matsuo

Department of Chemistry, Faculty of Science, Hiroshima University,
Higashisenda-machi, Naka-ku, Hiroshima, 730 Japan

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1. INTRODUCTION

Bryophytes have long been considered to be insignificant in the economy of man except for those mosses used in packing, plugging, and decoration, and raw Sphagnum and peat. In Japan, however, the horticultural use of bryophytes, especially of mosses, has been popular in gardening and landscape tray planting. In China several species of bryophytes (mainly mosses) are used as medicine. Recent progress in bryological science has greatly changed our understanding of bryophytes as useful plants. The importance of bryophytes relates above all to their usefulness as indicators of soil-, water-, or air conditions and to the actual and potential use of their chemical components as biologically-active agents. Furthermore, the elegant beauty of evergreen bryophytes seems to have become more highly appreciated by people in our modern material civilization.

We should not forget another important fact that bryophytes, notwithstanding their minuteness, are indispensable agents in the economy of nature. As KETCHLEDGE (1962) stated, "Mosses play such an important role in the total balance of nature. Unlike most higher plants, mosses are of nearly universal occurrence in plant communities. Although inconspicuous, they perform essential functions in maintaining the health and vigor of wildland habitats and thus indirectly serve man."

The present contribution entitled "Applied Bryology" provides a review of both old and modern studies and essays on the use of bryophytes. Some important papers were not available to us; nevertheless, they have been cited by requotation from other literature. As to the significance of bryophytes as indicator plants, the present account is limited because this topic is separately treated in this volume by H. MUHLE. We know well that bryophytes are valuable subjects for research in several plant sciences, such as cell biology, genetics, experimental morphology, physiology, paleoecology, plant geography, and ecology. Reference to these subjects is not pursued here as such matters are beyond the scope of "Applied Bryology" as we have defined it.
2. USES AS MATERIAL FOR BEDDING, PACKING, PLUGGING, AND STUFFING

Several archeological records prove that in the past mosses were used in a variety of ways, especially as material for bedding, packing, plugging, and stuffing owing to their soft and elastic texture. Mosses are also suitable for this purpose because they require no special treatment except drying. Dickson (1973) presents a review of reports on such used in Europe; examples of the uses are: 1) padding a mesolithic flint blade with Hylocomium brevirostre to protect the user's hand, 2) wads of Isothecium myosuroides and Homalothecium sericeum between timbers, 3) plugging seams and cracks of boats or canoes with Neckera complanata and many other moss species, 4) packing a dagger and a scraper in mosses, such as Sphagnum, Plagiomnium undulatum and "Hyphnum", 5) using Pseudoscleropodium purum, Rhytidiadelphus triquetrus, Hylocomium splendens, etc. in packing and stuffing.

Another archeological report by Seaward and Williams (1976) indicates that in Northumberland, England, mosses were probably used as bedding material for man and his domestic animals, and/or the absorption of water (and perhaps urine?) (analysis by volume of collected samples: Hylocomium splendens 55%, Rhytidiadelphus squarrosum 33%, Pseudoscleropodium purum 6%, 7 other species 6%), and in York, as packing material for the storage of fruit and vegetables in pits (Pleurozium schreberi 47%, Hyphnum supressiforme 27%, Hylocomium splendens 14%, Pseudoscleropodium purum 6%, 7 other species 6%). Other reports suggest that mosses may have been used as packing in soft leather slippers in Viking and early Medieval Trondheim, and that Ro-
mans at Beardson near Glasgow used mosses as toilet paper (BIRKS, 1982).

It is well known that *Polytrichum commune* has been used for bedding material and as stuffing for beds in Europe, especially by Laplanders; LINNAEUS, in his wanderings, often slept on such a bed (GROUT, 1947). LINNAEUS states, in his record of travels in Lapland, "*Polytrichum commune* grows copiously in the damp forests and is used for bed and bedding. They choose the starry-headed plants, out of the tufts of which they cut a surface as large as they please for bed or bolster, separating it from the earth beneath. This mossy cushion is very soft and elastic; and if a similar portion of it be made into a covering, nothing can be more warm and comfortable" (BLACK, 1979). Dillenius, in 1741, used the generic name *Hypnum*, derived from a Greek word for sleep, for pleurocarpous mosses. Such mosses would seem suitable for stuffing pillows and thus inducing sleep (CRUM, 1973). The moss-bed and -pillow that AL-LORGE (1937) observed in the Azores included *Thuidium tamariscinum*, *Pseudoscleropodium purum*, and *Hypnum cupressiforme*. According to HRDLICKA (1930; quoted from THIERET, 1956) who made a thorough anthropological survey in Alaska, moss was used in early Eskimo burials as a bed upon which to lay the bodies of the dead. A wooden scaphoid coffin (ca. 1300 years old) excavated at Ohira-cho, Tochigi-ken, Japan, contained scraps of *Aerobryopsis subdivergens* and some other mosses, which were considered to have been bedding material for the buried body (IWATSUKI & INOUE, 1971).

Several mosses have been reported to be used as plugging material for log cabins. Examples of mosses used in such a way are *Pleurozium schreberi* in northern Europe (RICHARDSON, 1981); *Hylocomium splendens* (most common), *Pleurozium schreberi*, *Hypnum cupressiforme*, and a few others in the Valais Suisse (DOIGNON, 1954); *Sphagnum* spp., *Hylocomium splendens*, *Rhytidiadelphus loreus*, *Racomitrium canescens*, etc. in Alaska (LEWIS, 1981). It is of interest that an aquatic moss, *Fontinalis antipyretica* has been used by Nordic people for filling spaces between chimney and walls to prevent the walls from burning; this moss was thus named by LINNAEUS "antipyretica" (= against fire).
In the Kii district of Japan, some large mosses, such as Thuidium kanedae, Hypnum plumaeforme, Rhytidiadelphus japonicus, and Hylocomium cavifolium, were used as a filling to stop a leak in a log dam which was temporarily constructed at the upper part of a river to gather timbers harvested from mountain forests (ANDO, 1957).

LEWIS (1981), who has experimented with using various species of mosses as plugging in his own cabins in Alaska where he lived for over 12 years, states, "I have found moss to be an excellent material for chinking log cabins, as have many others in the past and present. In many ways, it is preferable to more modern materials." This may be also true of its use as material for packing and stuffing in areas where suitable mosses are readily available. Some rigid mosses, such as Neokeria menziesii, Alsia abietina, and Antitriohia californica, are used in the western United States as moisture-retaining packing for vegetables (GROUT, 1902; FRYE, 1920). Rhytidiadelphus triquetrus is used for packing china and other fragile articles (GROUT, 1947). NOGUCHI (1952) has reported finding some mosses in an old box used to hold ancient (ca. 1000 years old) Japanese silk-clothes, including Aerobryopsis subdivertens, Meteorium helmintothalamum, Barbella determesii, and Neokera calcicola. These mosses, which grow hanging down from trees or rocks and are hence scarcely soiled, were used for packing clothes and fancy goods in ancient times.

3. HORTICULTURAL USES

Bryophytes have a variety of horticultural uses. They serve as: 1) soil additives, root-packing, and mulching materials, 2) ornamental material for pot- or bowl-cultivation and landscape trays (miniature landscapes), 3) ground cover of "Bonsai" (potted dwarf tree), and 4) ground cover in Japanese gardens (ISHIKAWA, 1974).
(1) **Soil additives, root-packing, aerial-rooting media, and mulching materials**

The use of mosses for these horticultural purposes has long been popular. Fresh *Sphagnum* mosses and *Sphagnum* peat have been especially important in this regard because of their high water-holding capacity, permeability to air and elasticity (ISHIKAWA, 1974; see Section 6 dealing with the use of peat mosses and peat). Fragmented plants of *Leucobryum bowringii*, *L. neilgherrense*, and occasionally *L. acabrum*, mixed with sand or soil, are used in Japan in soil mixes, which are especially appreciated for the cultivation of Rhododendron shrubs (INOUE, 1980). *Hypnum plumaeforme*, a large creeping moss common in Japan, is also used in the same way (ANDO, 1957). Several species of mosses, such as *Camptothecium arenarium*, *Rhytidiopsis robusta* (PERIN, 1962); *Thuidium delicatulum* and *Hypnum imponens* (ADDERLEY, 1964), have been found to be satisfactory in the culture of orchids. *Octoblepharum albidum*, a tropical member of the *Leucobryaceae*, is useful as a seedling medium (ARZENI, 1963).

(2) **Material for pot- or bowl-cultivation and landscape trays**

Some bryophytes, especially mosses, are employed in Japan as ornamental plants for container culture, which is a small horticultural art appreciated in the home (Fig. 4:1). Large dendroid mosses such as *Climacium japonicum* and *Rhodobryum giganteum* are very lovely and are sometimes planted in a bowl for decoration (ANDO, 1957). The beauty of these mosses suggests branched trees, palms, or tree-fern of a Lilliputian fairy land. INOUE (1980) explains how to undertake the bowl-cultivation of mosses and lists species suitable for it. They are: *Polytrichum commune*, *Atrichum undulatum*, *Racomitrium canescens*, *Bartramia pomiformis*, *Rhizogonium dosyanum*, *Climacium japonicum*, *Pleuroziop-sis ruthenica*, *Eurhynchium arbuscula*, *Hypnum plumaeforme*, and others.

Landscape tray ("Bonkei", "Bankei" or "Saikei") is an attractive horticultural art of Japan in which several mosses are effectively used. It is a miniature landscape created within
the confines of a small, shallow tray, which can be placed anywhere in the home (HIROTA, 1981). According to its components, the landscape tray is classified into three types: one is the moss landscape tray in which mosses are used as the main element but occasionally with an addition of lichens and a few small vascular plants in association with stones, soil, and sand (INOUE, 1978; Fig. 4:2); the second is the living landscape tray composed of living plants such as dwarf trees, shrubs, grasses, and mosses, and basic materials such as stones, soil, and sand (KAWAMOTO, 1980); and the third is the realistic landscape tray in which are used not only living plants but also artificial trees, flowers, and mosses, together with miniature objects such as houses, bridges, boats, people, and animals (HIROTA, 1981). Mosses are valuable for the landscape tray because they have an appropriate texture, retain their bright clean color throughout the year, and can withstand dryness (KAWAMOTO, 1980). Mosses arranged in harmony with other elements in a tray are suggestive of the endless variation of forests, bushes, and grassland, and in some cases they also express the sea and rivers. Liverworts, especially thalloid species such as Marchantia polymorpha and Conocephalum conicum, are not used because they spread rapidly beyond the original design and prevent poured water from reaching roots of other plants (KAWAMOTO, 1980).

Concise books by INOUE (1978, 1980) and OISHI (1981) are very helpful guides to learning the techniques of moss landscape tray design and planting. INOUE (1978, 1980) recommends the following species as suitable mosses to suggest landscape objects.

a. Dense forests: Atrichum undulatum, Pogonatum inflexum, Di-oranella heteromalla, Myuroclada maximovii, Cratoneuron filicinum.

b. Tall trees: Polytrichum formosum, Pogonatum inflexum, Di-oranum spp., Climaciurn japonicum, Pleuroziopsis ruthenica.

d. Cover of undulating mountains: *Bryum argenteum*, *Leucothrix neilgherrense*.

e. Lake water and snow: *Bryum argenteum*, *Leucothrix neilgherrense*, *Racomitrium lanuginosum*.

f. Rivers and sea: *Bryum argenteum*, *Leucothrix neilgherrense*.

OISHI (1981) cites *Rhizogonium dozyanum* as material for a show of deciduous and bamboo forests, and plants of *Rhodobryum giganteum* to accentuate landscapes.

Scenes in tray gardens are of two types: landscape and seascape. The former imitates mountains, plateaus, valleys, lakes, and swamps, whereas the latter shows oceans and islands. The following are examples of mosses used for each (ISHIKAWA, 1974).

a. Landscape: *Polytrichum commune*, *Leucothrix neilgherrense*, *Bartramia pomiformis*, *Rhizogonium dozyanum*, *Climacium japonicum*, *Cratoneuron filicinum*.


(3) As the ground cover of "Bonsai" (potted dwarf tree)

"Bonsai" is the art of growing sturdy and simple dwarfed trees in pots and caring for them so that they will reveal the innermost beauty of naturally aged plants. They represent the distillation of the best and most beautiful attributes given to them by nature (MURATA & MURATA, 1974). This horticultural art, which is popular in Japan and China, is here translated as "the potted dwarf tree" although this phrase does not fully describe the real heart of "Bonsai".

Mosses are not essential to "Bonsai", but they provide an important contrast to the tree that is the main element. A moss carpet serves to stabilize the soil and retain its moisture. Furthermore, mosses give graceful, old-age charm to the potted
dwarf tree. For ground cover of "Bonsai", species of low, small acrocarps with unpretentious beauty are favored because the mosses are a subtle enhancement of the potted tree (INOUE, 1980). Recommended mosses include: Atrichum undulatum, Leucobryum neillgherrense, Barbula unguiculata, Weissia controversa, Ceratodon purpureus, Funaria hygrometrica, Physcomitrium eury-stomum, Bryum argenteum, and Brachymenium exile. Most of these mosses grow in man-made habitats and can tolerate fertilized pot soils that are manured from time to time.

(4) Moss garden

Gardening is one of the polite arts that has developed in both the East and the West. In western countries, however, mosses have not been widely used as garden plants. They have usually been treated as pests in the garden, and those who wish to maintain well-kept lawns find mosses particularly annoying (MILLER & MILLER, 1979). In the Pacific Northwest of the United States, mosses flourish, covering the ground, trees and rocks in shaded areas, but even there they are not properly appreciated by gardeners – and one can actually obtain sprays with which to destroy them (STEERE, 1968). However, some lovers of beauty appreciate the color imparted to a landscape or a roof by a moss covering, and certain people have endeavored to increase the charm of their shaded walks by encouraging the natural growth of mosses and by transplanting suitable species (GROUT, 1931).

