Plant and Forest Dynamics in Response to Nitrogen Availability

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Abstract

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Theories and mathematical models were derived to analyse and predict plant and forest response to soil nitrogen (N) availability and atmospheric CO_2 concentration.

Soil carbon accumulation in response to long-term fertilisation was studied using measured soil C and ^{14}C of the organic layer in a pine forest in Northern Sweden. Fertilisation increased forest growth and drastically reduced long-term litter decomposition through effects on the decomposers. In 100 years, twice as much carbon would be accumulated in the forest soil where N addition is high as where no N addition occurs.

Root:shoot allocation of small plants was modelled using maximisation of relative growth rate, with and without explicit inclusion of N based maintenance respiration. The results agreed qualitatively with experimental data from birch and tomato plants and the agreement was considerably improved by the inclusion of maintenance respiration.

Senescence and resorption as mechanisms of maximising photosynthetic production were used to predict LAI and resorption efficiency in relation to canopy N. This theory explained the observed LAI for four investigated plant species: red amaranth (*Amaranthus cruentus*), soybean (*Glycine max*), rice (*Oryza sativa*), and sorghum (*Sorghum bicolor*).

Analytical expressions for forest photosynthesis, NPP, growth, LAI, root:leaf allocationand leaf N concentration were derived using a principle of maximal growth and optimisation of canopy N. Whole forest responses to N availability and atmospheric CO_2 were predicted from basic physiological parameters. The results agreed well with results of elevated CO_2 FACE experiments for sweetgum and loblolly pine trees.

Finally, the findings of reduced decomposition and increased growth in response to fertilisation and elevated CO_2 were evaluated in the context of the global carbon balance. A simple model of the responses of global carbon fluxes and pool turnover rates combined with a future scenario of CO_2 emissions was subjected to a strong fertilisation effect on the boreal forest components. The results indicate that massive fertilisation could temporarily halt the rising of the atmospheric CO_2.

Keywords: carbon-14, decomposer efficiency, litter quality, mechanistic model, N deposition, NPP:GPP, optimality, plant theory, resorption effciency, soil respiration.

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Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Franklin O, Högberg P, Ekblad A, Ågren G I. Pine forest floor carbon accumulation in response to N and PK additions - bomb ^{14}C modelling and respiration studies (Accepted for publication in *Ecosystems*).

II. Ågren G I, Franklin O. Root:shoot ratios, optimisation and nitrogen productivity. (Accepted for publication in *Annals of Botany*)

III. Franklin O & Ågren G I. 2002. Leaf senescence and resorption as mechanisms of maximising photosynthetic production during canopy development at N limitation. *Functional Ecology* 16, 727-733.

IV. Franklin O. Optimal growth principle controls forest production, allocation and leaf properties in response to elevated CO2 and nitrogen (Manuscript).

Foreword

This thesis is based on a collection of four papers on different, but related, subjects. The summarising overview is intended to explain the work in simple terms and place it in the context of the global carbon cycle. To make it understandable to a wider audience than scientists only, ease of reading has been favoured before scientific conventions. Details of background, methods and results can be found in the accompanying papers.

Ecosystems and people

Plants are more important than people are, because without plants there would be no people but without people… As stupid as it may sound, it illustrates the role of plants on the planet. All animals, including humans, are directly or indirectly depending on the production of plants for food. But not only for food. They also can help to save us from the escalating greenhouse effect.

Recently, people have started to worry about the carbon in the atmosphere, the rising level of carbon dioxide, CO_2, that is causing global warming through the greenhouse effect. Because CO_2 is a main part of the material of plant production, it is not surprising that it grows better the more CO_2 there is in the air. This means that increased plant growth has the potential to counteract atmospheric CO_2 elevation. But not only CO_2 is needed by the plants, they also need water and nutrients. Availability of nutrients, particularly nitrogen (N), restricts plant growth in most areas (Tamm 1991). Therefore, plant growth is commonly enhanced by human activities of fertilisation and air pollution causing nitrogen deposition.

