INVITED ESSAY

New Frontiers in Bryology and Lichenology

The Role of Bryophytes in Carbon and Nitrogen Cycling

Merritt R. Turetsky

Canadian Forest Service, Northern Forestry Centre, 5320-122 Street, Edmonton, Alberta T6H 3S5, Canada

Many chemical reactions at the Earth's surface are influenced by biota. Ecosystem ecologists study the flow of matter and energy in ecosystems composed of organisms and their abiotic environments. The study of ecosystem ecology can blur distinctions between 'basic' research and environmental management. How does our behavior (including urban development and land-use, water consumption, pollution) influence the movement of energy, water, and elements at local, regional, national or global scales? Will perturbations to chemical and energy cycles alter existing controls on ecosystem processes, and can we learn enough about them for effective regulation?

Plants are critical in regulating biogeochemical cycles. Their growth controls the exchange of gases that support life in our current biosphere, and affects soil development. As primary producers, they influence the distribution of energy for higher trophic levels. Understanding how plants influence ecosystem processes requires a multidisciplinary approach drawing on plant physiology and biochemistry, community ecology, and biogeochemistry.

Due to their unique physiology and ecology, bryophytes differ from vascular plants in influencing cycles of elements, energy, and water. For example, bryophytes have evolved an effective water relation system. Poikilohydry and desiccation tolerance allow bryophytes to tolerate longer periods of water stress than vascular plants, and to recover quickly with rehydration. With poorly developed conduction systems, water and solutes are taken up over the entire plant surface. Lack of both gametophyte stomata and effective cuticles in many species allows free exchange of solutions and gases across cell surfaces. Thus bryophytes often serve as effective traps for water and nutrients. This also makes them more sensitive to atmospheric chemical deposition than vascular plants.

Bryophytes also can tolerate a wide range of temperatures and are found in almost all terrestrial and aquatic environments, including harsh Antarctic environments where vascular plant cover is low (cf. Fogg 1998; Seppelt 1995). Without roots, bryophytes can colonize hard substrates like rock and wood that are poor habitat for vascular species. Bryophytes stabilize soils and prevent the loss of soil and nutrients via erosion, particularly on sand dunes (Martinez & Maun 1999) and in cryptogamic soil crusts (Eldridge 1999; Evans & Johansen 1999). Cation exchange on *Sphagnum* cell walls releases protons, generating acidity that may inhibit plant and microbial growth (Clymo 1963; Craigie & Maass 1966; Spearing 1972). Finally, bryophytes influence ecosystem succession (Brock & Bregman 1989) through terrestrialization of water bodies, deposition of benthic organic matter or paludification of upland systems. Bryophyte colonization often precedes the establishment of tree surfaces by other canopy-dwelling plants (Nadkarni et al. 2000).

Due to their physiology and life history traits, bryophytes influence ecosystem functions by producing organic matter, stabilizing soils or debris, trapping sediments and water, and providing food and habitat for algae, fungi, invertebrates, and amphibians. In this review, my objectives are to highlight several mechanisms by which bryophytes influence carbon (C) and nitrogen (N) cycles within and fluxes from ecosystems. As such, I will focus on how bryophytes fix, intercept, transform, and/or release C and N. My goals are to 1) introduce important processes controlling inputs and outputs of C and N in both terrestrial and aquatic ecosystems, 2) review work on the growth, decomposition, and leaching of bryophyte material, as well as biotic and abiotic controls on these mechanisms, and 3) suggest areas for future research that would advance our understanding of bryophytes in biogeochemical cycling.

Current address: U.S. Geological Survey, 345 Middlefield Rd. MS 962, Menlo Park, CA 94025 U.S.A. e-mail: mturetsky@usgs.gov

Bryophytes in Carbon Cycling

Carbon fixation by bryophytes.—One of the largest fluxes in the global C cycle is between atmospheric carbon dioxide (CO_2) and land vegetation (Houghton et al. 2001). Carbon derived from autotrophic fixation through photosynthesis comprises about half of all organic matter. Net primary production (NPP) represents the difference between gross primary production (total amount of organic matter produced per unit time) and plant respiratory losses. Net primary production on land is estimated globally at 60×10^{15} g C yr^{-1} (Schlesinger 1997).

Bryophytes directly influence the flux of C into ecosystems through their metabolism and growth rates. While estimates of bryophyte biomass have been characterized in various ecosystems, annual accumulations of C in plant material are more useful for studies of the C cycle. Carbon gains through NPP can be estimated through the net exchange of CO_2 (cf. Gaberscik & Martincic 1987; Lange et al. 1992; Tuba et al. 1998) or the annual production of biomass (cf. Clark et al. 1998; Ilyashuk 2002; Riis & Sand-Jenson 1997; Swanson & Flanagan 2001). With no need to quantify belowground root productivity, estimates of bryophyte growth can be more straightforward than for vascular plants. However, NPP measurements still can be time consuming and expensive, particularly if they involve gas sampling equipment.

Production rates of temperate, boreal, and polar bryophytes have been relatively well studied in comparison to tropical species. For example, NPP of feather mosses in the boreal forest ranges from 24–80 g C m^{-2} yr^{-1} (Bisbee et al. 2001; Swanson & Flanagan 2001). Growth rates of *Sphagnum* species vary widely, but can be very productive (Schofield 2001). For example, the growth of *Sphagnum* species in peatlands ranges from about 19–1,656 g m^{-2} yr^{-1} (data reviewed in Aerts et al. 1992; Rochefort et al. 1990; Vitt et al. 2003; biomass equal to about 48% C). Surprisingly, estimates of bryophyte NPP in polar regions can be comparable to growth in boreal or temperate regions. Fenton (1980) estimated that mean productivity of Antarctic *Polytrichum alpestre* ranges from 213–350 g m^{-2} yr^{-1} while productivity of *Chorisodontium aciphyllum* averages 162 g m^{-2} yr^{-1}.

