1 The Carbon and Nitrogen Cycle of Forest Ecosystems

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1.1 Introduction

Our understanding of the biology of major biogeochemical cycles came initially from, and is still based upon, field observations (Bolin et al. 1979; Clark and Rosswall 1981; Apps and Price 1996). This is in contrast to very advanced models, which explore the physics of the climate system and are based on laws of physics or chemistry with a mechanistic understanding of the underlying processes (Houghton et al. 1996; Bengtsson 1999). For the biologist, the responses of organisms reach far beyond physicochemical reactions, and they include genetically regulated changes in physiological pathways or activation of enzyme systems as part of acclimations and adaptations that are coupled with climate and species composition changes. Generic predictions thus remain elusive because there are too many species and pathways. Although climate greatly influences the biogeochemical cycles, models that include biology thus remain at a correlative level. Moreover, the cycling of elements like carbon (C) cannot readily be separated from the abundance, state and cycles of other elements, especially nitrogen (N) (Schulze et al. 1994) which, in turn, is tied to the cycling of other elements (Ulrich 1987). Nevertheless, detailed knowledge of the biology of C cycling and that of other major and minor elements is urgently needed because the Kyoto Protocol demands strategies to balance industrial emissions by biological C fixation (WBGU 1998; IGBP 1998). By this protocol, mankind is taking a first step to deliberately engineer the biology of the global C cycle; but without full understanding of the underlying processes, there is a risk of serious deleterious side effects (Schellnhuber and Wenzel 1998; Schellnhuber 1999). Forests are a major focus in this new endeavour of global engineering because of their high C storage capacity coupled with a relatively low demand for N (Melillo et al. 1996).

This book has the timely goal of elucidating the regulation of C and N pools and fluxes in forest ecosystems. We use European coniferous and deciduous forests along a transect of climate and pollution deposition as models, and include analyses of the role of biodiversity at plant, soil faunal and microbial levels in the determination of C and N cycles. Thus, we hope to understand limitations of resource use and supply in view of the new global engineering endeavour.