In addition to plants and pollution, there are also dead plants and soil microbes in the world. Dead plants (litter) and organic material are large reserves of carbon (C), waiting to be released as CO_2 to the atmosphere, or to be built on by production of more plant material. Dead plants are food for soil microbes that decompose and respire the dead plant material back to CO_2. In this process, nitrogen (N) is assimilated or released by the microbes, depending on the concentration of N in the litter. The microbes can also take inorganic N directly from the soil (N from fertilisers or deposition). If inorganic N is added by fertilisation or deposition, the microbes may use this N and depend less on decomposition of plant material to meet their needs. This can slow down the long-term decomposition process.

In summary, we are disturbing the carbon cycling between soil, plants and atmosphere in (at least) the

Box 1. *Explanation of terms*

Allocation	Distribution, sharing
Boreal forest	Mainly coniferous forests (e.g. pine and spruce) at northern lattitudes
C	Carbon
Canopy	All the leaves of a plant
Forest floor	The top layer of the soil consisting mainly of dead and decomposed plant parts (organic material)
LAI, Leaf Area Index	Number of layers of leaves above a unit ground area
Litter	Dead plant parts
Litter quality	Decomposability. Litter of high quality is easily decomposed.
Maintenance respiration	Respiration required to maintain a tissue
N	Nitrogen
N deposition	N originating from air pollutants
N resorption	Withdrawal of N before leaf shedding
Production, NPP	Photosynthesis - respiration
Relative growth rate	Growth rate per unit mass
Senescence	Leaf shedding controlled by the plant
Soil microbes	Bacteria and fungi that decompose litter

following ways: Plant fixation of CO_2 is increased by elevated CO_2 and N fertilisation, and carbon release from the soil is slowed down by N fertilisation. Fortunately, all these effects work against the greenhouse effect by increasing transfer of carbon from CO_2 in the atmosphere to storage in plants and soils.

In this thesis, I present work that deals with N and CO_2 effects on plant growth and decomposition. It also deals with the more internal affairs of plants: root-shoot allocation and canopy development. Finally, findings of the different papers are combined and their potential effects on global carbon fluxes are evaluated.

Theories, models and concepts

As a theoretical desktop ecologist, my work is based on theories, models and mathematics. Although some ecologists do not see it, they all use theories and models to interpret observations and draw conclusions. The aim of most of my work has been to develop mathematical theories and models to address the biological questions mentioned above, i.e. how plants and litter decomposition responds to nitrogen availability.

To develop a theory of how a system, e.g. a tree, works it is good to start by identifying some basic principle or purpose of the system. For a tree, the purpose is to maximise its fitness, i.e. the number of surviving offspring, or gene copies. Usually it is assumed that the fitness depends on something that is easier to measure, such as the growth rate, i.e. the faster it grows the sooner it can start spreading its genes. To maximise growth, available resources (e.g. N) should be invested in an optimal way, to maximise returns. All the plant theories developed here (papers II, III, and IV) are based on principles of maximal growth under given environmental conditions.

A model is always a simplification of a system and especially in ecology, systems must be hugely simplified to be understood. Only the most relevant processes should be included in the model. In addition, the use of appropriate concepts is important. For example, the concept of relative growth rate (the growth rate per unit mass) is useful for small plants where the whole plant is growing at a similar rate. However, this concept works less well for a large tree, which contains changing proportions of dead, slowly growing and fast turnover tissues. An extremely important concept in plant biology is the use of N as the basis for both photosynthesis and respiration (C loss). The reason for this is that N is a major constituent of the proteins that perform photosynthesis and cause respiration.

Paper I: Pine forest floor carbon accumulation in response to N and PK additions - bomb ^{14}C modelling and respiration studies

Fertilisation drastically increased forest growth and reduced long-term litter decomposition in a pine forest. In 100 years, twice as much carbon could accumulate in the forest soil where N addition is high as where no N addition occurs.

The investigated area was a Scots pine plantation in northern Sweden, where plots had been subjected to additions of N and PK in different amounts for 20 years (Tamm et al. 1999). Soil samples from the forest floor were taken, and each sample divided in three layers (L, F, and H-layer), for which the C and its ^{14}C enrichment were measured. Because of the past variation in atmospheric ^{14}C, the soil ^{14}C enrichment reveals when the carbon was fixed from the atmosphere. Nuclear weapons testing 1950-1963 caused a peak in atmospheric ^{14}C, which then has gradually declined (Harkness et al. 1996, Olsson 1993). Initial litter decomposition rates (Berg et al. 1991), soil respiration (CO_2 flux from soil) and tree growth (Gay et al 1994) were also measured at the site.