As noted above, a better understanding of bryophyte production in tropical regions is needed to understand the importance of these plants to terrestrial C sequestration. Productivity measurements on an areal basis are important for spatial extrapolation and modeling efforts, but are more difficult to estimate for epiphytic bryophytes than for ground layer species. Clark et al. (1998) reported tropical epiphytic bryophyte growth ranging from 122–203 g biomass m^{-2} yr^{-1}. The growth of canopy and gap species (~450 mg C per gram of initial thallus C yr^{-1}; Zotz et al. 1997) may be higher than that of understory bryophytes (~36.5 mg C per gram of initial thallus C yr^{-1}; Lösch et al. 1994).

Aquatic bryophytes often dominate vegetation in lakes (cf. Riis & Sand-Jenson 1997; Sand-Jenson et al. 1999), and bryophyte NPP can exceed that of epilithic or periphytic algae (Stream Bryophyte Group 1999). Aquatic bryophyte production can be comparable to growth in terrestrial systems, but varies widely with microhabitat and among species. For example, NPP ranges from $2–21 \times 10^{-4}$ g per g dry weight hr^{-1} for Norwegian *Sphagnum* (Lannergren & Ovstedal 1983), averages 10.4×10^{-4} and 8.2×10^{-4} g C per g dry weight hr^{-1} for *Jungermannia vulcanicola* and *Scapania undulata*, respectively (Miyazaki & Satake 1985), and averages 32, 41, and 157 g biomass m^{-2} yr^{-1} for Russian *Sphagnum denticulatum*, *Warnstorfia exannulata*, and *Fontinalis hypoides*, respectively (Ilyashuk 2002).

Slow diffusion in water minimizes the access of CO_2 to aquatic plants. While the PEP carboxylase enzymes of C_4 and CAM plants use bicarbonate (HCO_3^-) ions as a substrate during photosynthesis, rubisco (ribulose 1,5 bis phosphate carboxylase/oxygenase) fixes CO_2. The ability to utilize HCO_3^- was detected for some bryophytes (Penuelas 1985), but generally was inefficient (Bain & Proctor 1980). Many aquatic bryophytes will fix only free CO_2 (Glime & Vitt 1987; Raven et al. 1994). However, MacDonald et al. (1987) found that aquatic *Drepanocladus crassicostatus* gave older than expected ages because of uptake of ^{14}C-deficient C from an unknown source. Dissolution of old carbonate leads to a reduction of ^{14}C in dissolved C pools compared to the atmospheric C reservoir. Isotopic exchange in inorganic C species also will cause a ^{14}C-reduction in CO_2, and bryophyte assimilation of this ^{14}C-depleted C (as CO_2 or HCO_3^-) would lead to radiocarbon age estimates older than actual ages.

Controls on bryophyte growth.—Photosynthetic efficiency in bryophytes is internally controlled by factors such as the rate of photosystem electron transport (Schroeter et al. 1999) and leaf or plant morphology (Krupa 1984; Proctor 1982a). Environmental factors such as water, light, and nutrient availability also strongly influence C fixation by terrestrial bryophytes. Canopy photosynthetic active radiation (PAR) transmittance was significantly but weakly correlated to boreal feather moss production, but was not correlated to *Sphagnum* production (Bisbee et al. 2001). Increasing photoperiod length and radiation flux promoted the production of temperate *Sphagnum* species, and the combina-

tion of declining photoperiod length and night temperatures induced dormancy in these mosses (Gerdol 1995).

Generally both high and low water contents can limit C uptake (cf. Jauhiainen & Silvola 1999; Schipperges & Rydin 1998; Silvola 1991; Titus et al. 1983; Zotz et al. 1997). Low water availability can inhibit photosynthetic enzyme activity, while slow CO_2 diffusion can be limiting at water saturation (Tuittila 2000; Williams & Flanagan 1996). Water contents below 500% were associated with declining photosynthetic rates of most *Sphagnum* species (Titus et al. 1983). Beckett (2001) found that basal stem segments of *Atrichum androgynum* were more sensitive to desiccation than apical segments. Using carbon isotopic discrimination (measure of the uptake of $C^{13}O_2$ relative to $C^{12}O_2$), Rice (2000) concluded that water limitation lowers chloroplastic demand and increases resistance to C uptake in vascular plants, but decreases resistance to C uptake in *Sphagnum* species.

Bryophyte response to water stresses; however, varies among species. Davey (1997) reported greater photosynthetic declines during dehydration in hydric than in xeric Antarctic species. Yet absolute rates of C fixation were higher in the hydric species throughout dehydration due to their high initial fixation rates (see also Lewis Smith 1999). High water content was most stressful for the cushion moss *Leucobryum antillarum*, while the growth of other tropical species, including *Frullania mirabilis*, *Herbertus divergens*, *Holomitrium terebellatum*, *Macromitrium cirrosum*, and *Phyllogonium fulgens*, was more limited by low water availability (Zotz et al. 1997). While future precipitation patterns are difficult to predict, it seems clear that altered moisture availability could substantially influence bryophyte growth.

As N is thought to limit plant growth in many terrestrial systems, bryophyte productivity commonly increases following N or combined N and phosphorus (P) additions (cf. Aerts et al. 1992; Gordon et al. 2001; Robinson et al. 1998; Rochefort et al. 1990; Smith 1993; Vitt et al. 2003). Fertilization may have long-lasting influence on bryophyte communities. Strengbom et al. (2001) found that bryophytes such as *Brachythecium reflexum* and *Plagiothecium denticulatum* were more abundant in experimental plots than in control areas 47 years following N applications. Other studies, however, have reported no changes or decreases in bryophyte growth with nutrient additions (Bergamini & Peintinger 2002; Davey 1999; Graglia et al. 2001; Press et al. 1998; Thormann & Bayley 1997; Walker et al. 1996), or have found differential responses among species (cf. Austin & Wieder 1987; Bates 1994; Gordon et al. 2001; Mitchell et al. 2002).

