

Impacts of Climate Change on Carbon and Nitrogen Cycles in Boreal Forest Ecosystems

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Abstract

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It is well known that soil carbon stocks decrease considerably in response to soil warming, but experimental data have shown that the loss of carbon declines within decades in apparent acclimation. An explanation to such findings is offered under the theoretical framework of ecosystem models in this thesis. Simulations of forest ecosystem responses to increased soil temperatures showed that the labile carbon in soil was reduced considerably within years after warming, although the structure and function of decomposer organisms remained intact.

Simulations of increased CO₂ also confirmed positive growth response in the short term. The response of soil carbon was similar, however predicted to be less than the increase of biomass. Nitrogen availability and negative feedback mechanisms of the plant soil system were critical to the results, indicating that nitrogen progressively limited the growth response.

Assumptions concerning the response of decomposing organisms to changes in soil nitrogen are crucial to the interpretation of the above. Positive nitrogen feedback was therefore implemented to test consequences of nitrogen additions, allowing for improved decomposer efficiency when inorganic nitrogen becomes available in the soil. Responses compared well with experimental results. Simulations of moderate inputs of slowly increasing inorganic nitrogen loads in the long term revealed counteracting feedback responses: the positive nitrogen feedback resulted in increased decomposer efficiency and biomass growth also increased as expected; negative nitrogen feedback appeared in the sense that the growth response was reduced due to decreased mineralisation.

An economic estimation of the net value of carbon sink capacity was also performed. The value of the carbon sink was given in relation to conservative estimates of total net values of important stocks and flows of forest natural capital – factors such as recreational values or hydrological services omitted. The net value of the carbon sink was suggested to amount to 3-50% of the net value of Swedish forests.

Keywords: boreal forest, climate change, continuous-quality theory, decomposer efficiency, G'DAY, generic decomposition and yield model, natural capital, satellite net national accounts, nitrogen productivity, Q-model, soil decomposition, soil warming.

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This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

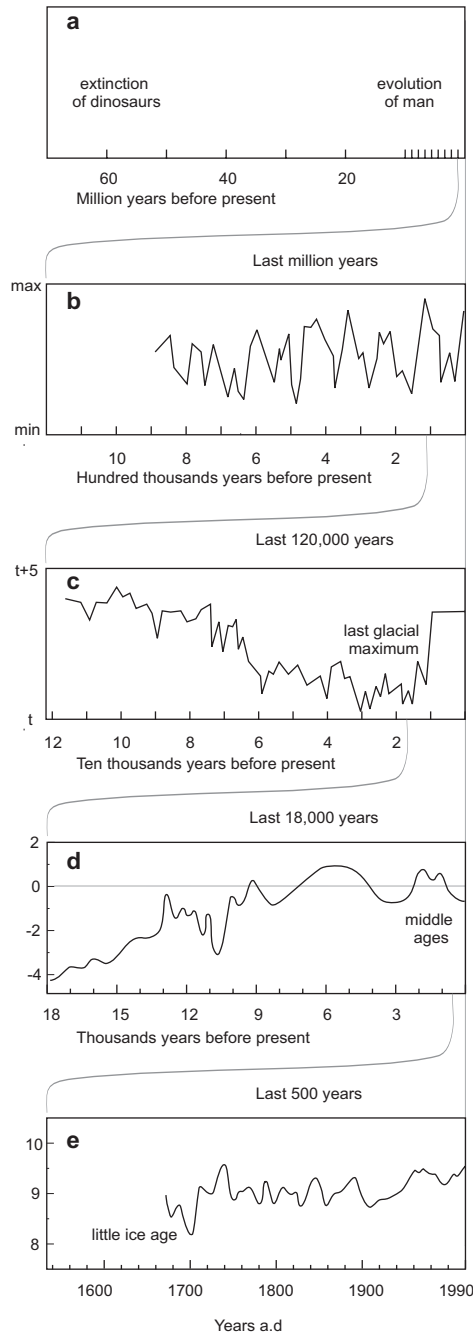
- I. Eliasson, P. (1997). Carbon fixation in Swedish forests in the context of environmental national accounts. In: *Climate change mitigation and European land-use policies* (eds. W.N. Adger, D. Pettenella & M. Whitby). Guilford and King's Lynn, UK, CAB International: 239-253.
- II. Eliasson, P.E., McMurtrie, R.E., Pepper, D.A. *et al.* (2005). The response of heterotrophic CO₂-flux to soil warming. *Global Change Biology* 11(1): 167-181.
- III. Pepper, D.A., Eliasson, P.E. McMurtrie. R.E *et al.* (2006). Simulated mechanisms of N feedback on positive forest CO₂ response. *Global Change Biology* 13(6): 1265-1281.
- IV. Eliasson, P.E. & Ågren, G.I.A. Feedback mechanisms of soil mineralisation rate and timing of growth response in a boreal forest ecosystem. (Manuscript).

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Anthropogenic influences on climate change and nitrogen supply

On a global scale, emissions from fossil fuels and other anthropogenic sources are estimated to increase atmospheric CO₂ by approximately 7 million tonnes carbon per year (IPCC, 2007), leading to increase of global surface temperatures during the 20th Century. The increase in temperature in the northern hemisphere was greater in the past century than in any other century during the past millennium. Increased temperature alters global wind patterns, storm tracks and temperature patterns in both hemispheres. As result of the warming, total precipitation in the northern hemisphere has increased by 5-10% and heavy rain events have become more frequent. Ironically, this is not the case in arid regions (*e.g.* the Mediterranean, Africa and parts of Asia) where water is naturally a scarce resource. Instead, the observed frequency and intensity of droughts have

Fig. 1. History of global climatic change in different time resolutions. *a:* The perspective of million years. *b:* Estimated variation in global ice volume based on O₂ isotopes in deep sea cores. *c & d:* Fluctuations in global mean temperatures based on isotopes of O₂ in ice cores over the past 120,000 & 18,000 years, *d* shows difference from present temperatures. *e:* Temperatures in central England over the past 300 years. Temperatures shown are in °C. Figures are from Cannell (1995) with kind permission of European Forest Institute.



probably increased in the South and El Niño events have become more frequent. As result of the warming, the ice cover of rivers, lakes and glaciers, including the Arctic ice, has retreated and thinned. Permafrost has thawed and global mean sea levels have risen by 100-200 mm. The warming has effects on timing of plant flowering, bird arrival, dates of breeding season and emergence of insects, as well as on the migration patterns of plants, insects and animals.

The above is the concise summary of assessments taken mainly from the Synthesis Report of the Third Intergovernmental Panel on Climate Change (IPCC) presented six years ago (IPCC, 2001a). The likelihood of these estimates and projections was confirmed and in some cases strengthened in the Fourth IPCC report (IPCC, 2007), which stated that future trends based on projections for the 20th Century are 'virtually certain' and that it is 'very likely' that the continued greenhouse gas emissions will cause even larger changes in the 21th Century.

There are still sceptics arguing that the causes of global warming are unknown or primarily the result of natural processes. Exceptions to the consensus above argue that the climate of the Earth and the chemical composition of the atmosphere have a long history of dramatic changes and that changes have been much more drastic in a perspective of millions of years than during the past millennium. It cannot be denied that considering only global mean temperature and our knowledge of the historical variations (see *Fig. 1*), climate change during the past 1000 years may not seem alarmingly drastic (Harrington, 1987; Dickinson, 1989; Cannell, 1995; Petit *et al.*, 1999; Bertrand *et al.*, 2002). The current increase in global mean temperature during recent decades is more drastic than at any time during the Anthropocene, however, and this increase is caused by human activities (IPCC, 2001b).

Furthermore, the production and application of nitrogen for human use has grown exponentially during the past three decades (Matthews, 1994; Galloway & Cowling, 2002). Alterations to the nitrogen cycle by the conversion of atmospheric nitrogen to biologically available forms, such as mobilisation of nitrogen from natural long-term geological and biological storage pools and extensive use of nitrogen-fixing crops, has at least doubled the rate of anthropogenic nitrogen input to the terrestrial nitrogen cycle (Vitousek *et al.*, 1997). The increased nitrogen supply may have the potential to counteract the increased concentrations of atmospheric CO₂ through increased plant biomass production. However, the levels of nitrogen being deposited over most of Europe exceed the many estimates of critical loads of between 10-20 kg N ha⁻¹ y⁻¹ (Rosen *et al.*, 1992; Dise & Wright, 1995; Erisman & de Vries, 2000; Matson, Lohse & Hall, 2002; Nordin *et al.*, 2005). The likelihood that a region will undergo nitrogen saturation depends on the interactions between soil properties, land use, stand age, climate variation and the rates and history of nitrogen deposition (Ågren & Bosatta, 1988; Aber *et al.*, 1989; Aber *et al.*, 1998; Aber & Magill, 2004).

In summary, there is strong consensus among leading scientists that global warming does exist and that it most likely is predominantly caused by human activities such as fossil fuel combustion and changes in land use (IPCC, 2007; Science Academies of G8+5 countries, 2007). Atmospheric concentrations of CO₂

have increased by 30% and other greenhouse gases have increased by approximately 150% (methane) and 17% (nitrous oxide) over the past 1000-250 years (IPCC, 2001a, 2001b). Release of large quantities of reactive nitrogen to the global nitrogen cycle adds to the complexity of the altered global carbon cycle through the interaction between the carbon and nitrogen cycles.

