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Bryophytes and Herbivory

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Abstract – This paper reviews briefly some possible defenses available to bryophytes and provides experimental evidence that suggests the role of phenolic compounds and toughness in defense. It indicates that in some cases toughness or nutrition may outweigh phenolic deterrents in determining what invertebrates eat. When given, apparently, only phenolic content as a difference between two populations of *Fontinalis antipyretica*, the aquatic isopod *Asellus militaris* selected the plants with the lower phenolic content. Presence of higher concentrations of phenolic compounds in shade plants than in sun plants contradicts the Carbon/Nutrient Balance hypothesis and suggests that slow-growing bryophytes may differ from tracheophytes in producing defenses rather than other carbon compounds. This review indicates that bryophytes may exhibit multiple means of feeding deterrency and that further study is needed.

Ecology / phenolic compounds / secondary compounds / sun and shade / Isopoda / slugs / antiherbivory / defense / *Fontinalis*, *Polytrichum*

Traditionally botanists have considered bryophytes to be inedible, citing as evidence their safety in herbaria where beetles devoured any unprotected flowering plants. However, it is becoming increasing clear that this is not the case for all bryophytes. A great number of potential predators and pathogens, such as bacteria, fungi, nematodes, mites, insects, mammals, and other herbivorous animals, surround plants, and especially bryophytes, in a natural ecosystem (Rhoades & Cates, 1976; Taiz & Zeiger, 1991). Most animals and nearly all insects feed on plants. It seems unrealistic to consider that any plant could exist with no natural predators.

Plants have evolved to avoid over-predation in a variety of ways (Harborne, 1988; Smith, 1990). Howe and Westley (1988) presented three defense systems, based on tracheophytes: 1) **mechanical** protection on the plant surface, including spines, thorns, and hairs, 2) **obstructive** protection involving complex polymers or silica crystals that reduce plant digestibility, and 3) **secondary chemical defense** through plant toxins that kill or repel herbivores at very low concentrations (Taiz & Zeiger, 1991).

Bryophytes are limited in the types of mechanical defenses they can possess by their small size and simple structure. However, it appears that their long evolutionary history with a mutation rate equalling that of other plants (Wyatt

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et al., 1989) has afforded them a wide array of secondary compounds that can provide them chemical defenses (Liao, 1993). But making defense compounds requires energy and therefore comes at a price, and it is that price that drives the evolution that makes some plants, including bryophytes, edible and others not. This mini-review will examine several examples of bryophyte consumption and avoidance to suggest reasons some bryophytes may be avoided.

WHO EATS BRYOPHYTES?

Actually, there are animals for which mosses form a considerable proportion of the diet (Prins, 1982), especially in the arctic tundra (Longton, 1984). Invertebrates are much more likely consumers of bryophytes than mammalian browsers. What may be inconspicuous to a mammalian browser can be home to these smaller organisms. Studies reviewed by Richardson (1981) and Gerson (1982) confirm that mosses are eaten by some species of crustaceans, gastropods, mites, tardigrades, and many groups of insects.

Mosses may also serve as an emergency food. In the Negev Desert Loria and Herrnstadt (1980) observed harvest ants (*Messor* spp.) feeding on moss capsules in a winter when no other food sources were available. When tracheophyte foliage is unavailable in winter, even populations of caribou and reindeer may eat mosses, the amount changing between localities and years (White & Trudell, 1980). In a feeding experiment in which lemmings on Devon Island were offered fruiting material of *Funaria arctica*, only capsules were eaten, a fact that may be related to the high lipid content of some moss spores (Pakarinen & Vitt, 1974), but as you will see below, it may instead or additionally relate to locations of phenolic concentrations within the plants.

