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ECOLOGY AND THE CYCLING OF CARBON AND NITROGEN

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INTRODUCTION

Carbon (C) and nitrogen (N) are two of the most important elements that affect the soil's productivity and environmental quality (1). Carbon is found throughout nature in a wide variety of forms and particularly in soil as 1) complex organic compounds (e.g., $C_xH_{2x}O_x$) derived from living organisms, 2) carbonate minerals such as calcite ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$), and 3) carbon dioxide (CO_2) and methane (CH_4) as decomposition endproducts. Nitrogen is an essential element of plants, animals, and microorganisms that is a part of chlorophyll, enzymes, amino acids, and proteins, which are necessary for growth and development of organisms. In soil, the quantity of N in organic matter and as clay-fixed ammonium (NH_4^+) far exceeds quantities in plant-available forms of nitrate (NO_3^-) and NH_4^+.

CARBON AND NITROGEN CYCLES

Carbon and N occur in various forms and undergo transformations from one form to another, primarily through biochemical manipulations involving enzymes (2, 3). Enzymes are catalysts of very specific reactions that function either 1) intracellularly within plants, microorganism, or soil animals or 2) extracellularly in soil solution or attached to soil colloids.

The forms and fluxes of an element are commonly illustrated in a cycle following the principles of conservation of mass (i.e., elements are transferred from one molecule to another). The C and N cycles have global dimensions with terrestrial, aquatic, and atmospheric components of major significance (4, 5). The sun initiates a chain of energy reactions, which drive elemental cycles. The elemental cycles of C and N interact closely with the water cycle, as water is a fundamental internal component of life and a major transport mechanism of nutrients.

Autotrophic fixation of atmospheric CO_2 by plants captures the energy of the sun within organic compounds via the process of photosynthesis (Fig. 1). Inorganic N is taken up by plant roots and synthesized into amino acids and proteins during plant development. Plants are eventually consumed by animals or microorganisms, transferring portions of this stored energy through biochemical processes into various cellular components. Once in soil, the C cycle is dominated by the heterotrophic process of decomposition, i.e., the breakdown of complex organic compounds into simple organic constituents. Mineralization is the complete decomposition of organic compounds into mineral constituents:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

$$R\text{–}NH_2 + H_2O \rightarrow R\text{–}OH + NH_3$$

Immobilization of N occurs simultaneously with N mineralization when soil organisms consume inorganic N to meet the demands for new body tissue. Net N mineralization occurs when gross N mineralization exceeds that of N immobilization.

ENVIRONMENTAL INFLUENCES ON SOIL MICROBIAL ACTIVITY

The dominant organisms responsible for decomposition of organic matter and associated mineralization of C and N are soil microorganisms, composed of bacteria, actinomycetes, fungi, and protozoa (6, 7). Soil fauna also indirectly affect C and N cycling by 1) comminuting plant residues and exposing a greater surface area to soil microorganisms, 2) transporting plant and animal residues to new locations in the soil to facilitate decomposition, interaction with soil nutrients, or isolation from environmental conditions, 3) inoculating partially digested organic substrates with specific bacteria and enzymes, and 4) altering physical characteristics of soil by creating burrows, fecal pellets, and distribution of soil particles that influence water, air, nutrient, and energy retention and transport. With suitable environmental conditions, soil microorganisms grow rapidly in response to the availability of organic substrates rich in C and N.

Soil Temperature

Temperature controls both plant and soil microbial activity, although not at the same level (Fig. 2). Plant and

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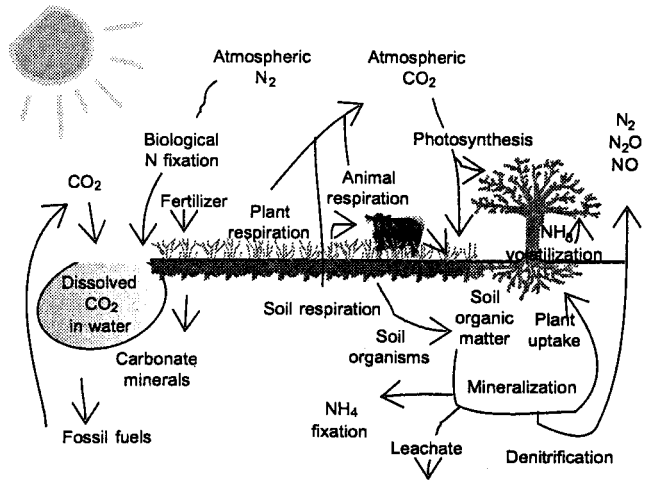