Ecology, the economy and climate change

Setting aside the altruistic perspective, our concern about environmental change can be seen as a socio-economic consideration of how we define the value of the present and future state of the environment in terms of human welfare. The perspective may extend from the present and up to a number of future generations depending on individual preferences. Indicators of environmental health and assessments of vulnerability as laid out by the IPCC reports have demonstrated what constitutes ‘dangerous anthropogenic interference with the climate system’ to the United Nations Framework Convention on Climate Change (UNFCCC). The UNFCCC is often referred to as the ‘Kyoto Protocol’ after the first principal update of the treaty, in which mission limits were agreed. It is acknowledged that the scientific basis for the IPCC Third Assessment Report involves value judgements influenced by considerations concerning development, equity and sustainability (IPCC, 2001a) and this is also in agreement with the mission as laid out by UNFCCC (Climate Change Secretariat of the UNFCCC, 1994). A socio-economic dimension of climate change is thus addressed, reflecting the underlying concerns for human welfare. Important decisions are likely to be further influenced by value judgements when policymakers make priorities and take decisions in the interest of social communities based on scientific conclusions. The concerns underlying our interest in the ecological consequences of climate change in the natural sciences are thus based on the aim of optimising the well-being of present and future generations in communities on national and international levels. It is therefore important to agree on definitions and understand not only the scientific basis, but also how to optimise welfare under economic restrictions. The state of the environment and the state of the economy are both more or less measurable entities, although not well integrated. The uncertainties concerning the value of inputs and outputs of the amounts of carbon ‘re-routed’ into economic system as displayed in *Fig. 2* highlights the necessity of incorporating environmental science into welfare economics (or vice versa). The problem for economists trying to optimise environmental resources is firstly that physical and economic metrics do not easily compare. Secondly, the value and cost of depletion of natural capital is difficult to theoretically define in the prevailing neo-classical economic theory. The challenging obstacle is that monetary value is understood in terms of market price and is derived from supply and demand under theoretical restrictions. Stocks and flows of carbon entering the economic system can easily be quantified in monetary terms as long as they are recognised on markets. The so-called external effects of economic activity on the utility of environmental

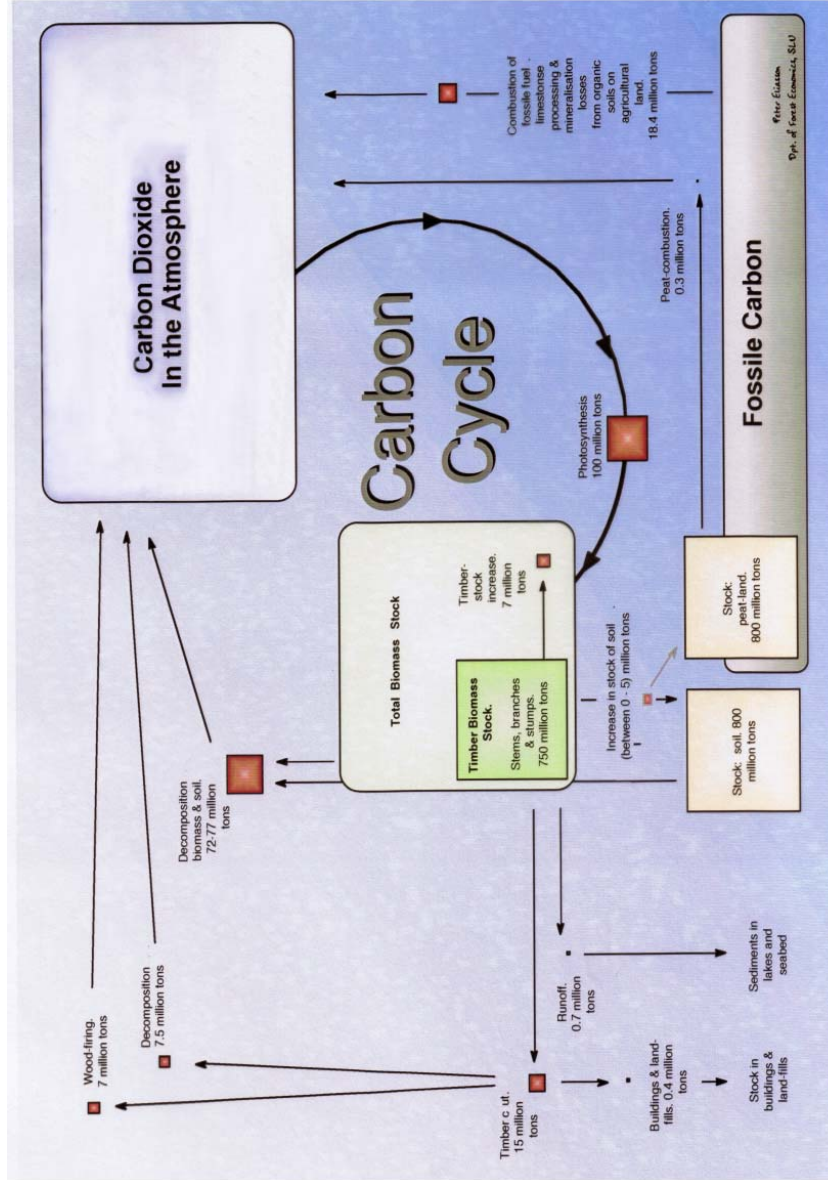


Fig. 2. The carbon cycle in Swedish forests as measured in tons of carbon. Area of the boxes is proportional to estimated volumes except for those drawn with rounded corners. For further details, see Paper I (Eliasson, 1997)

stocks and flows cannot easily be monetarised because they are not traded on markets. It is thus the utility of non-marketed and intangible goods and services, such as all possible consequences of CO₂ emissions that are difficult to quantify.

There is still no international consensus on how to properly measure the contribution of the environment to the economy and the impact of the economy on the environment. To that end, in 1993 the United Nations proposed a System of Integrated Environmental and Economic Accounting (SEEA) as an effort to implement a measuring system for the interaction between the economy and the environment in a coherent and consistent data framework. The latest revision of the SEEA was undertaken in 2003 under the joint responsibility of the UN, Eurostat, the International Monetary Fund (IMF), the OECD and the World Bank (United Nations *et al.*, 2003). The development and implementation of SEEA are still in an experimental stage. Aggregates from SEEA will of necessity be less precise than those coming from the System of National Accounts (SNA) (United Nations, 2007) due to the inherent difficulties in deriving values of non-market resources (e.g. Skånberg, 2001; Boman *et al.*, 2003), and it might be said that many environmental values have greater appeal if expressed in terms of quality instead of quantity. Environmental policies based solely on outputs derived from the conventional SNA can be misleading, although indispensable indicators of economic performance. Experimental SEEA satellite accounts are therefore useful complements to the SNA towards a more sustainable path of development.

Terrestrial carbon cycle driven by growth and decay

Importance of terrestrial carbon

Changes in land use are a major source of the increasing concentrations of atmospheric CO₂ although estimates are uncertain (see 'residual land sink' below). Over the past two centuries, two-thirds of the terrestrial carbon losses have been due to deforestation. The land biosphere is also a major sink. The estimates shown in *Fig. 3* are compiled from different sources as compiled in Betts *et al.* (2005).

Gross Primary Production, GPP

Plants produce carbohydrates by absorbing solar energy in photosynthetic pigments generally termed chlorophyll. The harvested energy in the form of electrons is absorbed in a sequence of reactions in high energy molecules (NADPH). The chlorophyll molecules regain electrons from water molecules leaving O₂ as a residual product. This residual product is the origin of the Earth's atmospheric oxygen. The above reactions result in increased concentrations of H⁺, creating high potential in chloroplasts of leaf cell membranes and enabling the synthesis of ATP, another high energy molecule. The atmospheric CO₂ diffused into the plant is reduced with the energy from NADPH and ATP the main enzyme

Rubisco, and a number of other enzymes in the so-called Calvin cycle, resulting in the overall photosynthesis reaction.

The use of CO₂ enrichment as a method to enhance plant productivity is well known in commercial horticulture and has long been used for many crops such as tomatoes, lettuce and cucumbers under optimal nutrient supply (Enoch, 1990). With sufficient light and open stomata, the actual photosynthetic rate depends on the supply of CO₂. Although photosynthesis requires CO₂, the relationship between CO₂ concentration and rate of uptake is not as predictable as might be expected. In addition to the atmospheric concentration of CO₂, the biochemical processes involved in photosynthesis are affected by temperature and the availability of nutrients and water. The temperature dependency of photosynthesis is mainly a result of temperature effects on enzyme kinetics. Water deficiency and dry air (high water vapour pressure deficit) mainly constrain photosynthesis through reduction in stomatal conductance and thereby the supply of CO₂. The exchange of gas in photosynthesising plants is substantial: for every gram of glucose formed in photosynthesis, 1.47 g of CO₂ is required (Larcher, 1995), corresponding to approximately 2.1 m³ of dry air under the current annual atmospheric CO₂ concentration ([CO₂]) of 382 ppm (Tans, 2007).

