CHAPTER 1
THE FAUNA: A PLACE TO CALL HOME

Figure 1. A bird nest in a New Zealand *Nothofagus* forest, exhibiting a potpourri of vegetal material, including bryophytes. Could that be *Dawsonia* on the left? Photo by Rosemary Lovatt.

Types of Interactions

When I first became interested in bryophytes, I turned to the aquatic habitat, a place I had loved as a child and young adult. This soon led me to the organisms that lived among them. But literature on the subject was extremely difficult to find. This did not seem to be a high priority topic among bryologists, and those who studied animals seemed to think bryophytes were unimportant.

It is with great pleasure that I write this book, because there are now many fascinating stories of bryophyte – animal interactions, from housing to building materials (Figure 1) to food to safe sites. It appears that ecologists are beginning to recognize the importance of bryophytes, including them in studies, and publishing their studies in a very wide array of journals. That literature is easier to find now due to the internet, and when contacted, these wonderful scientists have been willing to share their stories and their photographs with all of us.

Bryological Fauna

Imagine yourself as a tiny mite in the forest. Everything around you must seem gigantic! But there, amidst the rocks and pine needles, a miniature forest beckons. It is a moss. This moss is your home. Here you can feel secure, protected from the drying wind and flecks of sun, hidden from the hungry birds, yet able to find tiny morsels for your own diet.

The bryophyte world is full of life, creating a habitat unlike any other (Ramazzotti 1958). Yet we know almost nothing of it. What loss might there be if the mosses were to disappear? What bird might be unable to construct a nest? What ant would have no place to hide its winter cache of seeds? What lemming might freeze its feet? The animals of the forest and field, stream and rock, have a very different view of the mosses and liverworts from that of the human inhabitants of the planet.

The habitats provided by mosses and liverworts are widely varied and worldwide, from mosses on roofs (Corbet & Lan 1974) to epiphytes (Fly *et al.* 2002) to turf-forming moss polsters (von der Dunk & von der Dunk 1979). In this volume we will explore the wide-ranging sizes and uses of the bryophyte dwellers and users. We will compare the terrestrial habitat, where nematodes are often most abundant, closely followed by rotifers (Figure 2. Comparison of relative abundance (log scale) of common bryophyte-inhabiting invertebrate fauna. Redrawn from Sayre & Brunson 1971.), to the aquatic habitat, which can be quite different, and where Chironomidae (midges) are often the most abundant.

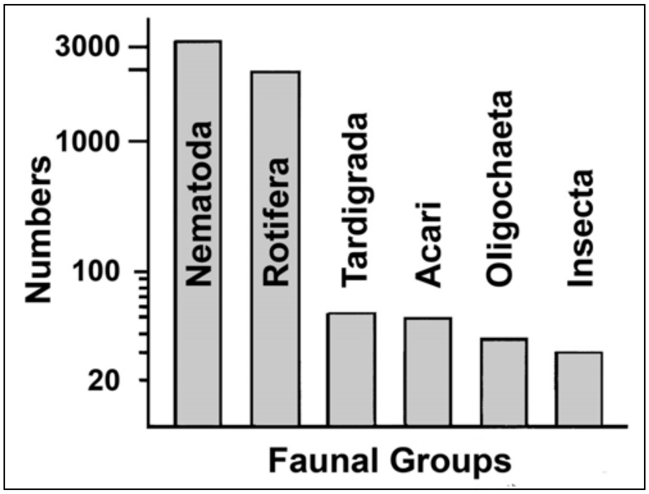

Figure 2. Comparison of relative abundance (log scale) of common bryophyte-inhabiting invertebrate fauna. Redrawn from Sayre & Brunson 1971.

Limitations

Bryophytes provide a habitat with a number of constraints that can prove to be of value to their tiny inhabitants. Most obviously, their small size limits the organisms that can live there. This affords small organisms protection from larger predators. And the bryophytes have a slow growth rate, permitting them to be a nursery to organisms that are initially small, but forcing these youngsters to leave before they are large enough to turn cannibal and consume their own offspring. The perennial nature of most bryophytes, rendering them present when many tracheophytes are absent or unable to provide cover, also provides a suitable overwintering habitat for numerous organisms, from the small ones living among the stems and leaves to the larger ones that live under them or use them as nesting material. Their C_3 habit permits the bryophytes to survive and sometimes even grow when the environment is cold and other plants are dormant, often absent above the substrate surface. Thus, in a world of predators, the bryophytes offer a safe site to numerous organisms that dominate this miniature world.