Recently PEARMAN (1982) drew attention to a nineteenth century "lichen and moss garden" established at Chatsworth, Great Britain, by reprinting an anonymous article from "Paxton's Magazine of Botany", Vol. 12, 1846. Reasons for making a garden of cryptogams are described as follows: "Mosses are, perhaps, the most beautiful and varied of all the cryptogamic race or plants; ... Most people who take any pleasure at all in the vegetable creation, will be delighted with the green verdure of a mossy carpet in a moist plantation, or when enveloping the arms of some fading forest-tree, or spreading over the rocks and stones beneath it; and we can readily conceive it
possible to transfer the same features to the garden, preserving each kind in mosses with its proper name." The list of cryptogams planted in the garden includes some 33 mosses, 4 liverworts, 23 lichens and one alga, among which nine mosses and the alga are marked as the most handsome. The nine species of mosses are: Plagiomnium undulatum, Rhizomnium punctatum, Dicranella heteromalla, Dioranum scoparium, Thamnobryum alopecurum, Bylocomium splendens, Neokera crispa, Polytrichum commune, and P. piliferum.

ANDO (1972) in a visit to Dove Cottage, Grasmere, in the English Lake District, the home of poet laureate, W. Wordsworth from 1799 to 1808, was impressed by a small but lovely garden behind the cottage where a verdurous cushioned bed of Polytrichum commune invaded by scattered plants of flowering daffodils was making an attractive show. He (ANDO, 1972) has also admired a beautiful wallgarden decorated with both colorful flowers and elegant mosses at M. & Mme TAILLARD's home in Corcy, France.

Mosses have received greater appreciation in Japan where they have long been considered a precious attribute of gardens. First, they are useful as an evergreen ground cover in much the same way as lawn grasses are used in western gardens; second, they give a peculiar beauty and ancient look to gardens by clothing trees, rocks, and stone lanterns (ANDO, 1957). Foreign visitors to Japan are intrigued by the unique features and beauty of Japanese moss gardens, many attractive examples of which are to be seen at various Buddhist temples and palaces in Kyoto, an ancient capital of Japan. Several Japanese authors have presented reports or introductions to moss gardens, especially those in Kyoto (ISHIKAWA, 1960, 1961, 1973, 1974; ISHIKAWA et al., 1953, 1954; IWATSUKI & KODAMA, 1961; ANDO, 1971; INOUE & OHASHI, 1983).

The conscious use of mosses as ground covers in Japanese gardens began in the latter part of the 16th century when the tea garden, "Roji", appeared and developed (ISHIKAWA, 1973; IGI, 1982). The tea garden is a garden of reduced size designed to harmonize with the ideals of the tea ceremony ("Chano-yu"). In
arranging such gardens, the primary objective is to create an atmosphere that is conducive to the serene state of mind necessary for full appreciation of the tea ceremony (NAKANE, 1968). The tea garden is thus required to be aged and natural in appearance and to reflect both elegant taste and a quiet mood of serenity. For creating such a calm and profound atmosphere, mosses have been appreciated as the best material because of their varying tones of green, soft texture, and the pleasing form of the individual tufts and carpets.

Before development of the tea garden, gardens in Kyoto were mostly large planted areas with ponds and islands, and pavilions. One example is the garden of Saihoji Temple in Kyoto (Fig. 5). This garden is now famous for its extensive growth of mosses, and thus is popularly called "Koke-dera" ("Moss temple"). Mosses, however, were not part of the original design (ISHIKAWA, 1973). The topographic setting of Kyoto is such that the surrounding mountains help to insure constant humidity which is favorable to the growth of mosses. This circumstance has automatically led to the development of moss gardens in Kyoto. Accordingly, mosses in Saihoji Temple are considered to have first appeared spontaneously as a result of the favorable setting of the garden. In later years growth and maintenance of the mosses have been encouraged by careful management and transplanting.

A Japanese garden of another unique type is the stone garden ("Seki-tei") or the dry garden ("Kare-sansui"), which is characterized by an abstract design reflecting the spirit of Zen Buddhism. The harmonious beauty of these gardens issues from the simple pattern formed by the arrangement of stones, white sand, and mosses (ISHIKAWA, 1973). The most famous example is the stone garden of Ryoanji Temple in Kyoto (Fig. 6:1). The fifteen stones, arranged into five groups upon a rectangular bed of white sand (336.6 m²) have provoked more commentary and speculation than perhaps any other single Japanese garden (BRING & WAYEMBERGH, 1981). No vascular plants are seen anywhere in the arrangement; only small patches of moss (Polytrichum commune) surround the groups of stones. The stones on white sand are suggestive of mountains rising above the clouds
or islands over the sea, and moss can become forests, shrubs, or grassland developed on them.

One more exceptionally simple but uniquely beautiful garden is seen in a corner of the main garden of Sanboin Temple, Kyoto (Fig. 6:2). It consists only of white sand and five patches (three circular and two guitar-shaped) of moss (Polytrichum commune). These patches are modelled after saké cups and gourds used as saké bottles, which symbolize the famous banquet sponsored in 1598 at cherry-blossom time by the lord, Hideyoshi TOYOTOMI, the creator of the main garden of the temple (ANDO, 1963).

According to the reports by ISHIKAWA et al. (1953, 1954), IWATSUKI and KODAMA (1961) and our observations, the following species are representative mosses in Japanese gardens of Kyoto (ANDO, 1971). In this list those with two asterisks are the more common and important species; those with one asterisk are locally frequent.


e. On banks of the pond and in other damp places: Sphagnum palustre, Polytrichum commune**, Fissidens japonicus, Climacium japonicum.

f. In ponds: Chiloscyphus polyanthos, Riccia fluitans.
g. Species sometimes found in the garden but not desirable as ground cover: Pleurocarpous mosses such as Thuidium glaucinum, Braehytheium buchananii, Entodon attenuatus, Brotherella henonii, and Hyphnum plumaeforme; liverworts such as Bassania japonica, Heteroscyphus planus, Conocephalum oonicum, C. supradecompositum, and Marchantia polymorpha.

Polytrichum commune is a most commonly used moss in the gardens of Kyoto, especially in open sites, because of its soft beauty, ability to withstand sunlight, and firm attachment to soil. Plants of this species resist disturbance by the brooms or bamboo-rakes used to remove fallen leaves and other debris. In other districts the dominant mosses are sometimes different species than those in Kyoto gardens. For example, garden mosses in other places consist mainly of creeping species such as Plagiomnium autumn, Brotherella henonii and Hyphnum plumaeforme; in some dry sandy gardens, Raeomitrium canescens is used (TAKAKI, 1980, UETA & DEGUCHI, 1980; IGI, 1982). Hyphnum plumaeforme is not permitted in gardens in Kyoto, but is appreciated as a good material for the moss garden in drier regions (UETA & DEGUCHI, 1980).

Techniques of moss gardening

Many books dealing with the character of Japanese gardens and the technique of gardening have been published, and some of these are written in English (NAKANE, 1968; SEIKE et al., 1980; BRING & WAYEMBERGH, 1981). It is uniformly acknowledged in these books that mosses are useful as ground covers, but the technicalities of moss cultivation are not or scarcely mentioned.

IWATSUKI and KODAMA (1961) presented a short note in which they advised selecting species suited to the environmental conditions at given sites in the garden. They state that thalloid liverworts such as Marchantia polymorpha, Conocephalum oonicum, C. supradecompositum, and Phaeoaeos spp., and pleurocarpous mosses, for example Hyphnum plumaeforme, are not desirable and should be weeded. They further say that moss carpets are to be kept free of dead leaves and debris. It is stressed that no
fertilizer should be used for mosses. MIZUTANI (1975, 1976) and FUKUSHIMA (1979, 1980) give several hints on maintaining the vivid beauty of garden mosses: 1) preserving favorable habitat conditions, 2) constant weeding, 3) moderate watering (over watering should be avoided), 4) continual care to remove fallen dead leaves and dung of cats, dogs, and birds, and 5) keeping away harmful animals such as moles, slugs, crickets, and ants.

The most useful and comprehensible guide book of moss gardening is that of INOUE (1976). Contents of this book include: 1) how to select and collect the mosses, 2) mat transplanting and fragment scattering* of moss material (* crushed or cut fragments of moss plants are scattered on the ground, covered with thin soil, and then pressed down by a board), 3) light, moisture, and temperature conditions suitable for the growth of mosses, 4) planning and building a moss garden, 5) methods of planting mosses in the soil and stone-work, 6) seasonal management of mosses, 7) examples of moss gardens, and 8) species useful in the moss garden.

Another helpful manual of moss gardening was written by OISHI (1981) who is a prominent professional moss-gardener with rich experience. In this book techniques for vegetative multiplication of garden mosses by cutting, fragment scattering, and mat separating are explained with series of color pictures and line drawings. How to design moss gardens is treated in the manual of INOUE and OHASHI (1983), which includes many fine pictures of gardens. Mats of commonly cultivated garden mosses such as Polytrichum commune, Leucobryum neilgherrense, and Hypnum plumaeforme are sold at nursery shops in Japan.

In Western countries especially in the United States, the Japanese moss garden has been introduced and described in several articles in which the appreciation of mosses as garden plants is warmly encouraged (GROUT, 1931; KETCHLEDGE, 1963; PULLAR, 1967; McDOWELL, 1968; STEERE, 1968; SCOFIELD, 1970; FREE, 1974; MILLER & MILLER, 1979; MUMA, 1979; RICHARDSON, 1981; TUCKER, 1982).
4. USE AS MATERIAL FOR DECORATION

According to WELCH (1948) and THIERET (1956) who reviewed old and new uses of bryophytes, mosses have been used for decoration in several ways: 1) Dicranum scoparium for forming banks of green in shop window displays, 2) Rhytidadelphus loreus, R. triquetrus, and Hylocomium splendens as green carpets for floral exhibitions, 3) Climacium americanum fashioned into wreaths and crosses, 4) Hylocomium splendens for making moss roses, 5) Climacium dendroides (dyed) as a decoration for women's hats. In Victorian times mosses were much collected in England and sold in markets for decorative uses (RICHARDSON, 1981), and it was fashionable to compile albums of pressed mosses, seaweeds, ferns, etc. (personal communication from M.R.D. SEAWARD). Framed artwork with pressed, dried bryophytes is popular today (SAITO, 1973).

CLARKE (1902) reported interesting moss-wares sold in Boston (U.S.A.) for the decoration of ladies hats and bonnets with braids constructed of Pseudoscleropodium purum, and cords made of Neckera crispa; as neither species is native in North America, they were considered to have been imported from Europe. LOESKE (in HAEKEL, E.H. ed., Die Wunder der Natur, 1912; quoted from MANZOKU, 1963) illustrated a unique decorative arrangement of sporophytes selected from several mosses. In fact capsules of varied forms and colors, especially those of Splachnum species with purple or yellow skirt-like hypophyses suggesting fairly parasols, are showy enough to be used as ornamental miniatures.

ANDO (1972) recorded a shop window display made of Convalaria majalis and some mosses, such as Isothecium myosuroides, Pleurozium schreberi, Pseudoscleropodium purum, and Hypnum supressiforme, in Rambouillet, a town ca. 50 km southwest of Paris, which he visited during a May festival in 1970, and at Renne he also observed cushions of Leucobryum glaucum arranged to attract attention in a tailor's shop window.

Natives of New Guinea use mosses to decorate masks used on ceremonial occasions (RICHARDSON, 1981). Other uses of mosses
by the New Guinean natives were reported by VAN ZANTEN (1973): "The natives of the Wissel Lakes area strip the plant (Dawsonia cf. grandis) of its leaves, put it over a glowing fire, strip off the outer layers, split it in two pieces and plait them in a rope-netting; it is then used as a red decoration for netbags, etc. ... I have seen the natives of the Nebelyer Valley (Western Highlands) wearing stems of Dawsonia grandis in their hari and also as a green decoration in their bracelets."

Selected handsome mosses artificially colored a brighter green than their natural color are sometimes sold; for example bunches of dyed Climaecium dendroides were once sold in New York (BRITTON, 1902), and packs of dyed Rhytidadelphus triquetrus were on sale in Paris in the Christmas season (ANDO, 1972). Ornamental "water-flowers" made from dyed plants of Climaecium japonicum and imitation paper-flowers are sold in Japan; placed in a glass of water, these expand decoratively (MIZUTANI, 1963). Climaecium plants attached to miniature ornamental rocks are also used to imitate seaweeds in small aquaria (HORIKAWA et al., 1967). Living plants of some water bryophytes are also appreciated in aquarium; examples are: Vesicularia dubyana (BENL, 1958; COOK et al., 1974), Glossadelphus sollingeri (COOK et al., 1974), Rhacopilum aristatum, Fontinalis antipyretica, Amblystegium ripariu, Eurhynchium riparioides, Taxiphyllum barbieri, Vesicularia ferriei, Chiloscyphus polyanthos, Riccia fluitans, and Ricciocarpus natans (TAKAKI et al., 1982). These bryophytes are also useful to fishes in providing oxygen and egg-laying substrates.

5. MEDICINAL USES

In early times medicinal uses of plants were often suggested by the similarity of their shape and structure to some organ in the human body. The surface of some liverworts (for example, Marchantia polymorpha) presented patterns similar to those of cross sections of animal livers, and hence they were believed to cure ailments of the liver (MILLER & MILLER, 1979). Another example is Polytrichum commune, which is commonly called "hair-
cap moss" because it bears hairy calyptra: DILLENIUS said that an oil expressed from this moss was used by ladies of his time on their hair – a truly fine application of the doctrine of signatures (CRUM, 1973).

The North American Indians have used various plants as herbal medicines (LEWIS & ELVIN-LEWIS, 1977). According to FLOWERS (1957) who made a report on the ethnobotany of the Gasuite Indians of Utah, "several kinds of mosses, including species of Philonotis, Bryum, Mnium, and various matted hypnaceous forms, were used to alleviate the pain of burns. The moss was crushed into a kind of paste and applied as a poultice. These and similar forms were used as a covering for bruises and wounds or as padding under splints in setting broken bones. The moss was often kept soaked with cold or hot water." Indians in Alaska use moss by mixing it with grease to make salve (MILLER & MILLER, 1979). The northern Cheyenne Indians of Montana are known to use Polytrichum juniperinum in medicines (HART, 1981).