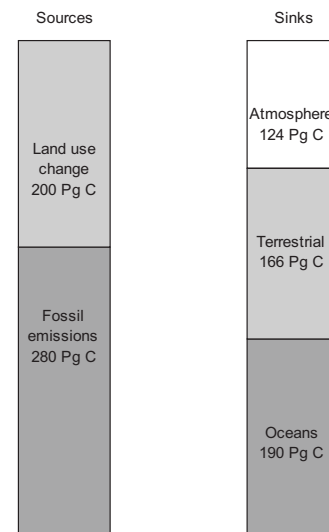


Fig 3. Estimated carbon sources and sinks over the last two centuries. Data from Betts *et al.* (2005) and references therein.

Plants are categorised as either C3 or C4 plants depending on differences in biochemical pathways associated with the Calvin cycle. It is mainly the influence of light intensity, leaf temperature and intercellular [CO₂] on the efficiency of CO₂ uptake that distinguishes C3 type plants from C4 (Björkman & Berry, 1973). Most C4 plant species are grasses adapted to warm climates and they contribute approximately 15% of gross primary production (GPP) in the global terrestrial biosphere (Lloyd & Farquhar, 1994). Cool growing season conditions favour C3 plants such as the boreal woody species investigated in this study and their photosynthesis is likely to respond much more to increased atmospheric [CO₂] than those with the C4 cycle (Kozłowski, Kramer & Pallardy, 1991).

The relationship between nitrogen supply and biomass growth is often expressed as nitrogen use efficiency (NUE), which is the ratio between the dry matter of biomass and the nitrogen incorporated during a specified time. Nitrogen-limited plants respond to addition of nitrogen primarily by increasing their leaf area index (LAI). It is the close relationships between photosynthetically active area, quantum yield and LAI that explain the growth response of plants to additions of limiting nutrients. The uptake of nitrogen in the plant is dependent on metabolic

synthesis and requires energy. The necessary energy is derived from photosynthesis, in itself dependent on chlorophyll and other compounds containing nitrogen. Extraction of energy derived from photosynthates such as nitrogen uptake is a respiratory process.

Autotrophic respiration, R_a

Respiration can in principle be seen as the reverse process of photosynthesis because O_2 is consumed and CO_2 and energy are released. Autotrophic respiration (R_a) is the result of metabolism in plant cells where different specialised plant cells use assimilated energy from photosynthates to maintain life-supporting functions of existent plant material, ion uptake and growth (Johnson, 1990). Rates of autotrophic respiration typically respond to climatic variables, most important of which is temperature but also humidity in atmosphere and soil, wind conditions, radiation and $[CO_2]$ in non-linear relationships. The release of autotrophic CO_2 is partly light-dependent and partly proportional to dry weight of the living biomass, hence the terms light respiration and dark respiration. Dark respiration can occur independently of light and continues during night-time and seasonal dormancy periods.

It is mainly the mechanisms of belowground respiration processes that are poorly known (Bond-Lamberty, Wang & Gower, 2004). Empirical relationships are difficult to establish because it is difficult to distinguish the sources of the autotrophic flux from roots and a more or less unknown community of decomposing organisms. One method to quantify the relative importance of autotrophic soil respiration relies on estimates of the difference between daytime and night-time respiration with corrections to climatic variables. Other methods of estimating autotrophic soil respiration are tree girdling and measurements of the relationship of ^{13}C to ^{14}C in the soil CO_2 efflux. Tree girdling interrupts root respiration with minimal disturbance to soil structure and water status while maintaining microbial respiration. Such experiments show that approximately half the average autotrophic respiration is derived from root respiration (Högberg *et al.*, 2001). Girdling, although a destructive technique, currently seems to be the most reliable method of estimating R_a/R_h . Uncertainties involve issues concerning the disruption of the symbiotic exchange of photosynthates and mineral nutrients between mycorrhizal fungi and roots (Kuzyakov, 2006; Trumbore, 2006). Different methods of estimating the soil CO_2 flux give rise to other uncertainties; *e.g.* the symbiosis above gives rise to an overlap in the definition of respiration by autotrophs (R_a) and respiration by heterotrophs (R_h) because the carbon source of the respiration from heterotrophic rhizomicrobial organisms is derived directly from roots (Killham & Yeomans, 2001).

Heterotrophic respiration, R_h

In terrestrial ecosystems, heterotrophic respiration (R_h) mainly occurs below ground as a result of decomposition of soil organic carbon (SOM) in a continuum of different stages of decay. Decomposition is the process by which more or less

complex organic molecules are disintegrated, partly into CO₂ and partly into a quality continuum of different by-products. Plant residues and SOM are often categorised depending on the rate at which they are decomposed. The most common method of determining the quality of substrates is by fractionation into solubility classes (Mellilo *et al.*, 1989; Johansson, Berg & Mentenmeyer, 1995). Most plant-soil simulation models use concepts similar to the above fractions as a simplified abstraction where inputs of plant litter to SOM is grouped into pools (Bolker, Pacala & Parton, 1998; Six *et al.*, 2002a; Six *et al.*, 2002b).

Fractions of recalcitrant plant residues may increase during decomposition, partly because recalcitrant fractions are less attractive to decomposers and partly because decomposition of labile fractions may leave chemically stable by-products. Moreover, during the processes of decomposition, SOM is subsequently enriched with the addition of complex molecules such as proteins and polysaccharides from the dead tissue as result of the turnover of decomposing organisms themselves. Insights about the structure and composition of the decomposer community are therefore important in understanding SOM decay rates. Estimates of the availability of SOM to decomposers are often used as a measure of soil quality (Ågren & Bosatta, 1997).

Role of nitrogen for the carbon cycle

The nitrogen cascade

The inherent potential of carbon storage at high altitudes, limited by factors controlling soil nitrogen mineralisation rates, is vast considering that the soils generally have C/N ratios that are less than half, or as low as one percent, of those in plant biomass. Thus, mineralisation of one unit of soil carbon theoretically makes nitrogen available for two to hundreds of units of plant carbon. The factors limiting rates of soil mineralisation in the boreal zone are therefore of crucial importance to the global carbon balance. The growth response to the addition of anthropogenic nitrogen can thus be seen as limited by nitrogen supply and it has been suggested that the addition of anthropogenic nitrogen to terrestrial ecosystems enhances net carbon storage by 0.1 to 1.3 Pg C yr⁻¹ (Townsend *et al.*, 1996; Vitousek *et al.*, 1997).

It has been shown that the growth response to additions of nitrogen declines and eventually ecosystems receiving heavy nitrogen deposition may reach nitrogen saturation, a state in which the system has no further capacity to retain nitrogen. Nitrogen saturation, often accompanied by a loss of Mg and Ca ions and soil acidification, has been described as either when nitrogen losses equal nitrogen deposition or when availability of inorganic nitrogen exceeds the demand from micro-organisms and plants (Ågren & Bosatta, 1988; Aber *et al.*, 1989; Tamm, Aronsson & Popovic, 1995; Aber *et al.*, 1997; Cannell & Thornley, 2000).

Production of plant biomass limited by availability of nitrogen in soil

Production of plant biomass is limited by nitrogen availability over much of Earth's surface, in particular at high latitudes where a third or more of the terrestrial carbon is stored, mainly in boreal forests, but also in temperate forests, temperate grasslands and tropical savannah (Tamm, 1964; Schlesinger, 1977; Post *et al.*, 1982; Schlesinger, 1997; Aerts & Chapin III, 2000). The potential for plant production in terrestrial ecosystems on a global scale is usually limited by the availability of nitrogen or phosphorus (Vitousek & Howarth, 1991), important elements in the molecular structures necessary for efficient photosynthesis. When insufficient amounts of nitrogen are available to plants, greater amounts of carbohydrates are converted into storable forms, such as starch and fat, and allocated to synthesis of lignin and other secondary metabolites (Larcher, 1995). In the boreal zone, it is the availability of nitrogen that limits plant growth (Tamm, 1991): the net uptake of nutrients is proportional to plant growth in young plants when nutrient supply is optimal (*e.g.* Ingestad & Kähr, 1997 and references therein), and it is well known that the shoot/root ratio and thus LAI increase in response to addition of nitrogen and other nutrients involved in the synthesis of new tissue (Ericsson, 1995).

Net carbon gain per unit nitrogen is linearly correlated to the amount of nitrogen available in the leaf (the nitrogen use efficiency of photosynthesis) and thus indirectly in soil. This is not the only reason why availability of nitrogen is crucial for understanding the influence of climate change on the carbon cycle. Plant nitrogen uptake mainly occurs in the rhizosphere, where roots interface with decomposers either through chemical exchange in the soil-water solution or directly in symbiosis with others that actively exchange their nitrogen for root carbohydrates (mycorrhizae). Soil nitrogen availability is primarily determined by the residual of release (mineralisation) and retention (immobilisation) of nitrogen because the origin of the nitrogen that decomposers release is bound in organic compounds. Consequently, rates of CO₂ released to the atmosphere by decomposers are associated with the release of inorganic nitrogen.

