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I INTRODUCTORY CHAPTERS

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1

The Ecological Value of Bryophytes as Indicators of Climate Change

NANCY G. SLACK

Bryophytes are the most successful group of plants other than angiosperms in terms of their numbers of species, geographical distribution on all continents, and their habitat diversification. There are at least 10,000 species of mosses and over 6000 liverworts. All three groups of bryophytes, also including the hornworts, were the earliest green plants to move to the land; each group has had a very long evolutionary history, probably more than 400 million years. All three groups, derived from a green algal ancestor, evolved separately from one another and from vascular plants through this long period. Although the great diversity of tropical bryophytes is often cited, Rydin (2009) pointed out their important contribution to biodiversity in northern ecosystems: 7.5% of the world's bryophyte species are found in Sweden, whereas only 0.8% of vascular plant species are found there.

Bryophytes are unique among land plants in that their dominant stage is the haploid green gametophyte rather than the much shorter-lived diploid sporophyte. They differ from vascular plants in other ways as well, in aspects that make them excellent environmental monitors. They inhabit a very wide range of ecosystems, habitats, and specific microhabitats, including substrates on which vascular plants cannot live. Many species are able to live in nutrient-poor conditions, and are adapted to respond rapidly physiologically to intermittent periods favorable for photosynthesis.

Morphology and physiology

Bryophytes lack the roots, xylem, and phloem of vascular plants. The great majority are ectohydric, that is, without internal conducting tissues. They absorb water and nutrients over the whole surface of the gametophyte. Water

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moves through externally, in capillary spaces around leaf bases, in hairs (tomentum) on stems, and in paraphyllia on the stems of some bryophytes. A few groups, particularly the Polytrichaceae and the larger Mniaceae, do have an internal water-conducting system composed of a central strand of hydroids (Hébant 1977). Some complex thallose liverworts in the Marchantiales conduct water internally around and within cell walls. Mosses of genera like *Polytrichum* and *Dawsonia* are thus able to grow tall, but they have not developed lignin; there are no bryophyte trees. The great majority are indeed very small, although both aquatic bryophytes such as species of *Fontinalis* and many pendant epiphytic bryophytes may grow very long. Bryophytes are very specific to particular microhabitats; they have diversified greatly ecologically in the course of their evolution. Many strategies have evolved that have enabled sympatric congeneric species to survive in separate niche spaces (Slack 1997). The relatively recent diversification of bryophytes is correlated with the evolution of angiosperms, especially forest trees, providing new niches for both mosses and liverworts. There has also been much speciation of tropical liverworts and the evolution of adaptations of mosses for epiphytic life. In many groups of mosses, repeated reduction has occurred in the course of evolution of mosses for xeric and ephemeral habitats.

Acrocarpic mosses, those that produce sporophytes at the tips of usually erect main stems, were the earliest to evolve and most still live on terrestrial substrates, rocks and soil. A few groups are successful as epiphytes; for example, the Calymperaceae. Many pleurocarpous mosses, those that produce lateral rather than terminal sporophytes and are often prostrate and highly branched, are found in many habitats. They may be terrestrial, particularly on forest floors and in wet environments; others are aquatic. Many pleurocarps are epiphytic, particularly in the tropics. Virtually all are perennial, whereas some acrocarps are annual or ephemeral, as are some liverworts. All bryophytes are C_3 plants; anthocerotes alone have a carbon-concentrating mechanism.

Mosses have many specialized structures, some of which have physiological functions. For example, leaf axillary hairs secrete mucilage for juvenile leaves, thus preventing dehydration (Buck & Goffinet 2000). Paraphyllia, small leaflike or filiform structures on pleurocarpous moss stems, add photosynthetic surface area. Lamellae, sheets of cells with chlorophyll usually on the upper surface of the leaf in Polytrichaceae and some Pottiaceae, serve physiological functions. Not only do they restrict water loss, but probably can be viewed more importantly as an adaptation for increasing the area for CO_2 uptake when well supplied with water and thus photosynthetically active. One can estimate the ratio between CO_2 uptake and projected leaf area. There is a clear correlation between this value and 95% irradiance (Proctor 2009). The very great majority of

