Assessment of the relative importance of nitrogen deposition, climate change and forest management on the sequestration of carbon by forests in Europe

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ABSTRACT

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This report summarizes results of studies assessing and predicting changes in forest growth and carbon sequestration in forests and forest soils in response to various scenarios with respect to changes in CO_2 concentration, climate (precipitation and temperature), atmospheric deposition (N and S deposition) and forest management (forest management scenarios), using empirical and process oriented models, respectively. This was done by evaluating measured stand based forest growth rates in the period 1995-2000 versus causal agents using data gathered in nearly 400 European Forest Ecosystems, using both statistical and process based models. The major finding of the statistical evaluation was an estimated increase in growth between 1-2 %, depending on tree species, per kg N deposition, that is approximately equal to an estimated carbon sequestration in trees of 20-40 kg carbon per kg nitrogen deposition. The process based model studies give a comparable range in carbon sequestration. Results from process based model studies, including the studies presented in this report, and from N fertlizer experiments indicate a slightly lower carbon sequestration per kg N input in soils, implying an estimated carbon sequestration in trees and soils between 30-70 kg C/kgN. Results also show that N deposition was the major cause of increased growth in the past and at present, but in the future, an increase in CO_2 and temperature is predicted to be more important. Temperature increase leads to an increased growth in boreal climates but in Central and Southern Europe the effect is opposite due to increased drought stress.

Keywords: carbon sequestration, nitrogen deposition, climate change, forest growth, forest ecosystems, process based models, empirical models

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Preface

This report mainly summarizes results of an EC funded project that aimed to assess and predict changes in forest growth and carbon sequestration in forest ecosystems in response to changes in CO_2 concentration, climate (precipitation and temperature), atmospheric deposition (N and S deposition) and forest management (forest management scenarios). The project was funded by DG Agriculture in the context of Forest Focus and it makes use of data that are gathered within the context of the European Scheme on the Protection of Forests against Atmospheric Pollution (EC) and the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests of UN-ECE).

The report is a compilation of papers that are mostly submitted to the journal "Forest Ecology and Management". It only includes one paper, that refers to the "generalizations for European forests based on the Intensive monitoring data" that has been published already namely: De Vries, W., G. J. Reinds and P. Gundersen and H. Sterba, 2006. Impacts of nitrogen deposition on carbon sequestration by forests in Europe. Global Change Biology 12: 1151-1173 (Chapter 7). All other papers that are submitted to the journal "Forest Ecology and Management". To give insight in the responsibility of the various authors for the contents of this report, the names related to the various titles are given below.

Empirical modelling at the Intensive monitoring plots

Solberg, S., M. Dobbertin, G.J. Reinds, W. de Vries, K. Andreassen, H. Lange, P. Garcia Fernandez and A. Hildingsson, 2007. The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical stand growth model (Chapter 1).

Laubhann, D, H. Sterba, W. de Vries and G.J. Reinds, 2007. The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical tree growth model (Chapter 2).

The process based model SUMO

Wamelink, G.W.W., H.F. van Dobben and F. Berendse, 2007. Vegetation succession as affected by decreasing nitrogen deposition, soil characteristics and site management: a modelling approach (Chapter 3).

Wamelink, G.W.W., H. F. van Dobben, J. P. Mol-Dijkstra, E. P.A.G. Schouwenberg, J. Kros, W. de Vries and F. Berendse, 2007. Effect of nitrogen deposition reduction on biodiversity and carbon sequestration (Chapter 4).

Process based modelling at the Intensive monitoring plots

Mol-Dijkstra, J. P., G. J. Reinds, J.Kros, B. Berg and W. de Vries, 2007. Modelling soil carbon sequestration in forest soils on intensively monitored plots in Europe in response to N deposition (Chapter 5).

Wamelink, G.W.W., H.J.J. Wieggers, G.J. Reinds, J. Kros, J. P. Mol-Dijkstra and W. de Vries, 2007. Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on growth and carbon sequestration of Intensive Forest Monitoring plots in Europe (Chapter 6).

Generalizations for European forests based on the Intensive monitoring data

Pussinen, A., Nabuurs, G.J., H.J.J. Wieggers, G.J. Reinds, G.W.W. Wamelink, J. Kros, J. P. Mol-Dijkstra and W. de Vries, 2007. Modelling long term impacts of environmental change on mid- and high-latitude European forests and options for adaptive forest management (Chapter 8).

Evaluation

De Vries, W., J. Kros, G.W.W. Wamelink, G.J Reinds, H.J.J. Wieggers, J. P. Mol-Dijkstra, S. Solberg, M. Dobbertin, H. Sterba, D. Laubhann, M. van Oijen, M.A. Sutton, C. Evans and P. Gundersen. The impact of nitrogen deposition on carbon sequestration by terrestrial ecosystems (Chapter 9)

Results from the statistical evaluation and from process based model studies indicate a carbon sequestration response in trees to nitrogen deposition of 20-40 kg C/kgN. Modelling studies, including those presented in this report, and N fertlizer experiments indicate a slightly lower carbon sequestration per kg N input in soils, implying an estimated carbon sequestration in trees and soils between 30-70 kg C/kgN. Results also show that N deposition was the major cause of increased growth in the past and at present, but in the future, an increase in CO_2 and temperature is predicted to be more important. Temperature increase leads to an increased growth in boreal climates but in Central and Southern Europe, the effect is opposite due to increased drought stress.