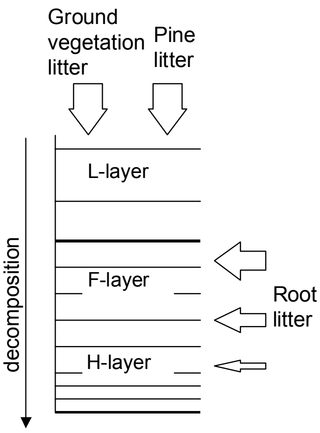

Fig. 1. Model representation of the forest floor. To estimate litter input and decomposition, these carbon fluxes are balanced to match measured C and ^{14}C in the layers.

A model of C loss through litter decomposition (Ågren & Bosatta 1998) was combined with calculations of C inputs from litter production for the different fertilisation treatments. This model was fitted to the measured C and ^{14}C data from the soil (Fig. 1).

The model allows a mechanistic description and separation of effects on substrate and decomposers. The results revealed that the fertilisation treatments had reduced the respiration/production ratio of the decomposers, i.e. they respired less CO_2 for each amount of litter that was consumed than they did in the unfertilised (control) plots. Furthermore, the reduction of litter quality (decomposability) as the litter is decomposed was increased by fertilisation (see also Ågren et al. 2001). Together these effects reduced the rate of CO_2 respired from the litter relative to the rate of litter quality degradation. This caused more build-up of low-quality, slowly decomposing material and an overall reduction in soil respiration in the fertilised treatments compared to the control. Over the years, this has resulted in a substantial increase in soil organic material in the fertilised soils.

Increased litter production also contributed to increased soil carbon in response to fertilisation, although reduced decomposition rate is the main cause of the observed and potentially large increases in forest floor carbon storage. Root production was largely unaffected while shoot:root ratio was increased. The results suggest that these effects are in progress in areas where N deposition is high, such as in Central Europe.

Paper II: Root:shoot ratios, optimisation, and nitrogen productivity

Root:shoot allocation is explained as a consequence of maximisation of relative growth rate in response to soil nitrogen availability.

Plants respond to N availability by changing their root:shoot ratios. This ratio is increased if N availability is reduced. One hypothesis used to explain this allocation is that plants optimise their behaviour by maximising their relative growth rate. We investigate the consequences of this hypothesis by formulating two models for root:shoot allocation, with and without explicit inclusion of maintenance respiration. Maintenance respiration can be viewed as a cost, i.e. a loss of C, for keeping N in the plant and is proportional to the amount of N (Canell & Thornley 2000, Ryan et al. 1996). In the model, the relative growth rate is a linear function of plant nitrogen concentration (nitrogen productivity; Ågren & Bosatta 1998). This theory is applicable mainly for small plants, where effects of self-shading in the canopy are not yet important.

The model without respiration gives qualitatively reasonable results when comparing predictions with observed results from growth experiments with birch (Ingestad et al. 1994b) and tomato (Ingestad et al. 1994a, de Groot et al. 2002). The explicit inclusion of maintenance respiration improves considerably the agreement between prediction and observation and is for birch within the experimental accuracy. The root:shoot allocation is not directly influenced by light intensity, but can respond indirectly through N concentration changes in response to light intensity. This is in line with the results for root:canopy allocation in mature trees, described in Paper IV.

Further improvements will require additional details in the description of respiratory processes and the nitrogen uptake function. Plants growing under extreme nutrient stress may also optimise their behaviour with respect to other variables than relative growth rate. However, more complex uptake functions tend to obstruct the mathematical analysis and obscure the mechanisms controlling the root:shoot allocation.

Paper III: Leaf senescence and resorption as mechanisms of maximising photosynthetic production during canopy development at N limitation

The amount of leaves and the shedding (senescence) of leaves are explained as consequences of the plant maximising the profit, photosynthetic production, of its canopy N capital.

Leaf photosynthesis is modelled using the non-rectangular hyperbola model, which is well known for its ability to describe photosynthesis response to environmental factors (e.g. Hirose & Werger 1987).

