Forest Ecosystems: Nutrient Cycling

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INTRODUCTION

Nutrients are elements or compounds that are essential for the growth and survival of plants. Plants require large amounts of nutrients such as nitrogen (N), phosphorus (P), carbon (C), hydrogen (H), oxygen (O), potassium (K), calcium (Ca), and magnesium (Mg), but only small amounts of others such as boron (B), manganese (Mn), iron (Fe), copper (Cu), zinc (Zn) and chlorine (Cl) (micronutrients). Forest nutrient cycling is defined as the exchange of elements between the living and nonliving components of an ecosystem.[1] The processes of the forest nutrient cycle include: nutrient uptake and storage in vegetation perennial tissues, litter production, litter decomposition, nutrient transformations by soil fauna and flora, nutrient inputs from the atmosphere and the weathering of primary minerals, and nutrient export from the soil by leaching and gaseous transfers.

Each nutrient element is characterized by a unique biogeochemical cycle. Some of the key features of the major nutrients are shown in Table 1. Forest trees make less demand on the soil for nutrients than annual crops because a large proportion of absorbed nutrients are returned annually to the soil in leaf and fine root litter and are reabsorbed after biological breakdown of litter materials. Also, a large portion of nutrient requirement of trees are met through internal cycling as compared with agricultural crops.

Nutrient cycling in forest ecosystems is controlled primarily by three key factors: climate, site, abiotic properties (topography, parent material), and biotic communities. The role of each factor in ecosystem nutrient dynamics is discussed and illustrated with selected examples from boreal, temperate, and tropical zones. The importance of ecosystem disturbance to nutrient cycling is examined briefly, since some nutrients are added or lost from forest ecosystems through natural (e.g., fire, erosion, leaching) or human activity (harvesting, fertilization).

INFLUENCE OF CLIMATE

Large-scale patterns in terrestrial primary productivity have been explained by climatic variables. In aboveground vegetation, nutrient storage generally increases in the order: boreal $<$ temperate $<$ tropical forests (Table 2). In contrast, forest floor nutrient content and residence time increases from tropical to boreal forests, as a result of slower decomposition in the cold conditions of higher latitudes.

In subarctic woodland soils and Alaskan taiga forests, nutrient cycling rates are low because of extreme environmental conditions.[2] Arctic and subarctic forest ecosystems have lower rates of nutrient turnover and primary production because of low soil temperature, a short growing season, low net AET and the occurrence of permafrost. Low temperature reduces microbial activity, litter decomposition rates, and nutrient availability and increases C accumulation in soil.

In contrast with high latitudes, conditions in a tropical forest favor microbial activity throughout the year, which generally results in faster decomposition except in situations with periodic flooding, soil dessication, and low litter quality.[3] Rates of plant material decay are an order of magnitude higher in tropical soils than in subarctic woodland soils. The low storage of C and high amount of litter production in highly productive tropical forests contrasts with the high C storage and low litter production in boreal forests (Table 2).

INFLUENCE OF BIOTIC FACTORS

Nutrient cycles are modified substantially by tree species-specific controls over resource use efficiency (nutrient use per unit net primary production). Species vary widely in their inherent nutrient requirements and use.[4] These effects can be split into two categories: accumulation into living phytomass and production of various types of nutrient-containing dead

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Table 1 Features of the major nutrient cycles

Element	Uptake by the trees	Major sources for tree uptake	Limiting situations
Carbon	Atmosphere	Atmosphere	Atmospheric concentration may limit growth
Oxygen	Atmosphere	Atmosphere	Waterlogged soils
Hydrogen	Atmosphere	Atmosphere	Extremely acidic and alkaline conditions
Nitrogen	Soluble NO_3 and NH_4; N_2 for nitrogen fixing species	Soil organic matter; atmospheric N_2 for nitrogen fixing species	Most temperate forests, many boreal forests and some tropical forests
Phosphorus	Soluble phosphorus	Soil organic matter; adsorbed phosphate and mineral phosphorus	Old soils high in iron and aluminum, common in subtropical and tropical environment
Potassium calcium magnesium	Soluble K^+/soluble Ca^{2+}/ soluble Mg^{2+}	Soil organic matter; exchange complex and minerals	Miscellaneous situations and some old soils

phytomass. Rapid accumulation of phytomass is associated with a net movement of nutrients from soil into vegetation. More than half of the annual nutrient uptake by a forest is typically returned to forest floor (litterfall) and soil (fine-root turnover). The subsequent recycling of these nutrients is a major source of available nutrients for forest vegetation. The mean annual litterfall from above-ground vegetation increases from boreal regions to the tropics following the gradient of productivity (Table 2).

Nutrient availability is strongly influenced by the quantity and quality of litter produced in a forest. A high proportion of the variation in foliar N concentrations at the continental scale has been explained by differences between forest types, which in turn has large impact on litter quality and the nutrient content of forest floors. In many temperate and boreal forest ecosystems, microbial requirement for N increases or decreases with labile supplies of soil C. Increased microbial demand for N may temporarily decrease the N availability to trees during the initial decomposition of forest residues with a wide C/N ratio. Microbes immobilize N from the surrounding soil, relatively rapid for readily decomposable organic matter (needle litter), and more slowly for recalcitrant material (branches, boles).