The response of bryophytes to increasing N availability may depend on the history of background N deposition, as plants in areas of high N deposition may actually be limited by phosphorus or water (cf. Aerts et al. 1992; Baxter et al. 1992). Gunnarsson and Rydin (2000) and Vitt et al. (2003) suggested that *Sphagnum fuscum* NPP is inhibited above critical N loading rates between 14–34 kg ha^{-1} yr^{-1}. Higher deposition rates can exceed plant tolerance levels, potentially with toxic effects (Aerts et al. 1992; Gunnarsson & Rydin 2000) or may increase the competitiveness of vascular plants.

Understanding abiotic limitations on bryophyte productivity is essential for modeling plant growth under changing climatic or pollution regimes. Will N deposition stimulate bryophyte growth in various environments, or is primary productivity limited by water or phosphorus availability? If N pollution creates a fertilizer effect, will this response be short-lived (cf. Rochefort et al. 1990)?

Phosphorus tends to limit primary productivity in aquatic systems, and high P inputs have been correlated to high bryophyte productivity (Arscott et al. 1998). Productivity of aquatic bryophytes also can be limited by substrate stability (Englund 1991), light, or C (Wetzel et al. 1985). Growth rates of *Sphagnum subsecundum* and *Drepanocladus exannulatus* were greater at depth than near the surface in a Denmark lake, with deeper waters characterized by low temperatures, CO_2 supersaturation, and high nutrient enrichment (Riis & Sand-Jensen 1997). Boundary-layer resistance to C fixation may limit photosynthesis at low water-flow velocities, but this limitation is dependent upon plant morphology (Jenkins & Proctor 1985).

Dissolved organic carbon.—Carbon can be leached from plant biomass as dissolved organic carbon (DOC) (Moore & Dalva 2001). Microbes can readily utilize labile DOC. Remaining DOC can be comprised of highly refractory compounds with complex structures. Therefore, DOC can be utilized by microbes or can be lost from terrestrial ecosystems via runoff. Terrestrial DOC is transported to lakes (Stepanauskas et al. 2000), estuaries (Hopkinson et al. 1998; Raymond & Bauer 2001*a*) and oceans (Bauer et al. 2001; Hedges et al. 1997; Lobbes et al. 2000; Mitra et al. 2000; Raymond & Bauer 2001*b*), and represents an important transfer of energy and carbon from terrestrial to aquatic systems. Dissolved organic carbon has important chemical and ecological consequences in aquatic systems, as it alters the production of greenhouse gases, acid-base chemistry, trace metal speciation, P and N availability, and light attenuation (Bushaw et al. 1996; Gergel et al. 1999; Schindler & Curtis 1997).
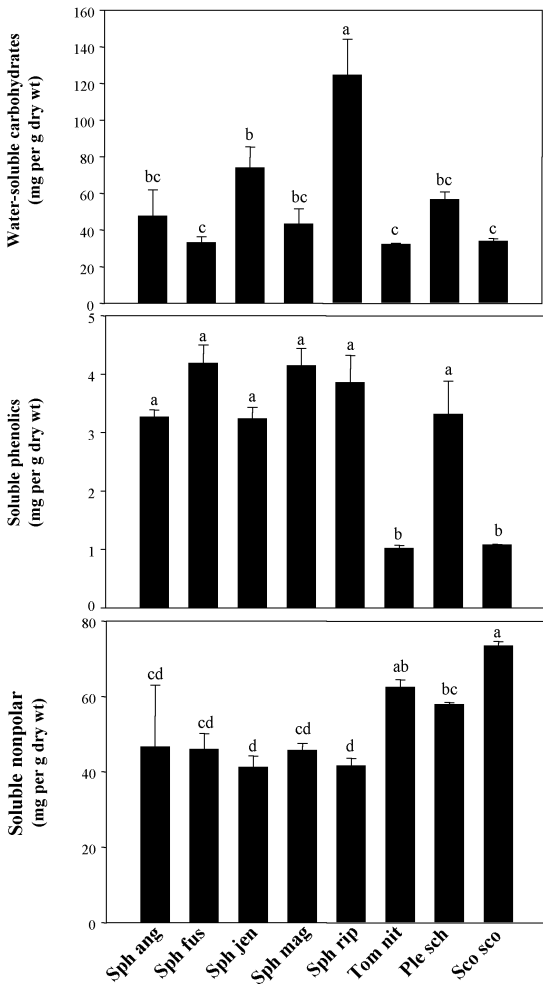
FIGURE 1. Concentrations of soluble components of moss litter collected from Canadian peatlands (data from M. Turetsky & S. Crow pers. comm.), including hot water-soluble carbohydrates, hot water-soluble phenolics, and soluble nonpolars (lipids). Data are means ± one standard error. Same letter superscripts denote non-significant comparison of means (one way ANOVA; species $p < 0.05$).

Plants influence DOC leaching through the production of soluble organic compounds. Bryophyte species common to boreal peatlands differ in water-soluble carbohydrates, phenolics, and soluble nonpolar compounds (Fig. 1). Concentrations of soluble sugars and polyols comprised up to 17% of *Frullania atrata* dry weight in the upper canopy of a montane rainforest, but were equivalent to only 6% of *Phyllogonium fulgens* dry weight in the lower canopy (Coxson et al. 1992). Pakarinen and Vitt (1974) concluded that greater amounts of soluble proteins and carbohydrates are associated with higher metabolic activity in green moss tissue and in hydric habitats.