The relation between institutes and names is as follows

- Wim de Vries, Wieger Wamelink, Gert Jan Reinds, Rick Wieggers, Janet Mol-Dijkstra, Hans Kros and Gert Jan Nabuurs: Alterra, Wageningen, the Netherlands.
- Ari Pussinen, European Forest Institute, Joensuu, Finland.
- Svein Solberg: Norwegian Forest and Landscape Institute, Ås, Norway.
- Mattias Dobbertin: Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland.
- Daniel Laubhann and Hubert. Sterba: University of Natural Resources and Applied Life Sciences, Department of Forest- and Soil Sciences, Institute of Forest Growth and Yield Research, Vienna, Austria.
- Marcel van Oijen: Centre for Ecology and Hydrology (CEH), Edinburgh Research Station, Scotland.

We thankfully acknowledge the European Commission, DG Agriculture and DG Environment, as well as The Dutch Ministry of Agriculture, Nature and Food quality, the Norwegian Forest and Landscape Institute, the Swiss Federal Institute for Forest, Snow and Landscape Research, the Austrian University of Natural Resources and Applied Life Sciences and the UK Centre for Ecology and Hydrology for their financing of the project. We also like to acknowledge the work carried out by a high number of experts at the national and international level with gathering and quality assurance of the various data sets that we used here, and in particular the assistance from many experts in the countries participating in this monitoring activity during the quality assurance of the data in this study, and for providing additional data such as plot ages.

Extended summary

Aim of the study

In the climate change discussion, the possibility of carbon sequestration of forests plays an important role. This report mainly summarizes results of an EC funded project that aimed to assess and predict changes in forest growth and carbon sequestration in forests and forest soils in response to various scenarios with respect to changes in CO_2 concentration, climate (precipitation and temperature), atmospheric deposition (N and S deposition) and forest management (forest management scenarios). The evaluation was done by both statistical models and process based models. The study aimed to supplement earlier studies on the impacts of environmental changes on a limited number of plots. This was done by evaluating measured stand based forest growth rates versus causal agents using data gathered in the "Pan-European Programme for Intensive and Continuous Monitoring of Forest Ecosystems" under the responsibility of the EC and ICP Forests.

Approach to the study

The basic method was to use: (i) empirical models to reconstruct and explain past forest growth in relation to environmental changes and (ii) process oriented soil chemical, hydrological and forest growth models to predict future effects of climate, deposition and management scenarios on forest growth and carbon sequestration. The research was carried out by: (i) the development of empirical statistical models at stand level and individual tree level and application at selected Intensive monitoring plots, (ii) the further development of the succession and stand growth model SUMO, (iii) the integration of SUMO with a hydrological model WATBAL2 and a soil biogeochemical model SMART2 and the calibration and application at selected Intensive monitoring plots and (iv) the upscaling of results using measured and estimated deposition and soil data at approximately 6000 so-called Level I plots and using growth data in a large scale European forest resource model (EFISCEN). Since the results implied a considerable impact of nitrogen deposition on present growth, being a red line through the whole report, a final overview article is included in which the impact of N deposition on carbon sequestration is summarized based on results from this study and available literature data.

More specifically, the four activities that were carried out in this study were:

1. *Empirical modelling at the Intensive monitoring plots:* This included an assessment of forest growth during a five year period on 363-382 Intensive Monitoring sites throughout Europe and application of empirical statistical models, at a stand level (363 plots) and at an individual tree level (382 plots), to gain insight in the deviation of the growth from expected values. This deviation was then related to environmental changes, including variations in climatic variables, nitrogen and sulphur deposition.
2. *Process based modelling:* This included the further development and integration of available process oriented soil chemical, hydrological and forest growth models (the model chain SMART2-SUMO-WATBAL2) into a spatial explicit model

system, predicting the impacts of changes in climate, deposition and management on carbon sequestration by forests and forest soils, focusing on the further development of the succession and stand growth model SUMO.

3. *Scenario analyses with process-based models at the Intensive monitoring plots:* This included the validation and calibration of predicted changes in hydrology, soil chemistry and forest growth by the model system on measured data at the Intensive Monitoring sites in the considered time period and investigating effects of plausible scenarios for climate change, atmospheric deposition and forest management on forest growth and carbon sequestration by the developed and validated model system.
4. *Generalizations for European forests based on the Intensive monitoring data:* This included the upscaling of the impacts as assessed by the process based models to all European forests scale by use of data in so-called Level I plots and by use of the EFISCEN European forest resource model, including different scenarios for climate change, atmospheric deposition and forest management.