BRYOPHYTE ANTIFEEDANTS

One strategy for suppressing herbivory is the presence of some chemical deterrent that would render plant tissue unpalatable, or toxic. Richter (1929) commented on odors of bryophytes, a feature suggesting a possible deterrency, and the pungent odor of flavonoids of *Fontinalis* drying in the lab is well known (Bendz & Svensson, 1971; Glime, pers. obs.). Asakawa and coworkers (1976) reported a pungent component in *Porella vernicosa* and a “mossy” odor in *Frullania*, and Crum (1991) suggests odors as a means of identifying several liverwort species.

Mosses and liverworts taste bad to humans, if that has any relevance to other animals. Richardson (1981) describes the taste of most species as being like raw green beans, while others have a strong peppery taste, such as in *Dicranum*. Crum (1973) describes the Asian moss *Rhodobryum giganteum* as having a sickeningly sweet taste when fresh, one that makes you want to rinse your mouth. Asakawa (1990b) reports that *Gymnocolea inflata* has a persistent bitter taste and results in vomiting when it is chewed for only a few seconds. It is likely that these unpleasant tastes and odors are the products of secondary compounds such as phenolic compounds or terpenes.

There are numerous terpenes and phenolics, and liverworts in particular show a wide variety of sesquiterpenes, bibenzyls, flavonoids, and other phenolics (Asakawa *et al.*, 1980, 1982a, b; Asakawa, 1982, 1990a; Markham, 1988; Zinsmeister & Mues, 1988; von Schwartzenberg *et al.*, 2004). Terpenes are lipids synthesized from acetyl CoA via the Mevalonic acid pathway. Asakawa (1990a) points out that most of the liverwort defensive compounds seem to be terpenoids and lipophilic aromatic compounds located in the oil bodies. He has shown that these substances are effective in deterring the African army worm *Spodoptera exempta*.

The term phenolic compound embraces a wide range of plant substances that have an aromatic ring bearing one or more hydroxyl substituents. Phenolic compounds are aromatic substances formed via the Shikimic acid pathway or the Malonic acid pathway in various ways. These substances tend to be water-soluble, since they most frequently occur combined with sugar as glycosides and they are usually located in the cell vacuole (Harborne, 1982). Among the natural phenolic compounds, of which several thousand structures are known, the flavonoids form the largest group, but simple monocyclic phenols, phenylpropanoids, and phenolic quinones all exist in considerable numbers. They all show intense absorption in the UV region of the spectrum and thus one might hypothesize that their original value was to shield the primitive bryophytes from the intensity of UV light encountered by living on land.

EXPERIMENTAL EVIDENCE

Given the presence of a wide array of phenolic compounds and terpenes, and evidence that some organisms do eat bryophytes, it is now our task to demonstrate that there is a connection between these deterrent compounds and herbivore avoidance.

Frahm and Kirchhoff (2002) reasoned that isolated compounds may not have the same deterrent effect as those combined effects normally present in bryophyte cells. They used alcohol extractions from *Neckera crispa* and *Porella obtusata* to determine their antifeedant effects. These extracts were sprayed in various concentrations onto iceberg lettuce leaves and the feeding activity of the slug *Arion lusitanicus* was compared on these with that on control leaves sprayed with only alcohol dilutions. The slugs ate lettuce equally with the extract and the control sprays, as well as on those leaves sprayed with just water. They likewise were not deterred by 0.025% extract from *Porella obtusata*, but they were somewhat deterred at concentrations of 0.05%. At higher concentrations they ate none of the leaves with *Porella obtusata* extracts.

But even this experiment has its problems. Other compounds, not alcohol-soluble, may have an effect on palatability, and the alcohol itself could present some sort of interaction. Many of these compounds are volatile, so the concentration could quickly diminish in air, whereas those in living cells would be released at full concentration when an invertebrate first crushes the cell. It appears that to understand the feeding relationships we need to examine them a number of different ways.