In China where herbal medicine is extensive and widely accepted bryophytes have been used as crude drugs and nearly 40 species are employed for various remedies. The medicinal bryophytes so far recognized as effective are as follows (DING, 1982):

Hepaticae: Frullania tamarisci, Reboulia hemisphaerica, Conocephalum conicum, C. supradecompositum, Marchantia polymorpha.

Musci: Sphagnum girgensohnii, S. magellanicum, S. palustre, S. squarrosum, S. teres (the four species, except S. teres which is applied for eye diseases, are used as surgical dressings), Ditrichum pallidum, Campylopus pyriformis, Oreoja martiana, Weisia controversa, Hydrogonium amplexifolium, Grimmia ovalis, Funaria hygrometrica, Tetraplodon bryoides, Bryum argenteum, Rhodobryum giganteum, R. roseum, Plagiommum cuspidatum, Rhizomnium punctatum, Plagiopus oederi, Philonotis fontana, Aneobryum filamentosum, Meteoriella soluta, Floribundaria flor-
bunda, Climacium dendroides, Haplocladium microphyllum, Cratoneuron filicinum, Amblystegium riparium, Entodon compressus, Hypnum calliclourum, Taxiphyllum taxivameum, Polytrichum commune.

Among these, the most important species are Rhodobryum giganteum and R. roseum (for cardiovascular disease, nervous prostration), Polytrichum commune (as an antipyretic, diuretic, hemostatic), and Haplocladium microphyllum (for tonsillitis, bronchitis, tympanitis, cystitis). Conocephalum cocteum and Marchantia polymorpha (mixed with vegetable oils) are used as ointments for boils, eczema, cuts, bites, and burns (WU, 1977; DING, 1982; ANDO, 1983). Successful experimental and clinical evaluations have been carried out on some species in China (DING, 1982). WU (1982) gave an interesting story about the medicinal use of Rhodobryum giganteum: "in 1976 the staff of the laboratory of the fourth medical school went to East Sezchuan to gather information of the use of mosses by peasants and found that Rhodobryum giganteum was used to cure angina. An ether extract of this species was found, on analysis, to contain volatile oils, lactones and amino-acids. This extract, when tested on animals, increased the rate of flow in the aorta of white mice by over 30%, causing a reduction in the amount of oxygen resistance. Thus Rhodobryum giganteum can be of use in the treatment of cardiovascular disease."

The following case is not directly concerned with a medicinal use, but it is closely related to the production of a chemical substance that is important in medicine and industry. Gallnuts, a source of tannic acid, are produced on leaves of Rhus javanica that have been parasitized by the aphid Schlechten-dalia chinensis. The production of gallnuts is associated with the growth of mosses, especially species of the Mniaceae, because gall aphids overwinter in cocoons that they make on the mosses. TANG (1976), quoted from WU, 1982) has studied a method for increasing the production of Chinese gallnuts and found that the numbers of aphids are closely related to the availability of their winter host plants – Plagiomnium maximoviscisii, P. auspidatum and P. vestoatum. The industrial management of
Mniaceous plants for increasing gallnut production is well developed in China where gall-making aphids are artificially raised on moss plants cultivated indoors under controlled conditions (ANON., 1981; ANDO, 1983).

Gallnuts have also been important in Japan where a technique for the more effective increase of gallnut production was devised after TAKAGI (1937) first found aphids wintering on Mniaceous plants. HORIKAWA (1947) studied the development of gallnuts and the life history of the aphid with special reference to their relation with bryophytes. Moss species hitherto known in Japan to serve as a winter host for the gall aphid are Trachyphyes micvophylla, Mnium sapporenses, Plagiomnium maximoviertii, P. acutum, P. vesicatum, Rhizomnium hattorii, and more rarely Pogonatum inflexum and Piesidens spp.

6. USES OF SPHAGNUM (PEAT MOSS) AND PEAT

A. Sphagnum (PEAT MOSS)

Peat mosses have the greatest monetary value among bryophytes. They have several uses that relate to their aseptic properties and high water-absorbing capacity.

(1) Horticultural uses

As already mentioned, fresh Sphagnum mosses are highly appreciated as soil additives, and as rooting-packing and mulching materials. Mixed with soil or spread over the ground, Sphagnum lightens soil mixture, discourages weed growth, and prevents excessive drying of the upper soil layers. Nurserymen use wet Sphagnum for shipping live plants and also as a medium for plant propagation (KETCHLEDGE, 1962). As an additive to soils, Sphagnum functions in the same way as peat does (see description under peat). Sphagnum is also a useful top dressing for seed flats to discourage damping-off fungi (MILLER & MILLER, 1979).
Use as a surgical dressing

*Sphagnum* has absorbent qualities superior to cotton and its antibiotic qualities are an added feature (SCHOFIELD, 1969). Owing to such properties, *Sphagnum* has been used as a surgical dressing. A paper by PORTER (1917), a series of articles by HOTSON (1918, 1919, 1921) and NICHOLS (1918a, b & c, 1920), and a review by THIERET (1956) give detailed information on this subject. During the First World War *Sphagnum* was widely used for dressing. The Germans were more active than the Allies in the utilization of *Sphagnum* dressings, and HOTSON (1921) has reported on the use of *Sphagnum* as a surgical dressing in Germany. According to NICHOLS (1918b, 1920), *Sphagnum* dressings were used extensively by the Allied armies also. The British used nearly a million dressings every month, and the Canadian Red Cross made over 200,000 per month. In the United States, 500,000 dressings were prepared between March 1918 and the war's end in November, after the American Red Cross adopted *Sphagnum* as a standard dressing material.

PORTER (1917) pointed out the following ways that *Sphagnum* pads are superior to cotton: 1) they absorb liquids about three times as fast, 2) they take up three to four times as much liquid as cotton pads, 3) they retain liquids much better and the dressings need be changed less frequently, 4) they distribute absorbed liquids more uniformly throughout their mass, 5) they are cooler, less irritating and softer, 6) they can be produced at much less expense. NICHOLS (1918a, b) writes that for surgical dressings, the more robust species of *Sphagnum* are superior to more delicate ones and that plants with large, closely set leaves and close-set branches are greatly preferable to those with small leaves and scattered branches. He named four important species of surgical value, *Sphagnum papillosum*, *S. palustre*, *S. magellanicum*, and *S. imbricatum*, which are of value in the order given. In China *Sphagnum girgensohnii*, *S. magellanicum*, *S. palustre*, and *S. squarrosum* have been used for this purpose (DING, 1982).

During the Second World War, the need to substitute *Sphagnum* for cotton never became critical (THIERET, 1956). The use of
Sphagnum dressings has declined because of the greater aesthetic appeal of a white cotton dressing (RICHARDSON, 1981).

(3) Miscellaneous uses

Dried plants of Sphagnum, together with other large mosses, have been used as bedding, packing, plugging, and stuffing materials (see Section 2). In Lapland and other northern regions, Sphagnum has domestic uses. STARK (1854) records of soft Sphagnum mosses citing Linnaeus' Flora of Lapland, "The Lapland matrons are well acquainted with this moss. They dry and lay it in their children's cradles, to supply the place of bed, bolster, and every covering; and bein changed night and morning, it keeps the infant remarkably clean, dry, and warm. It is sufficiently soft of itself, but the tender mother, not satisfied with this frequently covers the moss with the downy hairs of the reindeer, and by that means makes a most delicate nest for the new-born babe." Eskimo women have long used dried Sphagnum as diaper material (SCHOFIELD, 1969). Even recently the Chippewa Indians of Lac Vieux Desert in Michigan's Upper Peninsula put dry Sphagnum between babies' thighs to keep them clean (CRUM, 1973). LONTON (1973) reported a use of Sphagnum by Canadian Indians for bedding and diapering children. According to HOTSON (1921), serviceable pillows were made from loose Sphagnum in Germany during the First World War. These were used as rests under the hips and in the small of the back, as supports or for elevating the arms and legs of wounded people, and for head and neck rests in hospital trains.

Sphagnum has been used as insulating material. It traps much air both within the cells and among the plants and is consequently an excellent insulator (SCHOFIELD, 1969). HOTSON (1921) records that many Germans used dried Sphagnum during the War in their homes to keep milk warm or cool. The inside of a wooden or paper box was lined with Sphagnum plants and bottles of milk put in the center. HOTSON (1921) also reported that in Germany a fairly good and cheap cloth was made by mixing Sphagnum with wool and weaving them together. Another interesting
use is packing live frogs, worms and some insects with moist Sphagnum for shipment (RICHARDSON, 1981).

Sphagnum has antibiotic properties. Eskimos mix it with fat to make a salve (SCHOFIELD, 1969). Dried Sphagnum is sold in herb shops in China for use in the treatment of hemorrhages and eye diseases, (HU, 1945; quoted from RICHARDSON, 1981). DING (1982) mentions that Sphagnum teres (mixed with certain other herbs) is used in China as an internal decoction for eye diseases.

B. PEAT

Peat is formed from plant remains the decomposition of which is hindered by anaerobic conditions resulting from poor drainage (STEWART, 1977). Among the plants that form peat, mosses, particularly Sphagnum moss, contribute substantially to deep peat deposits. Peat has inherent characteristics such as a low density, a high porosity, cation exchange capacity, and thermal and acoustical insulation properties (RUEL et al., 1977). Peat may be utilized in the following general ways: 1) chemical conversion, including combustion, for recovery of the energy in peat, 2) mechanical preparation of peat products, e. g., as a soil conditioner, and as a filter for waste water, etc., 3) extraction of peat components such as waxes (LINDSTRÖM, 1980).


(1) Use as fuel

Peat has long been used as a fuel. It has certain advantages and disadvantages for this purpose. Among its advantages are:
1) ease of harvesting because deposits are located at or near the surface, 2) low sulfur content, and hence its use poses less of a pollution problem, and 3) a heating value superior to that of wood and about equal to that of lignite. Among the disadvantages are that 1) it contains 70 to 95 percent water, which must be reduced before burning, 2) it is generally located remote from major users and, therefore is costly to transport, and 3) the harvesting operation may pose environmental problems (BOFFEY, 1975).

The UNERG Report on Peat (1980) indicates that about 40 percent of the total annual world production of peat (220 million tons, most of which is produced in the USSR) is used as fuel, and estimates that the total amount of fuel-peat resources worldwide is equivalent to 100,000 million tons of oil, which is close to 50 percent of the known gas reserves. At least 40-50 countries have exploitable peat resources. Potential use throughout the world by the year 2000 has been estimated 40-60 million tons of oil equivalent (HINRICHSEN, 1981).

Peat is now an important source of fuel in northern Europe, namely, in Finland, Sweden, Ireland, the Federal Republic of Germany, Poland, and the Soviet Union. In some of these countries, such as the Soviet Union and the Republic of Ireland, peat is burned to generate electricity (Miller, 1981). The Soviet Union burned an estimated 70 million tons of peat in 1975, mostly to produce electricity in 77 power plants, and Ireland used and estimated 3.5 million tons in the same year, accounting for nearly a third of its total energy needs (BOFFEY, 1975). According to a more recent report (RICHARDSON, 1981), the use of peat fuel in Ireland has further developed. Three million tons of milled peat (dried to 55% water content) power seven electricity generating stations that supply about 20 percent of the national requirement, a million tons of machine turf (small blocks of peat dried to 35% water content) are used for domestic fuel, and about a half million tons of peat briquettes (compressed peat, 10% moisture) are burned for steam and heat in industry.

Finland has announced plans to make itself 40 percent self-
sufficient in energy within the next several years by utilizing indigenous supplies of peat and wood (MILLER, 1981). In Sweden, it is anticipated that during the 1980s industrial and municipal heating and power generation from peat will increase substantially. In northern Sweden a pulp and paper company has recently rebuilt its existing oil burners to enable combustion of pulverized peat imported from Finland. By 1983, the company plans to start its own full-scale harvesting of approximately 1,000 hectares of milled peat (SUMMERTON, 1981).

In the United States peat has not been much used as a fuel because the process of preparing peat for fuel is costly, and thus it is not cheap enough to compete with fuels in general use (THIERET, 1956). There, interest in peat as an energy source began with a strike of coal miners in 1903. After 1903, the U.S. Geological Survey undertook an assessment of the peat resources of the United States, and the U.S. Bureau of Mines also began to investigate peat and to explore possible uses for it (MILLER, 1981). Renewed interest in peat as fuel began in the United States in the 1970s as a result of the energy crisis. In 1975 the Minnesota Gas Company applied for a long-time lease on some 491 square miles of state-owned land — containing an estimated 200,000 acres of peat — with the announced hope of eventually building a plant that would convert the peat to synthetic natural gas (methane) (BOFFEY, 1975). In North Carolina, since 1975, First Colony Farm, which embraces 372,000 acres of peatland, has been developing plans to mine woody peat for fuel, either to be burned directly for generation of electricity or converted to synthetic gas. The farm's harvestable peat is estimated as more than 400 million tons, which is believed to be enough to fuel four 400-megawatt power plants for 40 years or an 80-million-cubic-foot-per-day gasification plant for nearly 50 years (CARTER, 1978).

To use peat as a fuel, several problems must be overcome including harvesting and transportation, drying, and conversion into more burnable fuel. "The technology of peat", as outlined by LINDSTRÖM (1980), describes these matters with particular attention to the last problem. Peat can be harvested as milled peat, sod peat, or hydraulic peat, a method now under
development. Peat is also suitable for production of low and intermediate Btu gas, as well as hydrogen, ethylene, SNG (synthetic natural gas), methanol, and Fisher Tropsch gasoline. Peat may also be converted in its wet condition directly to oil in a liquefaction process. However, the major use for peat during the next decade will be as a fuel for production of heat and/or electricity in advanced combustion processes including cold combustion of hydrogen produced from peat in fuel cells.