Empirical modelling at the Intensive monitoring plots

Empirical statistical models at stand level (Chapter 1)

In this study use was made of an extensive data set of intensively monitored forest plots with 5-year growth data for the period 1994-1999 to examine the geographical pattern and investigate the impact of N deposition and climatic parameters on growth. Evaluations focused on the influence of nitrogen, sulphur and acid deposition, temperatures, precipitation and on a drought index (precipitation minus potential evapotranspiration during the growing season) calculated as deviation from the long-term mean. The study included the main tree species Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Common beech (*Fagus sylvatica*) and oak (*Quercus petraea and Q. robur*) and was based on data from 363 plots. The major variable we focused on is relative growth, i.e. actual measured growth in percent of expected growth. Expected growth was modelled using site productivity, stand age and a stand density index. Relative tree growth was then calculated as actual growth in % of expected growth. The site productivity, assumed to be given by site conditions and past environmental conditions, was either taken from expert estimates or computed from site index curves from Northern, central and Southern Europe. The model explained between 18% and 39% of the variance with site productivity being positively related and age negatively related to actual growth.

The various models and statistical approaches were fairly consistent, and indicated a fertilizing effect of nitrogen deposition, with one percent increase in site productivity per kg of nitrogen deposition per ha and year. This was most clear for spruce and pine, and most pronounced for plots having soil C/N ratios above 25. Also, we found a positive relationship between relative growth and summer temperature, i.e. May-August mean temperature deviation from the 1961-1990 means. The cause-effect relationship here is however, less certain. Other influences were uncertain. Possibly, sulphur and acid deposition have effects on growth, but these effects are obscured by, and outweighed by the positive effect of nitrogen deposition, because of co-linearity between these variables. Drought effects were uncertain also, and one reason for this might be large uncertainties in the precipitation data: Precipitation measured on some 50% of the plots correlated poorly with the precipitation data obtained from European wide databases. The major finding of this study was a positive relationship between higher than normal volume growth on one hand and nitrogen deposition on the other hand. The average estimated increase was 1% per kg of N deposition, which was estimated to correspond with an increase between 33 and 49 kg wood per year or 16-25 kg C per kg N.

Empirical statistical models at individual tree level (Chapter 2)

This study also focused on the influence of changing temperature, precipitation and deposition especially of sulfur and nitrogen compounds on forest growth, but at individual tree level. The data base consisted of 654 plots of the European intensive monitoring program (Level II plots). Due to restrictions for data to be used only 382 plots were used in 18 European countries, limiting the study to the same four tree species as the stand level study: Norway spruce, Scots pine, Common beech and oak. An individual tree growth model was developed with size (dbh), site (soil, temperature), competition (basal area of larger trees and stand density index) and environmental-change (temperature change, nitrogen and sulfur deposition) as explaining parameters. As dependent variable basal area increment was used. Using a mixed model approach, all models for the tree species show a high Goodness of fit with Pseudo-R^2 between 0.334 and 0.442. Breast height diameter and basal area of larger trees were highly influential variables in all models. Increasing temperature showed a positive effect on growth for all species except Norway spruce. Nitrogen deposition showed a positive impact on growth for all four species, but the influence for common beech was not very significant. Comparable to the stand level study, an increase of 1 kg N ha^{-1} yr^{-1} corresponded to an increase in basal area increment between 1.20 % and 1.49 % depending on tree species. Considering an average total carbon uptake for European forests near 1730 kg per hectare and year, this implies an estimated sequestration of approximately 21-26 kg carbon per kg nitrogen deposition.

Process based modelling: the SUMO model

In this study, use was made of the vegetation succession model SUMO which is closely linked to the soil model SMART2. In the original SUMO model, the biomass development of five functional plant types is simulated as a function of nitrogen availability, light interception and management. The model simulates the change in biomass distribution over functional types during the succession from almost bare soil via grassland or heath land to various forest types. The processes modelled in the original SUMO model are extensively described in Appendix 1 of this report.

Impacts of nitrogen deposition and management on vegetation succession (Chapter 3)

After many years of increasing nitrogen deposition, the deposition rates are now decreasing. A major question is if this will result in the expected positive effects on plant species diversity. Long-term experiments that investigate the effects of decreasing deposition are not available. Model simulations may yield insight in the possible effects of decreasing nitrogen deposition on the vegetation. The SUMO model was thus validated on three sites in the Netherlands and one site in the UK.

The aboveground biomass of two grassland vegetation types was simulated properly, as well as the above ground biomass of heath lands during succession of sod removal. Some of the stages of forest succession were simulated less well, but the calculated biomass in the older stages agreed with the measured values.

To explore the long-term effect of a decrease in nitrogen deposition we applied the model to a heath land and a pine stand. In the heath land a major change was predicted as a result of decreasing nitrogen deposition in combination with turf stripping. The dominance of grasses changed into a dominance of dwarf shrubs, whereas at continuing high levels of nitrogen deposition grasses remained dominant. In contrast, the simulations indicated only very small effects of a decreasing N deposition in pine forests. This difference is due to the removal of excess nitrogen by management (turf stripping) in the heath land, whereas the more extensive management in the forest hardly removes any nitrogen from the system. The main conclusion from these examples is that a decrease of nitrogen deposition may retard succession, and consequently increase biodiversity in heath land but probably not in forest. The effects of declining N deposition depend on the amount of N that is removed from the system as a consequence of the various management regimes.