In a leaf, the photosynthetic capacity is controlled by the amount of N per leaf area, while the actual photosynthesis is limited by the light intensity. Because of this, plants distribute their available N proportional to the light intensity at different levels in the canopy (Field 1983).

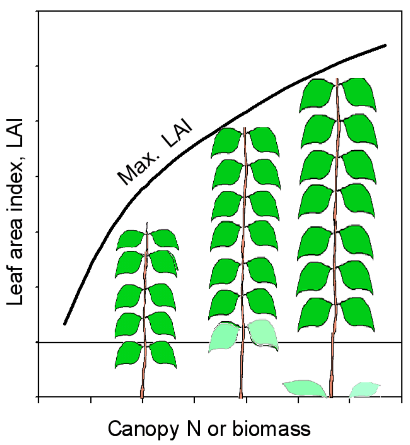

Fig. 2. As the canopy grows it reaches the max. LAI curve and starts shedding bottom leaves. Height grow continue but bottom leaves are dropped. When more N is taken up LAI can increase.

When the canopy grows, new leaves emerge on top of the old leaves and leaves at the bottom of the canopy become more and more shaded (Fig. 2). Their photosynthetic capacity is then reduced by transfer of their N to the top of the canopy. Eventually the bottom leaves become unprofitable and are discarded, after their assets of N have been withdrawn (resorbed). The theory implies that this happens when the potential gain from photosynthesis of resorbed and transferred N from the leaf is larger than the current photosynthetic production in the leaf.

This theory explained the observed amount of leaves per ground area (LAI) for four investigated plant species: red amaranth (*Amaranthus cruentus*), soybean (*Glycine max*), rice (*Oryza sativa*), and sorghum (*Sorghum bicolor*) (Anten et al. 1995). It is predicted that, per leaf area, the litter N: green leaf N ratio decreases with LAI, with N per leaf area and with decreasing soil N availability.

Paper IV: Optimal growth principle controls forest production, allocation and leaf properties in response to elevated CO_2 and nitrogen

Forest growth is considerably increased by elevated CO_2 and the resulting increase in rate of C storage in wood will remain as trees get larger, unless soil N limitation becomes more severe. This and other trends in forest response to elevated CO_2 are explained, solely as adaptive allocation responses to soil N availability and the well-established CO_2 effects on leaf photosynthesis.

While Paper II only considered small plants with no canopy N distribution effects, and Paper III only included the canopy, this paper aims to grasp a whole forest, or at least, a tree plantation. Based on a principle of maximal growth (biomass increase) and optimal amount of tree N, a tree model was developed (Fig. 3) and analytical results derived. Optimal N results as a trade-off between respiration+litter production (C losses) and photosynthesis (C gain), which both are functions of N (e.g. Hirose & Werger 1995, Canell & Thornley 2000, Ryan et al. 1996). The total optimal N depends on the relative allocation of N between photosynthetic canopy N and N in organs that lose carbon through respiration, such as stem and roots. If N soil availability is reduced, more roots are needed for N uptake and N is allocated away from the canopy to new roots. This leads to reduction of canopy N, photosynthesis, growth, leaf area, and leaf N concentration.

Elevated CO_2 increases photosynthesis (Curtis & Wang 1998) and improves the balance between C assimilation and C losses. Trees become more efficient both regarding light use for C assimilation and regarding biomass production per assimilated C. Because increased N uptake is needed as growth is increased, more roots are produced. If N uptake is not increased in proportion to root mass, the root:canopy allocation is shifted towards more root allocation. Thus, the forest response to elevated CO_2 is determined by the N uptake efficiency of new roots. The model shows that growth of wood in elevated CO_2 can be substantially increased by fertilisation, which has also been observed (Oren et al. 2001). Furthermore, the optimal leaf N concentration is reduced as a consequence of the change in C and N flux balance.