Slugs Prefer Capsules

Jennings and Barkham (1975) found mosses in the feces of deciduous woodland slugs (*Arion* spp.), but considered that these may have been consumed inadvertently along with other plant material. In their subsequent feeding experiments, the bryophytes (*Atrichum undulatum*, *Hypnum cupressiforme*, *Thuidium tamariscinum*) all had low palatability scores. The low digestibility of some moss leaves, with a high ratio of cell wall to cell contents, can cause them to appear disproportionately high in fecal matter. Most non-bryophyte plant material is unrecognizable.

Several studies indicate that sporophytes of bryophytes are more commonly consumed by slugs than gametophytes (Pakarinen & Vitt, 1974; Loria & Herrnstadt, 1980; Longton, 1984; Davidson *et al.*, 1990). In our laboratory feeding trials (Liao, 1993), slugs ate sporophytes of several taxa more frequently than they ate gametophytes, especially when the capsules had expanded, but were still green. Davidson *et al.* (1990) found that slugs normally leave the seta, and once the capsule is brown, the rate of consumption decreases considerably. I have likewise observed slugs eating only capsules of *Brachythecium* in the field (Fig. 1). Slugs also discriminate between taxa; Liao (1993) found that the slugs ate the capsules of *Funaria hygrometrica* in preference to the other species in his trials. The protonemata of *Brachythecium rutabulum* and *Funaria hygrometrica* are also

Fig. 1. Slug grazing on *Brachythecium*, apparently removing the capsules and leaving only setae. Photo by Janice Glime.

eaten as frequently by slugs (*Arion subfuscus* and *A. rufus*) as are immature capsules (Davidson *et al.*, 1990). Davidson *et al.* (1990) proposed that short-lived, pioneer plants (such as *Funaria hygrometrica*) make a lesser commitment of resources for defense against generalized herbivores, such as slugs, than do perennials, supported by the fact that *Funaria hygrometrica* (annual, pioneer) shoots are more acceptable to slugs than are those of *Brachythecium rutabulum* (perennial).

In order to look at the role of polyphenolics in antiherbivory of the bryophytes, Liao (1993) examined the eating habits of slugs on gametophytes and capsules of *Funaria hygrometrica*. In the first 4 days, the slugs consumed 59% of the expanded, green capsules. Within a week, 76% of the capsules were consumed. On the other hand, the leafy plants were rarely grazed. Previous studies showed that the mean ash-free caloric value of immature capsules of mosses is similar to or slightly lower than that of the leafy shoot (Forman, 1968, 1969; Rastorfer, 1976; Davidson *et al.*, 1990). Thus, there appears to be no energetic advantage to be gained by eating the immature capsules. After analyzing the phenolic content (total phenolics of the capsules = 25 mg/g fresh mass, leafy shoot = 82 mg/g fresh mass), Liao concluded that the high concentration of phenolics in the leafy shoots could account for the different levels of herbivory on capsules vs leafy shoots. Davidson *et al.* (1989) likewise found that the number and concentration of phenolic compounds can be greater in the shoot than in the immature moss capsules, explaining why young capsules were more likely to be eaten than the leafy plant.

It is already known that slugs in the Arionidae possess an impressive array of enzymes for digesting carbohydrates and are certainly capable of digesting cellulose (Evan & Jones, 1962; Hartenstein, 1982), but they do not possess polyphenoloxidase and cannot metabolize polyphenols (Hartenstein, 1982). Thus, their avoidance of leafy stems and preference for immature capsules is predictable.

Pillbugs Prefer *Polytrichum* Leaves to Stems

Davidson and Longton (1987) have suggested that *Polytrichum commune* may have a physical deterrent to herbivores, apparently discouraging feeding by slugs (*Arion hortensis*) on its leaves, whereas the slugs readily eat capsules and developing spores. Our lab has repeatedly done experiments with *Polytrichum juniperinum* and *P. commune* and found that pillbugs (Isopoda, *Porcellio*) would eat the leaves of *Polytrichum* species but avoided eating the stems, suggesting that the heavy texture of the stem might possibly have a role in the avoidance. It appears that the lignin-like compounds (Siegel, 1969; Downey & Basile, 1989; Edelmann *et al.*, 1998) in some mosses may serve a similar function to that of lignin in wood in deterring herbivory. Taiz and Zeiger (1991) claim that tracheophyte fibers with a tensile strength similar to that of steel wire may gain their strength from the combination of both lignin and extensin. The recent discovery of extensins (substances that strengthen cell walls) in *Physcomitrella patens* (Schipper *et al.*, 2002) suggests that these compounds may also contribute to toughness of some bryophyte tissues, but this remains to be explored in bryophytes.