Organic compounds with high availability of nitrogen are seen as high quality substrates and their decomposition should release nitrogen rapidly. The other side of the coin is that it has been shown that nitrogen additions reduce CO₂ evolution (Ågren, Bosatta & Magill, 2001) although no major differences in organic carbon chemistry have been seen in the upper forest floor (Sjöberg, 2003). Decomposition of nitrogen-rich substrates can therefore lead to a decrease in decomposition. One explanation in terms of decomposer efficiency could be that increasing availability of nitrogen in litter induces a shift in the microbial community towards more efficient microorganisms with a higher nitrogen demand.

There is much left to learn about interactions between decomposers and plants and properties of their substrate. As an illustration of this, it might be said that the term 'decomposers' is an imprecise expression as it refers to a number of heterotrophic soil organisms in a species richness so diverse that it is a challenge to even count

them (Hughes *et al.*, 2001). Two obvious categories of microbial decomposers are fungal and bacterial taxa. Other categories, not mentioned in any specific order, are mites, earthworms and collembola – admittedly another imprecision revealing the limitations in the author’s knowledge: although microorganisms play a central role in ecosystem response to global change-induced disturbance, much remains to understand about the processes involved in responses and feedback mechanisms of decomposers to environmental variables. Our ability to investigate the exact nature of that role is limited by disciplinary and methodological differences among *e.g.* microbial and ecosystem ecologists.

Lignin/N ratio is a useful chemical predictor of litter decomposability in the tropics and in the Mediterranean region. In the temperate region, however, there is no good chemical predictor of litter decomposability (Mellilo *et al.*, 1989; Aerts, 1997). Experimental results examining the responses of decomposition to additions of nitrogen are contradictory and pose challenges to our full understanding. Responses may depend on levels of current background deposition of anthropogenic nitrogen and deposition history (Knorr, Frey & Curtis, 2005). The temporal dimension seems also to have implications in addition to the above, as the response of litter mass loss rates may initially be positive or negative (Fog, 1988; Ågren, Bosatta & Magill, 2001; Franklin *et al.*, 2003). The application rate, type of nitrogen fertiliser litter quality, ambient deposition and the time of observation were all found to have a positive or negative influence on litter mass loss rates in a review of 24 studies of nitrogen addition on decomposition (Knorr, Frey & Curtis, 2005).

Net ecosystem production and the carbon balance

Approximately half of gross primary production (GPP) is lost in the metabolism (R_a) of the primary producers during photosynthesis. Net primary production (NPP) thus refers to:

$$NPP = GPP - R_a \quad (1)$$

Net ecosystem production (NEP) is calculated by subtracting the heterotrophic respiration (R_h) from NPP:

$$NEP = NPP - R_h \quad (2)$$

The amounts of carbon sequestered in forests depend on climatic conditions, soil properties and the extent to which the forests are managed. NPP and R_h theoretically balance in old growth stands if viewed over very long time periods extending over several forest fires, insect outbreaks and other natural calamities. Measurements over relatively short time periods have shown examples of carbon-neutral old growth stands in northern Europe (Valentini *et al.*, 2000). Managed

forests in the boreal zone typically sequester carbon at annual rates of approximately $2.5 \text{ t C ha}^{-1} \text{ yr}^{-1}$ (NEP), but the variability is considerable depending on factors such as climatic conditions and human activities (Bolin *et al.*, 2000). The sink capacity of forests in different world biomes can range from negative (Lindroth, Grelle & Morén, 1998) in a perturbed boreal system up to nearly $6 \text{ t C ha}^{-1} \text{ yr}^{-1}$ in a Amazonian tropical rain forest (Malhi, Baldocchi & Jarvis, 1999). The challenge to summarise and close the terrestrial carbon balance depends critically on how we manage to interpret the balance of $\text{GPP} - (\text{R}_h + \text{R}_a)$. An overview of estimated carbon stocks on a global scale shows that 45% of global carbon is stored in the living biomass of tropical forests, while the main store of SOM carbon (23%) is probably sequestered in the soils of the boreal zone. The estimates of belowground biomass, suffer from much uncertainty, fine roots because sampling and observation methods are destructive and disrupt the development of root turnover; soil carbon densities because sampling methods are limited to soil depth and because of the profuseness of stones and boulders in glacial soil profiles (Liski, 1995; Trumbore, 2000). Data such as those shown in *Table 1* are thus uncertain.

Table 1. Magnitude of carbon stocks in global biomes of (Bolin *et al.*, 2000)

Biome	Area, 10^9 ha	Vegetation C	Soil C	Total C
Tropical forests	17.6	212	216	428
Temperate forests	10.4	59	100	159
Boreal forests	13.7	88	471	559
Tropical savannas	22.5	66	264	330
Temperate grasslands	12.5	9	295	304
Deserts and semi-deserts	45.5	8	191	199
Tundra	9.5	6	121	127
Wetlands	3.5	15	225	240
Croplands	16	3	128	131
Total	151.2	466	2,011	2,477

In a theoretical plant-soil ecosystem, assimilation of carbon in biomass and release of carbon through respiration must balance if climatic and other environmental properties are held constant. A natural ecosystem is seldom in true equilibrium on an inter-annual or annual basis because of the stochastic nature of weather. It is the influence of climatic variables and environmental parameters that determines the sign and amplitude of the actual deviation from steady-state. Current estimates show that net uptake of CO_2 by global plant production is in the magnitude of 60 million tonnes per year and the amount of CO_2 released as a result of decay is on the same level as estimated by the IPCC in 2001. The same source reported differences between release and uptake of CO_2 over longer time periods ranging from approximately 0 to 1 million tonnes per year on a global scale.

The fast increase in the use of anthropogenic nitrogen has been suggested to account for the residual land sink (Schimel *et al.*, 1995; Nadelhoffer *et al.*, 1999; House *et al.*, 2003). The residual land sink was formerly called the ‘missing sink’ and relates to difficulties in estimating sources and sinks of CO₂ emissions from deforestation over forest re-growth: observed net uptake of CO₂ by the land biosphere implies that there must be an uptake by terrestrial ecosystems not evident if in estimates of land use change. Degradation of forests has been more extensive in the tropics over the past few decades than in the rest of the world. Consequently during the industrial era, forests have disappeared in 25 countries, while forest cover and biomass in managed Boreal forests increase {Betts, 2005 #1923; Denman, 2007 #1899; Nilsson, 2003 #1898}. In addition to possible growth response to nitrogen deposition, the sink may be explained partially by afforestation, reforestation, and forest management mainly in Europe, North America and China .

Models as research tools – materials and methods

The advantage of using models is that complex interactions can be evaluated in a consistent manner. Rates of photosynthetic assimilation, autotrophic and heterotrophic respiration and nitrogen mineralisation typically respond differently to climatic variables, often in non-linear relationships. Models allow hypothetical scenarios and facilitate quantitative and qualitative analysis of interactions and feedback mechanisms.

The usefulness of a model relies on its level of simplification and the intended use. Modelling results may none the less attract disapproval, with arguments that they are either too simple or too complicated. Such objections cannot be denied; considering geographical maps as models illustrates the dilemma of scaling. Maps of different scales serve different purposes such that a regional map for example, although useful locally, is less useful on a global scale. A map on a one-to-one scale would obviously be both unrealistic and useless.

Considering possible interactions and feedback mechanisms in plant-soil ecosystems, it becomes obvious that ecosystem models are useful tools to examine theories and test how previous findings in plant and soil sciences may interact. In this thesis, two different ecosystem models, G'DAY and Q, were employed to explore the effects of climatic change on boreal forest ecosystems.

G'DAY

G'DAY incorporates several aspects of forest ecophysiology. Gross photosynthesis is calculated by taking into account the separate contributions of beam and diffuse radiation (Medlyn *et al.*, 2000) and the biochemically-based

photosynthesis model of Farquhar & Caemmerer (1982). Thus, growth depends on canopy leaf area, diffuse radiation incident at the top of the canopy, $[\text{CO}_2]$ and leaf nitrogen content. Plant maintenance respiration is assumed to be a constant fraction of NPP to GPP. Plant nitrogen uptake depends on nitrogen mineralised from litter and SOM pools. Mobile nitrogen in stem wood and nitrogen in foliage is retranslocated. These processes affect the C/N ratio in foliage and hence photosynthetic capacity as described in (McMurtrie *et al.*, 2000).

The soil sub-model tracks carbon and nitrogen dynamics in four litter pools (surface structural (u), below-ground structural (v), surface metabolic (m), and below-ground metabolic (n)) and three SOM compartments (active (a), slow (s), and passive (p)), all with contrasting decomposition rate constants which have been derived empirically (Parton *et al.*, 1987). The soil compartments, representing fractions of substrate carbon, are interlinked by carbon flows. The amounts of carbon transferred from one pool to the next are proportional to the amounts of carbon resident in each donor pool. The same temperature activity factor $A(T_{soil})$ scales all fluxes between the litter and SOM compartments.

Plant carbon enters soil through the litter compartments (u , v , m and n) and the rate of influx is thus determined by plant growth and allocation, turnover (senescence) rates and size of the plant carbon pool of origin. Lignin and nitrogen in foliage and root litter (L_f & L_r) influence carbon allocation to the SOM compartments (a , s and p).