(2) Agricultural and horticultural uses

Peat is important as a soil conditioner and is commonly used for agricultural and horticultural purposes. With certain additives, it serves as a superb soil for greenhouse crops, potted ornamentals, and tree seedlings, and it can be used to improve garden soils when they are too coarse or too heavy (SJÖRS, 1980). The properties of peat which make it an ideal additive to mineral soils for growing plants are: 1) it increases the water storage capacity of soils with coarse texture, 2) it provides air spaces in soils with fine texture (e.g. clay), 3) it improves the nutrient-holding capacity of all soil types (STEWART, 1977). Furthermore, the buffering capacity of soil is increased by the presence of peat, which helps maintain a more or less constant pH in spite of the addition of fertilizer or water containing dissolved mineral salts (MILLER, 1981). Undecomposed, long-fiber peats make lasting mulches (MILLER, 1981). Their high water-holding and antiseptic qualities make them admirable for this purpose. In Ireland one million cubic meters of light, fibrous, slightly decomposed moss peat are produced for horticultural purposes. It is mainly exported to several other countries, generating as much as 7 million pounds a year in foreign currency (RICHARDSON, 1981).

MILLER (1981) describes other interesting uses. Peat is appreciated as material for mushroom beds. Pulverized peat is mixed with fertilizer to reduce caking before and during application. Peat is processed into several kinds of biodegradable con-
tainers for growing plants. Decomposed peat of fine texture with fertilizer and a wetting agent added is compressed into disks or squares and dried. Upon rewetting, these expand into cylinders or cubes appropriate for seed germination and the rooting of cuttings. [See also "Peat and its use in horticulture" (161 pp., Helsinki) by V. Puustjärvi (1977), which unfortunately was not available to the authors.]

Peat is otherwise used as basic material for a certain type of landscape tray [see (2) of Section 3], a unique horticultural art of Japan. Peat, which is called "keto" in Japanese horticultural terminology, is first dried and then, after being mixed with hot water and kneaded, becomes malleable. Such elastic peat paste is molded with a spatula to create mountains, rocks, islands and plains in the miniature landscape (Hirota, 1981).

(3) Use for treating waste water

Because of its physical and chemical characteristics, peat, especially Sphagnum peat, is effective as a filtering and adsorption agent and is used for the treatment of waste water containing heavy metals, organic substances such as oils, detergents and dyes, and microorganisms. Constituents of peat bear polar functional groups, such as alcohols, aldehydes, ketones, acids, phenolic hydroxides, and ethers that can become involved in chemical bonding. Furthermore, the physical structure of peat is highly cellular and permeable. The specific adsorption for dissolved solids such as transition metals and polar organic molecules is quite high because of these characteristics (Coufal & Lalancette, 1976). Ruel et al. (1977) reviewed this subject, and the following information is mostly derived from this source.

According to a series of studies by Coufal and Lalancette (1971, 1972, quoted from Ruel et al., 1977; 1976), the process of using Sphagnum peat to remove heavy metal ions in solution, for example, Ag, Cd, Cu, Cr, Fe, Hg, Ni, Pb and Sb, is divided into three steps: 1) contact of waste water with the peat,
2) drying the peat by mechanical pressure, and 3) burning the peat and reclaiming the metals. COUPAL and LALANCETTE (1976) reported on the characteristics and performance of a machine of 20,000 gal./day capacity used for the treatment of industrial waste waters. They concluded, "The use of peat moss appears as a very cheap and convenient method for the treatment of used waters. The main advantages of this method of treatment are the simplicity of the system, its very broad scope in terms of pollutants eliminated, its ruggedness and its ability to accept rather wide variations of effluent composition."

An experiment described by POOTS et al. (1976) showed that peat is a suitable adsorbent for acidic blue dye, although the time necessary to reach equilibrium was long (two hours). Peat is also used as an absorbent agent for oil spills. Furthermore, it is a potential filtering agent for oily waste waters in vegetable oil and margarine factories. This use is being explored in Canada and Finland (RUEL et al., 1977). Active carbon, an important adsorptive substance in many chemical industries can be produced from peat. The potential use of peat for making coke and activated charcoal is expected, although market studies must still be done (RUEL et al., 1977).

(4) Peat for paper and construction materials

In the early twentieth century in Sweden, wrapping paper and pasteboard were made from peat, and in 1920's in the United States, there was a manufacturing plant for this purpose near Capac, Michigan (MILLER, 1981). Some Russian plants use a process whereby raw peat is pressed and heated to form slabs for the insulation of domestic housing and refrigerators, although such slabs crumble and break easily (SUKHANOV, 1972; RUEL et al., 1977).

Recently, further uses of Sphagnum peat for construction materials have developed through the use of binders for solidification and strengthening. Two new materials for construction have emerged, "peatcrete" (OLIVIER, 1971; AITCIN, 1972; both
quoted from RUEL et al., 1977) and "peatwood" (AITCIN et al., 1972; quoted from RUEL et al., 1977).

a. Peatcrete

Peatcrete, light-weight concrete, is a hydraulically pressed mixture of screened Sphagnum peat, Portland cement, and water. Although it is relatively low in mechanical strength and water resistance, peatcrete has the following advantages: 1) the peat moss need not be dried, 2) the binder is low in cost, 3) is fireproof, 4) ease of sawing and nailing, 5) can be cast and moulded into any shape, 6) continuous process production, and 7) low density (0.7 to 1.2 Sp. Gr.; 45-70 lb/ft^3) (RUEL et al., 1977). Until properties of peatcrete have been fully evaluated, it is difficult to predict its commercial future. However, this new product is a promising building material.

b. Peatwood

Screened Sphagnum is dried, blended with the powdered phenolic resin, and pressed into a heated mold. According to RUEL et al. (1977), the principal advantages of "peatwood" in construction include: 1) attractive texture, 2) good strength (although sensitive to moisture, 3) sawed, nailed, screwed, and glued with ease, 4) quick hardening, 5) light weight (40-60 lb/ft^3), and 6) high rate of continuous production in any shape or form.

c. Other expected materials

Two other new construction materials made from peat are now under study. One, "peatfoam", which is comparable to styroform, is an ultra-light material based on peat moss and foamed resin. The other, "peatcork", is a synthetic cork derived from the coarse fraction of peat (RUEL et al., 1977).
Other uses of peat and importance of peat bogs

Peat is used in the making of Scotch whisky. Sprouted barley malt is put on screens in kilns above a peat and coke fire. The pungent peat smoke permeates the malt, and the aroma persists even through distillation (MILLER, 1981). Several products such as acetic acid, carbonic acid, alcohol, ammonia, nitrates, oils, and waxes, have been obtained from peat, but those substances can be made more economically by other methods, and hence, the virtue of peat for such uses are presently of little importance.

Archeological and paleobotanical importance of peat deposits are well known and are discussed by some authors (MILLER, 1981; RICHARDSON, 1981). The acidic, anaerobic character of peat bogs has been effective in preserving plant parts, remains of animals including man, and archeological materials such as tools, clothes, weapons, jewelry, and boats. By the analytical study of pollen grains and spores in peat deposits, past changes in vegetation and climate in the bog’s vicinity may be traced. Recently BARBER (1981) carried out an extensive study on the peat stratigraphy and climatic change at Bolton Fell Moss, Cumbria, England. He gave detailed descriptions of the peat stratigraphy and also made analyses of plant macrofossils and pollen and obtained radiocarbon dates of the sediments. Results of this study establish a close relation between peat stratigraphy and climatic changes during the past 2,000 years. He has found several interesting facts, for example, that Sphagnum imbricatum was dominant in periods of warm, dry summers, whereas it disappeared under wetter and/or cooler conditions. The well-known theory of cyclic regeneration of hummocks and hollows during bog growth was rejected as a conclusion of his study.

In some countries, e.g., Japan, peat deposits occur in only limited areas, and many peat bogs, especially those located on mountains, are appreciated by tourists because of their spacious landscape with unique vegetational and floral aspects. Ozegahara and Yashimagahara moors in central Japan are famous raised bogs that are favored with excellent scenic
beauty and attract a great many visitors (HORIKAWA et al., 1967).


7. BRYOPHYTES AS FLOOD- AND EROSION CONTROLLERS AND AS SEED BEDS FOR HIGHER PLANTS

It has been widely recognized that bryophyte carpets on the forest floor and on tree trunks aid in moisture conservation and flood prevention. Many species of bryophytes have special features that enable water to be absorbed and retained. Experiments of HORIKAWA (1952) show that some bryophytes absorb from 3.2 to 12 times as much water as the weight of the dried plants. For example, water absorption (weight when wet/weight when dry) was 12.0 in Haplomitrium mnioides, 9.8 in Hylocomium cavifolium, 6.7 in Plagiomnium maximovii, 4.0 in Bazzania pompeana, and 3.2 in Trachymnium micropyllla. In comparison absorption by dead leaves of conifer trees, Cryptomeria japonica and Pinus densiflora, was only 1.9 and 1.7, respectively.

The delicate green web of protonemata and tufts or mats of bryophytes covering exposed ground such as bare banks and sand dunes are quite effective in preventing soil erosion (WELCH, 1948). CONRAD (1935) reported that Barbula unguiculata, Weissia controversa, and Bryum sp. were pioneers on new road banks and valuable in erosion control in Iowa. WHITEHOUSE and McALLISTER (1954) stated that Atrichum zanthopelma and other species of Atrichum, and Pogonatum brachyphyllum, which are widespread in Texas on sandy or clayey banks, aid in preventing soil erosion. The same situation was described by ANDO (1957) for Japanese species of bank-growing bryophytes, such as Atrichum undulatum, Pogonatum inflexum, Trematodon drepanellus, Pohlia flexuosa, Nardia assamica, and Blasia pusilla.
RICHARDS (1929) presented some notes on the colonization of coastal sand dunes at Blakeney Point, Norfolk, England. The common pioneers recognized there were *Bryum pendulum*, *Tortula ruraliformis*, *Ceratodon purpureus*, *Brachythecium albicans*, and *Camptotheceum lutescens*. *Tortula ruraliformis* was most abundant and formed a close and effective covering on the surface of the dunes. LEACH (1931) reported the importance of *Polytrichum piliferum* and *P. juniperinum* as a binder of unstable sand in the British Isles. These species, which are both first colonizers of sand, produce tough long underground "stems", and from these rhizome-like shoots numerous soil-binding rhizoids spring. Sand on plants of *P. piliferum* induces abundant development of rhizoids on apical shoots and also causes prolific branching. The species is thus able to survive being buried by wind-blown sand and thereby also effectively maintains its soil-binding capacity. MARSH and KOERNER (1972) studied a role of *P. piliferum* in stabilizing sand slopes along the shore of Lake Superior, Michigan.

GIMINGHAM (1948) observed the role of *Barbula fallax* and *Bryum pendulum* as colonizers and surface stabilizers of a sand dune at Luskentyre on the west coast of the Isle of Harris, Outer Hebrides, Scotland. Shoots of *B. fallax* grow sympodially with a regular periodicity, and rhizoids, which are produced abundantly on below-ground stems, bind together sand particles and further interweave with rhizoids of other shoots keeping the whole cushion compact and difficult to detach from soil. Stabilization of soil erosion-faces is insured by such patterns of growth. Shoots of *Bryum pendulum* buried by blown sand elongate rapidly without producing leaves until at the new sand surface innovations with leaves are formed. Abundant rhizoids develop from the leafless parts of stems just below leafy regions. Plant of *B. pendulum* can thereby maintain themselves in regions of moving sand in the young dunes. BIRSE et al. (1957) studied the effects of burial by sand on dune mosses in Scotland. First colonizers of mobile dunes were *Bryum pendulum*, *Tortula ruraliformis*, and *Ceratodon purpureus*. These mosses have the ability to grow up through the sand deposited on them and to re-establish a moss colony on re-emergence. JOHNSON
(1962) noted that Rhacelopus pilifer is a sand-binding moss on the east coast of Malaya.

STUDLAR (1980) studied trampling effects on bryophytes by trail surveys and experiments at a site near Mountain Lake, Virginia, U.S.A. She recognized that trample-resistant structural features and high generative abilities of some bryophytes contribute to their importance as potential inhibitors of soil erosion. For example, even after 4,200 passages over 28 days, Ditrichum pallidum showed little damage—the small shoots were evidently cushioned by each other and by burial in the soil. After trampling ended, secondary protonemata and shoot-buds were produced from stems and leaves of intact plants and shoot fragments.

As suggested by CONRAD (1935) and BAYFIELD (1976), it is practical to sow spores and vegetative fragments of some species of bryophytes on bare areas where erosion is likely to occur. We further note that submerged bryophytes also serve as erosion controllers.

Aquatic mosses such as Hygrohypnum, Brachytheoium, and Amblystegium, which clothe stones and soil along the bed and banks of streams, are often densely packed with sand and soil trapped from flowing water (GROUT, 1912).

It has long been known that bryophytes are in many cases important at early stages of vegetational succession. Their contributions to the formation of soil and to the preparation of habitats favorable to the growth of higher plants are of great value to man (WELCH, 1948). STARK, as early as in 1854, stated in reference to the sequence of vegetational change, "The first vegetation that appears on new building evidencing itself by green stains, on recently raised reefs, and on volcanic ashes, is composed chiefly of the young coniferous shoots of Mosses; and when these have by their decay prepared a small film of vegetable mould, they yield their place to plants of more complicated structure, till at length trees of colossal growth cover what was once a barren waste. This fact alone shows their vast importance in the economy of nature." DEBRECZY (1969) reported
the important role played by bryophytes in the vegetational succession at places near Balatonoberland, Hungary.

Moss carpets, probably owing to their water retentive ability, play an important part as seed beds for flowering plants (RICHARDS, 1932). NICHOLS (1918d) noted that in northern Cape Breton Island, Nova Scotia, Canada, seeds of a pioneer-tree of pastures, *Picea glauca* germinates most prolifically in carpets of *Polytrichum*. According to CRUM (1972), old logs matted with mosses, such as *Drepanoclados uncinatus* and *Hypnum imponens*, are important in the establishment of seedlings and establishment of *Tsuga canadensis* and *Betula alleghaniensis* in the beech-maple-yellow birch-hemlock upland of the Great Lakes Forest Formation. CROSS (1981) observed in the Killarney oak-woods of southeastern Ireland that seeds of *Rhododendron ponticum* germinated almost exclusively in bryophyte beds. According to RICHARDS (1950; quoted from THIERET, 1954), terrestrial mosses are important in keeping soil in the most favorable condition for the growth of trees. In parts of Germany removal of mosses from forest floors has had an ill effect on tree growth. ORLOVA (1977), in a survey of Murmansk conifer species, found that the moss cover affected the survival of spruce seedlings.