Fig. 1 Generalized diagram of the C and N cycles in soil.

soil microbial activity are limited by low temperature resulting in low photosynthetic potential, as well as low decomposition potential. For many plants, net photosynthetic activity is optimized between 20 and 30°C, because at higher temperatures plant respiration consumes energy for maintenance. In many temperate soils, microbial activity is maximum near 30°C and decreases at higher temperatures. An intermediate temperature is often ideal for maximizing C retention in soil, where optimum plant activity outdoes soil microbial activity.

Soil Water Content

The greatest diversity of soil microorganisms is found under aerobic conditions, where maximum energy is obtained. However, there are a number of soil bacteria that thrive under anaerobic conditions, in which alcohols, acetic acid, lactic acid, and CH_4 become C endproducts via fermentation, and nitrate is converted to N gases (e.g., N_2, N_2O, NO) via the process of denitrification. Soil C and net N mineralization are maximized at an optimum balance between soil moisture and oxygen availability (Fig. 3). Significant denitrification occurs at water-filled pore space >70%, resulting in what appears as reduced net N mineralization.

Soil Texture

Soil texture can influence both the quantity of C and N accumulation in soil and their potential mineralization. Potential C mineralization is often greater in coarse- than in fine-textured soils, which may be due to both increased microbial predation by soil fauna and greater accessibility of organic substrates in coarse-textured soils. Organic C and N can also be protected from decomposition when bound within soil aggregates, which are a coherent assemblage of primary soil particles (i.e., sand, silt, clay) cemented through natural forces and substances derived from root exudates and soil microbial activity.

Spatial Distribution of Organic Substrates

Distribution of organic substrates in soil has a major impact on potential C and N mineralization. Potential C mineralization is often several-fold greater in the rhizosphere (i.e., 0–5 mm zone surrounding roots) than in bulk soil. However, because of the high demand for N by plant roots and the stimulated soil microflora, net N mineralization is often lower in the rhizosphere because of immobilization of N.

The soil-surface often contains greater quantities of organic matter than at lower depths due to surface deposition of plant residues, as well as highest plant root activity. The soil-surface usually undergoes the most extreme drying/wetting cycles and has the greatest exchange of gases, both of which contribute to enhanced soil microbial biomass and activity. Tillage of soil with traditional agriculture redistributes the organic substrates uniformly within the tillage layer, often resulting in stimulated soil microbial activity from disruption of organic substrates protected within stable soil aggregates. Minimum soil disturbance with conservation tillage practices can reduce oxidation of soil organic matter and preserve more C within soil, which can have implications for potentially mitigating the greenhouse effect (8).

ORGANIC SUBSTRATE QUALITY

The quality of organic substrates has a major influence on the rate of decomposition and the transformations that occur in soil. Plant residues do not vary greatly in total C concentration on a dry-weight basis (e.g., 37–47 mg g^{-1}), but do vary in the suite of C compounds, which determine its quality or conversely its resistance to degradation. The diversity of organic compounds attacked by soil microorganisms is extensive (e.g., organic acids, polysaccharides, lignins, aromatic and aliphatic hydrocarbons, sugars, alcohols, amino acids, purines, pyrimidines, proteins, lipids, and nucleic acids). Almost all naturally occurring organic compounds, and even most synthetic organic compounds, are susceptible to decomposition, given the appropriate environment, microbial community, and time (9, 10). Generally, the primary components of