Effect of nitrogen deposition reduction on biodiversity and carbon sequestration (Chapter 4)
Global warming and loss of biodiversity are among the most prominent environmental issues of our time. Large sums are spent to reduce their causes, the emission of CO_2 and nitrogen compounds. However, the results of such measures are potentially conflicting, as the reduction of nitrogen deposition may hamper carbon sequestration and thus increase global warming. Moreover it is uncertain whether a lower nitrogen deposition will lead to a higher biodiversity. In this study we forecast that a gradual decrease in nitrogen deposition from 40 to 10 kg N.ha^{-1}.yr^{-1} in the next 25 years will cause a drop in the net carbon sequestration of forest in The Netherlands to 27% of the present amount, while biodiversity remains constant in forest, but may increase in heath land and grassland.

Scenario analyses with process-based models at Intensive monitoring plots

Modelling forest soil carbon sequestration by three different approaches (Chapter 5)
Information on soil carbon sequestration and its interaction with nitrogen availability is rather limited, since soil processes account for the most significant unknowns in the C and N cycles. In this paper we compare three completely different approaches to calculate carbon sequestration in forest soils. The first approach is the limit value concept, in which the soil carbon accumulation is estimated by multiplying the annual litterfall with the recalcitrant fraction of the decomposing plant litter, which depends on the nitrogen and calcium content in the litter. The second approach is the N balance method, where carbon sequestration is calculated from the nitrogen retention in the soil multiplied with the present soil C/N ratio in organic layer and mineral topsoil. The third approach is the dynamic SMART2 model in combination with an empirical approach to assess litterfall inputs. The comparison is done by first validating the methods at three chronosequences with measured C pools, two in Denmark and one in Sweden, and then application on 192 intensive monitoring plots located in the Northern and Western part of Europe. Considering all three

chronosequences, the N balance method was generally most in accordance with the C pool measurements, although the SMART2 model was also quite consistent with the measurements at two chronosequences. The limit value approach generally overestimated the soil carbon sequestration. At the intensive monitoring plots, the limit value concept calculated the highest carbon sequestration, ranging from 160 to 978 kg ha^{-1} yr^{-1}, followed by the N balance method which ranged from 0 to 535 kg ha^{-1} yr^{-1}. With SMART2, we calculated the lowest carbon sequestration from -30 to 254 kg ha^{-1} yr^{-1}. All the three approaches found lower carbon sequestration in Northern Europe (latitude above 60 degrees) compared to Central and Southern Europe (latitude from below 60 degrees. Considering the validation of the three approaches, the range in results from both the N balance method and SMART2 model seems most appropriate.

Modelling impacts of changes in nitrogen deposition, climate change and carbon dioxide concentration on carbon sequestration (Chapter 6)
Changes in the Earth's atmosphere are expected to influence the growth and therefore carbon accumulation of European forests. We identify three major changes: (1) a raise in carbon dioxide concentration, (2) climate change, resulting in higher temperatures and changes in precipitation and (3) a decrease in nitrogen deposition. We adjusted and applied the hydrological model WATBAL, the soil model SMART2 and the vegetation model SUMO to asses the effect of expected changes in the period 1990 up to 2070 on the carbon accumulation in trees and soils of 166 European forest plots. The models were parameterized using measured soil and vegetation parameters and site-specific changes in temperature, precipitation and nitrogen deposition. The carbon dioxide concentration was assumed to rise uniformly across Europe. The results were compared to a reference scenario, consisting of a constant CO2 concentration and nitrogen deposition (data of 1990) while repeating the temperature and precipitation between 1960 and 1990 up to 2070.

The assumed rise in carbon dioxide concentration gives a rise in carbon accumulation all over Europe. Inversely, the assumed decrease in nitrogen deposition causes a decrease of carbon accumulation all over Europe and for all modelled tree species. Climate change leads to a predicted decrease in carbon accumulation in the South of Europe and an increase in the North. When the scenarios are combined an increase in biomass accumulation is predicted at most of the sites, with a raise in growth rate mostly between 0% and 100%. Only at a few sites in the south the carbon sequestration in trees is decreasing, due to an increased drought stress caused by a decrease in precipitation and an increase in temperature. An analysis of variance shows that climate change explains the major part of the variance, followed by the CO2 rise. The effect of the change in nitrogen deposition is relative small because of the relative small difference in nitrogen deposition and because soil and vegetation processes keep the nitrogen cycling relatively constant.

The predicted effects of a change in the investigated environmental variables on soil carbon sequestration are generally lower than on carbon sequestration by the trees but the magnitude is similar and also the dependence on location (latitude). As with trees, we predicted a net soil carbon release from at several sites in the south. Overall, we conclude that where nitrogen deposition was a major driver for a change in forest growth in the past, it is climate change and to a lesser extent CO2 change that will mainly determine forest growth in the future.