1.2 The Carbon and Nitrogen Cycles

Ecosystem C and N cycles are strongly coupled by several nested loops driven by the activity of specific organisms with specialised abilities to carry out a very diverse set of functions that transform and store C and N products.
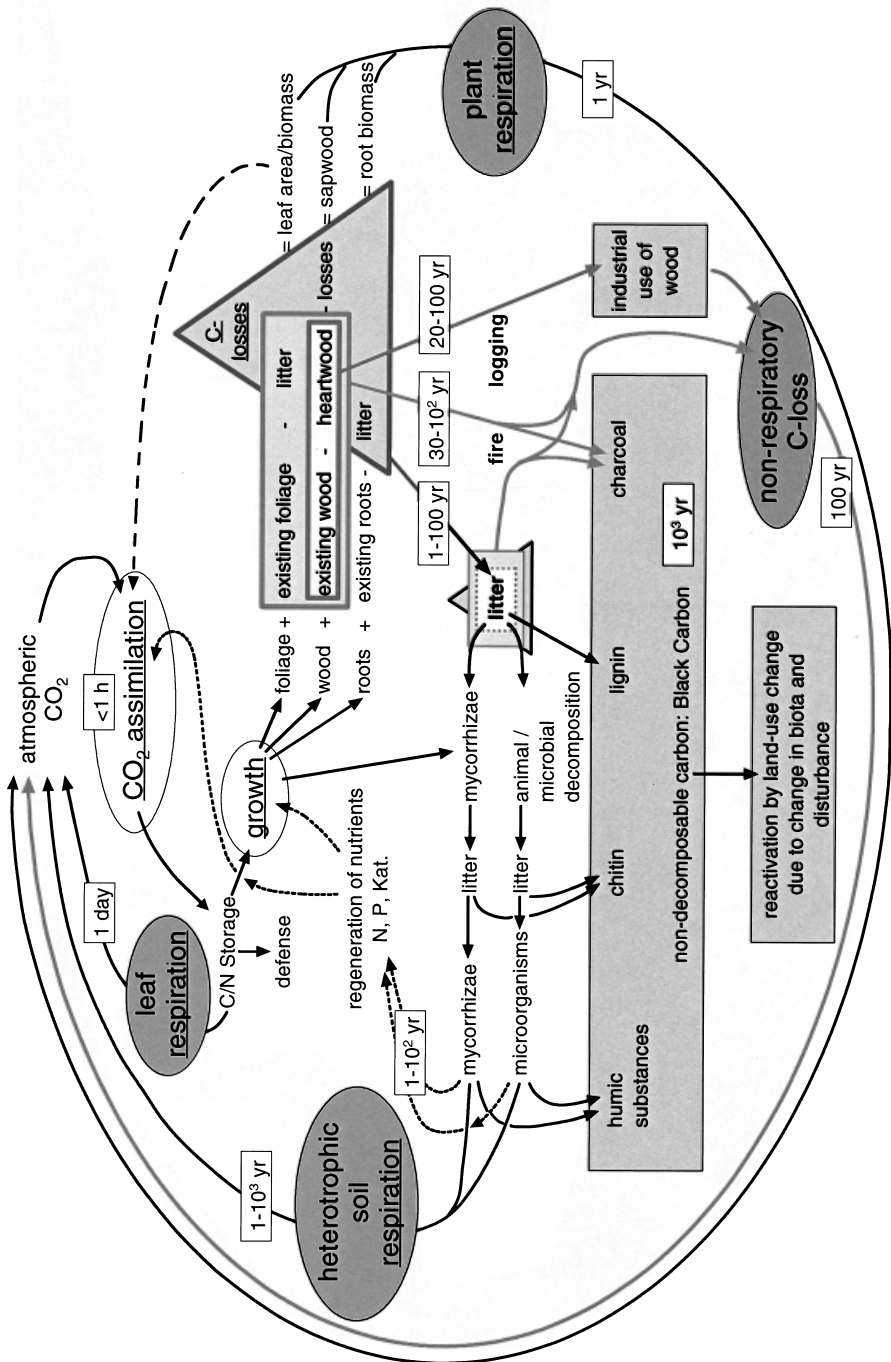
The C cycle (Fig. 1.1) begins with the process of CO_2 assimilation by plants. This is virtually an instantaneous process, depending on light energy. CO_2 assimilation determines the delivery of assimilates to the plant internal store, which may then be used for growth, reserve or defense (Chapin et al. 1990). In trees, growth adds biomass as foliage, wood and roots (Schulze and Chapin 1987; Stitt and Schulze 1994). However, this process is not simple. For example, the allocation of C to leaf growth leads to a positive feedback on the C-assimilation capacity of the tree, but there is an upper limit in tree canopies for leaf development, because there is a maximum leaf area index, depending on the availability of light and on leaf orientation, i.e. the distribution of foliage in three-dimensional space (Monsi and Saeki 1953). Growth is essential in plants because they operate as open systems for which the formation of new tissue offsets the internal cellular clock of cell senescence in ageing tissues. There is an upper limit for growth determined by the balance of assimilation and respiration, as growth with its associated respiration cannot exceed the cost of maintenance. Plants solve this dilemma by aptosis (Havel and Durzan 1996), in which some living tissue dies and is either shed as litter or, as in the case of heartwood in trees (Leopold 1980; Pennell and Lamb 1997), is retained to serve structural purposes. The processes involved have different time constants (or turnover rates), such as seconds or days for assimilation, and perhaps from growing seasons to years for senescence and abscission of plant parts. This further complicates the common practice of integrating growth processes over annual periods. Nevertheless, the difference between assimilation and respiration, which is equivalent to growth above and below the ground is commonly used as resulting quantity, known as net primary productivity (NPP).

