Ecosystem element cycling

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An **ecosystem** consists of all the biological organisms and the physical environments they occupy within a defined area [9]. The actual boundaries of an ecosystem are generally defined by researchers studying the ecosystem, who are usually interested in understanding the processes that control some aspects of ecosystem dynamics. Thus, the spatial domain of an ecosystem might range in size from a small pool of water in a tundra landscape to the tundra ecosystem of the Kuparuk River Basin in northern Alaska [4]. Ecosystem dynamics are changes in the biological and physical characteristics of ecosystems through time. The biological organisms in an ecosystem are responsible for a number of processes that affect ecosystem dynamics. For example, plants obtain carbon as carbon dioxide from the atmosphere through the process of photosynthesis, herbivores obtain carbon by consuming plants in an ecosystem, carnivores obtain carbon by eating animals in an ecosystem, and decomposers obtain carbon from dead organisms in an ecosystem. Physical processes also affect ecosystem dynamics. For example, the leaching of dissolved organic carbon in water flowing through the soil of an ecosystem is one path through which terrestrial ecosystems may lose carbon to aquatic ecosystems like rivers (*see* **Rivers, canals and estuaries**) and **lakes**. For our purposes here, ecosystem element cycling refers to the cycling of elements such as carbon within an ecosystem, as well as the flow of elements into and out of an ecosystem.

This entry has several purposes:

1. to provide some basic biological and physical background on processes responsible for ecosystem element cycling
2. to briefly describe generalized carbon and nitrogen cycles in terrestrial ecosystems
3. to discuss human modification of the global carbon and nitrogen cycles.

Biological Background

Biological organisms are composed predominantly of water, which can be responsible for well over 50% of the 'wet mass' of organisms. The 'dry mass' of organisms, which is composed of other molecules, is often referred to as **biomass**. There are four basic types of molecule that are important in maintaining and building biomass of organisms in an ecosystem: carbohydrates, fats, proteins and nucleic acids. Carbohydrates and fats are important because energy is stored in chemical bonds involving carbon atoms, and energy is released as carbohydrates and fats are transformed into carbon dioxide and water in the presence of oxygen, a process referred to as aerobic respiration. Thus, to release the energy required to maintain and build biomass, oxygen is obtained from the environment and carbon dioxide and water are released to the environment. Carbohydrates and fats are also important components of cell structure, e.g. cell walls in plants and cell membranes in animals. Proteins are important molecules because as enzymes they are responsible for catalyzing biochemical reactions. In addition, proteins are important to the structure of organisms, because muscle, hair, claws and horns are rich in protein. In contrast to carbohydrates and fats, proteins contain substantial amounts of nitrogen in addition to carbon. Nucleic acids are important molecules because they contain information, the 'genetic blueprint', for building the proteins that catalyze certain biochemical reactions, depending on the structure of those proteins. In addition to carbon and nitrogen, nucleic acids also contain substantial amounts of phosphorus. To maintain and build tissue, biological organisms also require a number of other elements besides carbon, nitrogen and phosphorus. For example, sodium and potassium are important ions in many biochemical reactions and calcium is an important structural element in bones. Biological organisms must obtain the needed elements in adequate quantities to avoid disease and death. Thus, the flow and cycling of elements in an ecosystem is important to maintain the function and structure of biological organisms in the ecosystem.

Biological organisms in an ecosystem are involved in sequestering elements from the physical environment, cycling elements in the ecosystem and releasing elements to the environment. For example, green plants sequester carbon from the atmosphere through the process of photosynthesis, herbivores and carnivores cycle carbon through the ecosystem, and decomposers release carbon back to the atmosphere. It is important to recognize that organisms do not necessarily have a single function with respect to ecosystem element cycling. For example, while green plants sequester carbon from the atmosphere through the process of photosynthesis, they also release carbon to the atmosphere through the process of aerobic respiration (*see* **Forest carbon cycling**), as do herbivores and carnivores. In addition, as should be obvious, each organism in an ecosystem is involved in the flow and cycling of many elements.