Flushing of soluble organic compounds decreas-

es the retention of C in plant and litter layers. Solute flushing is related to bryophyte desiccation tolerance. Carbohydrate pools that accumulate during dehydration can be leached during rewetting (Proctor 1982*b*; Wilson & Coxson 1999). Wilson & Coxson (1999) measured pulse releases of organic C equivalent to ~15 kg ha^{-1} from mats of subalpine *Hylocomium splendens* following rain events. Between 23–75% of this soluble C originated from the living *Hylocomium* mats. The release of soluble sugars from epiphytic bryophytes in tropical forest is equivalent to 122 kg ha^{-1} yr^{-1} (Coxson et al. 1992). Carleton and Read (1991) measured carbohydrate leakage from *Pleurozium schreberi* following drying events, and concluded that these carbohydrate-rich leachates are capable of supporting mycorrhizal fungal growth. Soluble carbohydrates also can be transferred to infected *Pinus contorta*.

Some DOC in peatlands is transported downwards into the peat and can be taken up by microbes (Charman et al. 1999; Chasar et al. 2000). Dissolved organic C also can be exported from peatlands, and DOC in streams and lakes tends to increase with the area of wetlands or peatlands in the watershed (Carpenter et al. 1998; Elder et al. 2000; Schindler et al. 1997). DOC export can be a significant loss of C from terrestrial ecosystems, and was equivalent to 12% of an ombrotrophic bog's annual C storage (Fraser et al. 2001).

Leaching of DOC from peatlands may increase with warmer temperatures and accelerated decay (Freeman et al. 2001), permafrost degradation, or drought-rewetting cycles (Fenner et al. 2001), or may decrease in response to drier conditions under low runoff (Moore et al. 1998). More research is needed to understand the long-term fate of bryophyte-derived DOC in terrestrial and aquatic ecosystems.

Decomposition and implications for soil carbon.—As plants die, C in organic matter is degraded through bacterial and fungal respiration. Generally, decomposition rates vary as a function of temperature, moisture, and the chemical composition of litter. Bryophytes may influence microbial activity by providing microhabitat for invertebrates (cf. Gersen 1982; Merrifield & Ingham 1998) that can break down soil particles and increase surface area for microbial activity. Bryophytes also can harbor microfungi that decompose organic C (cf. Thormann et al. 2002; Tsuneda et al. 2001). Bryophytes also influence decay by reducing soil temperatures and/or increasing soil moisture (Eckstein 2000; Sveinbjornsson & Oechel 1992; Van Cleve et al. 1983). Bryophytes have low thermal conductance, and can increase water availability through external capillary action. Wetter soils reduce the efficiency of aerobic heterotrophic respiration, and

can create anaerobic hotspots, possibly leading to the production of trace gas such as carbon dioxide and nitrous oxide.

Bryophytes appear to produce litter with poor organic matter quality. Bryophytes are not able to synthesize lignin, which is broken down by few microorganisms. Therefore, it seems reasonable to expect that bryophyte litter would decay more rapidly than vascular material. However, bryophytes generally produce organic matter that decomposes very slowly. For example, moss litter decomposed more slowly than vascular litter in a broad leaf forest in southwestern China (Liu et al. 2000), Scots pine forest (Berg 1984), boreal peatlands (Aerts et al. 1999; Thormann et al. 2001), Alaskan tundra (Hobbie 1996), and in sub-Antarctica (Smith & Walton 1986).

Slow rates of bryophyte decomposition could be caused by low N concentrations, particularly in *Sphagnum* material with an abundance of dead hyaline cells. Large concentrations of phenolics and nonpolar compounds in bryophyte tissue also will inhibit decay. Water-soluble phenolics (see Fig. 1) are actively excreted by some *Sphagnum* species (Rasmussen 1994). Polyphenolic networks with structures similar to vascular lignins or tannins have been identified in mosses (Verhoeven & Liefveld 1997; Williams et al. 1998; Wilson et al. 1989). These compounds can mask cellulose, further inhibiting microbial breakdown (Verhoeven & Liefveld 1997) and can make cell walls impenetrable to fungal hyphae.

Bryophytes may also have antimicrobial properties. Verhoeven and Toth (1995) showed that the addition of *Sphagnum* homogenates to *Carex* and *Sphagnum* litter inhibited the decay of both plant types. Flavanoids isolated from five species of mosses had antibacterial effects against *Enterobacter cloaceae*, *E. aerogenesm*, and *Pseudomonas aeruginosa* (Basile et al. 1999). Banderjee and Sen (1979) tested the antibiotic activity of 52 bryophyte species, and found that 56% of all species were active against at least one bacterial species.

Bryophyte tissue is strongly chelating (cf. Painter 1991), so competition for essential metals may limit microbial activity (Basiliko & Yavitt 2001). Finally, bryophytes tend to have high cation exchange capacity, and acidity generated through proton release from cation exchange sites (cf. Clymo 1963; Spearing 1972) may inhibit microbial populations and/or activity.

Decomposition rates, however, can differ widely among bryophyte species. Most notably, the common peatland hummock species, *Sphagnum fuscum*, decays more slowly than other mosses in a range of microhabitats (Belyea 1996; Johnson & Damman 1991; Rochefort et al. 1990; M. Turetsky & S. Crow, pers comm.). Understanding species-specific decay rates in relation to biomass production and tissue chemistry may help in identifying the mechanisms controlling the slow breakdown of bryophyte litter, and hence the accumulation of dead bryophyte remains as peat.