Stems of *Polytrichum* are tough, tough enough to be used to make rope (Dickson, 1973), brooms (Thieret, 1954), and baskets (Bland, 1971). It is reasonable to hypothesize that toughness of the stem serves as a deterrent to herbivore

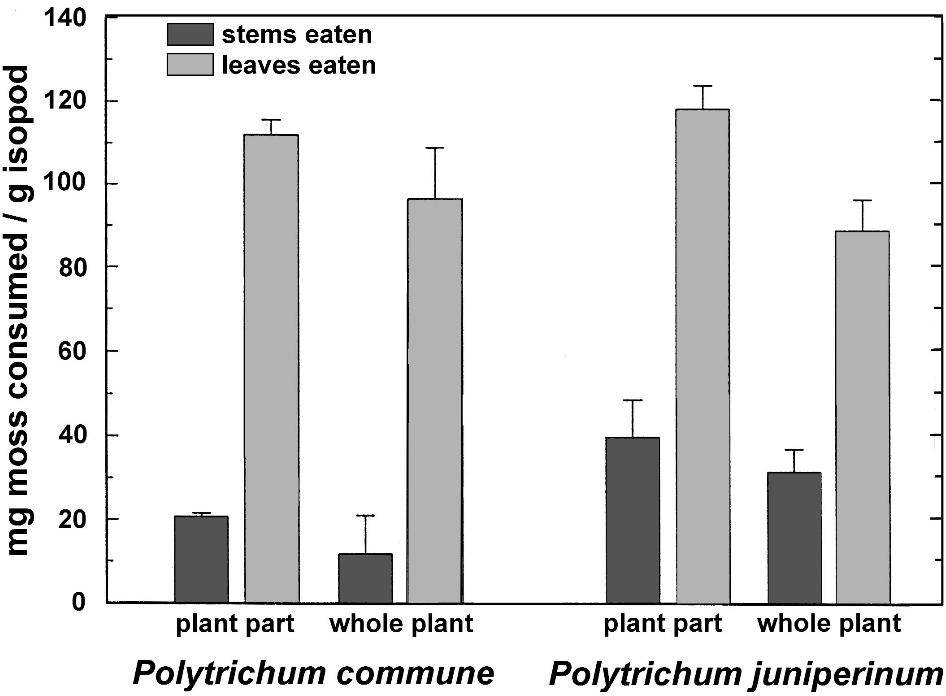

Fig. 2. Comparison of consumption by isopods (*Porcellio*) on stems and leaves of *Polytrichum commune* and *P. juniperinum*. "Plant part" indicates that only leaves or stems were provided; "whole plant" indicates stems with leaves intact were provided. Vertical bars represent 1 standard deviation. Based on unpublished data of Weston, Liao, and Glime, MTU bryology lab.

(slug) grazing. To test the hypothesis that it could be toughness, and not phenolic compounds, that deters isopods from eating stems of these mosses, our bryology lab (Weston, Liao, and Glime) provided isopods (*Porcellio* sp.) with *Polytrichum juniperinum* and *Polytrichum commune* as their sole food source and compared the phenolic content of stems and leaves.