Modelling impacts of environmental changes on carbon sequestration and green house gas emissions of European forests

The project also includes upscaling to Europe. An estimate of the net exchange of green house gases, focusing on net carbon (C) pool changes and long term C sequestration in trees and soils, was made on a European scale based on model results from Intensive monitoring data and soil information available at level I plots. Furthermore, the impact of various scenarios on climate change, atmospheric deposition and forest management on forest growth and carbon sequestration on a European scale was assessed by incorporating results on carbon sequestration in response to these scenarios by the process oriented SMART2-SUMO-WATBAL2 model system into the European forest resource model EFISCEN.

Impacts of nitrogen deposition on carbon sequestration by forests in Europe (Chapter 7)

An estimate of net carbon (C) pool changes and long term C sequestration in trees and soils was made at more than 100 Intensively Monitored forest plots (Level II plots) and scaled up to Europe based on data for more than 6000 forested plots in a systematic 16km x 16 km grid (level I plots). Carbon pool changes in trees at the Level II plots were based on repeated forest growth surveys At the level I plots, an estimate of the mean annual C pool changes was derived from stand age and available site quality characteristics. Carbon sequestration, being equal to the long term C pool changes accounting for CO_2 emissions due to harvest and forest fires, was assumed 33% of the overall C pool changes by growth. Carbon sequestration in the soil were based on calculated nitrogen (N) retention (N deposition minus net N uptake minus N leaching) rates in soils, multiplied by the C/N ratio of the forest soils, using measured data only (level II plots) or a combination of measurements and model calculations (Level I plots). Net C sequestration by forests in Europe (both trees and soil) was estimated at 0.117 Gton.yr^{-1}, with the C sequestration in stem wood being approximately 4 times as high as the C sequestration in the soil. The European average impact of an additional N input on the net C sequestration is estimated at approximately 25 kg C per kg N for both tree wood and soil. The contribution of an average additional N deposition on European forests of 2.8 kg.ha^{-1}.yr^{-1} in the period 1960-200 is estimated at 0.0118 Gton.yr^{-1}, being equal to 10% of the net C sequestration in both trees and soil in that period (0.117 Gton.yr^{-1}). The result of this study implies that the impact of forest management on tree growth is most important in explaining the C pool changes in European forests.

Modelling impacts of changes in nitrogen deposition, climate change and carbon dioxide concentration on the forest growth and carbon sequestration of European forests (Chapter 8)

As described in Chapter 6, the process based model chain SMART2-SUMO-WATBAL was applied to 166 intensive monitoring forest plots of mid and high latitude Europe to evaluate the effects of expected future changes in carbon dioxide concentration, temperature, precipitation and nitrogen deposition on forest growth (net annual increment. These results were used in the large scale forest scenario model EFISCEN (European Forest Information SCENario model) to upscale impacts of environmental change and to combine these results with adapted forest management. Because of the few plots available, Mediterranean countries were excluded from the analyses. Results are presented for 23 European countries, representing 109 million hectares of forests. We predict significant impacts of environmental change on mid and high latitude European forests. Under a no climate change scenario, an increased fellings scenario caused an increase in fellings from approximately 3.8 - 5.3 $m^3.ha^{-1}.yr^{-1}$ from in 2000 to 2010, to reach a stable growing stock volume between 170 and 180 $m^3.ha^{-1}$. Climate change increased this possibility to 90% (from 3.8 to 7.2 $m^3.ha^{-1}.yr^{-1}$). The growing stock in 2100 increased to 279 $m^3.ha^{-1}$ under base felling level, but under environmental change, the rise was up to 381 $m^3.ha^{-1}$ in 2100. The average carbon stock of whole tree biomass was 72 $Mg.ha^{-1}$ carbon in 2005 and it increased to a predicted 104 $Mg.ha^{-1}$ carbon in 2100 under base fellings, but environmental change enhanced the build up of carbon stocks to up to 143 $Mg.ha^{-1}$. An average 35-40% higher increment is thus foreseen for 2100 compared to a no environmental change scenario. The largest relative growth rate change is foreseen for the Nordic countries, with up to 75% growth increase.

The impact of nitrogen deposition on carbon sequestration by terrestrial ecosystems (Chapter 9)
In this study, we present estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in forests, heathlands and moorlands, based on: (i) empirical relationships between measured NEP and nitrogen deposition in the field, accounting for other influencing factors, (ii) results of 15N experimental data on the fate of N, combined with C/N ratios in forest ecosystem compartments, (iii) results of long-term (15-30 year) low dose N fertilizer experiments on the C pool in biomass and soil and (iv) model simulations predicting carbon response to environmental change including N deposition. The results of the various studies are all well in agreement and show that the range in above ground accumulation of carbon in forests is generally within 15-30 kg C/kg N. For heathlands and moorlands, values are lower. A range of 5-15 kg C/kg N has been observed based on low dose N fertilizer experiments. The uncertainty in carbon sequestration per kg nitrogen addition in soils is larger than for above ground biomass and varies on average between 5-35 kg C/kg N. All data together indicate a total carbon sequestration that on average is below 50 kg C per kg N deposition.

One of the major results of the complete study described in this report is the relatively large present impact of N deposition on carbon sequestration in European forest ecosystems and the predicted much larger impact of climate change and change in CO_2 concentration in the future.