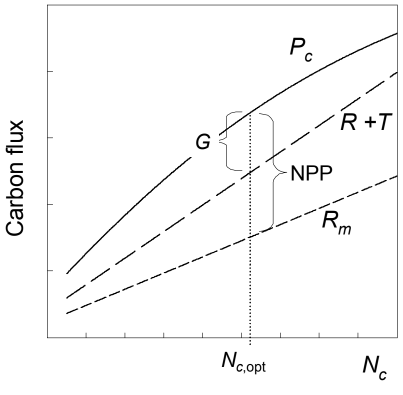

Fig. 3. The optimal canopy N ($N_{c,\text{opt}}$) is the N_c that maximises growth (G), which is the difference between canopy photosynthesis (P_c) and respiration + turnover ($R+T$). Maintenance respiration (R_m) and $R+T$ are linear functions of N_c, while P_c is a saturating function of intercepted light and N_c.

Another result is that the

NPP:photosynthesis ratio is insensitive to soil N availability but decreases with tree size.

The predictions of the model agree well with the results of elevated CO_2 FACE-experiments with loblolly pine (Hamilton et al. 2002) and sweetgum trees (Norby et al. 2002). In FACE-experiments, whole forest stands are subjected to elevated CO_2 without any physical barriers, which makes them the most realistic CO_2 experiments yet.

Plants and litter versus the greenhouse effect

As mentioned in the introduction, fertilisation and elevated CO_2 itself both work against elevated CO_2 and the greenhouse effect. As atmospheric CO_2 is further elevated, will the CO_2 elevation eventually be slowed by forest growth? Will it be stopped if forests are fertilised?

To address these questions I used a simple model (Box 2) of the global carbon balance to investigate the impact of fertilisation of the boreal forest under a scenario of rising atmospheric CO_2.

The global carbon pools and fluxes 1996 (Schlesinger 1997) were used to calibrate the mean residences times of the carbon pools for 1996 (Fig. 4). I assumed no changes in C uptake of the oceans, forest destruction and the “missing sink”, i.e. the 1.7 Pg C/y removed from the atmosphere to some undetermined place. Future carbon emissions from fossil fuel burning were taken from IPCC (Intergovernmental panel of climate change), which predicts future CO_2 emissions based on different scenarios of global development. The used scenario (“B2”, 0.9 Pg / year linear increase; IPCC 2003) is in the middle of the range of possible scenarios for future CO_2 emissions.

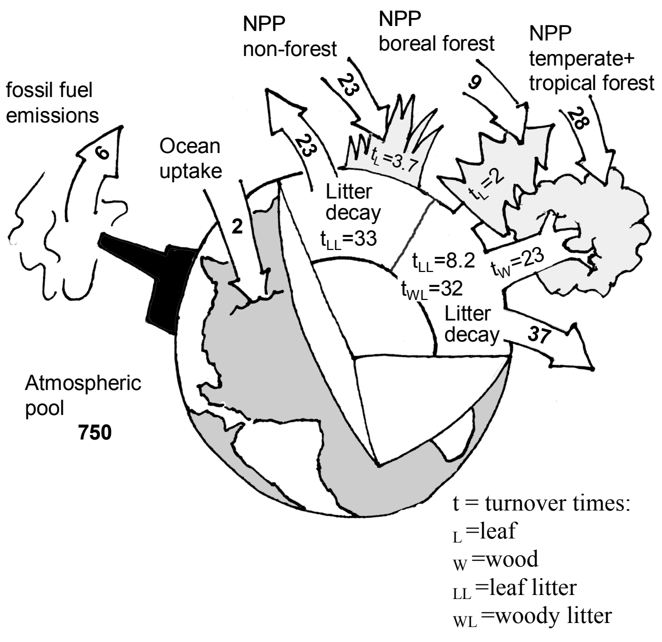

Fig. 4. Global carbon fluxes (Pg/y) in 1996. The same turnover times were used for both boreal and temperate+tropical forests and soils. Turnover times were calculated assuming a 3.2 Pg/y increase in atmospheric CO_2. (Schlesinger 1997). Pg=10^{15}g. Vegetation and soil C pools are given in Fig. 5.

I predicted the carbon pools 100 years from 1996, based on the effects of CO_2 and forest production estimated in Paper IV, i.e. production is increased by elevated CO_2. Based on the effects of fertilisation on production (Paper IV) and of reduced long-term litter decomposition (Fig. 5), I imposed a considerable fertilisation effect on the boreal forest starting 2004 (Box 2). No other vegetations or soils were subjected to the fertilisation, while the CO_2 level affects all vegetation.