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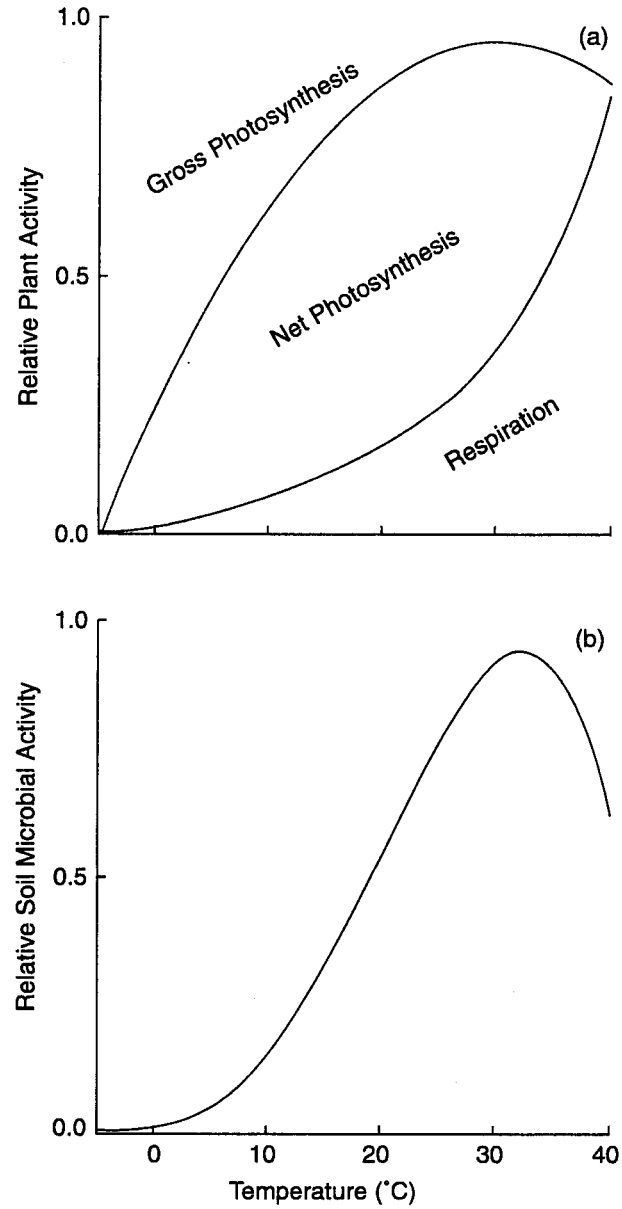

Fig. 2 Typical responses of plant and soil microbial activities to temperature.

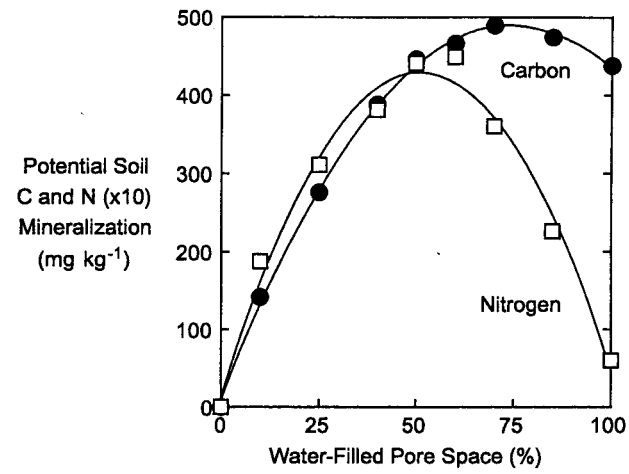

Fig. 3 Responses of potential soil C and N mineralization to water-filled pore space in Typic Kanhapludults in Georgia, U.S. Air-filled pore space is 100−(water-filled pore space).

plants can be categorized according to the relative rate of decomposition: rapid (sugars, starches, fats, and proteins), intermediate (cellulose and hemicellulose), and slow (lignin and lignocellulose). Young plants are of high quality and low resistance to decomposition, whereas with aging, lignin and polyphenolic concentrations increase, resulting in greater resistance to decomposition. Low N concentration of organic amendments usually results in temporary net N immobilization into microbial biomass, which grows rapidly in response to the availability of organic C. Soil microbial biomass maintains a C:N ratio of 10 ± 5. Following a proliferation of microbial biomass that depletes the source of readily decomposable organic C:N in excess of microbial demands becomes mineralized and available for plant uptake (Fig. 4). In general, plant residues with C:N ratio >40 will result in longer periods of net N immobilization.