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moss leaves, including the greatly modified leaves of *Sphagnum* mosses, consist of one layer of cells, as do those of most liverworts apart from the Marchantiales. The dominant gametophyte stage of bryophytes is thus directly exposed to many environmental factors. Sexual reproduction in bryophytes, as in ferns, requires water for the transfer of swimming sperm to the egg. Antheridia and archegonia are often on different plants; the majority of mosses are dioicous. In some taxa male and female plants are widely separated geographically. It is thus not unexpected that bryophytes have evolved many types of asexual reproduction and dispersal. Fragments of the gametophyte can produce new plants, probably the main means of dispersal to new sites of many mosses, including *Sphagnum*. “Fragile” leaves, part of which regularly break off, have evolved in a variety of moss families. Specialized propagules such as gemmae are found very commonly in leafy liverworts and in many mosses. Flagella or flagellate branches occur in both acrocarps and pleurocarps. Bulbils on the rhizoids occur in some moss genera, particularly *Bryum*. These dispersal methods are very efficient. Leafy liverworts colonize almost every decorticated log in moist temperate forests in eastern North America, many by gemmae rather than by spores. *Tetraphis pellucida*, with its gemmae in specialized “splash cups,” can be found on almost any rotten stump within its range. In addition, most moss sporophytes have capsules with peristome teeth that actively disperse spores. Peristomes have evolved, as for example in epiphytic mosses, to disperse spores efficiently in many different habitats. In the Splachnaceae, the dung mosses (coprophiles), spores are dispersed by insects, mainly by flies attracted to their special odors, with some coevolutionary parallels to insect pollination in angiosperms. The relationships of the species of *Splachnum* and other genera in the family to each other, to their substrates, and to environmental factors are complex (Marino 1997). The populations of some species have decreased in recent times, causing concern about land use practices and possibly climate change.

Bryophytes as Air Pollution Monitors

Bryophyte leaves, in contrast with those of vascular plants, do not have a thick cuticle. They are also, as noted above, ectohydric, obtaining their water and nutrients through the surface of the whole gametophyte. In addition, bryophytes are often exposed on rocks, tree bark, and soil. For all these reasons they are very close to, and in some respects at the mercy of, the environment. They have long been extensively used, as have lichens, as air pollution monitors, especially of sulphur dioxide and nitrogen oxides. Some species of mosses, especially epiphytes such as *Antitrichia curtipendula* and epiphytic species

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of *Orthotrichum*, are especially sensitive even to relatively low levels of pollutants compared with other mosses (Rao 1982; Porley & Hodgetts 2005). SO_2 in particular damages plasma membranes and causes chlorophyll to degrade. Some mosses were found to accumulate SO_2 one hundred times more efficiently than the leaves of vascular plants (Winner 1988). A great many studies of bryophytes as air pollution monitors have been carried out in many countries, including Britain, particularly from an early date (Burrell 1917). Some studies are ongoing, particularly in China and other areas heavily impacted by air pollution.

Desiccation tolerance

Desiccation tolerance has evolved in many bryophytes and is currently being intensively studied physiologically and by using techniques of molecular biology. It is important in terms of current climate change scenarios in which precipitation as well as temperature is predicted to change in the near future on a global scale. The mechanisms of true desiccation tolerance (as opposed to drought tolerance) are quite different from those of vascular plants; caution must therefore be used in making climate change predictions from vascular plant data alone.

A great variety of organisms show desiccation tolerance, including not only bryophytes and lichens but many other plants as well as animals and microorganisms. In bryophytes desiccation tolerance varies greatly among species, even for those in relatively moist environments, such as temperate forest epiphytes, and even for "similar" pleurocarps like *Hylocomium splendens* and *Rhytidiadelphus squarrosus* (Proctor 2000). Some mosses and leafy liverworts that live in continually moist or semi-aquatic habitats have not evolved (or have lost) desiccation tolerance. On the other hand, many epiphytes, such as *Ulota crispa*, which live on intermittently very dry bark even in generally moist forests, have evolved or retained desiccation tolerance.

Among desert mosses, desiccation tolerance is extremely well developed. Species of *Syntrichia* (*Tortula*) have been much studied. They can lose almost all of their water without disruption of cell structures; cell membranes and those of cell organelles remain intact. Experiments with *Syntrichia* (*Tortula*) *ruralis* show very rapid re-establishment of normal net photosynthesis in the renewed presence of water as was found in my early experiments on *Ulota crispa* (Tobiessen *et al.* 1979) and more recent ones (Tuba *et al.* 1996). Other experiments using chlorophyll fluorescence techniques show that recovery of photosynthesis is not affected by either chloroplast or cytoplasmic protein synthesis. It thus appears to be a matter of reassembly of pre-existing components rather than synthesis of new ones, also known as "constitutive" desiccation tolerance.

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Most bryophytes live in conditions of intermittent water availability. They spend their lives either fully turgid during or after rain (especially desert bryophytes) or dry and metabolically inactive. They are actually drought-evaders rather than drought-resistors. The latter strategy is characteristic of most desert vascular plants, which have evolved storage organs, long roots, as well as transcription and protein synthesis after a slower drying period than that which bryophytes often experience.