Carbon flows according to G'DAY are depicted in *Fig. 4*. The input to the active SOM pool (a) represents turnover by active decomposers and is a function of the outflows of the non-lignified carbon compounds from structural pools (u and v) and the metabolic litter pools (m and n), plus re-circulation of carbon from the slow (s) and passive (p) pools. Output from the active pool is largely allocated to the slow pool under the influence of a constant soil texture factor (Parton *et al.*, 1993). The output of lignified carbon compounds from the structural litter pools entering the slow pool represents an intermediate fraction of carbon that is physically and/or chemically protected from decay. Output from the slow pool is largely allocated to the active pool. The small flux of carbon into the passive pool, representing SOM fractions that are physically protected and chemically resistant to decomposition, is derived from the active and slow pools.

Fluxes associated with heterotrophic respiration (R_h) and the carbon transfers out of each pool are proportional to the amount of carbon resident in each pool. Carbon release (R_h) is calculated from the sum of fluxes of CO_2 out of each pool. The sum of carbon release therefore depends on NPP, lignin and nitrogen contents of living biomass and the carbon content of each soil pool.

Mineralisation of nitrogen depends on quality and quantity of litter and SOM, decomposition, soil temperature and soil moisture content. The total nitrogen mineralisation rate in soil is given by the sum of each pool, their size and $A(T_{soil})$ in similarity to carbon mineralisation, although constrained to certain boundary values of C/N in each pool.

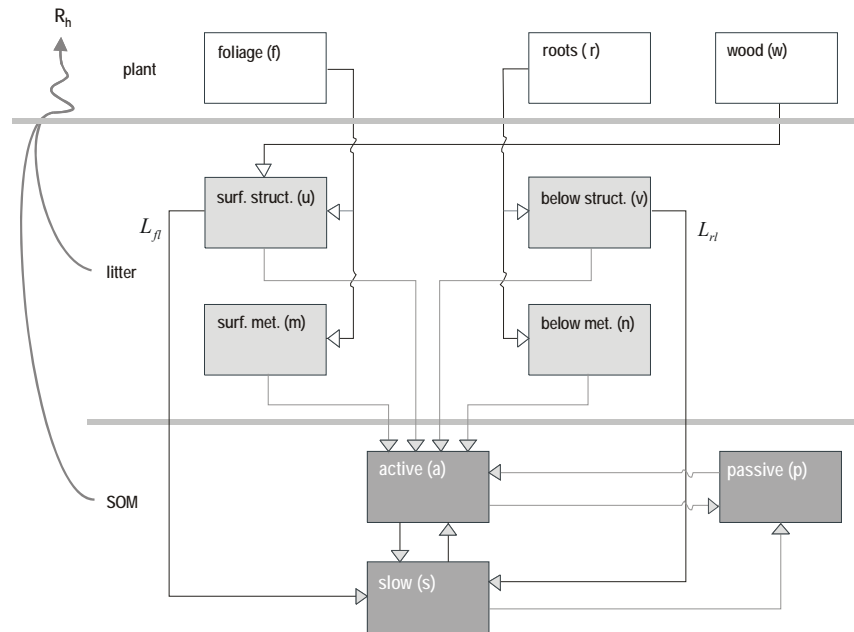


Fig. 4. Carbon flows in litter and soil in the G'DAY model. Plant compartments are no shaded, litter compartments are light grey and soil organic matter (SOM) compartments dark grey

The plant sub-model accumulates carbon and nitrogen in pools of foliage, wood and fine root biomass. Minimum levels of C/N in leaf and fine root limit the plant uptake of mineralised nitrogen. Surplus nitrogen goes into the pools of stem non-structural, stem structural, branch and coarse roots, which are also constrained by minimum C/N ratios. Excess nitrogen from the plant carbon and nitrogen pools above, with the exception of the stem non-structural pool, accumulates in a mineral nitrogen pool in the trees until there is a plant demand for mineral nitrogen in excess of what is available in the soil nitrogen pool. The output of nitrogen from the trees is coupled to litter production and occurs at the current C/N of the tissue in question.

Under nutrient limitation, decreasing leaf C/N ratio is a positive feedback to NPP because litter fall rates are calculated by assuming constant senescence rates: an increase in NPP therefore results in raised levels of litter nitrogen, which is subsequently released in the soil. The feedback may also be enhanced by increased light interception because LAI is calculated as a constant fraction of specific leaf

area (SLA) over leaf biomass. The effect of the feedback will eventually subside as a new balance between leaf gain and leaf litter-fall is established.

A new decomposition sub-model (*Fig. 5a & b*), with a greater mechanistic integrity, provides a relevant framework for studying carbon and nitrogen mineralisation as a set of interacting biological, physical and biochemical processes. The model is highly sensitive to parameters describing the retention of nitrogen by microbial biomass. This sensitivity highlights the important role of microbial biomass in nitrogen cycling in forest ecosystems, at least over the short term. Carbon and nitrogen mineralisation simulated by the new model is sensitive over the short term to a particular set of parameters:

over the short term:

d_{met} – specific decomposition rate of metabolic litter pool at ground surface

d_{cel} – specific decomposition rate of cellulosic litter pool in soil

recalcitrant fraction of the decomposer pool that consists of labile (α_{lab}) and more recalcitrant; ($\alpha_{res} = 1 - \alpha_{lab}$), and

β_{lig} – dependence of decomposition rate of lingo-cellulosic litter pool on lignin content

over the long term:

d_y – specific decomposition rate of young SOM pool, and

S_y – humification coefficient for young SOM pool.

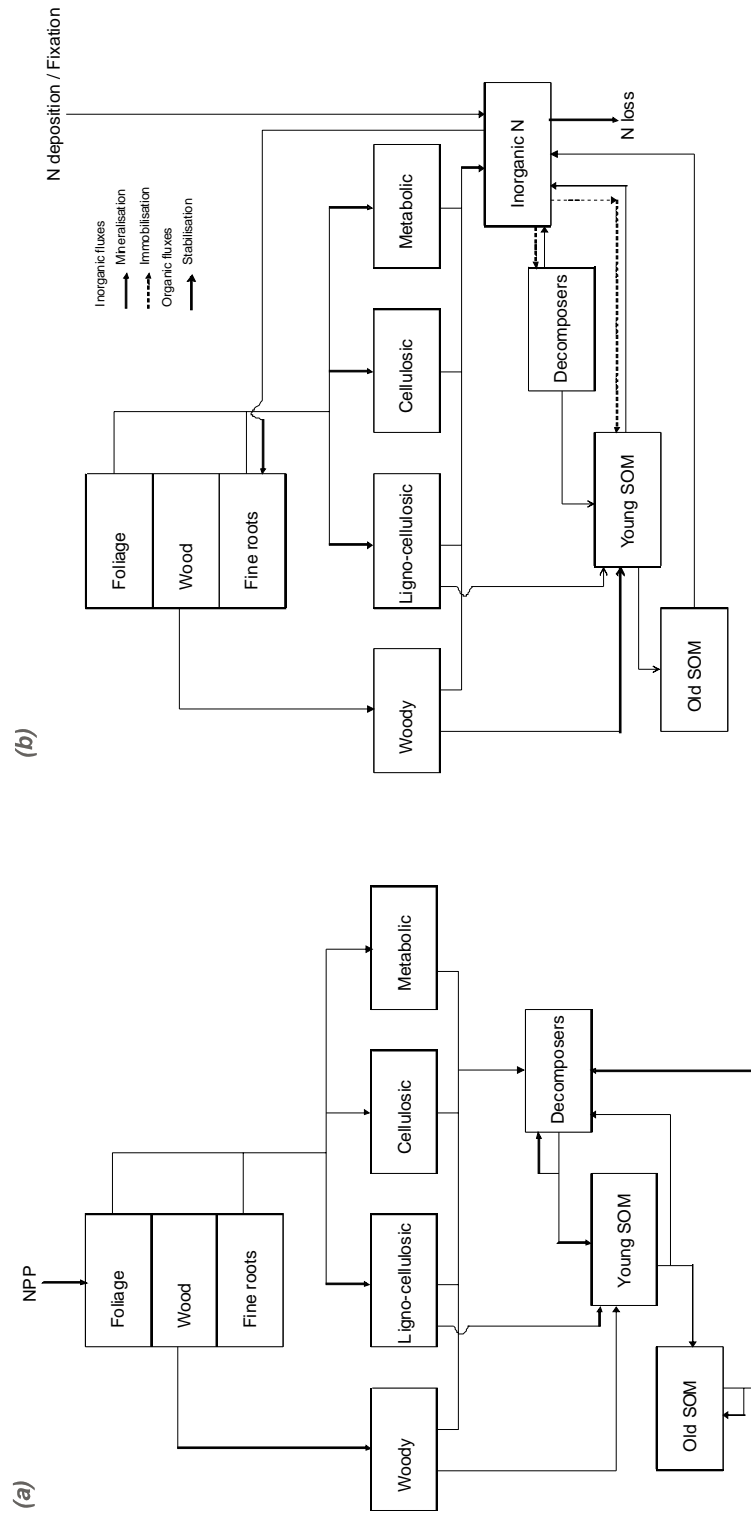


Fig 5. Figure 1 Pools and fluxes of *a.* carbon and *b.* nitrogen in G'DAY.