Methods – The isopods and mosses were collected in the vicinity of Houghton, Michigan, USA. Mosses were divided into three types of food: stems alone, leaves alone, and stems with leaves for each of *P. juniperinum* and *P. commune*. For each test, the food type and isopods were placed into deli food containers (7.5-12.5 cm deep, 3 cm in diameter, n=3). A wet sponge was form-fit into the container with a form-fitted paper towel on top. Each container had approximately 100 mg of the appropriate air-dried moss parts and 500 mg of live isopods (*Porcellio*) that had been starved for 72 hours. The controls had an equivalent amount of moss with no isopods and its change in mass was used to control for moisture changes. The containers were sealed with cellophane that had small holes to allow air flow. After 72 hours, the remaining moss parts and isopod feces were removed and air-dried, then weighed separately.

Protein in each moss type was determined by the Bradford (1976) method with BSA as the standard. For each analysis, 100 mg of sample was crushed to a powder with a mortar and pestle in 3-5 ml liquid nitrogen. Samples

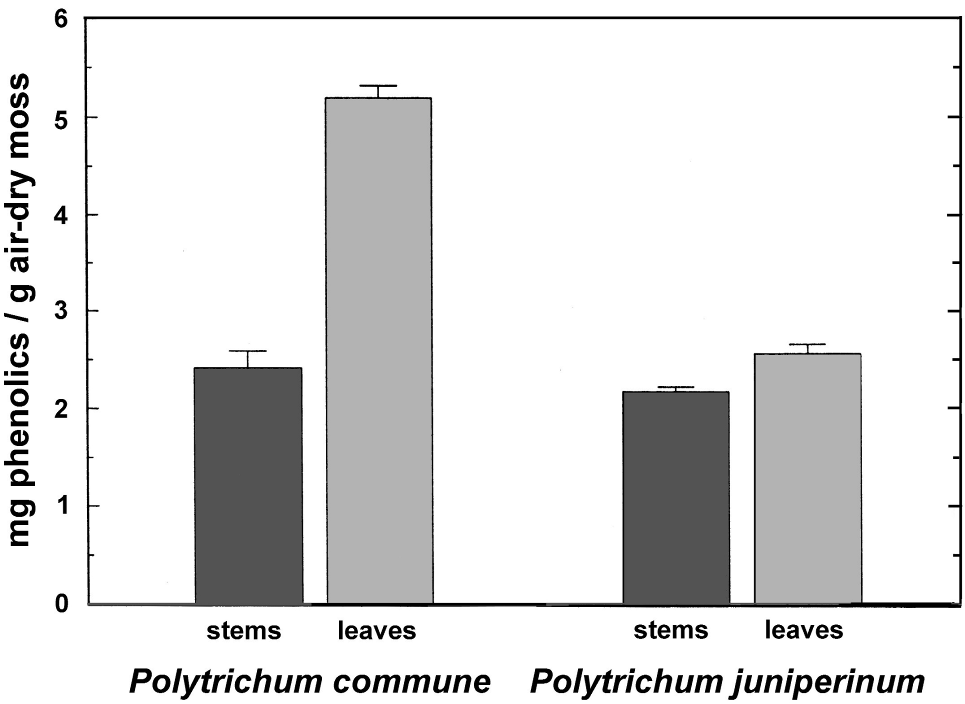

Fig. 3. Phenolic content, based on Folin-Dennis method, for *Polytrichum commune* and *P. juniperinum* stems and leaves. Vertical bars represent 1 standard deviation. Based on unpublished data of Weston, Liao, and Glime, MTU bryology lab.

were added to 1.5 ml K-phosphate buffer and vortexed for 5 seconds, then centrifuged at 12000X for 15 minutes. A tube of 820 µl solution with three replicates (10, 20, and 30 µl samples) was compared spectroscopically for each plant type to the standard BSA curve derived from 0, 5, 10, 20, 30, 40 µl BSA made up to 820 µl solution.

To measure phenolic content, air-dried moss parts (200 mg samples with three replicates) were crushed to a powder in 3-5 ml liquid nitrogen and placed in 50% methyl alcohol at 95°C, vortexed for 5 seconds, and left to cool for 24 hours. They were then centrifuged at 12000X for 20 minutes and 30, 60, and 90 µl samples of each treatment tested by the Folin-Dennis test (Swain & Hillis, 1959).