Rates of net N mineralization are higher and retention of foliar N is lower in temperate and tropical than

Table 2 Nutrient distribution in different forest ecosystems

	Vegetation ($Mg\,ha^{-1}$)	Forest floor ($Mg\,ha^{-1}$)	Soil ($Mg\,ha^{-1}$)	Residence time (year)
Carbon				
Boreal coniferous	78–93	37–113	41–207	800
Temperate deciduous	103–367	42–105	185–223	200
Tropical rain forest	332–359	7–72	2–188	120
Nitrogen				
Boreal coniferous	0.3–0.5	0.6–1.1	0.7–2.87	200
Temperate deciduous	0.1–1.2	0.2–1.0	2.0–9.45	6
Tropical rain forest	1.0–4.0	0.03–0.05	5.0–19.2	0.6
Phosphorus				
Boreal coniferous	0.033–0.060	0.075–0.15	0.04–1.06	300
Temperate deciduous	0.06–0.08	0.20–0.10	0.91–1.68	6
Tropical rain forest	0.2–0.3	0.001–0.005	0.06–7.2	0.6
Potassium				
Boreal coniferous	0.15–0.35	0.3–0.75	0.07–0.8	100
Temperate deciduous	0.3–0.6	0.050–0.15	0.01–38	1
Tropical rain forest	2.0–3.5	0.020–0.040	0.05–7.1	0.2

in boreal forest soils. Nitrogen limitation of productivity, therefore, is weak in tropical forests and increases from temperate to boreal and tundra forest systems. Trees may obtain organic N and P from the soil via mycorrhizae or by relocation from older foliage prior to abscission, and thereby, partly reduce their dependence on soil as a source of inorganic nutrients. Increased understanding of the fundamental relationships between soil properties and plant nutrients requirements will most likely come from examination of plant–fauna–microbe interactions at root surfaces (rhizosphere), rather than in the bulk soil.

INFLUENCE OF ABIOTIC FACTORS

Forests have distinctive physiographic, floristic, and edaphic characteristics that vary predictably across the landscape within a climatically homogeneous region. Differences in the elemental content of parent material influence the tree species composition between and within a landscape unit. For example, wind deposited soils, which support hardwood or mixed wood forest, are likely to be fine textured with high nutrient supplying capacity. In contrast, outwash sands that often support pine forests are coarse textured and infertile.

Heterogeneity within the landscape results in sites differing in microclimatic conditions, and physical and chemical properties, which produces different geochemical reaction rates and pools of available nutrients in soil. Soil type and topographic–microclimate interactions are important feedbacks that influence biological processes, such as the rate of N mineralization in soil. Low P availability is a characteristic of geomorphically old, highly weathered tropical, subtropical, and warm temperate soils.[3] The type and age of parent material from which the soil is derived can influence the base status and nutrient levels in soil. Soils in glaciated regions are relatively young and rich in weatherable minerals. Mineral weathering is an important source of most nutrients for plant uptake, with the exception of N. Nutrient availability is regulated by the balance between weathering of soil minerals and precipitation, adsorbtion, and fixation reactions in soil.

Edaphic conditions can exert a strong influence on forest productivity and produce considerable variation in nutrient cycling processes. Soils with low N, P, or pH support trees with low litter quality (high in lignin and tannins that bind N) that decomposes slowly. Edaphic limitations on growth may be compensated for by an increase in rooting density and depth. Some late-succession or tolerant species have a shallower root distribution relative to intolerant pioneer species and are adapted to sites where nutrients and moisture are concentrated at the soil surface. In contrast, nutrient uptake from sub-soil horizons is more important in highly weathered warm temperate soils where nutrient depletion takes place deeper in the soil.

ROLE OF DISTURBANCE

Disturbances such as fire, harvesting, hurricanes, or pests affect nutrient cycling long after the event. In fire-dominated ecosystems, intensive wildfire results in a horizontal and vertical redistribution of ecosystem nutrients. Redistribution results from the combined effects of the following processes: 1) oxidation and volatilization of live and decomposing plant material; 2) convection of ash particles in fire generated winds; 3) water erosion of surface soils; and 4) percolation of solutes through and out of the soil. The relative importance of these processes varies with each nutrient and is modified by differences in fire intensity, soil characteristics, topography, and climatic patterns. Expressed as a percentage of the amount present in vegetation and litter before fire, the changes often follow the order:

$$N > K > Mg > Ca > P$$

Harvesting removes nutrients from the site and interrupts nutrient cycling temporarily. The recovery of the nutrient cycle from harvest disturbance is dependent partly on the rate of re-establishment of trees and competing vegetation. Re-vegetation may occur within months in the tropics, 2–5 years in temperate regions, and longer in boreal and tundra regions.[5] Recovery assumes that the soil's ability to supply nutrients to plant roots has not been altered by disturbance. If nutrients cannot be supplied by the soil at rates sufficient to at least maintain the rate of growth of the previous forest then fertilization may be necessary to maintain site productivity.

Nutrient cycling and the impacts of disturbance on nutrient cycling, have been examined thoroughly in many representative world forests. The impact of natural disturbances and management practices on nutrient cycling processes are generally characterized of the stand or occasionally on a watershed basis. There is a growing demand from policy makers and forest managers for spatial estimates on nutrient cycling at local, regional, and national scales.

The availability of N, P, and K in soil largely determines the leaf area, photosynthetic rate, and net primary production of forest ecosystems. Forest management practices that produce physical and chemical changes in the soil that accentuate the cycle of nutrients between soil and trees, may increase forest productivity. Clear-cut harvesting and site preparation practices (mechanical disturbance, slash burning) remove nutrients from soil in tree components and by increased surface runoff, soil erosion, and off-site movement of nutrients in dissolved form or in sediment transport. In the tropics, potential negative impacts associated with complete forest removal and slash burning are greatest because a larger proportion of site nutrients are contained in the living biomass. Environmental impacts associated with clear-cutting and forest management in general, are confounded by climatic, topographic, soil, and vegetation diversity associated with the world's forests. Best forest management practices can be utilized to control negative impacts on nutrient cycling.

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