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THE INTERNAL NITROGEN CYCLE BETWEEN MICROORGANISMS, VEGETATION AND SOIL

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ABSTRACT

The major portion of the global nitrogen cycle occurs between vegetation and soil, only minor exchanges generally taking place with the atmosphere and the hydrosphere. Nitrogen conversions in soil are briefly reviewed and a global flow chart for soil nitrogen is presented. The turnover times of nitrogen in various components of this global system are compared with its turnover times in some selected ecosystems. It is shown that 95 % of the nitrogen flow in the global terrestrial system is restricted to the plant-microorganism-soil system; only 5 % of the total flow is concerned with exchanges to and from the atmosphere and the hydrosphere.

INTRODUCTION

Annual nitrogen transfers between soil and vegetation by far exceed other global nitrogen transfers. In the present paper the internal nitrogen cycle in the vegetation – soil system is compared with the external global nitrogen cycle (Söderlund & Svensson, 1976). In the estimates of the global cycle Söderlund & Svensson concentrated on the exchange processes between the pedosphere, hydrosphere and atmosphere (inputs/losses in Fig. 1), paying only limited attention to conversions in the soil – most of which are mediated by microorganisms.

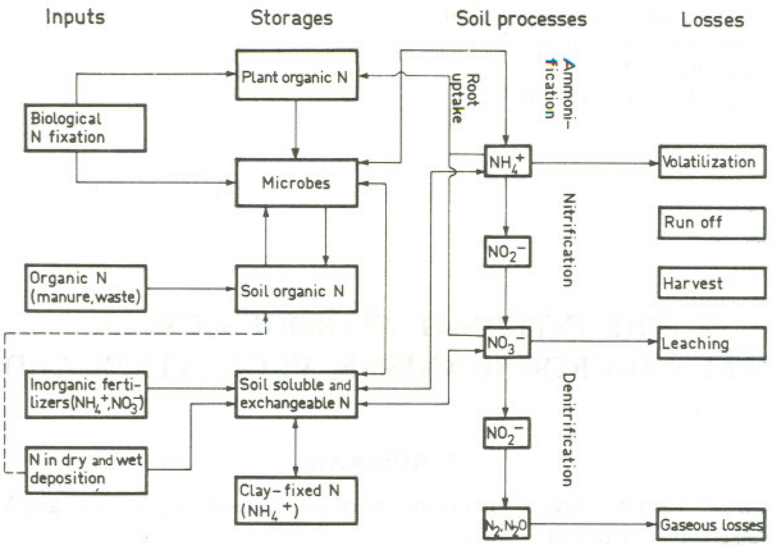


Figure 1. A flow chart for nitrogen in soil (modified from an original by Keeney & Gardner, 1970; used by permission).

NITROGEN CONVERSIONS IN SOIL

The vegetational cover of the earth is dependent on inorganic nitrogen for growth, and the amounts of plant-available ammonium- or nitrate-nitrogen at any one time are usually limiting. The ammonium nitrogen in soil water is in equilibrium with exchangeable inorganic nitrogen, which is bound to clay minerals and organic colloids. The amounts of exchangeable and soluble inorganic nitrogen rarely exceed 2 % of total soil nitrogen (Harmsen & Kolenbrander, 1965). Ammonium can also be fixed to clay minerals in such a way that it becomes unavailable, and amounts of fixed nitrogen have been reported attaining levels above 40 % of total soil nitrogen (Young, 1962); a global average of 5 % was estimated by Söderlund & Svensson (1976). The major part of soil nitrogen occurs, however, in organic form and must be mineralized to inorganic nitrogen before it can be taken up by plants. There are thus several forms in which nitrogen occurs in soil (cf. Fig. 1).

Molecular dinotrigen is fixed by certain bacteria and blue-green algae, becoming bound in the form of protein in biomass. Biological nitrogen fixation is one of the major inputs of nitrogen to the soil system. This organic nitrogen is mineralized to ammonium-N by microorganisms, this being one of the most important processes in soil. The ammonium nitrogen can either be taken up by plant roots or by microorganisms and utilized for growth or oxidized to nitrite and nitrate (nitrification), mainly by certain bacteria (*Nitrosomonas* spp. and *Nitrobacter* spp.). Nitrate can also be utilized by plants and microörganisms as a nitrogen source; under certain conditions it can serve as an electron acceptor for microorganisms and be reduced and released as molecular nitrogen (or nitrous oxide).