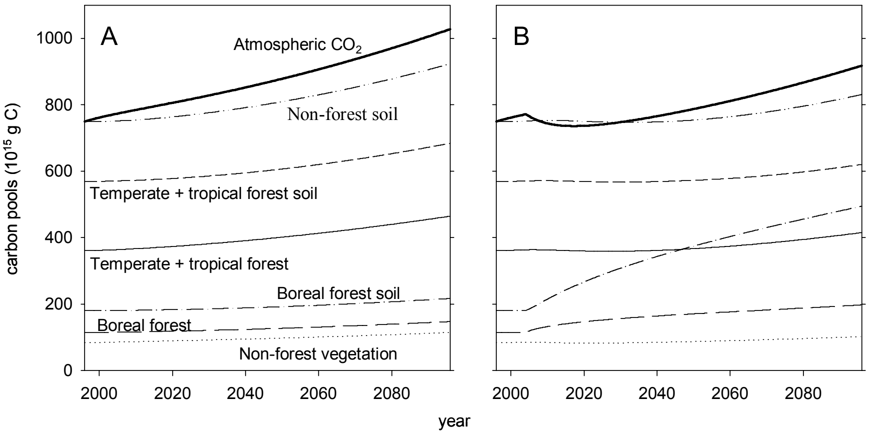

Fig. 5. Global carbon pools in response to rising atmospheric CO_2 and N fertilsation of the boreal forest. A) without fertilisation, B) fertilisation of the boreal forest starting 2004. Details of the model are given in Box 2.

Without fertilisation, the atmospheric CO_2 will rise to about 1030 Pg or 495 ppm. This is less than the 600 ppm that IPCC predicts for the same scenario. IPCC have a more complex model and may take into account additional factors, such as future changes in forest destruction or water availability. However, the purpose of the simple model used here is not to evaluate the accuracy of quantitative predictions, rather it is an initial analysis of the potential magnitude of the effects of a given scenario.

Initially, the fertilisation of the boreal forest reverses the rising CO_2 through a rapid build-up of forest biomass and litter. But after about 20 years, CO_2 emissions catch up with the C sequestration in the boreal forest and the atmospheric CO_2 levels starts rising again. Thus, the fertilisation of the boreal forest temporarily halts the atmospheric CO_2 increase, but only temporarily unless emissions from fossil fuel are reduced. In a longer time perspective, the forest soil C pools may reach a new equilibrium and their carbon storage will be saturated. On the other hand, the more elaborate model of decomposition used in Paper I indicates that N addition could reduce the long-term decomposition rate to the point of a never-ending soil C build-up.

These results contrast to widely cited conclusions that N deposition makes a minor contribution to forest C sequestration (Nadelhoffer et al. 1999). One explanation for the different conclusions is that Nadelhoffer et al. (1999) did not include any effects of reduced long-term decomposition in response to N deposition.

Box 2. Global carbon flux model

Carbon fluxes:

$$\frac{dA}{dt} = \mathit{fossil\ fuel} + \mathit{forest\ destruction} + \sum_i \frac{LL_i}{t_{LL_i}} + \sum_j \frac{WL_j}{t_{WL_j}}$$
$$- \mathit{ocean\ uptake} - \sum_i \mathrm{NPP}_i - \mathit{unknown\ uptake}$$

$$\frac{dL_i}{dt} = \mathrm{NPP}_i \cdot (1 - a_i) - \frac{L_i}{t_{L_i}} \qquad \frac{dW_j}{dt} = \mathrm{NPP}_j \cdot a_j - \frac{W_j}{t_{W_j}}$$

$$\frac{dLL_i}{dt} = \frac{L_i}{t_{L_i}} - \frac{LL_i}{t_{LL_i}} \qquad \frac{dWL_j}{dt} = \frac{W_j}{t_{W_j}} - \frac{WL_j}{t_{WL_j}}$$

Symbols:
A = atmospheric C
L = Leaf C, W = wood C, LL = leaf litter C, WL= woody litter C
t = turnover times
a = fraction NPP allocated to wood production

Indices:
i = non forest vegetation, boreal forest, temperate+tropical forest
j= boreal forest, temperate+tropical forest

CO2 concentration and fertilisation effects:

$$\mathrm{NPP_y} = \mathrm{NPP_0} \cdot \left(1 + 1.035 \cdot \frac{A_y - A_0}{A_0}\right) \text{ for all unfertilised vegetation.}$$

$$\mathrm{NPP_y} = 1.54 \cdot \mathrm{NPP_0} \cdot \left(1 + 0.89 \cdot \frac{A_y - A_0}{A_0}\right) \text{ for fertilised forest.}$$

In addition, the turnover times of litter in the boreal forest was doubled in response to fertilisation.