Empirical modelling at the Intensive monitoring plots

1 The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical stand growth model

Abstract

Forest growth in Europe has increased. Data from Intensive Monitoring Plots for a five years period were the basis to examine the influence of environmental factors on forest growth. Evaluations focussed on the influence of nitrogen, sulphur and acid deposition, temperatures, precipitation and on a drought index calculated as deviation from the long-term mean. The study included the main tree species Norway spruce, Scots pine, common beech as well as European and sessile oak and was based on data from 363 plots.

As many other factors besides nitrogen and temperature influence tree growth, expected growth was modelled using site productivity, stand age and a stand density index. Relative tree growth was then calculated as actual growth in % of expected growth. The site productivity, assumed to be given by site conditions and past environmental conditions, was either taken from expert estimates or computed from site index curves from Northern, central and Southern Europe. The model explained between 18% and 39% of the variance with site productivity being positively related and age negatively related to actual growth.

The various models and statistical approaches were fairly consistent, and indicated a fertilizing effect of nitrogen deposition, with one percent increase in site productivity per kg of nitrogen deposition per ha and year. This was most clear for spruce and pine, and most pronounced for plots having soil C/N ratios above 25. Also, we found a positive relationship between relative growth and summer temperature, i.e. May-August mean temperature deviation from the 1961-1990 means. The cause-effect relationship here is however, less certain. Other influences were uncertain. Possibly, sulphur and acid deposition have effects on growth, but these effects are obscured by, and outweighed by the positive effect of nitrogen deposition, because of co-linearity between these variables. Drought effects were uncertain also, and one reason for this might be large uncertainties in the precipitation data: Precipitation measured on some 50% of the plots correlated poorly with the precipitation data obtained from European wide databases. The major finding of this study was a positive relationship between higher than normal volume growth on one hand and nitrogen deposition on the other hand. The average estimated growth increase per kg of N deposition was estimated to correspond with an increase between 33 and 49 kg wood per year or 16-25 kg C per kg N.

1.1 Introduction

1.1.1 Environmental changes and forest growth

Forest growth is, in addition to its economical relevance, an important indicator of forest condition and is often used to study the effect of environmental changes, such as air pollution and climate change (Waring, 1987; Dobbertin, 2005). It can thus be considered as an early warning indicator for long-term forest vitality changes. Forest growth is also a prerequisite for carbon sequestration and influences indirectly e.g. the biodiversity or the quality of water percolating into ground water resources. The emission of sulphur dioxide and oxidized nitrogen compounds has increased massively after 1945 with a peak in emissions near 1965 for SO_2 and near 1980 for NO_x. In the 1980s, scenarios of a general decline in forest growth in Europe due to these increased pollutants were pictured (Ulrich et al., 1979). However, these scenarios of a general tree decline have not materialized, possibly due to successful efforts in emission reduction. On the contrary, many reports of increased growth of forest stands were published since the early 1990s (Pretzsch, 1992; Spiecker et al., 1996; Boisvenue & Running, 2006).

In an EU-wide study, Spiecker et al. (1996) found growth increases for the Central European countries, while the studies on growth in the Nordic countries were not conclusive. The number of reported studies was limited, and the studies contained a number of uncertainties such as the role of past management. Recently, Boisvenue and Runnings (2006) reviewed the evidence for the effect of climate change on natural forests since the middle of the last century and found in three out of four studies increased forest productivity and in only 10% recent decline in productivity.

Increased net primary productivity has been hypothesized to be due to increases in atmospheric CO_2 concentrations (e.g. Melillo et al., 1993), nitrogen deposition (Nadelhoffer et al., 1999b) and temperature, increasing the growing season (e.g. Myneni et al., 1997; Hasenauer et al., 1999; Menzel & Fabian, 1999; Linderholm, 2006) and change in management, such as litter raking, thinning type, genetic selection (Spiecker et al., 1996). Using a modelling approach, temperature has been claimed to be relatively unimportant, whereas the combination of CO_2 rise and elevated N deposition may account for a 15-20% increase in forest net primary productivity (Rehfuess et al., 1999). In this context, N deposition is claimed to be most important.

A recent EU-project (RECOGNITION) specifically analyzed the possible causes of growth increases in Europe. It included the analysis of control plots in former fertilizer trials, a retrospective analysis of height increment on selected ICP-Forests level II sites (Kahle et al., 2005) and a process-based modelling approach using selected intensive monitoring sites for calibration and validation (Karjalainen et al., in press). The study found increased height growth of Scots pine, Norway spruce and common beech of around 25% as compared to 40 years ago (Kahle et al., 2005). It concluded that nitrogen deposition is the main cause of the observed height growth increase (Karjalainen et al., in press). The number of sites used in the project was, however, limited as it ranged in the three studies between 9 and 28 sites per species.

1.1.2 Objectives

The present study aims to supplement earlier studies on the impacts of environmental changes on a limited number of plots by statistically evaluating measured stand based forest growth rates versus causal agents using data gathered in the "Pan- European Programme for Intensive and Continuous Monitoring of Forest Ecosystems". These data are gathered within the context of the European Scheme on the Protection of Forests against Atmospheric Pollution (EC) and the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests of UN-ECE).