The flows of nitrogen are summarized in Fig. 1. For more detailed discussions on nitrogen conversions in soil, the reader is referred, for example, to Jansson (1958), Allison (1965), Bartholomew & Clark (1965), Bremner (1967), Campbell & Lees (1967) and Paul (1976).

The mineralization of soil organic matter is slow as compared with many other soil conversions, and it has been estimated that generally only 1–3 % of the soil organic nitrogen is mineralized during a growing season (Bremner, 1967). Most plants can use either ammonium-N or nitrate-N, but some are more specialized and ecosystems can be characterized by the main forms of mineral nitrogen present (Table 1). The ammonium vegetation type is restricted to soils with a low pH, which limits the activity of nitrifying bacteria. The nitrate-type is confined to wet tropical forests and certain deciduous forests on soils with high pH.

In the present paper no attempt will be made to assess global rates of nitrification, inorganic nitrogen being treated as one pool of plant-available nitrogen.

Table 1. Ecosystem types classified by the main forms of mineral nitrogen (from Ellenberg, 1971).

NH_4^+–type	NH_4^+ – NO_3^-–type	NO_3^-–type
Taiga, dwarf-shrub tundra	Many temperate deciduous forest on loamy soil	Moist tropical lowland forest
Subalpine coniferous forest	Alluvial forest	Temperate deciduous forest on calcareous soil
Coniferous peat forest	Alder fen (*A. glutinosa*)	Fertilized meadows where soil is not wet, most gardens
Oak-birch forest	Many grassland types	
Calluna heath	Dry grassland on calcareous soil	Ruderal formations
Many swamps	Tropical savanna	
Raised *Sphagnum* bog	Some tropical forests	

A GLOBAL FLOW CHART FOR SOIL NITROGEN

The nitrogen cycle between vegetation, soil and microorganisms is schematically shown in Fig. 2. The storage values of nitrogen in plants, plant litter and soil organic matter were taken from Söderlund & Svensson (1976). The values presented by them, given in Tg, were converted to mean values per square metre by dividing by a total ecosystem area of $133 \cdot 10^{12}$ m^2 (Rodin *et al.*, 1975). The value for soluble and exchangeable inorganic nitrogen was estimated at 1 % of total soil nitrogen based on Harmsen & Kolenbrander (1965), who gave an upper limit of ca 2 %.

In order to estimate the amounts of nitrogen bound in microorganisms, a mean value of 100 g m^{-2} (dry weight) for microbial biomass in soil – an average of the data presented in Table 2 – was used. The percentage of nitrogen in microbial biomass varies considerably,

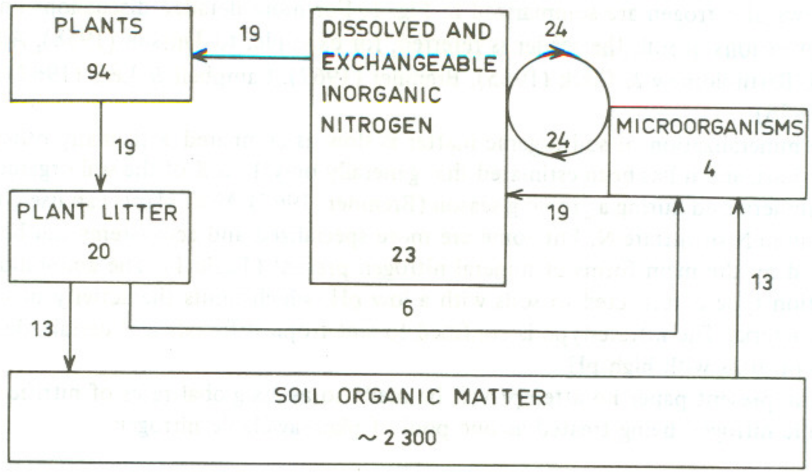


Figure 2. Storages (g m^{-2}) and transfers (g m^{-2} yr^{-1}) of nitrogen within the global plant-soil system.

depending on growth conditions, and actual determinations on microbial biomass from soil are lacking. Heal & MacLean (1975) gave a mean value of 6 % for nitrogen in soil microorganisms, while Ausmus *et al.* (1976) reported values of 4.0 % for soil bacteria and 2.8 % for fungal mycelia from a deciduous forest. Söderström (unpublished), analyzing fungal mycelia grown on a poor soil medium, obtained a nitrogen content of 4.0 %. For the present survey, a nitrogen content of 4 % was taken as a realistic average value for field conditions, giving a mean value of 4 g N m^{-2} in microbial biomass.