Peat accumulates where net primary production at the surface exceeds C losses throughout the soil column via decomposition, leaching, herbivory, fire, and other disturbance losses. Bryophyte remains are major components of peat deposits at northern latitudes (Fig. 2), and are important to soil C sequestration (cf. Harden et al. 1997; Rapalee et al. 1998). For example, bryophytes are estimated to comprise about half of the total peat density from 620 archived peat cores from continental Canada (Fig. 2; data catalogued in Zoltai et al. 2000). As noted above, peat accumulation may be promoted in some environments by the recalcitrant nature of bryophyte material. Additionally, losses of organic matter through herbivory tends to be lower for bryophyte litter than for many vascular plants (see Longton 1992; Pakarinen & Vitt 1974). Increased soil moisture also may accelerate peat accumulation by limiting aerobic decomposition and by diminishing intense fire combustion.

BRYOPHYTES AND NITROGEN CYCLING

Biological nitrogen fixation.—The atmosphere represents the largest global pool of N (Schlesinger 1997). In terrestrial ecosystems, N often is the most limiting nutrient to plant production. Plants need N for the production of chlorophyll and rubisco, and for proteins and nucleic acid construction. Nitrogen inputs to ecosystems include biological fixation, atmospheric deposition, and weathering. While anthropogenic deposition now doubles biological N fixation globally, the largest source of N in many pristine ecosystems is biological fixation. Certain prokaryote microorganisms use the nitrogenase enzyme to break the triple bonds of atmospheric N_2 and fix it into more soluble N species. Nitrogen fixation requires the expenditure of large amounts of energy (energy of N·N bond is 940 kJ/mol), some of which is supplied by metabolizing organic C. Symbiosis occurs between N-fixing cyanobacteria and hosts such as algae, fungi, bryophytes, and vascular plants. Thus, bryophytes influence biological N_2 fixation by forming facultative symbioses with cyanobionts such as *Nostoc* spp. (cf. DeLuca et al. 2002; Rai et al. 2000). The cyanobacteria can be epiphytic or endophytic, and can establish in a number of localities including gametophyte cavities and leaf crevices or margins (Dalton & Chatfield 1985; Granhall & Selander 1973; Rai et al. 2000).
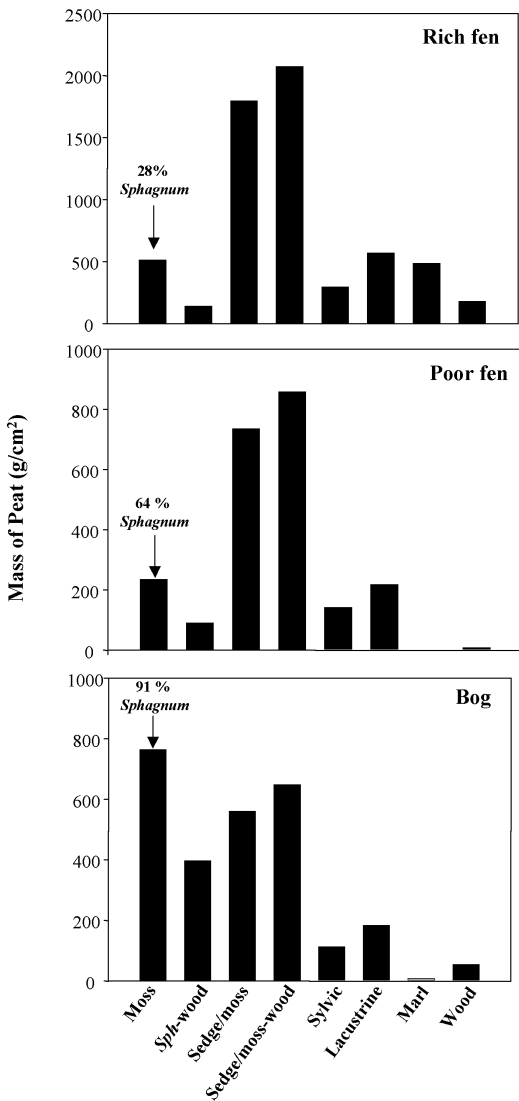
FIGURE 2. Mass of various peat types from approximately 620 peat cores collected in bogs, fens, swamps, and marshes across western Canada (catalogued in Zoltai et al. 2000). Each bar represents the cumulative mass of a single peat type in g cm^{-2}. I estimate that bryophytes comprise 45% of the total archived boreal peat while sedges and wood/sylvic material comprise 27% and 9% of boreal peat, respectively (assuming that *Sphagnum* with wood, sedge-moss, and sedge-moss with wood is 95%, 50%, and 47.5% moss-derived, respectively).

During N fixation, the cyanobiont receives carbohydrates (Steinberg & Meeks 1991) and provides N to hosts. Meeks et al. (1983) concluded that ammonium (NH_4^+) is the initial product of N fixation by symbiotic *Nostoc* associated with the hornwort *Anthoceros punctatus*. A small portion of N_2-derived ammonium (~10%) is assimilated by *Nostoc* and the remaining product is transferred efficiently to host tissue and utilized as amino acids. Basilier

(1980) showed that N fixed and exuded by *Nostoc muscorum* is readily transported along *Sphagnum* stems.

Many studies have quantified spatial patterns of N fixation, mainly through ^{15}N tracer applications or the acetylene reduction assay (i.e., acetylene is reduced by the enzyme nitrogenase to ethylene; requires use of a conversion rate between acetylene reduction and N fixation). For example, liverworts are important to N fixation in Hawaiian forests (Vitousek 1994), while soil crusts with *Bryum* spp. have higher fixation rates than crusts without moss in prairie grasslands (Giddens 1982). *Hapalosiphon flexosus-Sphagnum erythrocalyx* associations contribute about 400 mg N m^{-2} yr^{-1} on a tropical volcanic dome (Sheridan 1991). Polar bryophyte-cyanobacteria fixation range from 46–192 mg N m^{-2} yr^{-1} in Antarctica (Christie 1987; Davey & Marchant 1983; Nakatsubo & Ino 1987), and average 20 mg N m^{-2} yr^{-1} for associations with sub-Antarctic *Racomitrium lanuginosum*, *Jamesoniella colorata*, *Blepharidophyllum densifolium*, and *Clasmatocolea humilis* (Smith & Russell 1982).