Q

The Q model uses continuous quality theory to describe soil organic matter turnover and nitrogen productivity to describe plant growth (Ågren & Bosatta, 1998). The Q model was developed with the aim of analysing the carbon and nitrogen cycles and their relation to forest stand development (Rolff & Ågren, 1999). The model is based on the interaction between a soil subsystem and a plant sub-system, each being described in terms of their content of carbon and nitrogen, respectively. The model is named after one of its central variables, substrate quality (q).

Plants are represented in the model by different tree components and a 'grass layer' covering all vegetation other than the dominating tree layer (*Fig. 6*).

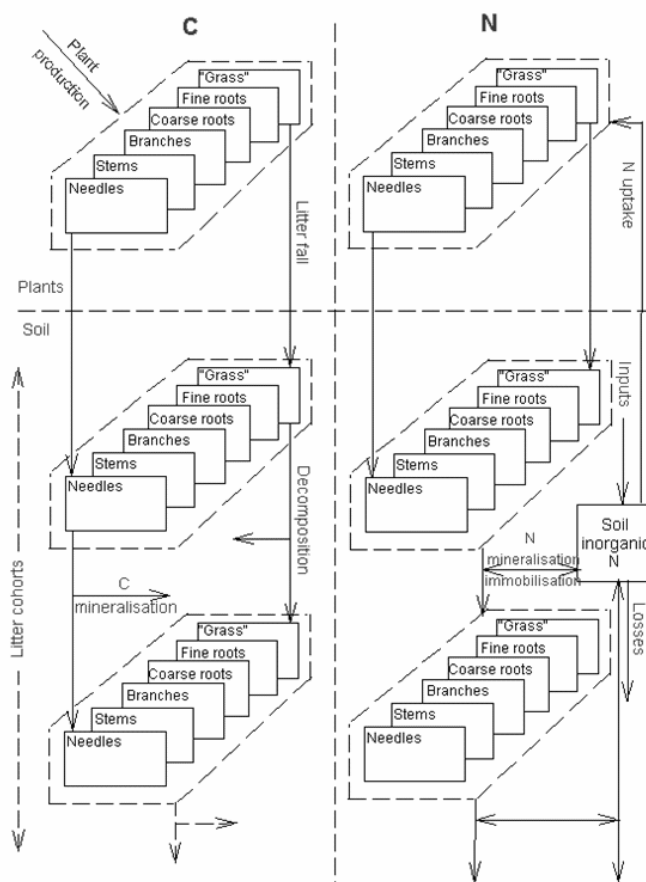


Fig. 6. Schematic view of the Q model.

For each plant component in the model there is one carbon and one nitrogen state variable. Normally, the grass plays a negligible role in the model. It is only after clear felling that the grass absorbs mineralised nitrogen that would otherwise have leached out of the system. This mechanism is designed to preserve nitrogen. The organic matter in the soil is divided into litter cohorts, thus keeping track of both the source of the material as well as the time of its appearance in the soil. The main aim of the model is to study long-term developments in forests. Q runs on a monthly time step and average air temperature is the only climatic driver. Nitrogen deposition is included as an external variable. Temperature only affects soil processes as it has been found that nitrogen productivity is insensitive to temperature (Ladanai & Ågren, 2004). Carbon dioxide concentration can easily be included. As of yet, there is a lack of experimental data available from which parameters can be estimated and effects of CO₂ have not been included.

Growth of needles is the key process described by the needle nitrogen productivity function:

$$\frac{dW_{needle}}{dt} = (a - bW_{needle})N_{needle} \quad (3)$$

where W_{needle} is the biomass of needles and N_{needle} is the amount of nitrogen in the total needle biomass. Parameters a and b are empirical. Growth of woody tree components is proportional to needle biomass. Fine-root growth also includes a function of needle nitrogen concentration that decreases fine-root growth as the needle nitrogen concentration increases. Age-related decline in forest production is controlled by the ability of the soil to supply nitrogen. The upper limit to needle biomass, a/b , is never attained because of needle turnover and the limitation from available nitrogen keeps N_{needle} down.

Litter fall occurs once per year and is calculated as a fraction of the biomass components. It is assumed that there is no litter formation from stem wood and coarse roots, except in the event of harvesting operations.

Each litter cohort of a given litter type is treated individually. During decomposition a litter cohort changes in two ways: (i) its quality decreases; and (ii) its mass decreases.

The substrate quality (q) changes when decomposers assimilate the substrate. The rate of change in the quality depends on the change in quality of a carbon atom being assimilated into decomposer biomass $\eta_1(q)$ ($\eta_1(q) = \eta_{11}q$) and the growth rate of decomposers per unit carbon $u(q, T)$ ($u(q) = (u_0 + aT)q^\beta$, where u_0 , a , and β are parameters). The linear temperature (T) response function, rather than the more conventional exponential response, is based on empirical data and can also capture variability in soil water availability because of the negative correlation between temperature and soil water (Andren & Paustian, 1987). The rate of change in quality is then calculated from the following equation:

$$\frac{dq}{dt} = -f_c \eta_1(q) u(q, T) \quad (4)$$

where f_c is the carbon concentration in the decomposers.

The fraction of a cohort remaining at a given time (g) is calculated from the quality reduction that the cohort has reached, calculated from the following relationship:

$$\frac{dg}{dq} = \frac{1 - e(q)}{\eta_1(q) e(q)} g(q) \quad (5)$$

Decomposer efficiency or production-to-assimilation ratio $e(q)$ is a critical function as it partitions the carbon flow into biomass and respiration. In the version used here, e_0 is a parameter $e(q) = e_0$.

Nitrogen mineralisation/immobilisation is calculated from the difference in nitrogen content in a litter cohort between the beginning and end of a monthly time step. The nitrogen concentration in a litter cohort r depends on the quality that it has reached according to:

$$\frac{dr}{dq} = - \left(\frac{f_N}{f_c} - 1 \right) \frac{1}{\eta_1(q)} \quad (6)$$

where f_N is the nitrogen concentration in the decomposers. As decomposition progresses, the nitrogen concentration in the substrate cohort gradually approaches that of the decomposers, f_N/f_c .

The nitrogen uptake by trees is proportional to the amount of available nitrogen, mineralisation plus inputs, and a function describing the extent to which tree roots occupy the soil. The grass takes up whatever nitrogen is left. There is, however, an upper limit on how much nitrogen the grass can take up. Nitrogen losses occur when the vegetation system lacks the capacity to utilise all the nitrogen that is available from mineralisation and inputs.

A previous version of the Q model has been used to analyse responses of pine forests to climate change (Ryan *et al.*, 1996a; Ryan *et al.*, 1996b). Harvesting effects were examined in Rolff & Ågren (1999). Temperature effects on soil organic matter decomposition (Ågren, 2000; Ågren & Bosatta, 2002) have also been analysed and large-scale effects of biomass harvesting on forest soil carbon stores predicted (Ågren & Hyvönen, 2002).

Weather variables

It is important in models driven by weather variables to include variability because responses are often non-linear. The implication of non-linearity in this context is that the responses to *e.g.* temperature taken from two different climate sequences with the same mean but different amplitude will be different. It is essential to reduce and isolate imposed perturbations in the simulations to well-defined events in order to track cause and effect of many interacting relationships in the model. The method of comparing the response as relative differences to steady-state allows for simple un-biased assessment. As mentioned above, there are currently no reliable methods to estimate actual status of carbon and nitrogen pools. Furthermore, if simulating a perturbation, such as soil warming, is difficult to evaluate responses to the warming in relation to inert responses initiated in the past (Bruun & Jensen, 2002). Such complications have can be circumvented by simulating a steady state system where all inputs and outputs initially balance as if the system were in steady-state.

G'DAY uses the mean of maximum and minimum daily air temperature greater than or equal to zero as soil temperature, and Q uses monthly mean temperatures. We used eight-year sequences of mean air temperature recorded at Flakaliden, near Vindeln in Northern Sweden (64°07'N; 19°27'E, alt. 310 m a.s.l.) (Bergh & Linder, 1999). In the simulations using the G'DAY model (Papers II & III), parameters were taken mainly from the Flakaliden site in all our simulations. Examples of tree physiological parameters used are relationships in the photosynthetic process, carbon and nitrogen allocation in trees, plant turnover and C/N ratios. Soil parameters are litter and SOM turnover rates, C/N ratios and nitrogen leaching (Linder, 1995; Roberntz & Stockfors, 1998; Medlyn & Jarvis, 1999; McMurtrie *et al.*, 2000; Medlyn *et al.*, 2000; McMurtrie, Medlyn & Dewar, 2001). The soil at the Flakaliden is a thin podsol, sandy, glacial till with an average depth of 120 cm and mean thickness of the organic layer of 4.3 cm. The site was planted after prescribed burning and soil scarification in 1963 and compared with steady-state conditions is still young.

Quasi-equilibrium in the models was initiated by looping the meteorological variables of an eight-year sequence of meteorological data on a daily resolution. The procedure of equilibrating the carbon and nitrogen pools in G'DAY requires the model to loop through thousands of years until the eight-year sum of net ecosystem production ($NEP = NPP - R_h$) is zero.