Physical Background

Although biological organisms play important roles in the flow and cycling of elements in an ecosystem, the physical environment is also involved in ecosystem element cycling. Physical processes involving air (the atmosphere), water (the hydrosphere) and soil (the pedosphere) play important roles in ecosystem element cycling [6]. The atmosphere is an important reservoir for both carbon dioxide and nitrogen, which can enter ecosystems through biological and physical processes. For example, in aquatic ecosystems the dissolution of carbon dioxide in water depends on the concentration gradient of carbon dioxide between air and water, and this gradient may depend on the sequestration of dissolved carbon dioxide by aquatic plants. Similarly, the atmosphere, which is approximately 80% gaseous nitrogen, is an important source of ecosystem nitrogen, which can enter through the physical deposition of ammonium and nitrate from the atmosphere as well as through biological nitrogen fixation of gaseous nitrogen.

The water cycle is important to ecosystem element cycles in a variety of ways. As organisms are predominantly composed of water, the availability of water is itself essential to the maintenance and construction of biomass in an ecosystem. The water cycle is also important to the flow of many elements into and out of ecosystems that occur via movements of water. For example, nitrogen may enter or leave an ecosystem dissolved in water as nitrate. The lateral flow of water across the terrestrial surface into the oceans is a means by which elements are transported from terrestrial ecosystems to aquatic ecosystems, including ocean ecosystems. The water cycle also influences many biological processes that cycle elements in an ecosystem. For example, the rate of carbon uptake from the atmosphere through the process of photosynthesis is generally low when the humidity of the atmosphere is low. Soil moisture may influence plant uptake of inorganic nitrogen released through decomposition of soil organic matter, as uptake may be limited by diffusion through the soil solution to the roots.

Soil properties and processes influence many aspects of ecosystem element cycling. Geochemical transformations of the parent rock underlying an ecosystem are responsible for the development of the mineral soil, which is the source of a number of elements that become incorporated into the biological organisms of an ecosystem. For example, the weathering of rocks is an important source of phosphorus, which usually becomes dissolved as phosphate, a form of phosphorus that can be taken up by plants. The physical properties of soils also influence ecosystem element cycling. For example, coarse-textured sandy soils hold less water than fine-textured clay soils. In addition, the chemical properties of soils are important to ecosystem element cycling. For example, soils vary in the degree of net negative charge depending on the number of hydroxide ions (OH^-) that are exposed to the soil solution. The hydroxide ions attract and bind to cations like sodium, potassium and calcium, which depending on the pH of the soil solution can be exchanged with the soil solution where the cations are available to be taken up by plants [7]. Finally, the organic matter of soils, which is derived from the senesced biomass of biological organisms, is an important reservoir of elements which are released by decomposition to the soil solution, where they are available for uptake by plants (*see* **Soil conservation and remediation**).

The Carbon and Nitrogen Cycles

As discussed earlier, the ability to acquire carbon and nitrogen is important to the maintenance and construction of biomass by biological organisms in an ecosystem. These cycles are also important to humans because the production of food and fiber by forest and agricultural ecosystems depends on these cycles. It is important to recognize that these cycles are linked together, as the availability of nitrogen can limit the uptake of carbon by ecosystems and the availability of carbon to nitrogen-fixing bacteria can limit the input of nitrogen to an ecosystem [5, 10]. Here, the basic features of carbon and nitrogen cycles in terrestrial ecosystems are described (Figure 1).

The carbon in green plants (C_V in Figure 1), which are referred to as photoautotrophs, is obtained from the atmosphere through the process of photosynthesis by using solar energy to chemically transform