The amount of nitrogen taken up by the primary producers was estimated from Bazilevich (1974) to be 19 g N m^{-2} yr^{-1}. This may be somewhat high, and for example Lieth (1975) estimated a lower value. The vegetation-soil system is considered to be in a steady state and the same amount as is taken up would consequently be returned in litter fall. It was further assumed that when plant litter has been decomposed to 40 % of its original

Table 2. Biomass of microorganisms (g m^{-2} dw) in various ecosystems.

Grassland	Pawnee, CO, USA	65	Andrews *et al.* (1974)
Grassland	Matador, Canada	195	Clark & Paul (1970)
Deciduous forest	Oak Ridge, TN, USA	97	Burgess & O'Neill (1976)
Deciduous forest	Meathop Wood, UK	46	Satchell (1971)
Coniferous forest	Jädraås, Sweden	240	Söderström & Clarholm (unpubl.)
Tundra	Stordalen, Sweden	80	Rosswall *et al.* (1975)
Tundra	Devon Island, Canada	20	Bliss (1975)
Mean value		~100	

weight, it has become so fragmented as to make it comparable with soil organic matter (Bunnell & Scoullar, 1975). This is a somewhat arbitrary assumption, but will probably be sufficient for the purpose of this paper. Organic nitrogen in plant litter or soil organic matter is mineralized by microorganisms and inorganic nitrogen is added to the pool of nitrogen in solution, which in turn is in equilibrium with the much larger pool of exchangeable and fixed inorganic nitrogen.

Apart from the nitrogen flowing through the microbial population in order to meet the need for inorganic nitrogen by vegetation (19 Tg yr^{-1}), nitrogen is also taken up by bacteria and fungi to meet their own nitrogen requirement in the production of microbial biomass. The estimated additional throughput of 24 g m^{-2} yr^{-1} of nitrogen was obtained by using the data given by Heal & MacLean (1975), viz. that the ratio of nitrogen throughput by microorganisms to nitrogen taken up by net primary production is 2.27; thus, a total of 43 g N yr^{-1} would pass through the microbial population in an average "global" terrestrial square metre.

From the data in Fig. 2, the turnover times of nitrogen in various comparments of the system can be calculated (Table 3). For comparison with global turnover times, data are also given for some selected ecosystems. The global turnover time of nitrogen in the vegetation is 4.9 years, the tundra and oak-hickory forest values being very similar. The turnover rates of nitrogen in the plant litter pool are also within the same order of magnitude for the four systems.

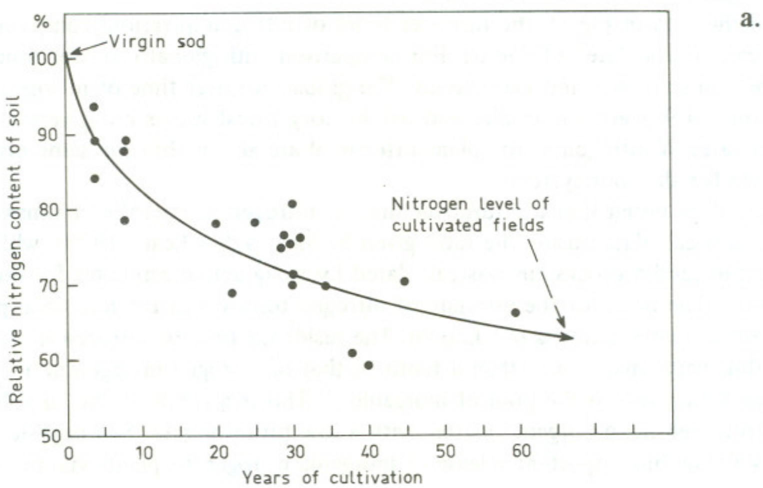
It should be noted that the turnover time of nitrogen in microbial biomass for the "world" was calculated using the ratio given by Heal & MacLean (1975), while the turnover for the tundra ecosystem was calculated by using actual estimates for microbial production. The basis for the estimate of nitrogen turnover in the microbial population for the other two systems is not known. The residence time of nitrogen in microorganisms is thus very small – less than a tenth of that of nitrogen in vegetation. There is also a rapid turnover in the pool of inorganic-N. This is a result of the large buffering pool of nitrogen in soil organic matter with a low turnover rate. Soil organic matter provides a slow but important release of inorganic nitrogen to plants via microorganisms.