In this study, we distinguish between stand growth determined by long-term site conditions, such as stand age and stand density, and stand growth influenced by recent changes in environmental conditions, such as anthropogenic depositions or climatic conditions. Site conditions are reflected in the past growth of the stands and can be substituted by site productivity, i.e. top height at a given stand age. We hypothesized that growth may deviate from the long-term expected growth due to four factors that vary geographically over the study area:

- Nitrogen deposition: current and historic N depositions are expected to gradually increase site productivity, but negative impacts have also been hypothesized;
- Soil acidification: soil acidification that depends on the current and historic acid deposition and on local soil conditions, may reduce forest growth due to root damage or to nutrient deficiency caused by caused by aluminium toxicity;
- Water availability: changes in water availability during the growing period which mainly depends on precipitation and on soil water storage capacity can substantially influence tree growth, due to drought stress;
- Temperature: increased temperature during the growing period may increase the growing period and thus growth in cold temperate regions, while in dry regions it may increase drought problems and cause reduced growth.

The key dependent variable in this study is relative growth, defined as actual growth in percent of the modelled expected growth. Expected growth is a measure of what growth rate is to be expected at each site, given the site and stand variables, without the effects of recent decades' (anthropogenic) influences. The expected growth values should reflect the long term growth potential, predating the period of eventual anthropogenic influences such as S and N deposition. Relative growth values that deviate from 100% will reflect either gradual change in site productivity or temporal deviations in growth caused by disturbances such as weather events.

1.2 Materials and methods

1.2.1 The Intensive forest monitoring database

The intensive monitoring plots were formally established since 1985, - and most data are gathered after 1994. In the period 1996 to 2003, Alterra, as a subcontractor of the EU has been responsible for the database activities (e.g. De Vries et al., 2003b). At this moment 863 permanent observation plots for Intensive Monitoring of forest ecosystems have been selected in 30 participating countries spread all over Europe. All plots are subjectively selected by each country, in order to represent typical forest types and growing conditions. The plots are typically designed as a 0.25 ha homogenous and rectangular area, which comprises one or more sub-plots for various monitoring activities. The selection of stands and the design of the plots vary from country to country. The comparability of results across countries is generally ensured by harmonized monitoring methods described in detail in manuals developed by international expert panels within ICP-Forests (Dobbertin, 2004), and by careful data handling, as further described below. The "core" activities are the assessment of tree crown condition, tree increment and the chemical composition of foliage and soil on all plots. Additional measurements on a sub-sample of the plots include atmospheric deposition, meteorological variables, soil solution chemistry and ground vegetation. The level-II database includes data from: (i) mandatory surveys on a 1-10 yearly basis, carried out at all plots (crown condition, at least once a year; chemical composition of needles and leaves, at least every 2 years; soil chemistry, every 10 years; increment, every 5 years) and (ii) optional surveys on a daily to biweekly basis, carried out on a subset of plots (atmospheric deposition, soil solution chemistry and meteorology). Data from two increment surveys for 654 plots were available for this study, mainly in the period 1995-2000. As growth variable we use stem volume growth per year and per ground area unit.

1.2.2 Forest data preparation

In this study we tried to avoid as far as possible country specific methods, which could lead to artefacts, i.e. "country effects". Hence, we calculated single tree volume functions, site productivity curves and site index values, using the same methods across all countries. Although the data came from a database on which many data quality checking procedures had been carried out, careful and considerable work was needed to obtain reliable growth data. It is evident that when many partners (countries) contribute to a database like this, there will easily be some variations in how data are submitted and how the partners have understood the manual for field measurements or data submission. The various data checking procedures are described in more detail below.

Plot selection

From a total number of 657 available plots in the database, we selected 363 (Table 1.1, Figure 1.1), after excluding plots from the study for various reasons. In order to have a large number of plots for each species, we selected plots where the main tree species were Norway spruce (132 plots); Scots pine (130); Common beech (65); and finally combined two similar oak species, Sessile oak (22) and Common oak (14). The number of oak plots is very low and has thus a low statistical power. The numbers of plots given here are the final counts after all exclusions as follows: We excluded 108 plots with other main tree species. Also, we required that the main tree species of the plot should comprise at least 70% of the basal area, and 43 plots were excluded for this reason. The rationale for this is that we will compare actual growth to expected growth derived from site index curves for pure stands. We also discarded plots when they were too young for the analyses, i.e. if they were reported to be in age classes 1 and 2 that is below 40 years (65 plots). This is important as we here apply an estimate of site productivity, which as far as possible should be based on each site's growth prior to the major anthropogenic influences. Hence, the trees on these plots should have a considerable fraction of their lifetime predating major deposition of N and S, and major changes in climate (Figure 1.2). Also, plots were discarded if they were classified as having irregular age (32 plots). A few plots (13) were excluded because they had been fertilized. We mandated that the growth period should be at least three years, and 12 plots were excluded as having less (see below). Finally, 27 plots were excluded for other reasons, such as missing tree diameter or height information; or obvious severe data errors. A number of plots were excluded for more than one reason, leading to a total number of 209 excluded plots. We can add here that we initially deleted 84 plots, that were no longer considered as level II plots, and which had not complete data. The final number of tree diameter measurements was 133,084, i.e. an average of 183 diameter measurements per plot and year.