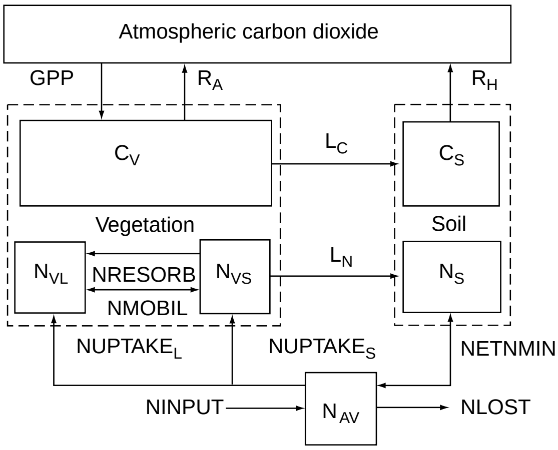

Figure 1 A generalized diagram of carbon and nitrogen cycling in terrestrial ecosystems. The pools of carbon and nitrogen are: carbon in the vegetation (C_V); structural nitrogen in the vegetation (N_{VS}); labile nitrogen in the vegetation (N_{VL}); organic carbon in soils and detritus (C_S); organic nitrogen in soils and detritus (N_S); and available soil inorganic nitrogen (N_{AV}). Arrows show carbon and nitrogen fluxes; GPP, gross primary production; R_A, autotrophic respiration; R_H, heterotrophic respiration; L_C, litterfall carbon; L_N, litterfall nitrogen; $NUPTAKE_S$, nitrogen uptake into the structural nitrogen pool of the vegetation; $NUPTAKE_L$, nitrogen uptake into the labile nitrogen pool of the vegetation; NRESORB, nitrogen resorption from dying tissue into the labile nitrogen pool of the vegetation; NMOBIL, nitrogen mobilized from the labile pool of the vegetation to the structural pool of the vegetation; NETNMIN, net nitrogen mineralization of soil organic nitrogen; NINPUT, nitrogen inputs from outside the ecosystem; and NLOST, nitrogen losses from the ecosystem

carbon dioxide to carbohydrates. The rate at which green plants transform carbon dioxide to carbohydrates is gross primary production (GPP in Figure 1). The energy costs to green plants in maintaining and constructing biomass results in a loss of carbon to the atmosphere as autotrophic respiration (R_A in Figure 1). The difference between GPP and R_A is net primary production (NPP), which represents the net amount of carbon that has been acquired by the green plants of an ecosystem over a specified period of time. Through senescence of tissue and mortality, a rate which is termed litterfall carbon (L_C in Figure 1), green plants in an ecosystem lose carbon to the soil where it becomes part of the pool of soil organic matter (C_S in Figure 1). Here, soil organic matter is decomposed by soil heterotrophs, which release carbon to the atmosphere as heterotrophic respiration (R_H in Figure 1). It is useful to note that plants also lose carbon to animals through herbivory, some of which is delivered to soil in fecal material that is not assimilated by animals and some of which is ultimately respired to the atmosphere by animals. As animals are heterotrophs, the term R_H includes respiration by animals.

Nitrogen enters the ecosystem (NINPUT in Figure 1) via biological nitrogen fixation of gaseous nitrogen or through the deposition of ammonium and nitrate. Plants are able to take up ammonium and nitrate from the soil solution, inorganic forms of nitrogen which are grouped together as nitrogen available for plant and microbial uptake (N_{AV} in Figure 1). Nitrogen that is taken up by plants can be directly incorporated into structural tissue (via $NUPTAKE_S$ into N_{VS} in Figure 1) or into storage as labile nitrogen for later use in constructing tissue (via $NUPTAKE_L$ into N_{VL} in Figure 1). Labile nitrogen can be mobilized from storage for the construction of structural tissue (NMOBIL in Figure 1). In addition, the resorption of nitrogen from senescing tissue (NRESORB in Figure 1), for example from deciduous leaves that are shed in autumn, puts nitrogen in storage that can be used in the construction of tissue at a later point in time. The resorption and mobilization of nitrogen into and out of storage represents the internal recycling of nitrogen within plants, and can be responsible for up to 80% of nitrogen used in constructing plant tissue [8]. The loss of nitrogen from plants to soils from senescence and mortality, which is termed litterfall nitrogen (L_N) in Figure 1, becomes incorporated into soil organic matter. The decomposition of soil organic matter by soil heterotrophs results in the mineralization of ammonium that enters the available nitrogen pool. Ammonium in the soil solution can also be taken up by soil heterotrophs to meet the structural nitrogen requirements of these organisms and may undergo additional transformations by being converted to nitrate by nitrifying bacteria. Because soil heterotrophs both supply and use forms of nitrogen that are available to plants, the net rate at which nitrogen is provided to plants is termed net nitrogen mineralization (NETNMIN in Figure 1). Nitrate in the available nitrogen pool can be lost from the ecosystem (NLOST in Figure 1) through the process of denitrification which releases gaseous nitrogen to the atmosphere or through leaching of nitrate in the soil solution that flows out of the ecosystem.