Table 3. Turnover time (yr) of nitrogen in various parts of the global terrestrial system and some selected terrestrial ecosystems. PP = primary producers, PL = plant litter, SOM = soil organic matter, MO = microorganisms, IN–N = soluble and exchangeable inorganic N.

Ecosystem	PP	PL	SOM	MO	IN–N	Reference
"World"	4.9	1.1	177	0.09	0.53	The present paper
Tundra mire	5.6	1.7	372	0.32	0.30	Rosswall *et al.* (1975)
Oak-hickory forest	4.1	2.9	150	0.15	0.19	Mitchell *et al.* (1975)
Mixed deciduous forest	4.0*	5.1	109	0.02	0.23*	Henderson & Harris (1975); Burgess & O'Neill (1976)

* Recalculated from data in the references.

In the estimation of nitrogen transfers in the "world" ecosystem, it was assumed that the system is in a steady state, since, at present, there is no conclusive evidence proving that world primary production is either decreasing, as a consequence of urbanization, forest cutting, etc., or increasing, as a consequence of the raised levels of carbon dioxide in the atmosphere or because of other climatic changes. It should be realized, however, that a steady state rarely occurs in isolated ecosystems in which nitrogen may either be increasing or decreasing. As examples, the changes in nitrogen content in the soil with time in a cropped ecosystems and a pasture are shown in Fig. 3. The nitrogen content of soil is thus very dependent on management practices, and increased land cultivation will surely affect the nitrogen content of the soil and consequently affect the total nitrogen cycle.



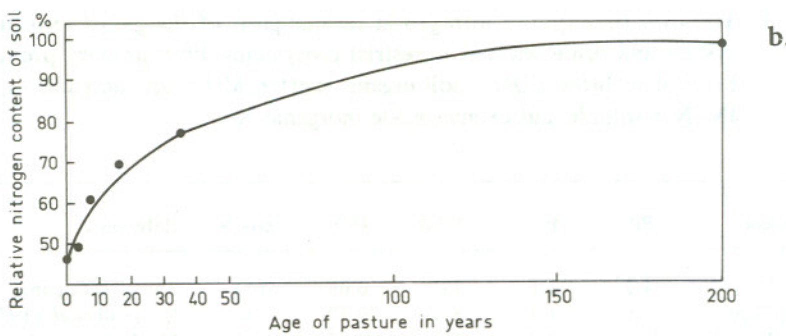


Figure 3. Changes in nitrogen content in the soil of a cropped ecosystem (a) (Jenny, 1941) and a pasture ecosystem (b) (Russell, 1973). Data used by permission of Professor H. Jenny (a) and Professor E.W. Russell (b).

Ecosystems conserve nitrogen by a more or less closed cycle of nitrogen between the vegetation and the soil, and it is generally agreed that the developmental stages of ecosystems tend to have a more open nutrient cycle as compared with the mature (climax) stages (Odum, 1969). The climax stages should be in a steady state – inputs should equal outputs – and since there is continuous input of nitrogen through nitrogen fixation as well as dry and wet deposition, a climax ecosystem may leak more nitrogen than one in the early stages of development (Vitousek & Reiners, 1975). The nitrogen cycle is also affected by the maturity of the ecosystem in other ways; it seems as if nitrification – at any rate in some ecosystems – is inhibited by the climax stages (Rice & Pancholy, 1972).

There are noticeable differences in the pattern of nitrogen cycling in various ecosystems – four of them are compared in Fig. 4. The desert ecosystem (Fig. 4a) has a large external cycle of nitrogen, and nitrogen fixation, ammonia volatilization and denitrification are very important parts of the total flow, accounting for more than 30 % of the transfers. Plant uptake of nitrogen accounts for only 21 % of the total nitrogen transfers within the system.