Results – In these experiments, the isopods ate significantly more leaves than stems, even when there was no other food choice (Fig. 2). Analysis showed that leaves of both *Polytrichum* species actually have a significantly higher content of phenolic compounds than do the stems (Fig. 3). Yet, isopods (*Porcellio*) ate leaves in preference to stems.

There are several possible explanations for this preference for leaves. First, the protein content is significantly higher in the leaves than in the stem (Fig. 4), making it nutritionally more valuable. And, as already discussed, the stem is tough in these *Polytrichum* species, perhaps making it more difficult to chew. Leaves are also more accessible because they would need to be removed to reach

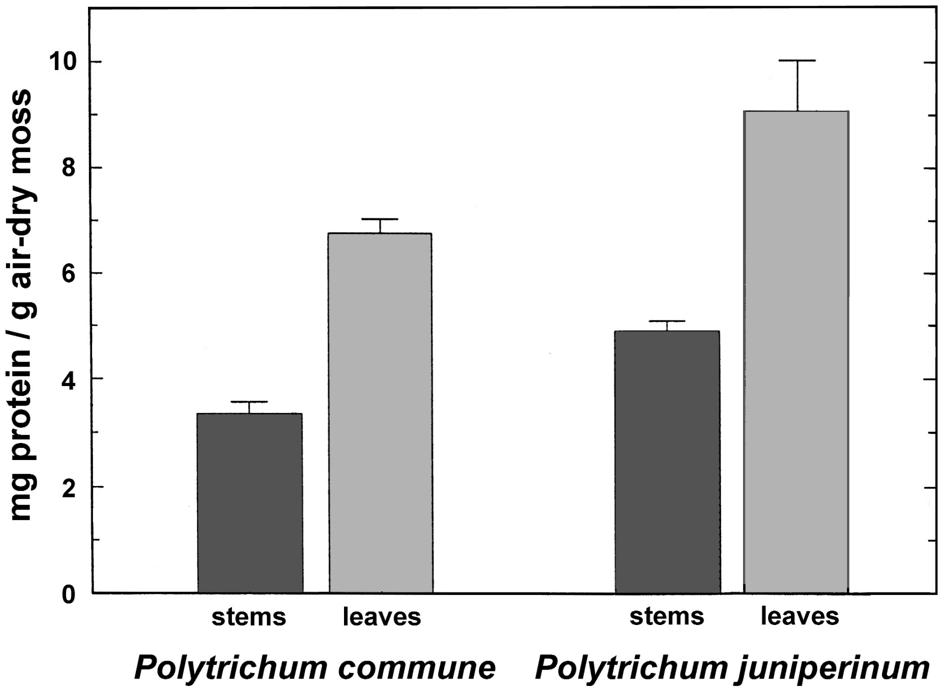

Fig. 4. Protein content, based on Bradford method (1976), for *Polytrichum commune* and *P. juniperinum* stems and leaves. Vertical bars represent 1 standard deviation. Based on unpublished data of Weston, Liao, and Glime, MTU bryology lab.

the stem, but since stems that had already had their leaves removed were likewise eaten at a lower rate than leaves alone (Fig. 2), this explanation is not supported.

Do Pillbugs Prefer Non-Apparent Mosses?

In 1976 several researchers independently proposed an "**apparency**" theory, stating that the type and degree of defensive commitment evolved by plants directly relate to the risk of discovery of the plant or plant tissue by herbivores (Feeny, 1976; Rhoades & Cates, 1976). Quantitative (dosage-dependent) defenses are characteristic of "**apparent**" plants that are easy for herbivores to locate, whereas qualitative (sensitivity to low dosage) defenses are characteristic of "**unapparent**" plants. This theory has not been tested for mosses.