Oliver (2009) discussed the development of true vegetative desiccation tolerance in bryophytes as a requirement for life on land, which very likely preceded the development of vascular tissue in tracheophytes. Vegetative desiccation tolerance is rare in vascular plants, but common, although as noted not universal, in bryophytes. Thus far only 158 species of moss, 51 species of liverwort, and one species of hornwort have been shown experimentally to have vegetative desiccation tolerance, but that number will likely increase rapidly with further experimental work. Most initial work was done on *Syntrichia ruralis*, but recent experiments have shown that the desert moss *Syntrichia caninervis* can actually survive rapid desiccation (within 30 minutes) to approximately –540 MMPa for up to six years, returning to normal metabolic activity upon rehydration (Oliver *et al.* 1993; Oliver 2009). Some bryophytes increase their level of desiccation tolerance after mild dehydration events prior to desiccation. Dehydration can be almost instantaneous and can also be a stressful cellular event.

In bryophytes it is not structural thickenings or other features of cell walls that are important in desiccation tolerance, as once thought, but inherent properties of the cellular components. Many bryophytes have mechanisms for cellular protection during the desiccation process, but this varies even within closely related species in one genus. In addition, the sporophyte generation may be less desiccation-tolerant than the highly tolerant gametophyte generation, as in *Tortula inermis* (Stark *et al.* 2007) Importantly, water loss in these mosses is too rapid for protein synthesis to occur; protein synthesis is very sensitive to loss of water from the cytoplasm and quickly ceases. Thus protein synthesis cannot account for cellular stability. Even if drying is slower, novel proteins are not transcripted during the drying process; the necessary proteins are already present in the cells in sufficient quantities. This contrasts with mechanisms in some of the few vegetatively desiccation-tolerant vascular plants, such as in “resurrection plants” (Selaginaceae). These involve a relatively slower drying process and the transcription of particular proteins by a range of dehydration-regulated genes. Oliver (2009) contends that there is a constitutive cellular protection mechanism that is “ready and waiting” to be challenged or activated by desiccation. Its effectiveness is at least clear in *Syntrichia ruralis* from the fact

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that the plasma membrane and cell organelle membranes remain intact during the drying process, as noted.

Desiccation tolerance is not yet fully understood in bryophytes but it does involve components present in the cells: sugars, largely sucrose, and protective proteins including antioxidants and enzymes involved in protection from the generation of reactive oxygen species (ROS). A genomic approach is currently being used to catalog genes whose products play a role in responses of bryophytes to desiccation and rehydration, but much remains to be resolved. The sequencing of the genome of *Physcomitrella patens* is an important tool. Even though *P. patens* is not a desiccation-tolerant species, researchers now have the ability to knock out and replace its genes, which will be a powerful tool for future work.

Future climate change, particularly in terms of changes in the geographic distribution of precipitation, is of course uncertain; many factors, particularly anthropogenic ones, are important. In some regions it is extremely likely that desiccation will become a problem; bryophytes may do better under such circumstances than vascular plants or animals.

Ecosystem functions of bryophytes

Bryophytes have important ecosystem functions that need to be considered. These functions of bryophytes have long been under study in many ecosystems in the temperate and boreal zones, in the tropics, and in the Arctic and Antarctic. These functions include high productivity and biomass accumulation in some ecosystems, as well as nitrogen fixation, nutrient cycling, food chains and animal interactions, colonization, vascular plant facilitation, mycorrhizal relationships (liverworts), and others. Many have been discussed extensively elsewhere (Rieley *et al.* 1979; Gerson 1982; Slack 1988; Bates 2000, 2009; O’Neill 2000; Duckett *et al.* 1991; Longton 1992; Sveinbjornsson & Oechel 1992; Porley & Hodgetts 2005; Rydin 2009; Vitt & Wieder 2009). Some are discussed in other chapters of this book for many of the ecosystems listed above.

Although in many environments vascular plants including forest trees are the dominant vegetation, in other environments, especially in the Arctic, the Antarctic, in alpine habitats in mountains above treeline and in bogs, fens, and larger peatlands, bryophytes are often the dominant plants in terms of both biomass and productivity. They also have important ecosystem functions in temperate rain forests as well as in wet high-elevation so-called “mossy forests,” where, however, liverworts rather than mosses usually predominate. Much of the earth’s boreal and arctic zones are covered by peatlands in which species of *Sphagnum* are dominant. These peatlands are very important as carbon sinks and

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are currently being impacted by climate change, a subject studied and discussed by several authors in this volume and previously by, e.g., O'Neill (2000) and Vitt & Wieder (2009). In addition to sequestering carbon, bryophytes in forests and elsewhere are important in water retention and nutrient cycling and also in relation to the vertebrate and invertebrate fauna (see references above).