While many studies have supported the importance of bryophytes as seed beds for higher plants, allelopathic interactions evidently occur between some bryophytes and other plants. Because of this relationship, the growth of seedlings of some tree species seem to be inhibited by certain bryophytes. This matter will be treated further in Section 10.

Very recently SLACK (1983) presented an appealing paper entitled as "Ecological importance of lichens and bryophytes: what happens if they disappear?" at the joint meeting of the Botanical Society of America and the Canadian Botanical Society, August 1983, at Grand Forks, North Dakota. She states, "Lichens and bryophytes have recently been shown to play a wide variety of roles in diverse ecosystems. In addition to their traditional role as pioneers in soil formation, soil retention, and colonization of difficult habitats not open to
other groups, recent research had elucidated their important roles in nitrogen fixation, nutrient cycling, and in the food chain of mammals." We here stress again the importance of bryophytes in the economy of nature, which also relates with human existence, and ask as Slack did, "What happens if they disappear?"

8. BRYOPHYTES AS ROCK- AND MINERAL BUILDERS

The important role played by bryophytes in the deposition of travertine (tufa) is well known and is reviewed by Richards (1932), Thieret (1956), and Richardson (1981). Travertine, a word that is from the ancient name for Tivoli, Italy, where there are large deposits of it, is a porous rock of calcium carbonate deposited from calcareous water. Since it has an attractive texture and is easily worked, it is much used for the interior decoration of buildings and for exteriors in tropical regions where there is no frost. It is called calcareous tufa when soft (The Encyclopedia Americana, Vol. 27, pp. 19-21, 1963 Edition).

As far back as 1864, Cohn (quoted from Thieret, 1956) studied the deposition of travertine in Tivoli and found that aquatic plants such as Chara and various algae and mosses growing in waters rich in calcium bicarbonate became encrusted with calcium carbonate. This was attributed to the activity of the plants, which in fixing carbon dioxide, brought about the precipitation of insoluble calcium carbonate. Emig (1918), who reported travertine formation in Oklahoma, also states that the mosses act only indirectly in the precipitation of calcium carbonate, principally by supplying a large surface area for the evaporation of calcareous water. In the temperate areas of Europe and North America, the chief tufa-forming bryophytes include the following species (Emig, 1918; Taylor, 1919; Richards, 1932; Flowers, 1933; Thieret, 1956): Fissidens fontanus, Hymenostylium recurvirostre, Didymodon tophaceus, Distichium capillaceum, Mniobryum albicans, Bryum pseudotreptorum, Philonotis calloarea, Eucladium verticillatum, Cratoneuron commutatum, C. .filicinum, Brachythecium rivulare, Cteni-
diurn mollusca, Hypnum revolution, Pellia fabbrioniana, and on a very small scale, Lophoria turbinata and Conocephalum conicum.

LA TOUCHE (1913) reported a very remarkable case of tufa formation observed in the Northern Shan States, Burma. There, a moss was involved in the development of a series of natural weirs across a river, which were from a few centimeters to more than 2 m high. The growth of the tufa-weirs was most active at the downstream edges where the condition seemed to be most favorable for the growth of moss. According to RICHARDS (1932), the moss was identified by Dixon as Barbula inflexa (= Hydrogonium inflexum).

It has been known that plants, particularly living bryophytes, play an important role in iron-ore deposition. TAYLOR (1919) found at springs in Otis, Indiana, and New Lenox, Illinois, that iron compounds in water penetrated the tissue of Brachythecium rivulare, which was abundant in the outlet of the springs, with the result that porous bog iron-ore formed. SHIIKAWA (1956, 1959, 1960, 1962) reported that Jungermannia vulcanicola, Sphagnum, and Polytrichum growing in mineral spring-water in northern Japan (northeast Honshu and Hokkaido) acted as effective depositors of limonitic iron-ore. Concerning limonitization by bryophytes, SHIIKAWA (1960, 1962) gave the following information.

1) Bedded limonitic iron-ores having a bryophytic pseudomorphic texture are commonly found in limonite deposits.

2) Bryophyte plants are limonitized from their basal parts upward, and precipitates composed of the ferric hydroxide show impressions of bryophyte structure. By microscopic observation, it is clear that limonitization has developed from the margin of both stems and leaves toward the interior, and tissues have been replaced by limonitic material.

3) The thickness of limonitic precipitates is 2-4 cm per year, and it is controlled by the growth rate of the bryophyte plants.

IJIRI and MINATO (1965) state that because Japan is poor in re-
sources of iron-ore, a plan was once considered to produce limonite ore artificially by the action of bryophytes cultivated in fields near ferruginous springs.

9. USES AS BIOINDICATORS

Interest in the value of bryophytes as environmental indicators has gradually increased during last 30 years, and at present it is not easy to keep up with the constant stream of published papers. As this important topic is reviewed by H. MUHLE in a separate chapter in this volume, we only give a general account of world studies; critical review is limited to the Japanese literature, which is mostly unavailable to foreign researchers. We also refer to some Chinese reports.

A. GENERAL VIEW OF STUDIES

(1) As ecological indicators

Most bryophytes have a sharply defined and rather narrow ecological ranges. This gives them great value as indicators of certain habitat conditions, probably greater than that of most flowering plants (RICHARDS, 1932), a fact confirmed by many studies. For example, BRINKMAN (1929), HÜRMANN (1974), and SIMON (1975) have found that certain bryophytes are fairly good indicators of soil quality in forests; ROMANOVA (1965), JEGLUM (1971), and PAKARINEN (1979) evaluated the indicator value of bryophytes for conditions of pH and water-levels in peatlands; BELL and LODGE (1963) showed that the occurrence of certain aquatic mosses was generally correlated with calcium or nutrient content in the water.

CAJANDER (1926), in his famous theory of forest types in Finland, used terrestrial bryophytes as one of the characterizing plants in classifying forest types. POSPÍŠIL (1975) reported the ecological significance of the mosses Pterogonium subsessile and P. ovatum as indicators of climatic sections in Czechoslovakia. Recently PIIPPO (1982) reported that certain
epiphytic bryophytes show a change from trees to rocks with increasing latitude, the area of their occurrence on trees depending on their climatic requirements. SJÖGREN (1975), who studied bryophytes as indicators of environmental factors in forests on the Island of Öland, states, "the preference of small annual bryophytes for particular pH, lime content, amount of sand or clay in fields, allows a short cut to a rough initial determination of fitness of a land for various crops."

(2) As paleoecological indicators

Paleoecologists should never ignore fossil bryophytes in sediments, since they are invaluable indicators of past flora, vegetation, and environment (BIRKS, 1982). Fossil mosses from Quaternary sediments, which are mostly assigned to extant species, are especially promising subjects for paleoecological studies. They provide information on small-scale communities and a way to assess in some detail edaphic conditions of the past (MILLER, 1980a). Studies and/or reviews on this problem have been made, in North America, by NICHOLS (1969), MILLER (1980a, b), and JANSSENS (1981, 1983), and, in Europe, by KIRK and GODWIN (1963), DICKSON (1973), and BIRKS (1982).

(3) As indicators of mineral deposits

Bryophytes, which are mostly perennial, concentrate many elements greatly in excess of the concentration in their soil or other substrate. Therefore, analyses of them may be more reliable indicators of the occurrence of minerals than are direct analyses of their substrate or surrounding water (SHACKLETTE & ERDMAN, 1982). For such geochemical evaluation, the potential value of bryophytes is higher than that of vascular plants (SEAWARD & BYLIŃSKA, 1980). Representative articles treating bryophytes as a guide to mineralisation are SHACKLETTE (1965a,b), WHITEHEAD and Brooks (1969), BROOKS (1972a), GIRLING et al. (1978), RICHARDSON et al. (1979), and SHACKLETTE and ERDMAN (1982). Contributions by LOUNAMAS (1956), MALYUGA (1964), BROOKS (1972b), and KOVALENSKII (1979) include a number of references
on the use of mosses in biogeochemical exploration. Many of these studies are concerned with prospecting for uranium.

Certain species of bryophytes are known to be closely associated with particular mineral deposits. The most remarkable example is that of the "copper mosses". These mosses are found on copper-bearing rocks or soils, but they also occur on ores of zinc, iron and lead which exist as sulfides, as well as at sulfur springs, and therefore, SCHATZ (1955) suggested that the term "sulphur mosses" might be more appropriate. The "copper mosses" (e.g., Cephaloziella massalongoi, Gymnoolea acutiloba, Mielichhoferia elongata, M. mielichhoferi, Soopophila ligulata) were discussed by PERSSON (1956), SHACKLETTE (1967), WILKINS (1977), and several other authors. BROWN (1982) critically reviews the literature on mineral nutrition in bryophytes, including a consideration of the value of bryophytes in biogeochemical prospecting.

(4) As indicators of water pollution

The potential use of aquatic bryophytes as indicators of the degree of water pollution is promising, although studies so far are fewer than those concerned with air pollution. Observations and discussions on this subject were made by EMPAIN (1973, 1978, KIRCHMANN and LAMBINOM (1973), FRAHM (1974), AVENA et al. (1975), McLEAN and JONES (1975), BENSON-EVANS and WILLIAMS (1976), WATTEZ (1976), BURTON and PETERSON (1979), LODENIUS (1980), SAY et al. (1981), SAY and WHITTON (1983), WEHR and WHITTON (1983a, b), and numerous others.

(5) As indicators of air pollution

It is well known that certain species of higher plants and many non-vascular plants, such as bryophytes and lichens, are very susceptible to gaseous and particulate air pollutants, and these plants can be used both to indicate the presence of air pollutants and to monitor concentrations of the pollutants (MANNING & FEDER, 1980). Bryophytes are especially useful in
this respect, and this is due to the following structural and ecological characteristics: 1) many species have a vast geographical distribution and grow in various habitats, 2) they have no epidermis and cuticle, 3) they usually obtain minerals from precipitation and dry deposition over the whole plant body, 4) some species (e.g., Hylocomium splendens) have layered habit and grow annually in distinct segments, 5) transport of minerals between the segments is very poor due to the lack of vascular tissue, 6) the accumulate metals unselectively in a passive way acting as ion exchangers, 7) they are mostly evergreen-perennial and can be sampled throughout the year, and 8) the treatment of material for chemical analyses is easy. "The First European Congress on the Influence of Air Pollution on Plants and Animals" held at Wageningen 1968 rightly resolved that cryptogamic epiphytes should be strongly recommended for general use as biological indicators, because they are so easy to handle and they show a vast range of specific sensitivity to air pollutants greatly exceeding that of most higher plants" (RAO, 1982).

Many papers have recently been published on such topics as: the effect of air pollution on bryophytes, element analysis of bryophytes on site and in herbaria, quantitative analysis of flora and mapping of polluted conditions based on bryophytes, and experimental studies by fumigation or transplanting. The literature on bryophytes in relation to air pollution has been reviewed by several authors such as LEBLANC and RAO (1975), RAO et al. (1977), MANNING and FEDER (1980), RICHARDSON (1981), RAO (1982), BROWN (1982), and GRODZINSKA (1982). The collection of summarized articles compiled by MASCHKE (1981) is a useful review of current studies on bryophytes as bioindicators of heavy metal air pollution. It includes representative contributions from the following countries: Sweden, Finland, Norway, Denmark, Poland, Great Britain, Germany, Switzerland, Canada, United Stated of America, and New Zealand.
B. STUDIES IN JAPAN AND CHINA

(1) Aquatic bryophytes

TAKAKI (1976, 1977) investigated aquatic bryophytes in the Katsuragawa river (Gifu Prefecture): Plagiomnium vesicatum, Amblystegium riparium, Bryhnia sublaevifolia, Eurhynochium riparioides, and Vesicularia ferriei were found, and their total coverage decreased gradually from the upper stream toward the midstream and disappeared almost entirely at the downstream. Amblystegium riparium was found to be absent in the upper part of the river with clean water, but began to appear at a station where the river deteriorated due to a polluted tributary that comes from a village. This species seems to be an indicator of more or less polluted water.

SATAKE and his co-workers (SATAKE & UEHIRO, 1982; SATAKE, 1983; SATAKE et al., 1983) analyzed elements of aquatic bryophytes (Jungermannia vulcanicola, Scapania undulata, Fontinalis antipyretica, Amblystegium riparium, Eurhynochium riparioides, and some others) and those in water in which the mosses were growing. They found that aquatic bryophytes are useful in monitoring heavy metal pollution because of their high ability to concentrate the elements. Mercury accumulation by J. vulcanicola and S. undulata was especially noticeable. The main chemical form in J. vulcanicola confirmed by X-ray photoelectron spectroscopy was a sulphur compound(s).

(2) Bryophytes in relation to air pollution and urban edaphic conditions

a. Floristic and phytosociological surveys

Since ANDO and TAODA (1967) reported the flora and ecology of bryophytes in Hiroshima City and discussed the relation between the growth of city-tolerant bryophytes and the urban environment, several authors have investigated bryophyte and lichen communities in relation to air pollution and particular edaphic conditions in urban or industrial areas of Japan.
TAODA (1972) analyzed the condition of epiphytic bryophytes in the Tokyo Metropolis to estimate the extent of atmospheric pollution. The metropolitan area treated was divided into five zones based on the decline in the species number and luxuriance or epiphytic bryophytes: 1) no bryophytes, 2) only a few species resistant to urban environments (e.g., Hypnum yokohamae var. kusatsuense) are rarely found, 3) the same species as those in the second zone and a few additional ones occur more frequently, 4) a greater diversity of species including those found in the suburban area (e.g., Entodon compressus) grow in moderate abundance, 5) several rural species such as Haplohyphnum sieboldii and Frullania muscicola, and some foliose lichens also occur. These five zones were arranged on a map with a geographical reduction corresponding to a decrease of the average concentration of SO₂ from over 0.05 ppm in zone 1 to below 0.01 ppm in zone 5 (Fig. 1). TAODA (1977) made a further study on bryophyte communities, epiphytic, epipetric, and epigeous, in the Tokyo Metropolis and discussed their ecology and distribution in relation to the degree of urbanization associated with air pollution, change of soil property, dryness, and direct human impact such as clearing and trampling.