A_y, $\mathrm{NPP_y}$ and A_0 , $\mathrm{NPP_0}$ are the atmospheric CO_2 concentration and NPP in year y and initial values (year 1996), respectively. Initial values of NPPs and turnover times are given in Fig. 4 and cabon pools in Fig. 5. The atmospheric C increase in 1996 was 3.2 Pg/y and the "unknown uptake" is 1.7 Pg/y.

Conclusions and implications

By the use of a mechanistic decomposition theory and ^{14}C variability, the soil C accumulation in a fertilised forest could be explained in terms of decomposer and substrate parameters. This gives a more detailed understanding compared to commonly used steady state pool turnover models. The results indicate that decomposition effects should be included when impacts of N deposition are evaluated.

Theories of root:shoot allocation and canopy development have been improved through application of maximal growth and production principles. The suggested principles for senescence and resorption provide a new basis for predicting dynamics of canopy LAI development.

A maximal growth principle made it possible to integrate forest responses to N and CO_2 in a simple analytical framework. This can explain observed trends in production, allocation, NPP:GPP ratio, LAI and leaf N concentration solely as consequences of an optimal acclimation response to changes in leaf photosynthetic rate and root N uptake efficiency. In the light of this theory, it should be possible to predict integrated whole forest stand responses to CO_2 from leaf physiological parameters and soil N availability. A better understanding of the root production - N uptake relation could further improve the model.

A simple global carbon flux model indicates that large-scale fertilisation of the boreal forest could have a considerable impact on the global carbon balance, particularly through reduced long-term decomposition. The global perspective on carbon fluxes illustrates the crucial role of plants and the importance of increased understanding of the interactions of nutrients and CO_2. For long-term predictions, the results emphasise the need to understand long-term organic matter decomposition.

References

Ågren G I, Bosatta E. 1998. Theoretical Ecosystem Ecology- Understanding Element Cycles. Cambridge University Press, Cambridge.

Ågren G I, Bosatta E, Magill A H. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. Oecologia 128, 94-98.

Anten N P R, Schieving F, Medina E, Werger M J A, Schuffelen P. 1995. Optimal leaf area indices in C3 and C4 mono- and dicotyledonous species at low and high nitrogen availability. Physiologia plantarum 95, 541-550.

Berg B, Booltink H, Breymeyer A,Ewertsson A, Gallardo A, Holm B, Johansson M B, Koivuoja S, Meentemeyer V, Nyman P, Olofsson J, Petterson A,Reurslag A, Staaf S, Staaf I,Uba L. 1991. Data on needle litter decomposition and soil climate as well as decomposition characteristics for some coniferous forest sites. Part 2. Decomposition data. Reports of Dep. of Ecology and Environmental Research, Swedish Uni. of Agr. Sci. 42.

Cannell M G R, Thornley J H M. 2000. Modelling the components of plant respiration, Some guiding principles. Annals of Botany 85, 45-54.

Curtis P, Wang X. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113, 299-313

de Groot C C, Marcelis LFM, van den Boogaard R, Lambers H. 2002. Interactive effects of nitrogen and irradiance on growth and partitioning of dry mass and nitrogen in young tomato plants. Functional Plant Biology 29, 1319-1328.

Field C. 1983. Allocating leaf nitrogen for the maximisation of carbon gain, Leaf age as a control on the allocation program. Oecologia 56, 341-347.

Gay C, Tamm C O, Aronsson A, Flower-Ellis J G K, Linder S. 1994. Ekologen Database. Collection of data from the Forest Optimum Nutrition Program.