Evidence for N fixation by associations between cyanobacteria and *Sphagnum* spp. is conflicting. Urban and Eisenreich (1988) concluded that N fixation rates (0.5–0.7 kg N ha^{-1} yr^{-1}) in a *Sphagnum*-dominant peatland were small compared to N deposition (10.4 kg N ha^{-1} yr^{-1}). Schwintzer (1983) did not find N-fixing cyanobacteria in association with *Sphagnum* in a minerotrophic peatland, while Basilier (1979) found that N fixation in coniferous forests occurred only with *Sphagnum* plants. *Sphagnum* symbioses contribute about 25 g N yr^{-1} to an entire aquatic system in Norway (Lannergren and Ovstedal 1983), and up to 20 g N ha^{-1} yr^{-1} to a subalpine forest ecosystem (Lambert & Reiners 1979).

Moisture availability appears to be important to N fixation (cf. Bentley & Carpenter 1980; Billington & Alexander 1983; Davey & Marchant 1983; Wojciechowski & Heimbrook 1984). For example, Line (1992) concluded that sub-Antarctic plants supporting N fixation, including *Jamesoniella colorata*, *Ditrichum strictum*, and *Andreaea* spp., were associated with moisture wicking through densely packed stems and leaves. However, Nakatsubo and Ino (1986) reported that mosses growing on dry sand in East Antarctica have higher N fixing activity than wet mosses near streams. Temperature also is a strong control on N fixation in polar regions (Davey & Marchant 1983; Smith & Ashton 1981).

Global change and altered land use could influence N fixation rates. Increased precipitation stimulates N fixation in cyanobacteria-*Hylocomium splendens* associations, while enhanced UV-B ex-

posure decreases fixation in cyanobacteria-*Sanionia uncinata* (Solheim et al. 2002). Disturbance has a negative influence on N fixation by microbiotic soil crusts in Colorado, causing 25–75% decreases in soil N (Evans & Belnap 1999), but wind or volcanic disturbance increases fixation by tropical *Hapalosiphon flexosus-Sphagnum erythrocalyx* (Sheridan 1991). High N fixation under bryophyte mats following fire may have replenished soil N in a Mediterranean forest (De Las Heras et al. 1996). Thus, disturbances can positively or negatively influence N fixation rates. However, interactions between climate and disturbance likely will be important to N fixation rates and N availability for plants and microbes.

Nitrogen assimilation by bryophytes.—Plants generally have access to inorganic N (ammonia and nitrate) and/or organic (cf. Lipson & Näsholm 2001) N. Absorption of N oxides by plants tends to be highest in areas of high metabolic activity. Once assimilated, NO_3^- and nitrite (NO_2^-) are reduced. Woodin and Lee (1987) measured high nitrate reductase activity (which catalyzes the reduction of nitrate to nitrite in plants) in *Sphagnum* capitula, and declining activity with depth throughout the stems. Nitrate reductase does not have a long lag phase in *Sphagnum*, allowing the plants to capitalize on even short-lived inputs of nitrate (Jauhiainen et al. 1998). Cultured cells of some bryophyte species; however, did not grow in media with NO_3^- as the sole N source (Takio 1994).

Bryophytes generally assimilate NH_4^+ more readily than NO_3^- (Brown 1992; Jauhiainen et al. 1998; Schuurkes et al. 1986). Liverworts such as *Jungermannia vulcanicola* and *Scapania undulata* used NH_4^+ as their major N source, with uptake rates ranging from 0.019–0.058 mg N per g dry weight hr^{-1} (Miyazaki & Satake 1985). Aquatic alpine bryophytes took up NH_4^+ at average rates of 4.3 mg m^{-2} hr^{-1} (Kopacek & Blazka 1994). Kahl et al. (1997) used ^{15}N-NMR to show that *Sphagnum fallax* incorporated $^{15}NH_4^+$ into glutamine and glutamate amino acids.

Low pH may inhibit NO_3^- assimilation (Rudolph et al. 1993), and acid-tolerant aquatic species such as *Sphagnum* and *Drepanocladus* rely heavily on NH_4^+ for N requirements (Glime 1992; Roelofs et al. 1984; Schuurkes et al. 1986). However, Press and Lee (1982) argued that *Sphagnum* mosses are adapted to low concentrations of both NH_4^+ and nitrate, the latter received largely during precipitation events. High NH_4^+ concentrations can suppress the activity of glutamine synthetase (primary enzyme of ammonia assimilation) (Baxter et al. 1992). Additionally, NH_4^+ can inhibit nitrate reductase activity and/or enhance the degradation of the induced enzyme (Rudolph et al. 1993). Ammonium

accumulation is associated with declining nitrate reductase activities in *Racomitrium lanuginsum*, *Rytidiadelphus loreus*, *Philonotis Fontana* and *Sphagnum* species (Rudolph & Voigt 1986; Soares & Pearson 1997; Woodin & Lee 1987).

Plants may utilize organic N for growth, particularly under N-limitation (Chapin et al. 1993; Näsholm et al. 2000; Streeter et al. 2000). Bryophytes are able to take up organic N such as amino acids or dipeptides (Brown 1992; Simola 1975, 1979). Kielland (1997) concluded that organic N is an important N source for arctic *Sphagnum rubellum* and *Cetraria richardsonii*.