In other studies on Chiba and neighboring cities along Tokyo Bay, TAODA (1980a) mapped air pollution based on epiphytic bryophytes and also assessed the degree of urbanization by the distribution of three liverworts: Marchantia polymorpha, Lunularia cruciata, and Conocephalum supradecompositum, the last being a species characteristic of more weakly urbanized or rural areas (TAODA, 1980b). NAKAMURA (1976) assessed the degree of urbanization by a different method in the same region: he first selected seven areas of different vegetation cover and cultural function and then analyzed the species number, abundance, growth form, and substrate type of bryophytes observed in each area. He was able to classify the region treated into four zones according to the urbanization level indicated by differences in the growth form and substrate requirement of the bryophytes.

UMEZU (1978) conducted a study of epiphytic bryophyte and lichen communities in evergreen broad-leaved forests scattered
Fig. 1. Maps showing the extent of air pollution in the Tokyo Metropolis.
1. Map based on $SO_2$ concentration. A and B, and a, b, ..., and 1 show the weather stations and air pollution observatories, respectively. 2. Map based on epiphytic bryophyte communities. For zones I-V, see the text. (TAODA, 1972).
in the Ube heavy-industrial region, western Honshu. The degree of naturalness estimated by the floral composition and coverage of epiphytic communities observed at 52 sites was classified into five grades, and their distribution pattern was compared with SO$_2$ levels recorded in the region. MITSUGI et al. (1978) using IAP values [Index of atmospheric purity determined on the basis of number, frequency-coverage and resistance factor of species (LEBLANC & DE SLOOVER, 1970)], examined the relation between air pollutants and epiphytic bryophyte and lichen communities in the eastern Harima industrial region of Hyogo Prefecture. A map based on the IAP values calculated at 59 sites was generally comparable with SO$_2$ isopleths. They also found the concentration of SO$_2$ and soluble matter in rain water had combined effects on epiphytic communities, the latter being more highly influential than the former. NARAGAWA et al. (1977) made a map of epiphytic communities according to their IAP values in Akoh City, Hyogo Prefecture, and compared it with a SO$_2$-isopleth pattern.

NEHIRA and UNE (1980, 1981), who investigated epiphytic communities of bryophytes in urban environments of Fukuyama and Hiroshima Cities, divided the respective areas into three urbanization zones based on floral composition and abundance of the bryophytes (Fig. 2). In the first zone epiphytic bryophytes were not found; in the second zone species preferring or withstanding the urban environment, such as Ventureilla sinensis, Fabronia matsumurae, and Frullania musoicola, Occurred; and in the third zone those characteristic of less-urbanized areas, e.g., Orthotrichum consobrium, Macromitrium japonicum, and Trocholejeunea sandviaensis, were observed in addition. NAKAMURA & IWATSUKI (1981) studied epiphytic bryophytes on trees of Cinnamomum camphora in and around Miyazaki City, southern Kyushu, with a population of about 250,000. Their study demonstrated that the quantity of bryophytes was largely affected by conditions such as age of trees, moisture, and light, but the floristic composition seemed to be more highly influenced by the degree of air pollution.

In some studies air pollution was assessed by the phytosociologically classified units of bryophyte communities. NAKANISHI
Fig. 2. Division of the urban area of Hiroshima City based on the floral aspect of epiphytic bryophytes. Closed or open symbols (classified by the number of bryophyte species) show the stands investigated. Areas of woody hills (surrounded by hatched lines) were excluded from the observation. 1: Hiroshima Station; 2, 3, 5, and 6: Parks; 4: Parts of the Peace Memorial Avenue (100 m broad) with planted belts. (NEHIRA & UNE, 1981).

and SUZUKI (1977) studied the bryophyte vegetation occurring on concrete blocks, granite stone walls, and soil in Hiroshima City and discussed the distribution of the 12 communities recognized in relation to the degree of urbanization and substrate conditions. NAKANISHI (1979) has analyzed the pollution-induced phytosociological changes of epiphytic communities in Kobe City. He recognized the following four epiphytic communities based on the data from 245 samples at 147 sites:

1) Sematophyllum pulchellum community (21 species total, 3 on average; characteristic to the inner struggle zone), 2) Fabronia matsumurae community (35 total, 6 on average; outer struggle zone), 3) Parmelia tinctorum community (41 total, 7 on average; quasi-normal zone), and 4) Parmelia caperata community (85 total, 11 on average; normal zone). He discussed the relationships between the distribution of these communities, IAP values (see LEBLAND & DE SLOOVER, 1970), and SO₂ levels.

The epiphytic vegetation of Ohtu City, located along the coast
of the Lake Biwa, east of Kyoto, was investigated phytosociologically by TAODA et al. (1981) who recognized three communities: 1) Hypnum yokohamae var. kusatsuense-Parmelia tinctorum community, 2) Hypnum yokohamae var. kusatsuense-Brothera leana community, and 3) Fabronia matsumurae-Frullania musciola community, each of which is further subdivided into two or three types. The distribution, succession and retrogression of these communities were discussed with reference to air pollution.

Environmental sciences have recently developed in China and the role of bryophytes is valued in monitoring air pollution. WU and LOU (1981) first introduced theories and methods in this field of study. LI and GAO (1981) investigated bryophytes growing in Shanghai, the most urbanized city of China, and showed that the development of bryophyte communities has been greatly influenced by air pollution. Some species were known to have disappeared due to air contamination; for example, Venturiella sinensis, which is an epiphytic moss described from Shanghai, has vanished from its type locality.

b. Monitoring by means of a bryometer

TAODA (1973a) has contrived a "bryometer", which is a small-sized, handy instrument for measuring phytotoxic air pollution. It consists of an air pump and a pair of growth chambers (ca. 55 cm³ each) made of transparent plastic for bryophytes to be tested. The air supplied to one chamber is purified by an activated-carbon filter, while that to the other chamber is not filtered. A pilot survey using this instrument in the Tokyo Metropolis with five moss- and one liverwort species was found to be reasonably effective in evaluating air pollution. Later TAODA (1976b) employed it to monitor air pollutants emitted from the petroleum chemical plants in Ichihara City, southeast of Tokyo. He suggested that gemmae of Marchantia polymorpha were suitable as test material for the bryometer.

YOKOBORI (1978) studied the degree of air pollution in and around the Kashima industrial area about 90 km east of Tokyo using bryometers established at nine sites in that area. The
effect of air pollutants was expressed by the growth ratio (un-filtered/filtered, in percentage) of gemmae of *Marchantia polymorpha* cultivated in the chambers. Degrees of aerial phyto-toxicity estimated by the growth ratio of gemmae during one week (repeated four times) showed a close correlation to the extent of pH values and electrical conductivity of rain water determined at each site. He further compared the bryometer tests to the concentration (means of daily maximum and their total) of four gaseous pollutants: SO$_2$, oxidant, NO and NO$_2$, measured at five autometer stations, and concluded that the degree of aerial phytotoxicity can be easily and conveniently estimated by means of the bryometer. An additional survey by the same method was subsequently carried out by YOKOBORI and TAODA (1980) in the same industrial area, achieving results which further support the usefulness of the bryometer.

The reasons for reduced occurrence or extinction of epiphytic bryophytes in heavily polluted areas must be considered not only for adult plants but also for early stages such as sporelings and protonemata. MITSUGI and NAKAGAWA (1982) have made some improvements in the structure and function of TAODA's bryometer and observed the effect of air pollutants on spore germination and the growth of protonemata by using the reformed bryometer.

c. Experimental studies in the laboratory

TAODA (1973b) made fumigation experiments to examine the effect of SO$_2$ on bryophytes. Most of the bryophytes treated (16 species collected from tree-trunks and 3 from concrete) were injured or killed by exposure to 0.8 ppm SO$_2$ for 10-40 hours (5-7 hours a day) or by 0.4 ppm for 20-80 hours. At 0.2 ppm for about 100 hours, acute injury, such as decoloration of shoots, did not occur, but chronic injury (poor growth of new shoots) was observed. Tolerance for SO$_2$ was higher in species more commonly found in urban areas (e.g., *Glyphomitrium humilium*, *Hypnum yokohamae var. kusatsuense*), while those of lower tolerance included rural species (e.g., *Orthotrichum consobrium* and *Schwetschkea matsumurae*), although some exceptions were
detected. It is noteworthy that *Bryum argenteum* which is a typical "weed" found frequently in city centers and considered toxitolerant, was very sensitive to SO$_2$ in samples tested either from bark or from concrete. He further observed that bryophytes in dry conditions were more tolerant to SO$_2$ than those in wet conditions. TAODA's study also shows that the toxicity of H$_2$SO$_3$ is stronger than H$_2$SO$_4$ at the same pH.

TAODA (1975, 1976a) assessed the chemical characters of soils associated with urbanization by CLEMENTS and GOLDSMITH's (1925) method of control phytometer. In this study he employed a pair of bryophytes showing a distinct contrast in ecological requirement, *Marchantia polymorpha*, a typical urban nitrophilous liverwort, and *Pogonatum akitense* which occurs on non-basic soils in rural and mountain environments. Gemmae of *Marchantia* and protonemata of *Pogonatum* were cultivated in aqueous extracts of several soils, which varied in pH and electrical conductivity, collected from different sites in and outside the cities of Tokyo and Nagoya. The growth rate of the gemmae and protonemata were compared with changes of pH values and electrical conductivity of soil extract. Correlations (positive in *Marchantia* gemmae and negative in *Pogonatum* protonemata) where shown between the growth of the tested plants and the increase of urbanization demonstrated by soil characters, namely, the rise of both pH values and electrical conductivity of soil extract. MITSUGI et al. (1982) demonstrated that the bioassay of spore germination and protonemal growth in urban epiphytic species such as *Fabronia matsumurae* and *Venturiella sinensis* cultured on the agar medium with rain water added is a sensitive indicator for evaluating air pollutants.

TAKAOKI and MITANI (1982) contrived a simple phial instrument useful for SO$_2$ fumigation of bryophytes and lichens, and used this to study the effect of SO$_2$ on the rate of photosynthesis and respiration in thalli of *Marchantia polymorpha*, *Conocephalum conicum*, and *Parmelia tinctorum* (MITANI & TAKAOKI, 1982, 1983). Their studies showed that *Parmelia tinctorum* was most sensitive to SO$_2$ and that *Conocephalum conicum* was more resistant than *Marchantia polymorpha*, although it is less frequent
in urban areas than *Marchantia*. It was known that the injury was more extensive in samples fumigated in the light than those in the dark. They also observed that chlorophyll degradation occurred more gradually than the decline of photosynthesis, namely, the visible symptoms of injury appeared later than invisible damage.

10. BIOLOGICALLY-ACTIVE SUBSTANCES FROM BRYOPHYTES

It is generally known that bryophytes, even herbarium specimens, are hardly ever attacked by micro-organisms and insects. In addition, many bryophyte species have their own particular odors and tastes; furthermore, certain bryophytes have been used for medicinal purposes (see Section 5). These bryophyte characteristics may be attributed to chemical constituents inherent in their structures. However, although preliminary chemical investigations on oil bodies of liverworts were done at the beginning of this century (LOHMANN, 1903; MÜLLER, 1905), detailed studies were neglected until about 20 years ago because of difficulty in collecting sufficient pure material from a single species. Development of analytical equipment and methods for isolation and determination of the structure of chemical constituents accelerated in the 1960s. Since then many important organic compounds have been isolated from a wide variety of plants, including bryophytes, to clarify their structures and biological roles.

Several groups or researchers (BENDZ et al., 1962; HUNECK, 1963; MARSILI & MORELLI; 1968; HAYASHI et al., 1969; BENEŠOVÁ et al., 1969; KNOCHE et al., 1969; VALIO et al., 1969; MARKHAM et al., 1969) undertook interesting phytochemical investigations on the secondary metabolites of bryophytes, using these advanced techniques. Subsequently, investigation of chemical constituents of bryophytes, especially lipophilic compounds, has been advanced by new research groups (SUIRE, 1970; PRYCE, 1971a; KARUNEN, 1971; CONNOLLY et al., 1972; ANDERSEN et al., 1973; MUES & ZINSMEISTER, 1973; ASAKAWA et al., 1975). At the present time, phytochemical investigations are being carried
out mainly in two areas: one is on the chemical structure and biogenesis of the constituents of bryophytes with respect of the phylogenetic relationships among bryophytes or between bryophytes and other plants; the other is to obtain biologically-active substances effective on bryophytes themselves, as well as other kinds of plants and to animals including man.

In this section our review is of studies on the biologically-active substances produced by bryophytes in the following six categories: 1) fragrant odors and particular tastes, 2) antimicrobial substances, 3) plant-growth regulators, 4) deterrents to attacks from predators including fish, 5) allergenic contact dermatitis, and 6) anti-tumor and cytotoxic substances. ASAKAWA (1981) reviewed on the same topic, but many important studies have been completed since then, especially in Japan. Biochemical and phytochemical investigations of bryophyte constituents having biological roles have only begun quite recently; in most cases, only a small sample has been used to test these activities because of difficulty of obtaining sufficiently large samples. Most of the reports of various biological roles which suggest the occurrence of active substances have been qualitative rather than quantitative.

Successful methods of cell-suspension culture of bryophytes have recently been devised, and studies on cultured cells are currently being made by several authors (e.g. TAKEDA & KATOH, 1981; OHTA & HIROSE, 1982); biologically-active substances may soon be isolated by these techniques.

Biologically-active substances so far obtained from bryophytes have not yet been put to practical and economically viable use, but their potential usefulness may be fully appreciated. Expectations are high regarding future development of their possible applications as a source of medicinal drugs, together with new discoveries of even more effective substances.
Bryologists have recognized that some bryophyte species have characteristic odors. SCHUSTER (1966) cited LOHMANN's report of the distinctive aroma of some liverworts as follows: Leptolejeunea spp. have an intense and diagnostic odor of licorice; Conocephalum conicum has a very strong, mushroom-like smell; Moerckia spp. possess an intense, unpleasant odor; Riella an anise-like odor; Solenostoma obovatum has a carrot-like odor; Lophozia biorenata has a pleasant odor similar to cedar oil; Lophocolea heterophylla and L. minor possess a rather distinctive mossy smell; Geocalyx graveolens has a turpentine-like odor.

