

# SPECIAL FEATURE

## Within-Stand Nutrient Cycling in Wetland Ecosystems<sup>1</sup>

Within-stand nutrient-cycling studies have occurred primarily in temperate and tropical terrestrial ecosystems where plants generally have well-developed conservation mechanisms. We sought to determine the degree to which the findings and hypotheses developed from studies of terrestrial ecosystems were applicable to wetland ecosystems and, where appropriate, to develop new ideas and hypotheses relevant to wetlands. Less information is available for wetland ecosystems, particularly oligotrophic wetlands that experience changes in nutrient status through anthropogenic activities. The authors of this Special Feature were asked to address issues related to nutrient conservation, retention, and cycling among wetlands of different trophic status from a global perspective. Some hypotheses and predictions that the authors were asked to consider are:

1) Mechanisms that help conserve nutrients for plants in low-nutrient wetlands become less efficient as availability of the limiting nutrient increases. This hypothesis predicts that the efficiency of wetland plants to resist leaching and withdraw nitrogen (N) and phosphorus (P) prior to leaf abscission decreases as availability of a limiting nutrient increases. A corollary of this hypothesis is that sclerophylly and extended leaf longevity, typically characteristic of plants in low-nutrient habitats, decrease as nutrient availability increases.

2) High-nutrient litter decomposes faster and immobilizes smaller amounts of N and P than low-nutrient litter. This hypothesis predicts that decomposition rates of plants from high-nutrient wetlands will be greater than for plants from low-nutrient wetlands.

3) Plants growing in low-nutrient conditions have higher tissue C:N ratios, resulting in higher concentrations of carbon-based polyphenolics (tannins and lignin). This hypothesis predicts that, because of lower levels of polyphenolics, higher leaf-litter decomposition rates occur in high-nutrient wetlands. It also predicts that a greater percentage of the nutrient standing stock will be cycled via grazing pathways when nutrient availability is high.

The five papers consider these issues and others for arctic, boreal, temperate, subtropical, and tropical wetlands. Sven Jonasson and Gaius Shaver review internal nutrient-cycling processes in arctic and boreal wetlands where nutrient availability is usually low due to low temperatures and anoxic soils. Arctic vegetation typically has a higher percentage of biomass in perennial structures, resulting in lower rates of nutrient loss and reduced annual nutrient demand. Jonasson and Shaver find that plant and nutrient turnover increases with increasing soil fertility across gradients of nutrients and moisture. Vegetation composition apparently has little influence on nutrient turnover at the ecosystem level, and there is strong competition between microbes and plants for nutrients. Barbara Bedford, Mark Walbridge, and Allison Aldous review the literature and provide examples from their own research for patterns of nutrient availability and plant diversity in temperate wetlands in North America. They find that species diversity decreases across broad gradients from low to high nutrient availability but that the pattern does not hold within many vegetation types. They further note that interpretations of vegetation–nutrient patterns would benefit greatly by consideration of bryophytes. Bryophytes are major elements of some wetlands, and it can be expected that they would present a different pattern than higher plants. The authors' analysis suggests that most North American temperate wetlands are P-limited with some co-limited by N and P. Rien Aerts, Jos Verhoeven, and Dennis Whigham also consider temperate wetlands but focus on plant-mediated processes that influence nutrient cycling at the levels of individual species and ecosystems. Their review considers fens and bogs dominated by monocots (i.e., sedges and grasses) as well as scrub-shrub and forested wetlands. They conclude that rates of nutrient cycling are predicted best by N and P concentrations in mature leaves and that plant growth form predicts nutrient-cycling rates better than does wetland vegetation type.

<sup>1</sup> Reprints of this 69-page Special Feature are available for \$10.50 each. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington DC 20006.

Few studies of within-stand nutrient cycling have been conducted in subtropical and tropical wetlands. Curtis Richardson, Gloria Ferrell, and Panchabi Vaithyanathan report studies from the Everglades, an oligotrophic ecosystem impacted, in part, by nutrient runoff from anthropogenic activities. Everglades vegetation is P-limited, and species distributions are related to patterns of nutrient-use efficiency for two dominant species, cattail and sawgrass. Higher C:N ratios and higher concentrations of tannins occur in plants growing in P-deficient soils. Ilka C. Feller, Dennis Whigham, John P. O'Neill, and Karen McKee describe studies on the effects of P and N availability on within-stand nutrient cycling in a P-limited red mangrove forest in Belize. They demonstrate that increased P availability has a dramatic effect on N and P resorption efficiencies. Phosphorus enrichment causes a significant decrease in P-use efficiency and a significant increase in N-use efficiency. Because of lower P-resorption efficiency, litter from P-fertilized trees has >3 times as much P as litter from unfertilized trees.

Defining patterns of within-stand nutrient cycling of wetlands in response to nutrient availability is complex, and conclusions may vary at different levels of study from individual species to ecosystems. The complexities of wetland plant species and ecosystem responses to nutrient availability are demonstrated in this set of papers. Many questions, however, remain unanswered or poorly understood. Jonasson and Shaver conclude that organic-matter accumulation in arctic and boreal wetlands is primarily controlled by hydrology and soil temperatures. They also conclude that proposed relationships between decomposition and mineralization may not hold. Among the most poorly understood, yet potentially important, aspects of arctic and boreal wetlands are the roles of microbes in P and N cycling and utilization of organic N by plants directly or indirectly through mycorrhizae. Jonasson and Shaver also question the assumption that increased nutrient-resorption efficiency is characteristic of low nutrient availability. Aerts et al. conclude that comparisons of nutrient-use efficiency between bogs and fens will continue to be weak without additional studies of the resorption and nutrient-use efficiency of *Sphagnum* mosses. They call for additional studies of nutrient cycling in soils to allow a better comparison between fens and bogs. They suggest that low productivity in bogs may be controlled by other factors more than by N and P limitations. Bedford et al. conclude that it will not be possible to understand patterns of species diversity in wetlands without additional fertilization experiments in which ecosystem properties and species responses are evaluated. Richardson et al. provide evidence that within-stand nutrient-cycling efficiency and phenolic content of plants decrease as nutrient-poor subtropical wetlands receive additional P. They recognize, however, that their conclusions are based on few studies and the short- and long-term ecological consequences are poorly understood. Feller et al. demonstrate that more needs to be learned about the direct and indirect impacts of nutrient limitations on plants and secondary consumers. They suggest that efficient nutrient-conservation mechanisms provide red mangrove with a competitive advantage over sympatric mangrove species in P-deficient soils. They also conclude that increased availability of limiting nutrients alters nutrient-conservation patterns, resulting in mangroves becoming more "leaky" in response to eutrophication.

Finally, the papers deal with the appropriate indices for capturing the ecological and evolutionary significance of within-stand nutrient-recycling processes. The simplest comparison of nutrient reabsorption among species and sites is the nutrient concentration of senescent leaves (nutrient proficiency) relative to that of active leaves. Yet the ecological significance of nutrient-use efficiency at the community and ecosystem levels favors more quantitative use of resorption efficiency, or nutrient turnover. The papers demonstrate the need to develop indices that describe the ecological significance of nutrient-recycling processes, while not merely representing different expressions of concentration.

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