On the other hand, the ecosystem represented in Fig. 4b, a temperate deciduous forest, has very limited inputs/outputs, and both nitrogen fixation and denitrification accout for less than 1 % of the total nitrogen flows. This deciduous forest ecosystem is thus a very closed system, buffered by a large pool of nitrogen in the soil (Reichle, 1975).

The tundra mire (Fig. 4c) is selected to represent a system accumulating nitrogen in the form of soil organic matter (peat). Although the inputs from the atmosphere in the form of nitrogen fixation and dry and wet deposition are numerically small, they are very important for retaining the productivity of the system by counterbalancing the amounts of nitrogen annually made unavailable in the deeper peat strata.

The cut grass sward (Fig. 4d) is representative of a system which is largely influenced by man. Large amounts of commercial fertilizers are added annually in order to sustain productivity, but this also leads to important losses to the atmosphere through denitrification and perhaps ammonia volatilization, and also to leaching losses, which have been considered to be negligible in the other ecosystems shown. Large amounts of nitrogen are removed from the system in annual harvests. The system thus has large inputs/outputs, and is only prevented from running low in nitrogen by addition of fertilizers.

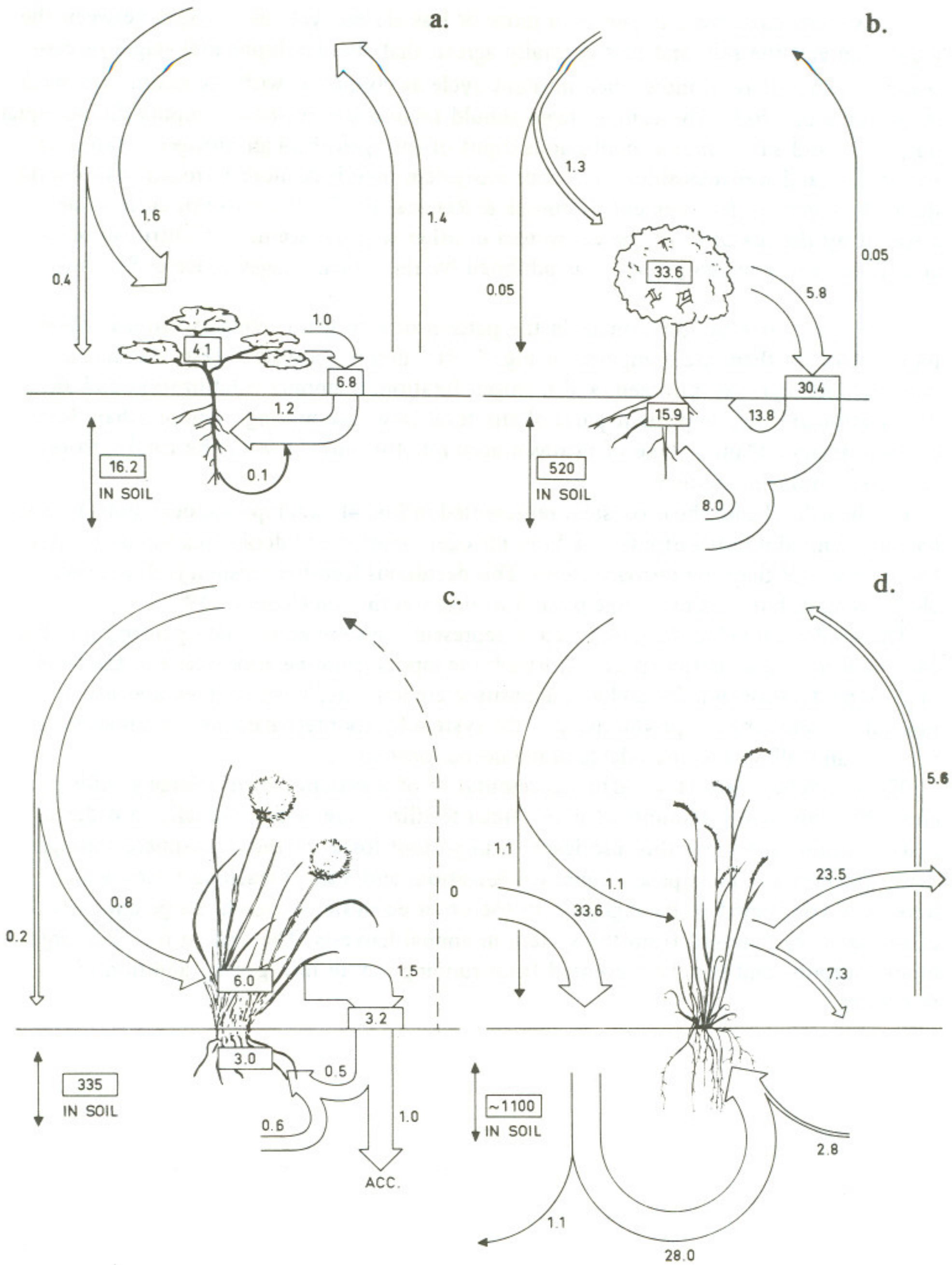


Figure 4. Ecosystem nitrogen cycles. a. desert ecosystem; b. deciduous forest ecosystem (a and b from Reichle, 1975; used by permission); c. tundra mire (data from Rosswall *et al.*, 1975); d. cut grass sward receiving a large amount of nitrogen fertilizers (336 kg ha^{-1} as NH_4NO_3) (data from Whitehead, 1970). The arrows are approximately proportional to the flows expressed as a percentage of the total flow in any one system. All values are in g m^{-2} yr^{-1}.