The Inhabitants

Large bryophyte mats typically host a wide variety of micro and macroinvertebrates (Ino 1992; Glime 1994; Peck & Moldenke 1999). The presence of a wide diversity of feeding strategies in a moss community suggests that the moss serves as a site of multiple pathways for nutrient cycling (Merrifield & Ingham 1998).

Fauna of mosses may be divided between those that are **bryophilous**, *i.e.*, those that typically live among mosses, and the casual visitor, sometimes referred to as **bryoxenous** (Ramazzotti 1958; Gadea 1964). Gerson (1982) divided these bryofauna into four categories:

bryobionts: animals that occur exclusively associated with bryophytes, *e.g. Cyclidium sphagnetorum* (a ciliate protozoan) on *Sphagnum* (see Figure 3)

bryophiles: animals that are usually associated with bryophytes but can be found elsewhere

bryoxenes: animals that regularly spend part of their life cycle among bryophytes

occasionals: animals that may at times be found associated with bryophytes but do not depend on them for survival

Figure 3. *Cyclidium* sp. This genus includes *C. sphagnetorum* that occurs only on *Sphagnum*. Photo by Yuuji Tsukii.

Those tiny organisms that live on the bed of a river or lake and are barely visible to the human eye are termed **meiofauna** – those that pass through a 0.500 mm sieve and are retained on a 0.045 mm sieve (International Association of Meiobenthologists 2008). Usage of this term has expanded to include organisms living on bryophytes that provide a moist film of water during at least part of the year. Maggie Ray (Bryonet 7 July 2005) stated that there are three groups of meiofauna that commonly live in the film of water on the bryophyte surface and that can achieve an **ametabolic** state. These are tardigrades, free-living nematodes, and rotifers. This **cryptobiotic** or **ametabiotic** state permits them to join the bryophytes in being dormant during those periods when the bryophyte is dehydrated or under a blanket of snow. She states that these cryptobiotic animals are "virtually indestructible." This permits them to survive environmental extremes such as high and low temperatures, high and low *p*H, very high pressure and very low vacuum, and low moisture. Upon return of the habitat to a "livable" and hydrated state, the animals absorb water, expand, and return to an active life. Hence, one might find eggs, "**tuns**" (stage in which body metabolism is undetectable), and cysts. Maggie points out that they do not age while they are in their cryptobiotic state and can remain that way for decades, making ideal study organisms for those interested in space travel and cellular research.

One particularly important **xerophytic** community is the **cryptogamic crust** (Figure 4) found in prairies and deserts. These bryophyte masses are associated with lichens and algae and inhabited by fungi, bacteria, and other micro-organisms. Among 38 taxa (nematodes, tardigrades, mites, arachnids, springtails, other small insects) in New Mexico, 29 occurred on mossy patches

(Brantley & Shepherd 2002). Twenty-seven species occurred on mixed lichen and moss patches, and 21 on lichen patches. Fifteen taxa occurred on all three types. Mosses supported the highest abundance, followed by mixed lichen and mosses, then by lichens. Richness and abundance were both higher in winter (March) than in summer (August) for all crust types in these dry habitats, reflecting differences in moisture stress.

Figure 4. A hydrated cryptogamic crust of *Syntrichia ruralis* and other desiccation-tolerant organisms. Photo by Michael Lüth.

Bryophytes can be especially important in contributing to species diversity of ecosystems. Sudzuki (1971) found that among 17 stations along five lakes on Mt. Fuji in Japan, the populations of rhizopods, gastrotrichs, rotifers, and nematodes were richest in the mosses. The mosses by Lake Kawaguchi had the highest overall species richness, ranging as high as 77 species, whereas gravels had richness as low as 19 species.