Soil Organic Matter

Soil organic matter is composed of a large variety of organic compounds that can be characterized in many ways. A useful separation of soil organic matter for modeling is based on the turnover times, whereby at least three pools can be defined: 1) active (composed of microbial biomass and light fraction material with a turnover time of <1 yr), 2) passive (composed of macroorganic matter and protected organic matter with a turnover time of 3–10 yr), and 3) slow (stable humus fraction with a turnover time of >100 yr).

LOSSES OF NITROGEN FROM SOIL

Nitrogen cycling in soil is different from that of C because of the more numerous transformations that can occur upon mineralization to an inorganic form (11). Mineralization of N from organic matter results in NH_4^+ released into soil solution. In the presence of nitrifying bacteria, NH_4^+ is converted to NO_3^-; a process called nitrification. The fate of NO_3^- in soil depends upon environmental conditions. Active plant growth in natural and agricultural systems would provide enough demand to reimmobilize N into

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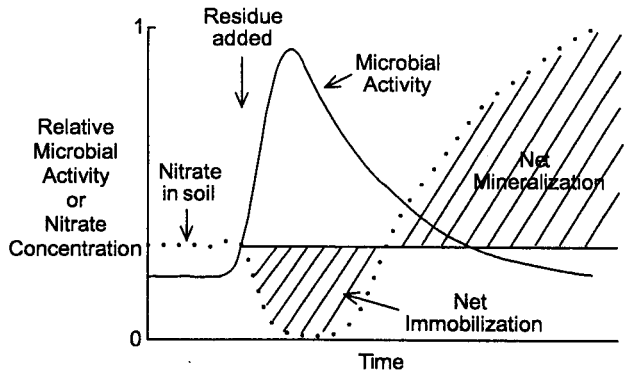

Fig. 4 Typical responses in soil microbial activity and soil nitrate concentration with the addition of plant residue relatively low in N concentration.

organic forms. However, NO_3^- can be used as an electron acceptor in place of O_2 under anaerobic conditions with a supply of soluble organic C, resulting in gaseous loss of N to the atmosphere via denitrification. In temperate soils with a net negative charge on colloidal surfaces, NO_3^- can readily leach into the vadose zone and contaminate groundwater. In tropical soils with a net positive charge, NO_3^- can be retained on anion exchange sites. Contradicting behavior of the cations, NH_4^+ and NO_3^-, occurs with respect to clay mineralogy.

Humans, as well as roving animals, impose great demands on the C and N cycles. Management of agricultural and forest land for food and fiber removes nutrients from soil for consumption and utilization elsewhere. Return of these nutrients to soil is possible when municipal and agricultural solid wastes and wastewater are applied to land. Losses of C and N from managed lands also occur through soil erosion, which transports nutrients via 1) water from overland flow into streams, lakes and oceans, and 2) air from exposed land.

Volatilization of ammonia (NH_3) to the atmosphere is possible when NH_4^+ is exposed to alkaline soil conditions. Significant ammonia volatilization can occur with surface application of urea fertilizer to nonacidic soils, from animal manures, and from green plant materials not incorporated into the soil.

FIXATION OF CARBON AND NITROGEN

Both C and N are biologically fixed from inorganic atmospheric forms to organically bound plant and microbial forms. As mentioned earlier, photosynthesis converts CO_2 from the atmosphere into organically bound forms in plants, algae, and cyanobacteria. Biological N_2 fixation is a unique transformation carried out by a number of bacteria, which convert N_2 gas into NH_3 for biological uptake. These bacteria are most prevalent in symbiotic relationships with plants, such as *Rhizobium* that forms nodules on the roots of clovers where the nitrogenase enzyme catalyzes the reaction. Fertilizer manufacturing converts N_2 gas into NH_3 in a similar manner without an enzyme, but rather large quantities of energy necessary to create the pressure required for the transformation.

Under certain conditions, both inorganic C and N can be chemically fixed in the subsoil. Carbon dioxide forms carbonic acid in water, which can precipitate with the basic cations, Ca^{2+}, Mg^{2+}, and Na^+, to form pedogenic carbonates. Inorganic C is most abundant in soils of the semiarid and arid regions. Ammonium can be fixed as nonexchangeable components of the lattice structure of 2:1-type clay minerals, which are especially prevalent in the subsoil of many younger soils.

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