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

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

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

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

Other Air Pollutants

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

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

UV-B Radiation

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

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

Radioactivity Indicators

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

Aquatic Bioindicators

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

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

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

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

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

Treatment of Waste

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

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

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

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

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

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

Horticultural Uses

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

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

Soil Conditioning

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

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

Culturing

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

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

Seed Beds

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

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

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

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

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

Moss Gardens

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

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

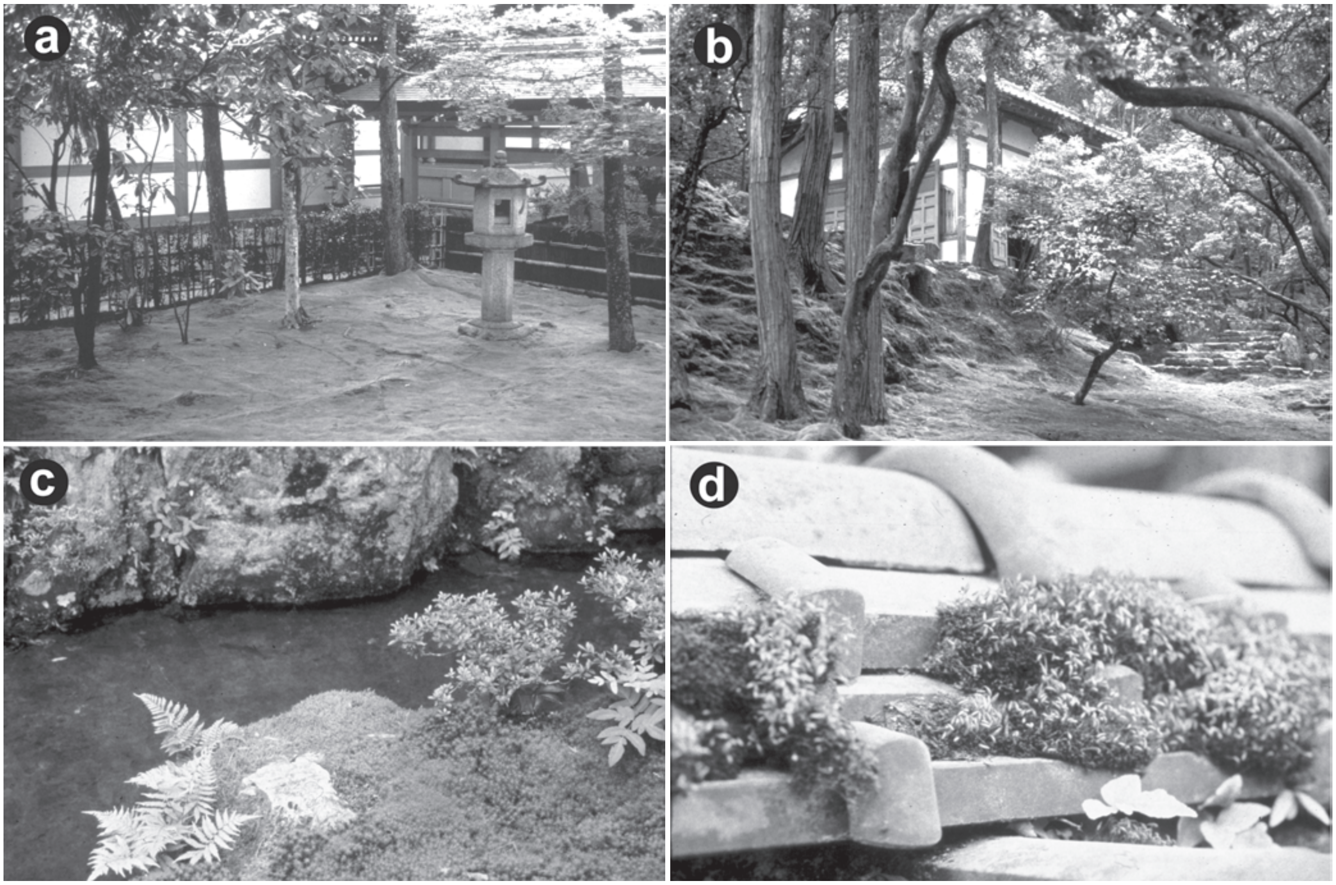

FIGURE 8. Moss gardens in Japan are designed to be restful. **a.** Mosses provide a look of tranquility. **b.** Mosses predominate at Kokedera (temple garden) in Kyoto. **c.** Mosses give small gardens an illusion of distance; stream and ferns provide scale. **d.** Mosses occupy tiles atop a moss garden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

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

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

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

Planting Techniques

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