Varga (1992a, b) has found that some rare bryophytes in Sweden [*Plagiobryum zierii* (Figure 5) & *Saelania glaucescens* (Figure 6)] harbor a bryofauna that helps in monitoring air pollution. Not only do the invertebrates have high concentrations of lead, but the fauna in polluted cushions is diminished compared to that from unpolluted sites.

Figure 5. Lead accumulates in the fauna of this *Plagiobryum zierii*. Photo by Michael Lüth.

Bryophytes are such an important part of the **niches** of some invertebrates that their name indicates they are "of the moss." A Google search for *muscorum* has revealed 33 of these names among the protozoa and invertebrates (Table 1), and there are probably more, as well as those with *bryophila* or *muscicola* and other bryological epithets such as *Cyclidium sphagnetorum* or *Bryometopus sphagni*.

Figure 6. *Saelania glaucescens* is a moss whose bryofauna can be used to monitor air pollution. Photo by Michael Lüth.

Table 1. Names of protozoa and invertebrates including *muscorum* as the specific epithet. The list was derived from an internet Google search, especially ITIS search, for *muscorum*. Accessed on 7 October 2008 at <http://www.itis.gov/servlet/SingleRpt/SingleRpt>.

Protozoa

Assulina muscorum (Rhizopoda)
Chilodontopsis muscorum (Ciliophora)
Gastrostyla muscorum (Ciliophora)
Histriculus muscorum (Ciliophora)
Holosticha (=*Keronopsis*) *muscorum* (Ciliophora)
Oxytricha (=*Opistotricha*) *muscorum* (Ciliophora)
Pusilloburius (=*Pseudoglaucoma*) *muscorum* (Ciliophora)
Rhabdostyla muscorum = *Opercularia coarctata*
Sathrophilus (=*Saprophilus*) *muscorum* (Ciliophora)
Steinia muscorum (Ciliophora) name validity not verified
Strongylidium muscorum (Ciliophora) name validity not verified
Stylonychia muscorum (Ciliophora)
Urostyla muscorum (Ciliophora)

Nematoda

Hemiplectus muscorum (nematode)
Prionchulus muscorum (nematode)

Arthropoda: Arachnida

Gnaphosa (=*Pithonissa*) *muscorum* (Araneae – spider)
Liochthonius muscorum (Araneae – spider)
Tegeocranellus muscorum (Acari – mite)

Arthropoda: Isopoda

Philoscia (=*Oniscus*) *muscorum* (moss wood louse)

Arthropoda: Pseudoscorpiones

Neobisium muscorum (Neobisiidae – moss scorpion)

Arthropoda: Insecta

Acerella muscorum (Protura)
Acrotona muscorum (Coleoptera: Staphylinidae)
Bombus (=*Apis*) *muscorum* (Hymenoptera: Bombidae – moss carder bee)
Anthrenus museorum = *Byrrhus* (=*Anthrenus*) *muscorum* (Coleoptera: Dermestidae)
Entomobrya (=*Degeeria*) *muscorum* (Collembola – springtails)
Leptothorax (=*Myrmica*) *muscorum* (Hymenoptera: Formicidae)
Liothrips muscorum (Thysanoptera: Thripidae)
Lissothrips muscorum (Thysanoptera: Thripidae)
Mniophila muscorum (Coleoptera – leaf beetle)
Neanura muscorum (Collembola: Neanuridae)
Peromyia muscorum (Diptera: Cecidomyiidae
Tetramorium muscorum (Hymenoptera: Formicidae – Guinea ant)

Mollusca

Pupilla muscorum (Gastropoda – snails)

Cover and Nesting Materials – Terrestrial

Moss mats and cushions can make ideal cover and nesting material for a variety of organisms. They serve to buffer both temperature and moisture, while providing sufficient spaces for gas exchange. There are many tiny spaces ideal for laying eggs and protecting young larvae from predators or desiccation. For larger organisms, the leafy stems are easily woven into suitable nests, and the projecting leaves render stability to the completed product. Thus it is not surprising to find that many organisms actually depend on bryophytes for their homes and shelters.

Bryophyte Individuality

But to what extent do individual bryophyte species differ in their provisions for these animals? Learner *et al.* (1990) found no relationship between taxon richness and macroinvertebrate fauna on bank slopes of river corridors where bryophytes were included in the assessment. This suggests that bryophytes might form functional groups that differ in their form from other plants but otherwise differ little within the functional group in the means by which they shelter organisms.