The method of initialising approximately steady state conditions in Q was different. Locale temperature data for the simulated stands, $T(L,E)$, were approximated from temperature data (T_F) with a monthly resolution from the Flakaliden site by adjusting temperatures for latitude (L) and elevation above sea level (E) using the following relationship:

$$T(L, E) = T_F + 43.59L - 0.6391E \quad (7)$$

The steady state was reached by first running the model with local climate and a set of initial soil carbon and nitrogen stores for 200 years with tree biomass developing from seedlings up to a mature forest stand. The resulting distributions of soil C and N were then entered as new initial soil states but mortality of stems and coarse roots during the 200 year period was represented by returning 1.5% and 4% respectively of the C and N accumulated in biomass to the soil. Maintaining the obtained soil stores of C and N these were scaled up or down and the simulations repeated until the theoretically maximum stem volumes at the age of culmination and corresponding to site index

Objectives of this work

The central interest in this thesis is the importance of environmental variables to the carbon sink capacity as determined by biomass production of plants and the outputs by respiratory release by decomposers in boreal forest ecosystems.

An introductory economic analysis is aimed to underpin the economic importance of the carbon sink and discuss the sustainability of forests sink capacity.

The main focus is on investigating the influence of three environmental variables to the inputs and outputs of the carbon balance: *(i)* sensitivity of decomposition to soil temperature; *(ii)* effects on carbon sink of increased concentrations of atmospheric CO₂; and *(iii)* how mineralisation rates are coupled to availability of inorganic nitrogen in soil.

Papers included

Including the carbon budget in national accounting – tools for policymakers (Paper I)

Forests provide more or less essential services contributing to social welfare. Not all of these utilities are subjected to market transactions and hence they are not included in the macroeconomic aggregates that are registered in national accounts. Accounts in a coherent and consistent data framework are the basis for the evaluation and comparison of economies in countries throughout the world. The current system of national accounts (SNA) integrates information about resource allocation in an internationally accepted framework allowing an assessment of past economic performances. Gross national product (GNP) is one of the important economic indicators resulting from the SNA.

The GNP has sometimes been interpreted as a measure of welfare, which is valid only if social welfare is understood to be synonymous with the value of all economic production, or consumption, in society. Mass media and policymakers sometimes use the expression 'economic growth' when referring to positive

changes in GNP, implying that production or consumption is a measure of welfare. Social welfare, however, has at least two major components that are poorly represented in the GNP: depreciation of the resource stock to some extent and the flow of non-market goods and services, including environmental qualities.

The main purpose of the experimental national net accounts outlined in Paper I (Eliasson, 1997) is to shed light on the economic importance of forests as carbon sinks, thereby indicating their key environmental service role. The simple argument is that if increasing concentrations of CO₂ in the atmosphere is a welfare problem, then reduction of atmospheric carbon has a value. Furthermore, if we want to optimise allocation of income from timber extraction and from the use of carbon sinks in the economy, it is important that the sinks are attributed a realistic value. It should be noted, however, that attaching a value for carbon sinks to the conventional net national product (NNP) is not an attempt to estimate welfare itself but to complement NNP with final products 'that are the penultimate ingredients of human well-being' (Eisner, 1988). Elaboration of theoretical restrictions and exact definitions of NPP can be found in (Dasgupta & Mäler, 2000).

Net values of forest production based on lower boundary estimates of market values of timber products, inputs from other sectors, increase in growing stock, silviculture, berries, mushrooms, game (meat), stock and production of lichen (reindeer fodder), changes in environmental stocks, biodiversity and exchange of cations are given in Hultkrantz (1992) and Eliasson (1994). The net value of carbon sinks is reconciled and updated in Paper I. Four different methods of calculating the value of CO₂ sequestration highlighted the uncertainty involved in assessing non-market monetary values. The estimated values of the carbon sink ranged from 3% up to 50% of national net income from the forest sector. However, the important conclusion from the exercise is that there is probably an upper limit to the carbon sink capacity. The upper limit of this future carbon storage capacity may amount to levels close to or above an unknown steady-state condition that prevailed sometime before industrialisation, when standing volumes of old-growth trees were well above present, more frequently perturbed by fires but less drained (Eliasson, 1992; Linder, 1992; Linder, Elfving & Zackrisson, 1997; Andersson & Östlund, 2004). The upper theoretical limit to standing volumes and soil carbon densities is possibly higher than the pre-industrial level due to anthropogenic eutrophication and silvicultural methods employed during the past millennium. Nevertheless, recent findings indicate that national soil carbon stocks have increased by 3 Tg yr⁻¹ in the period 1926 and 2000 and that stocks will continue to increase because soils are far from equilibrium (Ågren, Hyvönen & Nilsson, 2007).

Market solutions may efficiently allocate scarce resources to reflect the value of resources provided that there is supply and demand on monetary markets. This is the basis of neo-classical economic growth theory, where terms such as supply and demand define economic value and prices are suggested to moderate depletion of natural resources (Solow, 1957). The accumulated income from industrial activities such as the widespread use of fossil fuels has given returns on investments and increased welfare in monetary terms mainly in the industrialised

parts of the world. As opposed to welfare gains, however, costs have no doubt been distributed globally.

Increased temperature in soil and elevated atmospheric CO₂ (Papers II & III)

One large uncertainty in estimating the carbon balance is that much remains to be learnt about how decomposers respond to warming under natural circumstances. Paper II (Eliasson *et al.*, 2005) offers an explanation as to why soil CO₂ flux after experimental warming is initially very high and then declines within a few years. Simulations using G'DAY show that high quality soil carbon can deplete rapidly simply due to faster turnover rates; function and composition of the decomposing community remained the same in heated and non-heated soil. It is also implied that the storage of soil carbon with slow decay rates (*i.e.* with high sensitivity to changes in temperature) would decrease considerably in the long term as result of increased soil temperature. The development in the pools of G'DAY over ten years following a step increase in soil temperature by 5 °C in is shown in Fig. 7. Similar results are confirmed in other studies (Gu, Post & King, 2004; Knorr *et al.*, 2005).

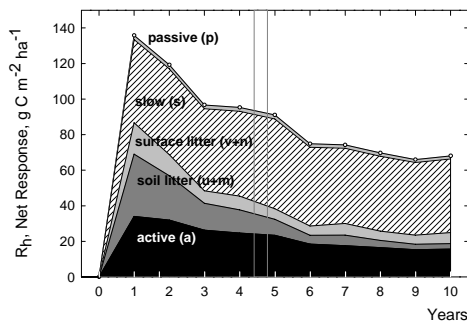


Fig. 7. Components of simulated total R_h shown as the difference between heated plots and control plots during the first decade of soil warming. Highlighted area shows the fifth growing season after warming commenced.

Paper III (Pepper *et al.*, 2007) deals with response in trees and soil to elevated [CO₂]. Besides being a greenhouse gas, a characteristic of CO₂ is that its concentration directly influences photosynthetic production. Increased atmospheric [CO₂] may stimulate photosynthesis under certain conditions because plant uptake of CO₂ takes place in openings on the surface of the leaves (stomata) with the loss of water (transpiration). Water and CO₂ are consumed during photosynthesis and are thus limits to production. The uptake of CO₂ is driven by diffusion, meaning that the flux rate is determined by the difference in concentration on either side of stomata. The stomatal aperture also determines how much water is lost from the plant because water diffuses in the opposite direction. Plants can thus make use of water more efficiently when the ambient concentration of CO₂ is high, resulting in improved nitrogen use efficiency.

The simulations in Paper III indicate that plant production may increase after a century due to enhanced nitrogen use efficiency in the photosynthetic processes. Consequently, the total plant carbon in the system increased as a first response and

soil carbon increased as result of the subsequent increase in plant litter input. However, the increase in plant carbon was not subsequently compensated for by the corresponding relative increase in plant nitrogen. Instead, G³DAY predicted gradual decrease in total plant nitrogen, further diluting biomass of total nitrogen, and a shifting allocation of ecosystem nitrogen to soil, although not in sufficient quantities to preserve total soil N/C ratio over 100 years as seen in *Fig. 8*.

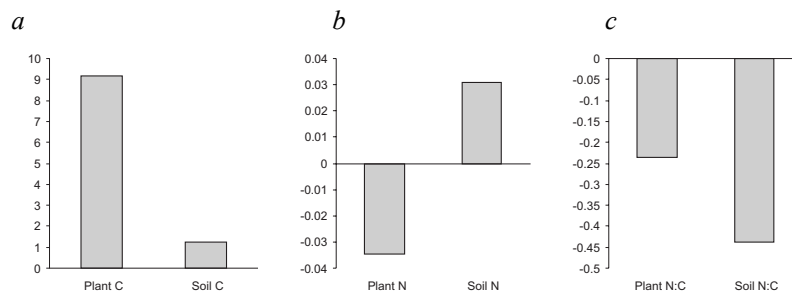


Fig. 8. Response in carbon and nitrogen pools averaged over 100 years of doubled [CO₂]. Change of carbon and nitrogen in t ha⁻¹, change in N/C × 10⁻³

The simulations showed that the total plant carbon increased for the first ten years after doubled [CO₂], although input of system nitrogen remained unchanged as a result of enhanced nitrogen use efficiency in foliage. However, there was no compensation for the increased demand for nitrogen in plant biomass, subsequently leading to increased C/N ratios in litter fall and resulting in less nitrogen released per unit carbon in decomposing litter and SOM.