Bryophytes generally are very efficient in assimilating N, and appear to rely mainly on atmospheric deposition. Tracer studies using ^{15}N highlight the mechanisms of N uptake and retention by plants under field or laboratory conditions. Li and Vitt (1997) showed that the moss layer in boreal peatlands captured nearly all of the ^{15}N label added as atmospherically deposited N. Mosses were more efficient at taking up added N than higher plants in an arctic wetland (Kotanen 2002), and an oligotrophic fen (Francez & Loiseau 1999). However, Lamontagne et al. (2000) showed that ground layer communities of lichens, mosses, and grasses on the Canadian shield absorbed less ^{15}N label than was stored in woody islands of *Picea mariana* and *Pinus banksiana*.

Bryophytes are competitive scavengers of N and reduce N availability for higher plants (cf. Svensson 1995). Vascular plants appear to differ from bryophytes in their N-use strategy, relying mainly on N mineralized from litter or soils taken up through roots (Bowden 1991; Malmer et al. 1994; Weber & Van Cleve 1984). *Sphagnum* species in particular are extremely efficient at capturing N, as the entire plant is able to absorb nutrients (Rudolph et al. 1993; Woodin & Lee 1987). Li and Vitt (1997) concluded that *S. fuscum* is more efficient at ^{15}N absorption than is *Tomenthypnum nitens* in boreal peatlands. Nitrogen uptake is more efficient in hummock species (i.e., *Sphagnum fuscum* and *S. rubellum*) that occur in dense canopies than in hollow species (i.e., *S. fallax*, *S. magellanicum*, *S. papillosum*, *S. pulchrum*) (Jauhiainen et al. 1998). *Hylocomium splendens* also shows efficient nutrient acquisition and recycling in subarctic woodlands, with N retained in biomass for 3–10 yrs (Eckstein 2000). Nitrogen-use efficiency in mosses at least partly is related to recycling during senescence. Eckstein and Karlsson (1999) observed *Hylocomium splendens* and *Polytrichum commune* recycling N from older segments into current year's growth. Older biomass turned brown during this N reallocation.

Epiphytic bryophytes may play an important role

in N cycling within canopies, though less is known about their N-use efficiency. Tropical epiphytes accumulated 1.8–3.0 g N m^{-2} yr^{-1} (Clark et al. 1998). Approximately 19 ± 2 and 45 ± 3% of this N was lost following two years of decomposition in the canopy and on the forest floor, respectively. Thus, annual net accumulation in epiphytic biomass was estimated at 0.8–1.3 g N m^{-2} yr^{-1} (Clark et al. 1998).

Nitrogen loading and bryophyte assimilation.— Nitrogen oxides or NH$_4^+$ concentrations in wet and dry deposition vary spatially, depending largely on regional sources of combustion, animal husbandry, and/or fertilizer production. Bryophytes tend to become less efficient at retaining N under high deposition (Aerts et al. 1992; Woodin & Lee 1987). Boreal *Dicranum majus* and *Pleurozium schreberi* were efficient in capturing ^{15}N at low dosages of 0.5 kg N ha^{-1}, but became less efficient at higher loading rates (Nordin et al. 1998; see also Aerts et al. 1992 for *Sphagnum*). Ammonium nitrate (NH$_4^+$NO$_3^-$) applications increased amino acid concentrations in *Sphagnum* (Nordin & Gunnarsson 2000) but NH$_4^+$ alone decreased organic acid concentrations in other bryophytes (Soares & Pearson 1997). Generally, N loading can alter plant productivity and patterns of N retention, and can also influence community composition by favoring nitrophilous species.

Bryophytes often are used in monitoring programs as indicators of N pollution in terrestrial and aquatic ecosystems (cf. Lopez et al. 1997; Penuelas & Filella 2001; Pitcairn et al. 2002; 1995; Woolgrove & Woodin 1996). Due to high cation exchange, mosses are efficient at sequestering nutrient cations (Bates 1994) and can take up compounds even at low concentrations. Pearson et al. (2000) used N concentrations and δ^{15}N values in mosses to document pollution sources. Urban pollution was dominated by N oxides (NO$_x$) leading to positive δ^{15}N values, while rural pollution was associated with ammonium (NH$_4^+$) yielding negative isotopic ratios.

Mosses also have been used for temporal assessments of N deposition. Woolgrove and Woodin (1996) documented increases in the N content of *Kiaeria starkei* over the past century. In addition, moss specimens from a Spanish herbaria showed declining δ^{15}N values and increasing N concentrations during the second half of the 20th century, marking the rise of N pollution (Penuelas & Filella 2001).

Nitrogen transformations and losses.—Due to the rapid uptake of N by plants and microbes, the majority of soil N occurs in organic forms. The release of N from organic matter is driven largely by microbial activity. However, similar to C cycling mechanisms described above, bryophytes may reduce the loss of organic N from ecosystems by decreasing decomposition, herbivory, and fire combustion. Nitrogen retained in recalcitrant compounds such as phenolics may be protected from microbial activity (Berg 1984). Clark et al. (1998) concluded that tropical epiphytic bryophytes sequester N largely from atmospheric deposition, converting inorganic N in mobile form into recalcitrant biochemical compounds. However, bryophytes may increase N availability for vascular plants if N slowly released from the breakdown of bryophyte litter can be taken up more efficiently (Oechel & Van Cleve 1986).

Dissolved organic N (DON) is released from plant organic matter through microbial breakdown or plant leaching. Protein N was leaked from both green and senescent segments of *Pleurozium schreberi* during drying events (Carleton & Read 1991). Williams et al. (1999) measured 0.03% of a ^{15}N label originally added as ammonium nitrate as DON in *Sphagnum* cores. Dissolved organic N concentrations from *Sphagnum capillifolium* were proportional to the amount of added inorganic N, but did not show the same relationship for *S. recurvum* (Williams et al. 1999).