Two communities of bryophytes on Signy Island in the Antarctic support this growth form or functional group suggestion for richness. Davis (1981) found that there was little difference in assimilation or respiration of the plant and faunal components of the *Polytrichum alpestre* and *Chorisodontium aciphyllum* turf compared to the *Calliergon sarmentosum*, *Calliergidium austro-stramineum*, and *Sanionia uncinata* mat with *Cephaloziella varians*, but among the faunal taxa (protozoa, Rotifera, Tardigrada, Nematoda, Acari, and Collembola) of these bryophytes, the standing crops of Collembola and Acari differed between the two associations. Thus, while richness differed little, the types of species did differ. Interestingly, it appeared that no bryophytes were eaten by these organisms. Rather, the bryophytes form unique habitats that provide safe sites for the small invertebrates that seek shelter there.

Bryophytes can play a role in the larger ecosystem picture as well, affecting organisms in other niches. Some mosses in the Antarctic provide habitat for a variety of arthropods indirectly rather than directly by modifying the underlying soil (temperature, moisture, structure) in ways that make it suitable for a variety of arthropods (Gerson 1969).

Food Value of Bryophytes

Because most bryophytes exist uneaten in herbaria around the world, biologists have long held the view that bryophytes are not effectively a part of the food chain. They have low caloric value (3.7-4.8 Kcal/g; Forman 1968, 1969; Rastorfer 1976a, b), large quantities of holocellulose and crude fiber (Walton 1985) that makes them hard to digest, and are often endowed with a plethora of secondary compounds (Asakawa 1981; see chapter on antiherbivory).

In comparison to evergreen and deciduous shrubs in the alpine tundra, with ~5,560 cal/g ash-free dry mass, bryophytes would seemingly provide considerably less energy (Bliss 1962). Nevertheless, the caloric values for twenty herbaceous tracheophyte species had a mean of 4,601±29 cal/g ash-free dry mass, whereas seven species of moss averaged 4,410±70cal/g, ranging from a high of 4,780 in *Polytrichum juniperinum* var. *alpestre* to 4,211 in *Sphagnum girgensohnii* (Figure 7), a difference hardly worth noting.

Ecologists have long considered that bryophytes had little to offer in nutritional quality (Pakarinen & Vitt 1974). Furthermore, some bryophytes even prevent their consumers from obtaining the nutrition from the non-bryophyte food they have just eaten by complexing the protein in ways that make it indigestible. Liao (unpublished) has found lignin-like protein-complexing tannin compounds in all the boreal forest mosses, except for *Sphagnum*, in his study.

In further support of this concept of low food value, we find that in the Antarctic, where bryophytes form the bulk of the vegetation, the invertebrates (protozoa, Rotifera, Tardigrada, Nematoda, Acari, & Collembola) form a diverse fauna among the bryophyte cushions. Yet despite the paucity of non-bryophyte plant food organisms, most invertebrates apparently do not eat the bryophytes (Davis 1981).

Figure 7. *Sphagnum girgensohnii*. Photo by Janice Glime.

Nevertheless, some animals seem to include liverworts (Barthlott *et al.* 2000), mosses (Smith 1977), and hornworts (Bisang 1996) in their diets. Even among the **apparent** (conspicuous) Antarctic bryophytes, which should be expected to have the highest quantity of antifeedant secondary compounds, some invertebrates are adapted to consume them. Weevils (*Ectemnorrhinus similis*) eat 37% of their body weight daily of the moss *Brachythecium rutabulum*, consuming 1.67 mg per day per individual weevil on Marion Island (Smith 1977). Tardigrades worldwide are adapted to living among and consuming mosses. Perhaps antifeedants are not as important to these organisms as we might suppose. How little we know of the physiological mechanisms that make these feeding relationships successful!

We know even less about the nutritive value of sporophytes. Yet several instances are known where capsules are a preferred food, especially for snails and slugs (Davidson *et al*. 1990). Stark (1983) found that 14% of the expanded capsules of *Entodon cladorrhizans* exhibited signs of grazing. Spores can have a lipid content of 30% while vegetative portions may have only 5% (Gellerman *et al.* 1972; Pakarinen & Vitt 1974). Even flowering plants have a lipid content of only 5% in the Arctic (Pakarinen & Vitt 1974).

