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INVITED ESSAY

New Frontiers in Bryology and Lichenology

The Role of Bryophytes in Carbon and Nitrogen Cycling

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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.

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