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Figure 5 shows the nitrogen cycle in the global system. The internal plant-soil-micro-organism cycle is larger by an order of magnitude than the fluxes to and from the global system. The global data on a square metre basis are approximately equal to those given for the deciduous forest ecosystem (Reichle, 1975) in that the flux to/from the soil to the atmosphere is ca. 10 % of that between the soil and the vegetation. The flows of nitrogen from soil-vegetation to the atmosphere-hydrosphere amount to only 5 % of the total annual transfers of nitrogen. In this respect the "world" ecosystem has a closed nitrogen cycle, hence the Earth can be regarded as a mature or climax ecosystem.

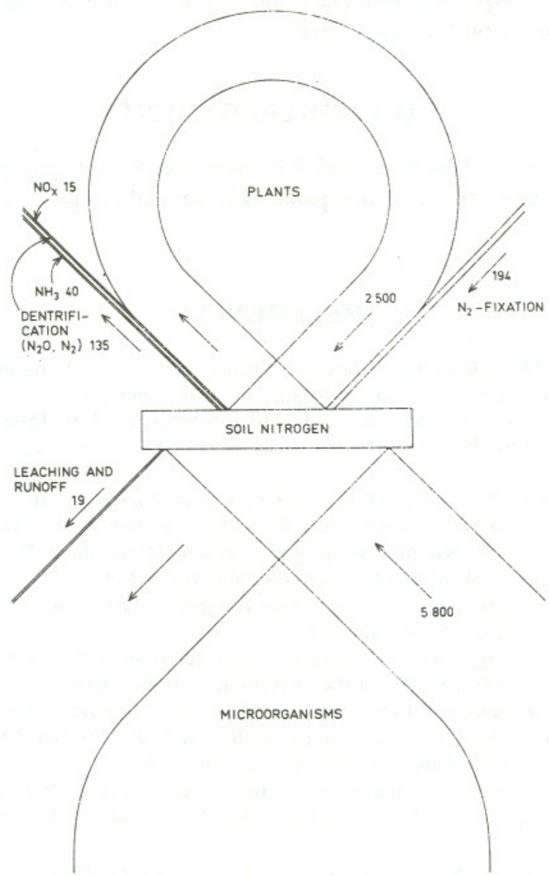

Figure 5. The global nitrogen cycle in the soil-vegetation-microorganisms subsystem. All values are in Tg (million metric tons) per year. The dimensions of the flows are proportional to the amounts. Input/output data are from Söderlund & Svensson (1976).

CONCLUSIONS

The biosphere has developed over millions of years to a mature system with a very closed nitrogen cycle. On a global scale, 95 % of the annual nitrogen flows occur within the soil and between soil and vegetation.

The Earth, as well as individual ecosystems, seems to have adapted to a fairly constant turnover rate for nitrogen in various components. Although the total magnitudes for the flows vary, the turnover rates for separate components are very similar.

At present, man-induced changes probably affect the prevailing patterns of nitrogen conversions only to a minor extent. However, a global view of nitrogen cycling undoubtly conceals very important regional and local effects of man's activities. It should be noted that small changes can have profound effects – for example the catalytic action of oxides of nitrogen on the ozone layer.

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