Not all functions of food are directly for nutrition. Particularly in northern climates, mammals, and perhaps other animals, seem to benefit from the large quantities of arachidonic acid in bryophytes (Al-Hasan *et al*. 1989). With a melting point of -49.5ºC, this fatty acid provides greater pliability for cell membranes at low temperatures. Prins (1981) suggested that this property may help to keep foot pads of Arctic rodents from freezing.

In any case, bryophytes appear to form an important component of the diet for a number of invertebrates and some Arctic mammals and birds. Gerson (1969) included among these the Collembola, Diptera, Hemiptera, Hymenoptera, Orthoptera, Cryptostigmata, and Acarina. These and many others will be discussed further in the succeeding chapters on individual groups.

Vitamins

Bryophytes may fill specific needs of animals when fresh food is scarce. For example, vitamin B_2 is not available in most plants, but *Barbella pendula* has a high content and causes no noticeable side effects when fed to puppies and chickens (Sugawa 1960). In fact, Sugawa claims that the animals thrive. Asakawa (1990) lists the species used by Sugawa, citing *Barbella pendula, B. enervis, Floribundaria nipponica, Hypnum plumaeforme, Neckeropsis nitidula*, and *Ptychanthus striatus* as all resulting in weight gain in chickens and puppies, implying that the presence of B_2 in these bryophytes may have been instrumental in that gain.

Food Chain Effects

Of concern when bryophytes enter the food web is the ability of bryophytes to retain high levels of radiation. When the Chernobyl accident occurred, bryophytes for hundreds of miles had elevated radiation (Daroczy *et al*. 1988), measurable in mosses two years after the accident (Elstner *et al*. 1987, 1989). These concentrated levels are further concentrated when they enter the food web, and lemmings, which consume them rather extensively in areas affected by the high radiation (Ericson 1977), are but one step into the food web of higher carnivores.

Seasonal Differences in Habitat and Diet

We know virtually nothing about the seasonal changes in diet of invertebrates that might involve bryophytes. And it is likely that bryophytes also change their nutritive value seasonally, but again we are ignorant. We do know that both invertebrates and vertebrates change habitats to survive or take advantage of the seasons (Ovezova 1989). Crafford and Chown (1991) hypothesized that curculionid beetles (Curculionidae: Ectemnorhinini) would gain a nutritional advantage by eating bryophytes at low temperatures. Indeed, the cryptogams provided the main source of energy for five out of six of these species on sub-Antarctic Marion Island.

While we seem to know nothing about seasonal diet changes of moss-dwelling invertebrates, we have, however, observed changes in the eating habits of the more conspicuous rodents. Lemmings are known to switch to bryophytes as winter approaches (Prins 1982a), perhaps taking advantage of the high content of arachidonic acid in bryophytes to maintain pliability of cell membranes in their footpads as they run around on frozen ground and snow.

Habitat Differences in Nutrient Availability

Even desert mosses form habitats for a variety of invertebrates (Kaplin & Ovezova 1986). Habitat can play a major role in food value (Figure 8). The avoidance of bryophytes as food seems to be supported where bryophytes form a dominant feature of the physiognomy, *i.e.* the Antarctic, so perhaps apparency theory does apply.

Davis (1981) reported that moss was eaten at a rate of less than 0.2 g m^{-2} yr^{-1} by two Antarctic moss invertebrate communities, despite tardigrades, nematodes, rotifers, protozoa, mites, and insects living among them. If such is the case, it supports the model of **apparency**, discussed regarding antiherbivory later in this volume, where the Antarctic bryophytes indeed are the most conspicuous photosynthetic food items available. One would suppose that to avoid herbivory where the slow-growing bryophyte is so conspicuous to would-be consumers, it must either have a high component of secondary compounds to inhibit feeding or lack sufficient food value to make consumption profitable.