Polytrichum is usually an apparent moss. Following the theory of apparency, it should therefore deter herbivory. In our lab, we have compared many taxa of apparent and unapparent mosses, but only a few will be compared here due to the loss of the phenolic and protein data. In a setup in our lab like that of the *Polytrichum* experiments above, when the pillbug *Porcellio* was given whole plants of only one of three mosses (*Polytrichum juniperinum*, *Pleurozium schreberi*, or *Thuidium delicatulum*), the pillbugs consistently consumed all of the *T. delicatulum*, all the leaves of *P. juniperinum*, and almost none of the *Pleurozium schreberi* during a week-long experiment. We have repeated this experiment many times with the same results. In boreal forest habitats, where such mosses as *Hylocomium splendens* and *Pleurozium schreberi* dominate the relatively dry conifer sites, bryophyte ground cover can be almost 100% (Longton, 1984), making the bryophytes very apparent to herbivores. Evolutionary theory suggests that the production of defensive chemicals should be greatest in habitats in which selective pressures for their use are highest (Rhoades, 1979). In this set of experiments, *Pleurozium schreberi* was the most conspicuous moss in its natural habitat and *Thuidium delicatulum* the least.

The phenolic content of *Pleurozium schreberi* was highest among the three mosses (Liao unpublished data) and could account for its being least preferred, even under starvation conditions, in these experiments. This is consistent with the findings of Smith *et al.* (2001), who found that the cranefly *Tipula montana* selected its food (bryophytes) based on maximizing growth, but with one exception. Despite growing best on a diet of *Pleurozium schreberi*, it was the least preferred moss in a series of 2-choice experiments. These few experiments suggest that there may be a connection between apparency and phenolic content, and that phenolic content may deter herbivory, but much more evidence is needed to make any generalizations for bryophytes.

Fontinalis Deters Herbivory

I have already mentioned the oily, somewhat unpleasant odor of drying *Fontinalis*. It appears that the aquatic moss *Fontinalis* is not palatable to snails, whether it is because of its structure that gets in the way of navigation or the moss itself is chemically undesirable. On the other hand, in Europe, the aquatic moss *Fissidens fontanus* is devoured by snails to the point that it does not occur in lakes with certain species of snails, unless it is able to grow among the bases of *Fontinalis* plants (Lohammar, 1954). Lohammar observed that in an aquarium snails do not eat *Fontinalis*. It appears that in lakes with these snails, the *Fontinalis* protects the *Fissidens* by surrounding it with something impenetrable or inedible.

Nevertheless, based on examination of feces, LaCroix (1996; Bowden *et al.*, 1999) has shown that the aquatic isopod *Asellus militaris* does in fact eat *Fontinalis antipyretica* in the field. In their study of *Fontinalis antipyretica* Liao and Glime (1996; Bowden *et al.*, 1999) found that this moss is not nutritionally inferior to other plants and thus should be prime food for many of the aquatic organisms that live there (Glime, 1994).

Aquatic Pillbugs Prefer Sun Plants of *Fontinalis*

LaCroix (1996) examined the relationship between the concentration of phenolic compounds and *Asellus militaris* herbivory, using *Fontinalis antipyretica* collected near Calumet, Michigan, USA. Phenolic compounds are often produced in response to stress, and for *Fontinalis*, living in full sun is often a stress condition