The epiphyllous liverwort Leptolejeunea elliptica has the most striking distinctive fragrant odor, and its occurrence can be easily recognized in the field by its odor. The original substance of the special odor of this liverwort was determined as p-ethyl anisol by spectral evidence and chemical synthesis, and it was obtained in high yield of about 80% (NAKAYAMA et al., 1979). Substances responsible for the characteristic odor of another liverwort, Isotachis japonica, were isolated by MATUSO et al. (1971), which included three aromatic esters, benzyl benzoate, benzyl cinnamate, and β-phenylethyl cinnamate. By using head-space-vapor method, which is widely used in the analysis of fragrant odors in plants, HAYASHI, MATSUO, and their co-workers examined the odors of about 40 species of liverworts: many monoterpenoid hydrocarbons such as α-pinene, β-pinene, camphene, sabinene, myrcene, α-terpinene, limonene, β-phellandrene, γ-terpinene, p-cymene, and terpinolene, and fatty acid methyl esters of low molecular weight were detected from Conocephalum conicum, C. supradeconstitutum, Wiesnerella denudata, Marchantia paleacea, Jungermannia vulcanicola, and others. It was ascertained that the characteristic odor of each liverwort was composed of a mixture of many compounds (HAYASHI et al., 1977).

As to the taste of some liverworts, MIZUTANI (1961) reported that Jamesoniella autumnalis had a taste like that of lilac, Porella vernicosa, even herbarium specimens, was strongly
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pungent, and *Rhodobryum giganteum* had a saccharin-like taste. ASAKAWA and ARATANI (1976) isolated a sesquiterpene dial, polygodial or tadeonal, which had been obtained from *Polygonum hydropiper* (Polygonaceae) (BARNES & LODER, 1962; OHSUKA, 1962), as a characteristic pungent substance present in *Porella vernicosoa*. The same pungent substance was later isolated from certain species of *Porella* closely related to *P. vernicosoa* (ASAKAWA, 1981). Furthermore, ASAKAWA et al. (1977), and ASAKAWA & TAKEMOTO (1978) studied the chemical constituents of *Triohocoleopsis sacculata* and *Pellia endiviifolia* to obtain new pungent substances, sacculatal (1) and its hydroxy derivative. Some sesquiterpenoids having the α-methylene γ-butyrolactone group in the molecules were also isolated as pungent substances from *Chiloscyphus polyanthos*, *Diplophyllum albicans* (ASAKAWA et al., 1979b), and *Wiesnerella denudata* (ASAKAWA et al., 1980a). HUNECK and OVERTON (1971) reported the isolation of the following unknown diterpenoids with a bitter taste: floerkein A and B from *Barbilophozia floerkei*, scarpanin from *Scapania undulata*, and gymnocolin from *Gymnocollea inflata*, structure of the last compound was most recently determined by X-ray analysis (HUNECK et al., 1983).

(2) **Antimicrobial substances (= Antibiotics)**

Bryophytes are almost free from attack by micro-organisms, and herbarium specimens usually need no special treatment against insects and micro-organisms. MADSON and PATES (1952) in a study to discover antimicrobial substances from almost all plant groups reported that aqueous extracts of some bryophytes such as *Sphagnum portoricense*, *S. strictum*, *Conocephalum conicum*, and *Dumortiera hirsuta*, inhibited the growth of the micro-organisms tested (*Candida albicans*, *Pseudomonas aeruginosa*, and *Staphylococcus aureus*). McCLEARY et al. (1960) tested the antibiotic properties of 12 species of mosses, and their results, based on differences of solubility of the active substances to the different solvents, suggested that several kinds of active substances were contained in this plant group. Later, many bryophytes were tested for their antibiotic properties against both gram positive and gram negative organisms (PAVLETIC &
STILINOVIC, 1963; WOLTERS, 1964; GUPTA & SINGH, 1971). McCLEARY and WALKINGTON (1966) found that the most antibiotically-active mosses are in the genera Atrichum, Dicranum, Mnium, Polytrichum, and Sphagnum, and they suggested that the active substances are probably polyphenolic compounds. PRYCE (1972a) reported the antifungal activity (25-100 μg/ml) of an endogenous growth inhibitor, lunularic acid (2). ASAKAWA et al. (1982a) isolated three prenyl bibenzyls from Radula spp. which inhibited the growth of Staphylococcus aureus at concentrations of 20-30 μg/ml.

BANERJEE and SEN (1979) examined the antibiotic activity of 52 species of bryophytes: extracts of each species with water and with several kinds of organic solvents were tested against gram positive and gram negative bacteria and fungi. They suggested, on the basis of solubility data and antibiotic spectra that the occurrence of a variety of antibiotic substances in bryophytes and also that the active substances, which were soluble in methanol, were to be found more frequently in liverworts than in mosses and anthocerotopsids. Interestingly, they found that the degree of antibiotic activity in a given species of bryophyte may depend on its age, the season of its collection, and the ecological niche which it inhabits.

Recently, MATSUO et al. (1982a, 1982b, 1983b) found that a methanol extract of Herberta adunca inhibited the growth of some pathogenic fungi, such as Botrytis cinerea, Phialoconidia, and Pythium debaryanum. Three antifungal substances named (-)-α-herbertenol (3), (-)-β-herbertenol (4), and (-)-α-formylherbertenol (5) were isolated from an extract of this liverwort, together with similar phenol derivatives, and their structures were established by extensive chemical degradation reactions. α-Herbertenol (I₅₀ 25-60 μg/ml) and β-herbertenol (I₅₀ 8-40 μg/ml) showed significant growth-inhibitory activity against the above pathogenic fungi which cause plant diseases. α-Formylherbertenol inhibited the growth of Botrytis cinerea at I₅₀ 15 μg/ml (MATSUO et al., 1982a). They also isolated a new dolabellane diterpenoid, (+)-acetoxyodontoschismenol (6) as an antifungal substance from Odontoschisma denudatum. It inhibited 20-40% of the growth of the above fungi at a concentra-
tion of 100 μg/ml (MATSUO et al., 1983a). ICHIKAWA (1982) and ICHIKAWA et al. (1983) tested the antimicrobial activity of more than 80 species of mosses and discovered that almost all the mosses treated had some antimicrobial activity. They isolated acyclic acetylenic fatty acids and cyclopentenonyl fatty acids, one of which completely inhibited the growth of the fungus causing rice blast, *Pyricularia oryzae*, at a concentration of 1 μg/ml. ISOE (1983) reported weak antibiotic activity by polygodial, a pungent substance contained in certain species of *Porella*.

(3) Plant-growth regulators

The growth of plants is generally regulated by both growth-promoting and growth-inhibiting hormones. One of the growth-inhibiting hormones, abscisic acid, is universally present in higher plants, and other plant hormones, such as auxin, gibberellin, cytokinin, and ethylene, are known to promote the growth of vascular plants.

Independent studies on growth-regulating substances in bryophytes by WILSON and SCHWABE (1964) and FRIES (1964) isolated new endogenous growth inhibitors from *Lunularia cruciata* and *Marchantia polymorpha*, respectively. These compounds proved to be plant hormones, inhibiting the growth and promoting the dormancy of liverworts. VALIO et al. (1969) determined that the structure of the growth-inhibitor lunularic acid (2) isolated from *Lunularia cruciata* was dihydrohydrangeic acid, which had an activity of about 30% inhibiting at a concentration of 10 μg/ml. Later, evidence for the identity of plant-growth inhibitors obtained from these liverworts was reported by HUNECK and PRYCE (1971) and PRYCE (1971a). Lunularic acid is widely distributed in liverworts but does not occur in mosses, hornworts, and algae; it corresponds to abscisic acid, a common growth inhibitor, known in higher plants and algae (PRYCE, 1972b; GORHAM, 1977a). Chemical synthesis of lunularic acid was performed by ARAI et al. (1972), and its growth-inhibitory activity on higher plants was tested by using the *Avena* straight growth test; it inhibited IAA-induced elongation of coleoptile
segments at concentrations of 10-30 μg/ml (ARAI et al., 1973).
GORHAM (1978) examined the growth-inhibitory activity in liver-
wort-gemmaling assays and in the cress-root growth test of this
compound and many other stilbenoid derivatives. The acid was
inhibitory to Marchantia gemmalings at $5 \times 10^{-9} - 10^{-7}$ M/gem-
maling (about 1-25 μg/ml in solution) and inhibited 20% of the
cress root growth at a concentration of $10^{-3}$ M. PRYCE (1971b)
and GORHAM (1977b) studied biogenesis and metabolism of the
endogenous plant hormone, and most recently, OHTA et al. (1983)
isolated an important precursor, prelunularic acid, in the bio-
synthesis of lunularic acid from suspension cultured cells of
Marchantia polymorpha to confirm the biosynthetic pathway.

LARUE and NARAYANASWAMI (1957) and SCHNEIDER and SHARP (1962)
presented evidence for the occurrence of the endogenous growth
regulators in Lunularia cruciata and Tetraphis pellucida, re-
spectively. SCHNEIDER et al. (1967) isolated an endogenous
growth hormone from Marchantia polymorpha and identified it as
indole-3-acetic acid. BEUTELMANN and BAUER (1977) isolated $N^6-
(\Delta^2$-isopentenyl) adenine, a sort of cytokinin, from a culture
medium of callus cells of the moss hybrid Funaria hygrometrica
x Physcomitrium pyriforme; concentration of the compound in
culture medium was determined at ca. $10^{-6}$ M. Occurrence of the
cytokinin in the moss callus had already been suggested by the
same authors (BAUER, 1966; BEUTELMANN, 1973). MUROMTSEV et al.
(1964) suggested the occurrence in mosses of a gibberellin-like
substance, another endogenous hormone.

A type of allelopathy between bryophytes and other plants is
sometimes encountered, which suggests that bryophytes produce
some allomones. GAVRILLOVA (1970) reported that an aqueous ex-
tract of the mosses Polytrichum commune and Sphagnum spp. in-
hibited the growth of Pinus and Picea seedlings, but stimulated
the growth of Larix seedlings. These results show the impor-
tance of moss cover for the development of forest communities.

In fact HUNECK and SCHREIBER (1972) tested the plant-growth
inhibitory activity of five terpenoids, gymnocolin, drimenol,
longiborneol, longifolene, and scapanin, and the endogenous
hormone lunularic acid, all of which were isolated from liverworts (and many lichen substances also) on cress root and oat seedling growth on infiltration into the seed. The terpenoids were found to be growth inhibitors at $10^{-3}$ to $10^{-4}$ M and growth promoters at $10^{-6}$ to $10^{-7}$ M, but lunularic acid showed only a weak effect on the growth of higher plants. BENĚŠOVÁ and HEROUT (1978) reported that an antifeedant substance, pinguisone (7) (BENĚŠOVÁ et al., 1969), which will be described later, and a novel sesquiterpene alcohol, myliol (8) isolated from Mylia taylorii (BENĚŠOVÁ et al., 1971; MATSUO et al., 1976), as well as indole alkaloids, had a high inhibitory effect in the wheat coleoptyle test.

α-Methylene γ-butyrolactone moiety in terpenoids is known as a common active site to many biological activities, such as allergic contact dermatitis and cytotoxicity. It has been reported that various sesquiterpene lactones obtained from liverworts had plant-growth inhibitory effects on the germination and root elongation of rice husk at concentrations of 50-200 μg/ml (ASAKAWA, 1981, 1982). The weak inhibitory effect (100-500 μg/ml) of a sesquiterpene dial, polygodial, and diterpene dials, perrottetinal A (9) and B (10), was also reported by ASAKAWA et al. (1979a).

In the course of investigations of liverwort terpenoids displaying plant-growth-inhibiting properties, MATSUO et al. (1979a, 1979c, 1981a, 1981b) isolated several kinds of active substances from Plagiochila semidecuvrens and P. ovalifolia together with their precursors. Their structures and absolute configurations were determined on the basis of extensive chemical reactions and spectral data to be (+)-ovalifoliene (11), (+)-plagiochiline A (12) (ASAKAWA et al., 1978), (+)-ovalifolienal (13) and their derivatives, (+)-ovalifolienalone, (+)-ovalimethoxy I, (+)-ovalimethoxy II, and (+)-9a-acetoxy-ovalifoliene, which possessed a novel ent-2,3-seco-alloaroma-dendrane skeleton. The plant-growth inhibitory activity of these novel acetyl hemiacetals was tested on rice seedlings and almost all of the compounds were found to inhibit the growth of leaves and roots at concentrations of less than 50 μg/ml. Ovalifoliene (11), plagiochiline A (12), ovalifolienal
(13), ovalimethoxy I, and 9α-acetoxyovalifoliene were very strong growth inhibitors showing 50% growth inhibition ($I_{50}$) at ca. 7, 14, 19, 13, and 12 μg/ml, respectively.

Furthermore, to study the relation between biological activity and chemical structure, the reaction products derived from the main constituent ovalifoliene were tested for biological activity, and it was shown that the inhibitory activity was due to the acetyl hemiacetal moiety. A γ-lactone derivative had almost the similar inhibitory effect as natural inhibitors, but derivatives of a ketone and a γ-lactone promoted the growth of roots at low concentrations (MATSUO et al., 1981d).

From another leafy liverwort, *Lepidosia vitrea*, a methanol extract of which showed plant-growth inhibitory activity, three sesquiterpene aldehydes were isolated. Their structures and absolute configurations were determined as (−)-isobicyclogermacrenal (14), (−)-lepidonzenal (15), and (+)-vitrenal (16) (MATSUO et al., 1979b, 1980b, 1981c), chemical synthesis of the last compound being carried out by MAGARI et al. (1982). These compounds almost completely inhibited the growth of leaves and roots of rice seedlings in concentrations of 50, 250, and 25 μg/ml, respectively (MATSUO et al., 1980a, 1984a, 1984b).