This nutritional profitability, as in tracheophytes, differs with habitat. In the high Arctic, not only do the percentages of N and C differ, but the hydric mosses tend to have a higher caloric value (4.57-4.97 kcal/g) and lipid content than do the mesic and terrestrial ones (4.50-4.69 kcal/g) (Pakarinen & Vitt 1974).

Caloric contents likewise differ among terrestrial habitats, with those of alpine regions seemingly lower than those of either coniferous forests (4169 cal/gdw) or northern hardwoods (4179 cal/gdw) (Figure 9; Forman 1968). Oakwoods have the least (3773 cal/gdw) among these studies.

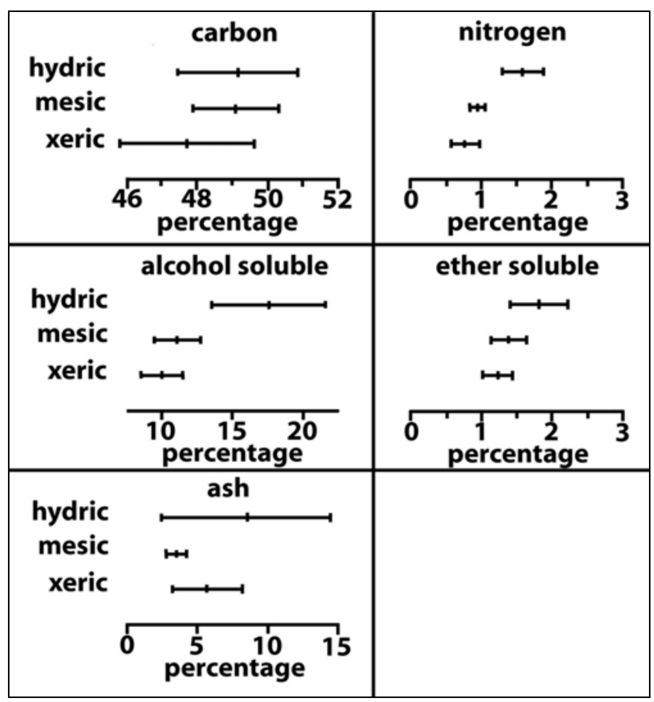

Figure 8. Mean food values (± 95% C.I.) of green (living) tissues based on ash-free dry mass of 35 species of Arctic bryophytes. Redrawn from Pakarinen & Vitt 1974.

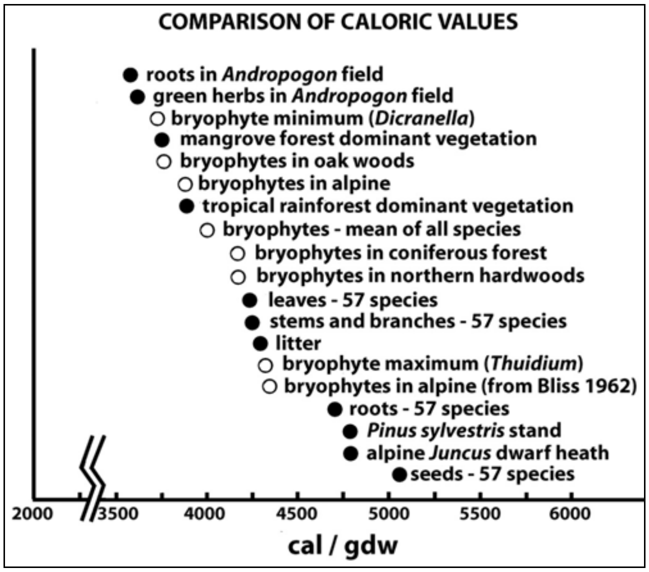

Figure 9. Caloric values (per gram dry weight) of bryophytes (open circles) compared to other plants and plant parts (solid circles). Non-bryophyte data are from Golley 1961; redrawn from Forman 1968.

Despite their seemingly lower caloric content, Arctic bryophytes seem to experience greater consumption by mammals than elsewhere (Prins 1982b). Prins (1982a) reported that mosses were found in 20% of Arctic stomach analyses but were only about 1% of the total amount of food consumed. It is clear that a lower proportion of net bryophyte production is grazed than for tracheophytes, and Longton (1984) concluded that bryophytes are utilized primarily via the detritus pathway. Ugh! If they have little caloric content when alive, it would seem that only the microbes could benefit when they are dead. Of course, once eaten they can go up the food chain. It appears that certain temperate animals eat mosses in very limited amounts. Unfortunately, our knowledge of feeding relationships with bryophytes in the tropics is meager.