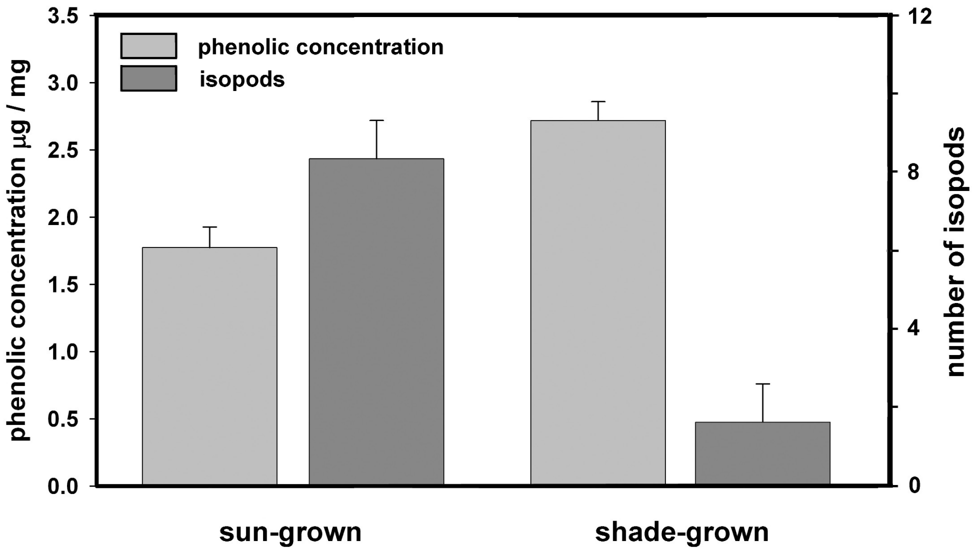

Fig. 5. Comparison of phenolic compounds (Folin-Dennis method) in sun and shade populations of *Fontinalis antipyretica* from near Calumet, Michigan, USA and the number of isopods found among branches of mosses of each type after 24 hours in an aquarium. n = 14 pairs of mosses with 10 isopods in each setup. Vertical bars represent 95% confidence intervals. Graph based on LaCroix (1996).

(Glime, 1984). LaCroix (1996), working with Liao and Glime in our lab, reasoned that if in fact *Fontinalis antipyretica* produces more phenolic compounds in full sun than in shade, it provides a means of testing effects of phenolic compound concentration within an intact set of mosses on herbivory. Surprisingly, LaCroix found that significantly higher concentrations of phenolics were produced in shady habitats, compared to sunny ones (Fig. 5). Nevertheless, this provided mosses with high and low concentrations of phenolic compounds within the same species and apparently the same physical structure.

When 10 pillbugs (*Asellus militaris*) were placed in each of 16 replicate containers (8 in 24 hours light, 8 in 24 hours dark, with paired mosses, one shade-grown and one light-grown), LaCroix (1996) found significantly more isopods on the sun-grown mosses in both light conditions (Chi-square $p<0.001$ for each experimental light condition; Fig. 5). However, in the field, he found five times as many *A. militaris* in samples from the shady habitat, indicating that preference for shade was more important to these isopods than phenolic deterrents. It would be interesting to test whether this moss produces phenolic compounds in response to herbivory. The lower content of phenolic compounds in the sun mosses contradicts the Carbon/Nutrient Balance hypothesis that predicts that secondary metabolites will be positively correlated with the carbon/nutrient ratio of the plant. Herms and Mattson (1992) indicate that shade decreases the C:N ratio by limiting carbon fixation, so we should have expected lower concentrations of phenolic compounds in the shade. However, this may not be the general case for slow-growing, shade-adapted mosses.

WHAT CONTROLS HERBIVORY?

We are far from a general answer to this question for bryophytes. However, the preceding experiments, although simple and in need of replication, indicate that bryophytes may follow many of the same principles as tracheophytes in defense against herbivory. Their high phenolic content, often exhibiting a number of different compounds presumably working together as antifeedants, suggest that these compounds may play a major role. And we know that bryophytes may distribute these compounds unequally within the plant, protecting the most vulnerable or most important part for the continuation of the species. We also know that invertebrates apparently eat some mosses and avoid others; correlations of avoidance with high phenolic content suggests that the phenolic content plays a significant role in this avoidance. But we cannot rule out physical structure and nutrient content as contributing factors to avoidance of certain species or parts of plants. And it is clear that other factors may override the phenolic deterrency in the preference of certain herbivores.

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