The annual cycle of plant part losses, arising in the form of the litterfall derived from above- and below-ground parts, feeds back to the heterotrophs of the ecosystem which use the energy stored in the organic matter and recycle nutrients as a major resource for further plant growth. However, the decomposer chain is by no means a single pathway. Several groups of organisms competing for discarded plant organic matter include bacteria, fungi and soil animals. In this context, symbiotic mycorrhizal associations between tree roots and fungi are especially important in forests because, while supported by carbohydrates received directly from the living plant, the fungi produce enzymes enabling nutrients such as N to be recycled from plant litter without mineralisation (Smith and Read 1997). At the same time, more complex residues like cellulose and lignin are comminuted by soil animals, degraded by saprophytic fungi, and recycled by bacteria, and new compounds are synthesised by the decomposing organisms. Despite these very specialised and diverse microbial activities, some particularly recalcitrant fractions of the litter or products of the decomposers are not degradable for the decomposer community involved. These left-over products accu-

Fig. 1.1. The ecosystezm carbon cycle. This figure illustrates the main fluxes of carbon in forest ecosystems, neglecting minor pathways through flowers and fruits and bark. Herbivory is assumed to be part of litter. The times that are depicted at the different cycles illustrate the usual integration time of measurements or the mean residence time. *Solid arrows* depict C fluxes, *gray arrows* depict nutrient fluxes, the *broken line* between leaf biomass and assimilation indicates a major feedback of C allocation. Black carbon encompasses the recalcitrant, nondecomposable fraction of humus, which to a large proportion consists of charcoal

mulate as humus (Meyer 1993; Zech and Kögel-Knabner 1994). This pool of residues serves a valuable ecosystem function because it acts as a temporary and reversible store of nutrients, including N, which can be exchanged against equivalent charges of other ions. However, under certain conditions, for example following a change in species composition in the flora, the humus itself can also be remobilised if the edaphic conditions or the decomposing organisms change. Decomposition of litter or humus may also lead to losses of dissolved C to groundwater.

The heterotrophic respiration associated with decomposition leads to a release of CO_2 from the ecosystem. This inclusion of heterotrophic respiration with the NPP term at the ecosystem level yields net ecosystem productivity (NEP = assimilation minus autotrophic plant respiration and minus heterotrophic respiration). The NEP term is what is measured using the eddy covariance technique, though it is then commonly called net ecosystem exchange (NEE), because these measurements generally are carried out over relatively short periods of time and do not include periodic or long-term disturbances (Schulze and Heimann 1998). NEP quantifies the change in C storage of the ecosystem, including growth of woody biomass and changes in soil C.

The decomposer chain is only one possible pathway for the breakdown of organic C. The above-ground biomass and the organic layer of the soil may also be consumed by fires, which produce charcoal on one hand but release CO_2, bypassing heterotrophic respiration, on the other. Harvest of trees is the other main process disrupting the forest C cycle. Harvest generates fresh litter on one hand, but extracts a major fraction of organic material and the associated elements (nutrients) from the ecosystem on the other, and this may affect soils in the long term (Schulze and Ulrich 1991). The C balance, including disturbances that export C from the ecosystem bypassing respiration, was termed net biome productivity, NBP (Schulze and Heimann 1998). Thus, NBP includes changes in soil C, excluding changes in woody biomass. Soil C may include a short-term component (changes during stand development) and a long-term component considering the effect of disturbances, e.g. during harvest. The recalcitrant component of soil C, which may originate from fire or from soil processes, is termed black carbon.

In the following text we will not deal with fire or logging, but we will try to unravel the interaction between plants and decomposers, which covers time constants between hours and millenia of years, and where the pool of soil C acts as an "ecological memory" that is regulated by parameters and organisms other than the assimilatory process, and which may significantly determine the actual rate and the interannual variability of NEE. The time lag between assimilation and dissimilation may serve as an indicator of the mobilisation of deposited organic material. In the forest ecosystems under investigation we may neglect N_2-fixation.

While nutrients appear as an environmental parameter in the C cycle where decomposers release nutrients that are required for new growth, the emphasis changes when inspecting the N cycle. In this case, C is substantially involved only for a fairly short part of the pathway, and a shuttle between organic an inorganic forms of N play a major role at all time scales.