Hirose T, Werger M J A. 1987. Maximising daily photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. Oecologia 72, 520-526

Hamilton J G, DeLucia E H, George K, Naidu S L, Finzi A C and Schlesinger W H. 2002. Forest carbon balance under elevated CO_2. Oecologia Berlin 131, 250-260.

Harkness D D, Harrison A F, Bacon P J. 1986. The temporal distribution of ”Bomb” ^{14}C in a forest soil. Radiocarbon 28, 328-337.

Ingestad T, Hellgren O, Ingestad Lund AB. 1994a. Data base for tomato plants at steady state. Methods and performance of tomato plants (Lycopersicon esculentum Mill. cv. solentos) under non-limiting conditions and under limitation by nitrogen and light. Department of Ecology and Environmental Research. Swedish University of Agricultural Sciences. Report 74. 50pp.

Ingestad T, Hellgren O, Ingestad Lund AB. 1994b. Data base for birch plants at steady state. Performance of birch plants (Betula pendula Roth.) under non-limiting conditions and under limitation by nitrogen and light. Department of Ecology and Environmental Research. Swedish University of Agricultural Sciences. Report 75. 38 pp.

IPCC 2003. Scenarios for future CO_2 emissions and atmospheric CO_2 concentration. IPCC website http://www.ipcc.ch/.

Nadelhoffer K J, Emmett B A, Gundersen P, Kjonaas O J, Koopmans C J, Schleppi P, Tietema A, Wright R F. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. Nature 398, 145-148.

Norby R J, Hanson P J, O’ Neill E G, Tschaplinski T J, Weltzin J F, Hansen R A, Cheng W, Wullschleger S D, Gunderson C A, Edwards N T and Johnson D W. 2002. Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. Ecological Applications 5, 1261-1266.

Olsson I U. 1993. A ten-year record of different levels of the ^{14}C activities over Sweden and the Arctic. Tellus 45, 479-81.

Oren R, Ellsworth D S, Johnsen K H, Phillips N, Ewers B E, Maier C, Schafer K V R, McCarthy H, Hendrey G, McNulty S G and Katul G G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411, 469-472.

Ryan M G, Hubbard R M, Pongracic S, Raison R J, McMurtrie R E. 1996. Foliage, fine-root, woody-tissue and stand respiration in Pinus radiata in relation to nitrogen status. Tree Physiology 16, 333-343.

Schlesinger W H. 1997. Biogeochemistry - An analysis of global change. Academic press.

Tamm C O. 1991. Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability. Ecological Studies 81, xii + 115 pp.

Tamm C O, Aronsson A, Popovic B, Flower-Ellis J K G. 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. Studia Forestalia Suecia 266.

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Trots det fasansfulla kaffet som serveras har många roliga diskussioner utspelat sig i fikarummet där väl alla EoM-are varit med nån gång och därmed ska känna sig tackade. Före detta EoM-are som jag kommer ihåg särskilt har livat upp stället både vetenskapligt och annars är bl a Peter Saetre, David och Matty.

Tack vare Barbros rådiga och ihärdiga insatser har jag fått ordning på nästan allt från reseräkningar till att fixa fram en dataprojektor. Hans Bonde har varit till stor hjälp med möbler och intressanta diskussioner om bildelar och politik. Tack till Kerstin Ahlström och övriga som bidragit till filmproduktion och småkrypsfotografering i labbet. Bengt ska ha tack för att jag fick åka med som kursassistent och fånga vattenödlor vid Barnens ö.

Niklas och Anna har inte bara lyst upp EoM och varit friska fläktar vid fikabordet utan även i världen utanför och fixat lodjur, slagugglor, filmer och kalas m.m, m.m.. Detta gäller även Patrik Karlsson och exjobbare som t.ex. Josefin.

Helt utanför SLU-världen har Peter Frisk, Mats Svensson och Peter Reigo bidragit med nya perspektiv på doktorandjobbets för- och nackdelar. Anders Rådéns grafiska och andra tjänster har besparat mig sisådär en kvarts miljon. Alexandra har förklarat vad "hermeneutics" betyder och har haft en mycket gott inflytande på många vetenskapliga och ovetenskapliga områden. Det gäller även för Åsa. Min familj får förståss inte glömmas även om dom antagligen undrat vad jag egentligen hållit på med för ett konstigt jobb.