Dissolved organic N can be exported from terrestrial ecosystems via runoff if it is not immediately immobilized. Chapman et al. (2001) found correlations between DON and DOC in upland streams. Unlike DOC, however, DON was not related to the amount of peatland cover in the catchment.

CONCLUSIONS AND FUTURE DIRECTIONS

Bryophytes generally fix C and N from atmospheric pools, reduce N availability for vascular plants and microbes, release dissolved compounds that are immobilized by soil microbes or lost via runoff, and transform C and N into recalcitrant organic matter. Bryophytes also can influence local soil climates by increasing soil moisture, decreasing soil temperatures, and changing the density of soil organic matter. Thus, bryophytes influence the apportionment of C and N ecosystem inputs, and indirectly influence the rate at which these elements are lost from ecosystems through litter decay, fire, and herbivory (Fig. 3). The field of bryogeochemistry will continue to develop as scientists merge traditional fields such as plant physiology, population and community ecology, geochemistry, and ecosystem modeling. Besides the questions and issues highlighted above, there are several knowledge gaps inhibiting our understanding of bryophytes in C and N cycling.

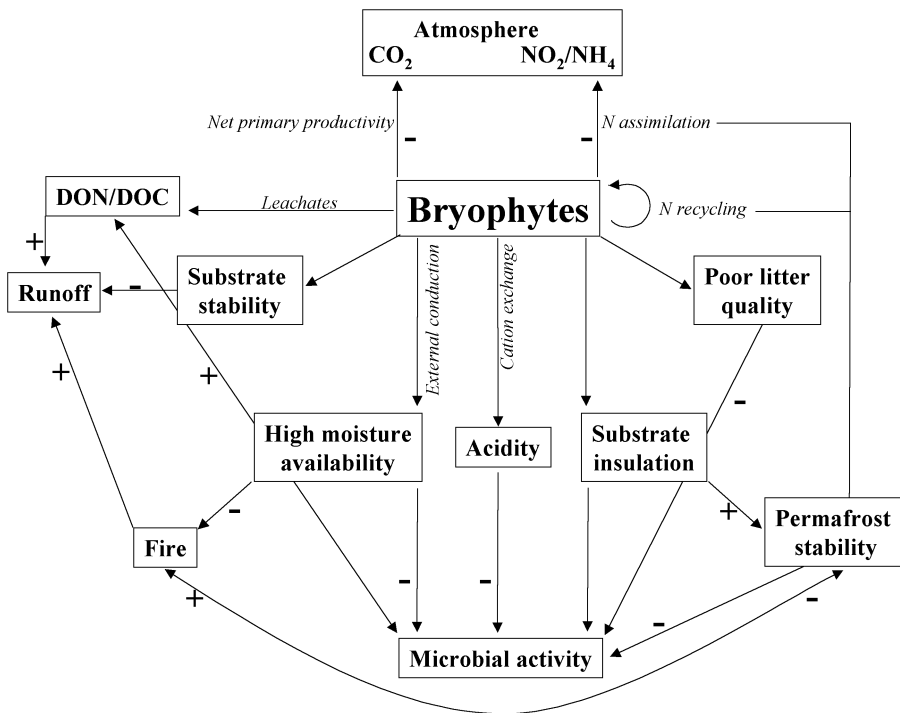i) Much of the research on bryophyte productiv-

FIGURE 3.   Schematic summarizing the influences of bryophytes on carbon and nitrogen cycling in terrestrial ecosystems, including positive (+) and negative (−) influences on microbial activity, fire and runoff.

ity has focused on mosses (Schofield 2001). More information on C and N retention by liverworts and hornworts will provide a more general understanding of nutrient cycling in and by Bryophyta *sensu lato*. Future efforts also should focus on tropical bryophytes, particularly looking at processes measured on an aerial basis,

ii) Bryophytes should clearly not be labeled as a single functional group. Recent work shows that bryophyte species respond differently to water and N limitations, and UV-B exposure, and that litter from various species decays differently. Can we group bryophytes in various ecosystems into useful categories (based on habitat, desiccation tolerance, life histories, etc.) that will be useful in predicting their role in biogeochemical cycling (see Chapin et al. 1996)?

iii) Biochemical and decomposition studies suggest that bryophyte material is of poor litter quality, yet we need a better understanding of the mechanisms controlling bryophyte chemistry (see Aerts et al. 1999; Hobbie 1996). How does litter quality vary among species or functional groups, and how does it influence more permanent C and N storage in ecosystems?

iv) Can bryophyte productivity be effectively scaled, for example, using ecosystem models or the normalized difference vegetation index (NDVI; see Bubier et al. 1997; Karnieli et al. 1996)?

v) How will changes in species diversity influence ecosystem processes or controls on ecosystem processes? Is genetic diversity also an important factor?

vi) What are the tolerance levels of various bryophyte species to N deposition? Will species disappear in response to N pollution (see Lee & Studholme 1992)? Does N deposition alter bryophyte biochemistry (Rasmussen 1994) and how will this influence litter and soil decay?

vii) Gignac and Vitt (1994) concluded that warmer and drier climates in western Canada will lead to decreased peatland area and bryophyte abundance. How will bryophytes in other regions or ecosystems respond to future climate and/or land use? Will global warming influence bryophyte chemistry, and how will this influence DOC leaching, C turnover, and C storage in ecosystems?

There are many exciting research opportunities available for the plant ecologist, biogeochemist, or budding bryogeochemist. Ultimately, understanding the role of bryophytes in the movement of elements, energy and water will be important contributions to our knowledge of both aquatic and terrestrial ecosystems.

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