Nitrogen (Fig. 1.2) enters into the biological cycle through N_2 assimilation or through oxidation by electrical discharge or combustion processes. From then on, N shuttles between reduced and oxidized inorganic N and organic N, which is mainly associated with amino acids, nucleic acid and wall materials such as chitin. The plant
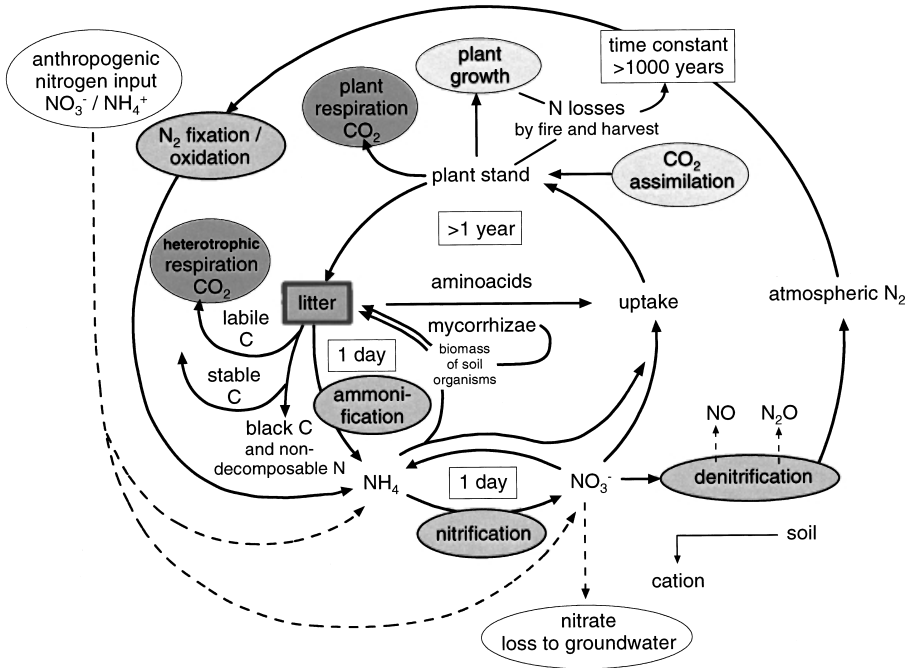
Fig. 1.2. The ecosystem nitrogen cycle. This figure illustrates the major pathways of N in forest ecosystems. The times that are depicted at the different cycles illustrate the usual integration time of measurements or the mean residence time. *Solid arrows* depict C fluxes, *broken arrows* illustrate the path of anthropogenically added N

cover can potentially use all forms of N, organic as well as inorganic. Generally, however, it assimilates inorganic N and releases organic N in form of litter. Depending on conditions, the N cycle shows a number of nested cycles during decomposition. Mycorrhizae are capable of breaking down proteins (Abuzinadah and Read 1986) and most likely contribute to the capacity of plants to take up amino acids from soils (Naesholm et al. 1998; Wallenda and Read 1999). Under nutrient-deficient conditions this process is very efficient, i.e. it may, in fact, compete successfully with other soil organisms. When more N is available, bacteria, decomposer fungi and soil fauna will mineralise organic N and release ammonium, which may again be utilised by other microorganisms for their own metabolism or structure, or be taken up by plant roots. If excess ammonium is available, and soil conditions are appropriate, a part of the ammonium may be converted to nitrate by nitrifying microorganisms. Nitrate may, in turn, be assimilated by microorganisms for their own metabolism, be taken up by plants or be denitrified, if conditions are suitable (mostly anoxic conditions). Excess nitrate may be leached to the groundwater. This latter process is associated with a loss of cations and soil acidification.

The N cycle, with all its shortcuts, is thought to be a closed system under natural conditions, especially if N is limiting; but the cycle can be disrupted by anthropogenic N deposition from industrial and agricultural sources. The input of ammonium and