Much information, some of it from recent studies (Bates 2009), is available on the functions of bryophytes in nutrient cycling, a function that is vital to vascular plants, both in terms of facilitation and competition. Nutrient cycling is important in a variety of ecosystems likely to be affected by continuing climate change, not only projected changes in temperature and precipitation, but also in increased atmospheric CO_2 and UVB. Bryophytes capture mineral nutrients by “facilitated diffusion,” which involves ion channels and carrier proteins and depends on the existing gradients of concentration and electric charge across membranes. They frequently accumulate chemicals in much higher concentrations than in the ambient environment, one important reason for the use of mosses for biomonitoring of air pollution. There are a number of sources of nutrients (as well as other chemicals) that bryophytes accumulate with both wet and dry deposition. Experiments have shown that they also obtain nutrients from the substrate on which they are growing (e.g., Van Tooren *et al.* 1988). An early study (Tamm 1953) showed that *Hylocomium splendens* growing under a Norwegian forest canopy received most of its mineral nutrients from leachates from the tree canopy, i.e., wet deposition. This was also true in ombrotrophic bogs; wet deposition supplied mineral elements to *Sphagnum* (Malmer 1988). Woodin *et al.* (1985) showed that in a subarctic mire in Abisko, Sweden, *Sphagnum* captured NO_3 during both natural precipitation and experimental treatments more efficiently than rooted vascular plants, which presumably compete for nutrients in such ecosystems.

In addition, Oechel and Van Cleve (1986) found that bryophytes can be important in obtaining nutrients from wet deposition (precipitation) as well as from dust and litter before they can be taken up by rooted vascular plants. Experiments by van Tooren *et al.* (1990) showed that bryophytes in Dutch chalk grasslands absorb nutrients and grow during fall and winter while higher plants are inactive, and release nutrients by decomposition in spring and fall; these nutrients are then used by higher plants. Many more examples of nutrient cycling involving bryophytes could be cited. All of these relationships in part depend on ambient environmental factors currently in flux as a result of global climate change. Continued monitoring is needed.

Although most of the nutrient cycling studies to date involve mosses, studies of the liverwort *Blasia* are of interest. *Blasia pusilla* is very common in pioneer communities formed after deglaciation in Alaska (Slack & Horton 2010).

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It contains nitrogen-fixing cyanobacteria (*Nostoc*). As reported by Bates (2009) from the work of J. C. Meeks and D. G. Adams, *Blasia* (as well as the hornwort *Anthoceros*, which also harbors *Nostoc)*, when starved of nitrogen compounds, releases a chemical signal that induces the formation of short gliding filaments of the *Nostoc*, called hormogonia. These eventually move into the ventral auricles of *Blasia* and after developmental changes generate *Nostoc* filaments with a large number of N_2 -fixing heterocysts; about 80% of the fixed nitrogen is leaked to the host *Blasia* in the form of $NH_{3.}$ Whatever the complex nature of this symbiosis, the molecular genetics of the switch in form of *Nostoc* is presently under study. In the Bering Strait region of Alaska, in this author's experience, *Blasia* is an early successional species. The plant dies, and mosses and vascular plant seedlings take part in the subsequent succession, presumably using the nitrogen leached from the *Nostoc*.

At the 2007 International Association of Bryologists (IAB) meeting in Kuala Lumpur, Malaysia, protocols were set up to be used internationally in monitoring bryophyte responses to various aspects of climate change. The responses of bryophytes are likely to interact in quite complex ways with climatic factors, often both earlier than and different from those of vascular plants. A great deal of recent research on bryophyte responses to all the above factors of climate change, both present and predicted, in diverse ecosystems and on several continents, is presented in succeeding chapters.

Although polar bears have recently been referred to, in relation to global warming, as the new "canaries in the coal mine," it is the bryophytes that deserve that title. They are sensitive not only to increasing global temperatures, but also to increasing carbon dioxide content of the atmosphere, to increasing UVB radiation, to decreasing precipitation in some regions, and to several factors affecting carbon storage, especially in peatlands. All of these effects have been studied by the authors of the succeeding chapters and by many others whose work they cite. Both monitoring and actual laboratory and field experiments are currently being conducted and their results, including those of long-term field experiments in a number of different ecosystems, from arctic and alpine to desert, are reported in this book.

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