Markham and Porter (1978) were among the first to take a global approach to examining the constituents of bryophytes. The differences are strongly influenced by the climate, especially temperature. In the Antarctic, bryophytes have higher C:N ratios than do tracheophytes, with larger amounts of holocellulose and crude fiber and lower energy levels, contributing to their undesirability as a food source (Walton 1985). Pakarinen and Vitt (1974) found that even within the Arctic, ratios could differ considerably, with mesic habitats having a higher carbon ratio (Figure 8). Furthermore, as the moss ages, its cellulose content increases, whereas in grasses it decreases (Walton 1985).

Long after Bliss (1962) initiated the study of Arctic and alpine plants and their nutritional value by examining the caloric and lipid content of alpine tundra plants, Sveinbjornsson and Oechel (1991) found little seasonal difference in lipid or carbohydrate content of *Polytrichum commune* or *Polytrichastrum alpinum.* Nevertheless, the variability suggests that seasonality of nutrients bears further investigation. Sugar and starch content were negatively associated, with high starch contents occurring in rhizomes and high sugar contents in shoots, suggesting that starch serves as a storage compound.

Consumption Rates

There are few quantitative studies of bryophyte consumption. Duke and Crossley (1975) calculated that a rock grasshopper, *Trimerotropis saxatilis*, consumed the moss *Grimmia laevigata* at a rate of 391 mg m^{-2} yr^{-1} in SE USA. On Marion Island in the Antarctic, an individual beetle, *Ectemnorrhinus similus,* ate a mean of 1.67 mg of *Brachythecium rutabulum* per day in feeding trials, equivalent to 37% of its body weight (Smith 1977). Davidson and Longton (1987) quantitatively investigated the consumption of several moss species by slugs (*Arion subfuscus* and *A. rufus*), as discussed in the chapter on invertebrates.

Moss litter is not easily broken down and depends on the moss fauna for consumption, returning to the ecosystem as feces (Frak & Ponge 2002). In alpine areas, other litter generally does not depend on fauna for its breakdown. The same secondary compounds that discourage herbivory also interfere with bacterial and fungal decomposition.

Summary

The small size of bryophytes affords protection from predators to small organisms. This also makes them a good nursery for many kinds of invertebrates. Their perennial nature also provides winter cover, not only for tiny invertebrates, but for larger amphibians and reptiles. Therefore, their potential for contributing to the biodiversity of the planet is enormous.

Bryophyte inhabitants may be classified as **bryobionts** (animals occurring exclusively on bryophytes), **bryophiles** (animals usually but not exclusively among bryophytes), **bryoxenes** (animals that spend part of their lives among bryophytes), and **occasionals** (animals that occur among bryophytes but do not depend on them for survival). **Meiofauna** are the tiny organisms on the bed of a river or lake, or in the moist film of a bryophyte.

One reason for the success of many invertebrate inhabitants is their ability to achieve an **ametabolic** or **cryptobiotic** state, thus becoming dormant when the bryophyte becomes dehydrated or frozen.

Bryophytes buffer both temperature and moisture, not only within the bryophyte community, but in the soil beneath them. Bryophytes differ considerably in their form, yet we know little about differences in communities among different species of bryophytes.

Scientists have assumed that bryophytes have little or no food value, but, nevertheless, isopods, lemmings, and a variety of other organisms do eat them. We know virtually nothing about seasonal changes in nutritive value of bryophytes, nor of seasonal diets of animals that feed on them. Only a few small rodents are known to switch to bryophytes in preparation for winter. Dangers lurk in areas with radiation accumulation in the bryophytes.

Habitat may select for nutritional quality, with alpine taxa having lower caloric values, hydric mosses having higher values and also higher lipid content. Coniferous and northern hardwood forest bryophytes have higher caloric values, bryophytes of oakwoods the least. As bryophytes age, cellulose content increases, further reducing palatability and energy availability.

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