Human Alteration of the Global Carbon and Nitrogen Cycles

Humans have substantially altered the global carbon cycle in several ways. First, nearly 50% of global NPP has come under direct human management though agriculture (including grazing of domestic livestock) and **forestry** activities [12]. Human activities result in adding approximately 7×10^{15} g of carbon (Pg C) yr^{-1} to the atmosphere through fossil fuel burning ($\simeq 5$ Pg C yr^{-1}) and tropical **deforestation** ($\simeq 2$ Pg C yr^{-1}). Of this amount approximately 4 Pg C yr^{-1} is absorbed by ocean and terrestrial ecosystems and approximately 3 Pg C yr^{-1} remains in the atmosphere, which is responsible for the current increase of approximately 1.5 ppmv CO_2 per year in the atmosphere. Greenhouse gases like CO_2 allow short-wave radiation to reach the surface of the earth, but trap long-wave energy that is radiated by the earth's surface. Thus, the increasing concentration of atmospheric CO_2 has been judged by the scientific community as probably being responsible for the **global warming** that has been occurring during the last century [3].

Humans have also substantially modified the global nitrogen cycle in several ways [11]. The fixation of nitrogen for fertilizer by industrial processes is approximately equal to the total biological nitrogen fixation of terrestrial ecosystems. The large amount of fertilizer applied on agricultural systems is thought to be responsible for the increasing concentrations of nitrous oxide, which like CO_2 is an effective heat-trapping gas that may be contributing to global warming. The application of fertilizers in agricultural ecosystems is also affecting aquatic ecosystems (*see* **Agricultural runoff**). For example, the nitrogen flux of rivers that empty into the North Atlantic Ocean has increased 2- to 20-fold since pre-industrial times in association with human use of fertilizer [2]. This increase has implications for humans, as high levels of nitrate in drinking water have health consequences. In addition, the high level of nitrogen in rivers has led to eutrophication of estuaries and coastal waters, which has been linked to toxic blooms of algae that have caused substantial mortality of fish and shellfish in estuaries. The burning of fossil fuels also releases nitrogen-based trace gases into the atmosphere. Some of this nitrogen is deposited into terrestrial ecosystems, with the highest levels in western Europe, in eastern China and in the eastern US. Because of interactions between carbon and nitrogen dynamics, the deposition of nitrogen has consequences for carbon dynamics of terrestrial ecosystems. High levels of nitrogen deposition have damaging consequences on ecosystem function, as negatively charged nitrates leach from the soil and carry away important cations such as potassium, calcium and magnesium [1]. Thus, the use of nitrogen fertilizers and the deposition of nitrogen on terrestrial ecosystems have the potential to decrease the overall fertility of soils, which has consequences for the function and structure of these ecosystems.

As human modifications of ecosystem element cycles have wide-ranging effects on biological and physical functioning of the earth, these modifications are also influencing global politics. For example, there is currently an intense international debate concerning the actions required to stabilize CO_2 concentrations in the atmosphere to prevent dangerous human interference with the climate system (*see* **Global environmental change**), and there are serious economic and environmental choices that depend on the stabilization scenario [13] (*see* **Economics, environmental**). Negotiations as part of the United Nations Framework Convention on Climate Change are setting targets for the reduction of fossil fuel emissions to stabilize the atmospheric concentration of CO_2. Because the present compliance with the reduction of **emissions** is largely based on the voluntary actions of individual countries, it is unlikely that targets will be met. Future negotiations will require more drastic actions. The use of fossil fuels by individual countries will certainly play a role in these negotiations. Additionally, the storage or release of carbon by terrestrial ecosystems in individual countries is relevant to the negotiations, and there are substantial statistical challenges to verify the changes in carbon storage of terrestrial ecosystems for individual countries.

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(*See also* **Meteorology**; **Nutrient cycling**; **Oceanography**; **Soil wetness index**)

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