The results are consistent with experimental data showing that nitrogen availability probably constrains the ecosystem responses of elevated CO₂ (Luo *et al.*, 2004; Reich *et al.*, 2006). The nitrogen constraint acts progressively, indicating that stimulation of plant growth in a future CO₂-enriched world may decline over time.

The assumptions concerning nitrogen availability are crucial. C/N ratios associated with C fluxes both to young SOM pools from litter pools or involved in SOM stabilisation processes were the most important processes in the CO₂ response.

Influence of nitrogen deposition on growth and decay (Paper IV)

Nitrogen deposition is currently considerably higher than during pre-industrial times and an interest in using nitrogen fertilisers to alleviate nitrogen limitations in forest ecosystems and thus increase biomass production requires that we understand the interactions between nitrogen and carbon in such ecosystems. Although knowledge is considerable, it has recently become obvious that our understanding of how the complication of additional nitrogen deposition will interfere with the turnover of soil organic matter is inadequate. In Paper IV (manuscript) we used the Q model to investigate the potential response of stands of Scots pine (*Pinus sylvestris* L.) to additional inputs of nitrogen, whether in the

form of single or consecutive pulse doses as in fertiliser applications or as slowly increasing deposition.

To account for the observed increase in decomposer efficiency with increasing inorganic soil N (Ågren, et al. 2001; Franklin et al., 2003) we introduced a feedback mechanism from available inorganic soil N (N_{inorg}) to decomposer efficiency (e_0) through a linear relationship:

$$e_0 = e_{00} + e_{01} N_{inorg} = e_{00} + e_{01} (N_{min} + N_{ext}) \quad (8)$$

The soil inorganic N comes from two sources, N mineralised from soil organic matter (N_{min}) and external sources, deposition and fertilisation, plus what has not been taken up by the vegetation (N_{ext}). However, N_{min} is a function of e_0 and for some time step Δt

$$N_{min} = \sum_{litter} u(q_{litter}, T) \left[\frac{N_{litter}}{e_0} - r_d C_{litter} \right] \Delta t \quad (9)$$

where $u(q_{litter}, T)$ is the growth rate of decomposers, N_{litter} and C_{litter} is nitrogen and carbon in litter, r_d is the N/C ratio in decomposers (see Paper IV).

Inserting eqn (8) into eqn (9) leads to a quadratic function in e_0 , which is has to be solved for each time step.

In addition to the obvious extra nitrogen available for plants and soil organisms, the nitrogen feedback mechanism resulted in a positive soil nitrogen feedback where decomposer efficiency increased with increasing nitrogen availability. The Q model accurately predicted the response to fertiliser additions, although the effect of the implemented feedback was small because the fertiliser dose overrode the expected effects on soil organic matter turnover. Simulations under slowly increasing nitrogen deposition during a century reduced ecosystem carbon storage. Two effects of the feedback was that it simultaneously acted on the inputs and outputs of soil carbon: Increased nitrogen retention in the soil reduced plant growth response, thus influencing litter input, while soil heterotrophic respiration was also gradually reduced due to increasing decomposer efficiency, but not enough to sufficiently balance the reduced litter input.

The simulation with continuously increasing nitrogen deposition of an extra 432 kg N ha⁻¹ deposited during 100 years increased the ecosystem carbon store by 110.4 Mg ha⁻¹ or an N use efficiency of 256 kg carbon (kg N)⁻¹. This is approximately equal to that estimated by Magnani *et al.* (2007) from eddy-covariance flux measurements in forest chronosequences if we assume that their wet N deposition values should be doubled to also account for dry deposition. On the other hand, our simulated N use efficiency was at least five-fold larger than that observed in a range of fertiliser experiments (Högberg, 2007; Hyvönen *et al.*, 2007). The main difference between our results and those of (Hyvönen *et al.*,

2007) was in the effects on tree growth, which were much larger in our simulations. A probable explanation for the diverging results is that in the simulations, there are almost no N losses (leaching or denitrification), which are certain to occur in fertiliser trials (Ladanai & Ågren, 2004).

Conclusions

Regarding the environmentally adjusted net national accounts in Paper I, it is a challenge for policy-makers to promote efficient resource use that maximises resource worth and reinvestment of that worth. Policy decisions in the past, which have led to the complications involving socio-economic impacts of climate change, were made on the basis of limited information in the sense that market prices do not sufficiently reveal changes in all natural capital. Prices can be seen as signalling devices indicating an excess of demand over supply. Judging from the general consensus concerning climate change, the current demand is for carbon sequestration, among other possible mitigating strategies, to be in excess of supply. When aiming to improve the assessment of the net value of natural, human and social capital in a sustainable fashion, the challenge is to estimate the value of non-marketed utilities in monetary terms, or any other comparable entity.

In this study, comparison of estimated values of the carbon sink with previous estimates of the net contribution of the forest sector to the national income suggested a value for the carbon sink capacity of 3-50% of net income. However, important factors such as recreational value and hydrological services were not included.

It was speculated that it is an oversimplification to assume that the sink capacity is sustainable, particularly in terms of living biomass. In the long run, new technologies must be developed for mitigating greenhouse gas emissions and for adapting to the climate changes that are already unavoidable.

Consequences in terms of environmental change over the coming few decades could cause major disruption to economic and social activities and demand immediate decisive action. Monetary estimates of the consequences of continued inaction are necessary to efficiently communicate the urgency to decision-makers on all levels. Consistency in economic methods is as important as reliable physical data and prediction of trends.

Although much is known about plant physiological responses to the main determinants of the terrestrial carbon sink, uncertainties concerning feedback mechanisms prevent reliable predictions. The simulated ecosystem responses to important environmental variables (and the experimental data upon which they are based) in this thesis show that increasing soil temperature decreases soil carbon storage, both in the long term and the short term. Labile carbon depletes rapidly (within decades) in response to increasing temperatures and the sensitivity of recalcitrant SOM to increases in temperature is considerable.

Simulated responses in this thesis suggest that what can be seen as acclimation of decomposers to soil temperature can be explained simply as partly an effect of depletion of labile carbon pools during the first decade of warming. The response of heterotrophic respiration (R_h) to elevated soil temperature in the model is attributed mainly to changing levels of carbon in pools with short time constants, reflecting the importance of high-quality soil carbon fractions. Using this approach, no down-regulation of temperature activity is required to explain observed patterns of R_h – acclimation may instead represent a natural system response leading to a transient increase in heterotrophic respiration followed by a decrease. If this is so, then it is not necessary to invoke any changes in the structure or physiology of the decomposer community. Whether the dynamics of the response to the warming should actually be termed an acclimation or viewed as a natural part of the system dynamics therefore becomes a question of definition.

The difference between the rates of nitrogen mineralisation and nitrogen immobilisation is crucial to how the carbon balance responds to increased $[\text{CO}_2]$. Simulations suggest that several processes may be important to the CO_2 response, most likely on different time scales. The immediate simulated CO_2 response depends on improved nitrogen use efficiency under elevated $[\text{CO}_2]$. The CO_2 response in the short term (first two decades), medium term (two-four decades) and long term (four centuries) depends on soil nitrogen availability. Thus, the difference between the rates of nitrogen mineralisation and nitrogen immobilisation will be crucial.

Turnover rates of decomposer and young SOM pools, and C/N ratios associated with carbon fluxes to these SOM pools from litter pools or to pools involved in SOM stabilisation processes, were the most important processes in response to doubled $[\text{CO}_2]$. Increased biological nitrogen fixation, added nitrogen input or more efficient use of ecosystem nitrogen should have a very important effect on the long-term CO_2 response, even if the carbon costs involved have a detrimental effect in the short to medium term.

The uncertainties concerning nitrogen fixers and how they respond to nitrogen deposition inevitably add to the uncertainty of the above responses. The simulations using the Q model reveal simultaneous positive and negative nitrogen feedback; nitrogen decomposer efficiency increases as inorganic nitrogen becomes available in soil, but reduces the response of growth to the fertiliser. The effect of the implemented feedback mechanism on pulse dose fertilisation confirms that the model behaves consistently in comparison with experimental data. The response is more significant under slowly increasing nitrogen deposition: the feedback mechanism reduces the carbon storage response to external nitrogen in the long term. However, the estimates of the carbon immobilisation effect of additional nitrogen in forests produced were considerably larger than those observed in fertiliser trials but on a par with observations based on eddy-covariance measurements. Accurately predicting the amount of added nitrogen that is retained in the system thus seems to be one of the questions for estimating the additional carbon sequestration.

This work indicate that the key uncertainties concerning the terrestrial carbon balance concern the processes involved in soil decomposition, although not directly addressed in all the included papers. Further integration of microbiological science into the models has potential to greatly improve the assessments of the impacts of climate change on carbon and nitrogen cycles.

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