(4) Deterrents to attacks from predators including fish

Although it was known that few bryophytes are fed on by insects and that they may therefore contain antifeedants (substances inhibiting feeding) effective in protection against insect attack, no chemical study of antifeedants in bryophytes appeared until 1971. WADA and MUNAKATA (1971) tested the feeding inhibitory activity of a unique sesquiterpenoid, pinguisone (7) against a polyphagous insect, *Spodoptera littoralis*. The threshold concentration of pinguisone which was isolated from *Aneura pinguis* was 0.25% (BENESOVÁ et al., 1969). A sesquiterpene hemiacetal, plagiochiline A (12) which was commonly distributed in *Flagiochila* (ASAKAWA, 1982) inhibited the feeding of an African worm *Spodoptera exempta* at concentrations
of 1-10 μg/ml (ASAKAWA et al., 1980b), and the compound also proved extremely poisonous to mice (MATSUO, 1983). The pungent sesquiterpenoid polygodial isolated from many species of *Porella* showed antiphagic activity against the same African insect, but it was not a universal antifeedant since the antifeedant level of this compound was not significant when tested against *Manduca sexta* and *Scolioptera Vaga* (KUBO et al., 1976). ASAKAWA (1981) reported that crude bitter principles obtained from *Gymnoaolea inflata* and *Jamesoniella autumnalis* had intense antiphagic activity against *Spodoptera* spp. Recently, GERSON (1982) reviewed interesting interactions between bryophytes and invertebrates.

KANASAKI and OHTA (1976) isolated a piscicidal component from *Marchantia polymorpha*. The active compound was identified as the sesquiterpene lactone (+)-costunolide whose piscicidal activity was TLM 2 μg/ml against kelle-fish (*Oryzia latipes*). Other sesquiterpene lactones, diplophyllin (17) and frullanolide (18), which will be described later, also had a piscicidal activity on the same fish (ASAKAWA et al., 1983).

(5) Allergenic contact dermatitis

It has been known that workers in the forest industries of France and Canada often suffer from allergenic contact dermatitis caused by certain chemical constituents of the epiphytic liverworts *Frullania* and *Radula* (KNOCHE et al., 1969; MITCHELL et al., 1969). KNOCHE et al. (1969) isolated a new sesquiterpenoid named (-)-frullanolide (18) from *Frullania tamarisci* and recognized it as an allergen causing allergenic contact dermatitis. Its structure was determined by chemical and spectral evidence to be eudesmanolide containing α-methylene γ-butyrolactone. An enantiomeric compound, (+)-frullanolide, which also had allergenic potential, was obtained from *Frullania dilatata*.

Alternatively, MITCHELL et al. (1970) reported that the results of patch test reactions in 12 species of *Frullania* were positive except for one species (*F. squarrosa*), and they iso-
Fig. 3. Biologically-active compounds isolated from bryophytes.
lated the known frullanolide from *F. nisquallensis*, the commonest species in British Columbia. They also reported that the positive patch test reactions were also recognized in some species of the family Compositae. To discover the cause of such dermatitis, MITCHELL and DUPUIS (1971), an MITCHELL et al. (1972) carried out extensive allergenic examinations of more than 100 kinds of sesquiterpenoids obtained from a wide variety of plants, especially the Compositae. They established that the immunochemical requisite of the molecular structure of the active compounds depended upon the presence of α-methylene γ-lactone moiety.

Besides the frullanolide described above, three other sesquiterpene lactone, (−)-oxyfrullanolide (19), (−)-cis-β-cyclostunolide (20), and (−)-eremofrullanolide (21), were isolated as allergens from *Frullania dilatata* (ASAKAWA et al., 1976). ASAKAWA (1981) described that "allergenic intensities between (−)-frullanolide (18) and its optical enantiomer, between (+)-epoxyfrullanolide and its enantiomer, were almost the same, indicating no chiral specificity against the allergenic activity." Many other kinds of sesquiterpenoids containing α-methylene γ-butyrolactone were isolated from several species of liverworts (ASAKAWA, 1981, 1982), most of which had already been isolated from higher plants and their allergenic activities had been tested (MITCHELL et al., 1971, 1972).

(6) *Anti-tumor and cytotoxic substances*

Since cancer-prevention studies are one of the most important subjects in modern natural sciences, many workers have tried to search for anticancer agents derived from natural sources. BELKIN et al. (1952-1953) tested many plant materials for any necrotizing capacity against Sarcoma 37 implanted in CAF1 mice, and found that the extracts, both with alcohol and with acid, of *Polytrichum juniperinum* produced gross and histologically demonstrable damage. Plant extracts exhibiting anti-tumor (actineoplastic) activity have received considerable attention, particularly in the last decade, and many sesquiterpenoids having α-methylene γ-butyrolactone as a partial structure were
evaluated for their growth-inhibitory potential against numerous models (e.g., HARTWELL & ABBOTT, 1969; KUPCHAN et al., 1971). The sesquiterpenoids costunolide and tulipinolide, which showed a reproducible inhibitory activity against the cell culture (KB) of human carcinoma of the nasopharynx, were isolated from the alcohol extract of *Liriodendron tulipifera* (Magnoliaceae) (DOSKOTCH & EL-FERALY, 1969). Zaluzanin, a sesquiterpene lactone, having inhibitory activity toward the P-388 lymphocytic leukemia test system, was obtained from the ethanol extract of *Zaluzania robinsonii* (Compositae; JOLAD et al., 1974). The above three sesquiterpenoids were later isolated from several liverworts (ASAKAWA, 1981, 1982): costunolide from *Conocephalum supra-decompositum*, *Frullania tamarisci*, *F. monocera*, *Marchantia polymorpha*, *Porella japonica*, and *Wiesnerella denudata*, and tulipinolide and zaluzanin C from *Conocephalum conicum* and *Wiesnerella denudata*.

In the first report on anti-tumor or cytotoxic active compounds of bryophytes, OHTA et al. (1977) isolated a new ent-eudesmanolide, diplophyllin (17), from *Diplophyllum albicans* and *D. taxifolium*. Diplophyllin, having α-methylene γ-lactone unit, showed significant activity (ED$_{50}$ 4-16 µg/ml) against human epidermoid carcinoma (KB cell culture). Its optical enantiomer, derived chemically from the compound isoanantolactone, also exhibited anticancer activity (ED$_{50}$ 20-37 µg/ml), but this was less than that of the natural diplophyllin. This result is the first demonstration of optical selectivity for this type of cytotoxicity.

Most recently, ASAKAWA et al. (1982b) presented the results of a study on cytotoxicity against the KB cell of the cyclic bisbibenzyl and acyclic bisbibenzyl derivatives obtained from liverworts: marchantin A (22) isolated from *Marchantia polymorpha*, *M. paleacea* var. *diptera*, and *M. tosana*, riccardin A (23) and B (24) from *Riccardia multifida*, and perrottetin E (25) from *Radula perrottetii*. The structures of these bisbibenzyl compounds were established by a combination of chemical and spectral evidence and the result of X-ray analysis. These bisbibenzyls (22), (23), (24), and (25) showed cytotoxicity against the KB cell at ED$_{50}$ 8.4, 10, 10, and 12.5 µg/ml,
respectively. They also reported that plagiochiline A (12) isolated from Plagiochila spp., a pinguinane sesquiterpene alcohol and a monoterpane ether obtained from Trocholejeunea sandvicenise also showed cytotoxicity against the KB cell (\( E_{50} \) 3, 12.5, and 12.5 \( \mu g/ml \), respectively).

11. OTHER TOPICS

Uses of bryophytes by animals other than man were reviewed by Richardson (1981) in which moss-feeding by mammals and birds, especially those living in northern areas, were discussed. Prins (1981) reported that in cold environments mosses are eaten by a variety of herbivores, both mammals and birds. He suggested as a possible reason that mosses supply polyunsaturated fatty acids such as arachidonic acid, which are not found in higher plants. One of the presumed effects of this substance is, he noted, to afford the herbivores better protection against the cold.

Sugawa (1960) studied the food value of powdered material of Barbella pendula, a hanging epiphytic moss distributed in southwestern Japan, to puppies and chickens. He found that this moss is rich in vitamin B\(_2\) and that mixed with food it caused no distaste and no ill effect. In fact the animals so fed gained more weight than the control.

Mosses are mentioned in many stories and poems in the literature of both western and eastern countries (Welch, 1948; Hat- tori, 1955; Takaki, 1972-1977). "Hikarigoke" (1954; tr. "Luminous Moss", 1967) by T. Takeda (1912-1976), a famous Japanese novelist, is a dramatic work dealing with the themes of cannibalism and human survival. In this story a faint golgen-green light from the luminous moss (Schistostega pennata) is the backdrop that reflects a struggle in man's mind in a dark cave that is the main scene of the drama. An operatic version of the drama has been created by I. Dan (music) and K. Arai (direction and stage), and it was played at the 15th Osaka International Festival (1972).
The most famous poem quoting a moss is, in Japan, the national anthem "Kimigayo" (His Majesty's Reign). B.H. CHAMBERLAIN, author of Things Japanese, translated the anthem as follows:

"Thousands of years of happy reign be thine
Rule on, my lord, till what are pebbles now
By age united to mighty rocks shall grow
Whose venerable sides the moss doth line."

12. LITERATURE CITED


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BELL, P.R. & E. LODGE (1963) - The reliability of Cratoneuron commutatum (Hedw.) Roth as an 'indicator moss'. J. Ecol. 51: 113-122.


BENL, G. (1958) - Java moss for decoration and as a spawning medium - a useful aquatic plant which has yet to be seen in Britain. Fish Keeping. Nov. 1958: 655.


FLOWERS, S. (1933) - On fossil mosses. Bryologist 36: 26-27, pls. XV-XVI.


GROUT, A.J. (1902) - Note (with no title). Bryologist 5: 78.


GROUT, A.J. (1931) - Mosses in landscape gardening. Bryologist 34: 64.


HORIKAWA, Y. (1952) - The amount of water absorption by some mosses. Hikobio 1: 150. (In Japanese.)


effect from the liverwort *Lepidozia vitrea*. 23rd Symposium on Chemistry of Natural Products, Symposium Papers, pp. 420-427. (In Japanese with English summary.)


MATSUO, A., K. UOHAMA, K. KAMIO & S. HAYASHI (1983a) - Structure of a new dolebellane diterpenoid from the liverwort *Odontoschisma denudatum*. 47th An-
nual Meeting of the Chemical Society of Japan, Proceeding Papers II, pp. 1130. (In Japanese.)


PRYCE, R.J. (1972a) - Metabolism of lunularic acid to a new plant stilbene by Lunularia cruciata. Phytochemistry 11: 1355-1364.
PRYCE, R.J. (1972b) - The occurrence of lunularic and abscisic acids in plants. Phytochemistry 11: 1759-1761.

PULLAR, E. (1967) - Ornamental mosses have landscape potential. The Japanese know how to use them. Plants & Garden 22(4): 32-34.


SCHATZ, A. (1955) - Speculations on the ecology and photosynthesis of the "copper mosses". Bryologist 58: 113-120.


SEAWARD, M.R.D. & D. WILLIAMS (1976) - An interpretation of mosses found


TAKAKI, N. (1976) - Preliminary report on the aquatic communities of bryo-
phytes in the Katsuragawa stream in Gifu Prefecture. In YATAZAWA, M. (ed.),
Effects of Fertilizers on Water Quality and Indicator Macrohydrophytes.
pp. 41-45.

TAKAKI, N. (1977) - Distribution of aquatic mosses in a rice field area.
In YATAZAWA, M. (ed.), Effect of Fertilizers on Water Quality and Indicator
Macrohydrophytes II. pp. 31-37. (In Japanese.)

TAKAKI, N. (1980) - Kurashi no naka no Hana. 8-gatsu, Koke (Plants in our

TAKAKI, N., R. WATANABE & Z. IWATSUKI (1982) - Bryophytes in aquariums for
summary.)

TAKAOKI, T. & K. MITANI (1982) - A simple method for the fumigation on

TAKEDA, R. & K. KATOH (1981) - Growth and sesquiterpenoid production by

TAODA, H. (1972) - Mapping of atmospheric pollution in Tokyo based upon

TAODA, H. (1973a) - Bryo-meter, an instrument for measuring the phytotoxic

TAODA, H. (1973b) - Effect of air pollution on bryophytes, I. SO2 tolerance

TAODA, H. (1975) - Evaluation of city soils based on controlled phytometer
(In Japanese.)

TAODA, H. (1976a) - Evaluation of city soils based on controlled phytometer
(In Japanese.)


Fig. 4. Samples of moss horticulture. 1. Bowl-cultivation of mosses enhanced by *Habenaria radiata* (in flower) and *Liriope minor*. Mosses are mostly *Polytrichum formosum* and those of lower cushion in the foreground are *Leucobryum neilgherrense*. 2. Moss landscape tray designed after a scene of undulating hills and a valley. Mosses covering the "hills" are *Cladopodium assurgens* and scattered hummocky clusters are *Pogonatum otarumense* (in the foreground) and *Leucobryum neilgherrense* (white ones), which suggest different features of the vegetation. Two stones (in the left back corner) and a few small herbs are added to accentuate the landscape. (INOUE, 1978).
Fig. 5. Moss garden of Saiboji Temple, Kyoto. 1. A view inside the gate. Both sides of the path are covered with *Polytrichum commune*, *Trachylostis microphylla*, and *Rhizogonium donyanum*. *Brachythecium buchananii*, which can withstand trampling, forms whitish-green belts near the path. 2. Part of the moss garden. The ground is entirely clothed with mosses, more common species of which are *Polytrichum commune*, *Leucobryum neilgherrense*, and *L. bowringii*. (ANDO, 1971).
Fig. 6. Unique gardens with moss in Kyoto. 1. Stone garden of Ryoanji Temple. The garden shows a simple pattern formed by the arrangement of stones, white sand, and moss (*Polytrichum commune*). Visitors are free to interpret the meaning of the garden. 2. A patched moss garden of Sanboin Temple. It consists of white sand and five patches (three circular and two guiter-shaped) of moss (*Polytrichum commune*), which are modelled after *saké* cups and gourds used as *saké* bottles. (ANDO, 1971).