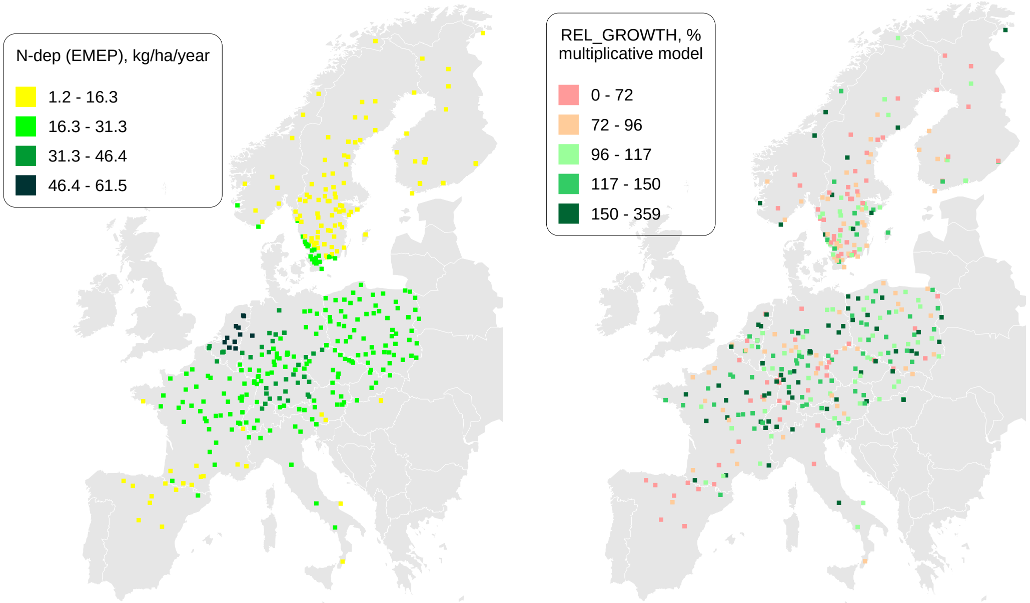

Figure 1.1 Nitrogen deposition and relative growth of the plots (class mid-point values alternative).

Table 1.1 The selected 363 Intensive Monitoring plots used in the study

Country	Spruce	Pine	Beech	Oak	Total
Austria	12		2	1	15
Belgium		2	4	1	7
Czech Republic	8				8
Finland	9	8			17
France	5	10	16	20	51
Germany	28	12	17	5	62
Hungary			1	1	2
Italy	3		7		10
Luxemburg			2		2
Norway	13	1			14
Poland	10	52			62
Slovak Republic	1		1	1	3
Spain		5	2	2	9
Sweden	42	35	9	2	88
Switzerland	1	1	4		6
The Netherlands		4		3	7
Total	132	130	65	36	363

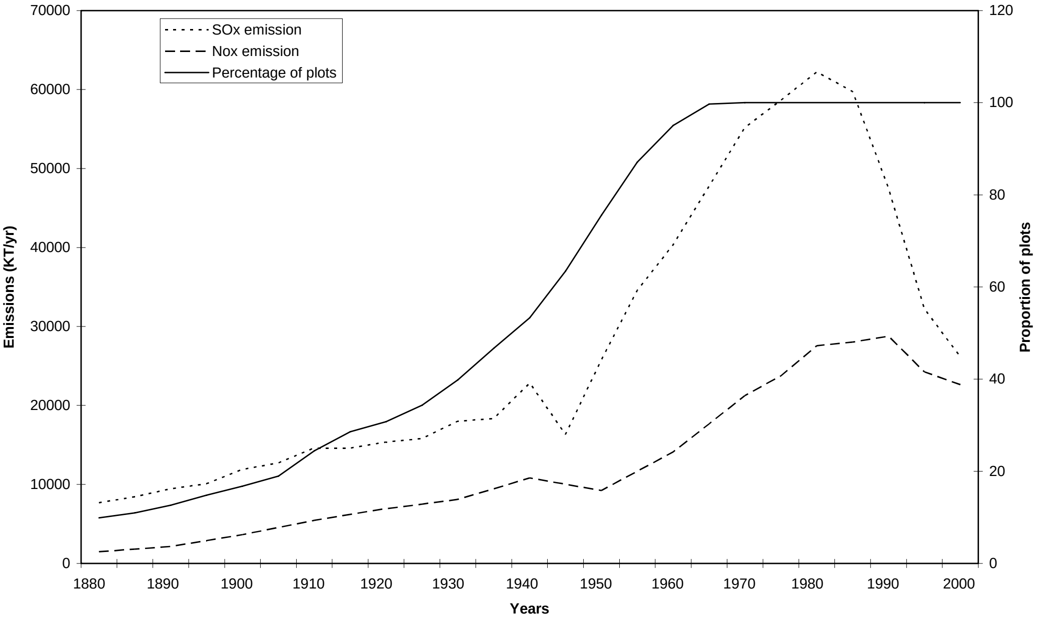

Figure 1.2 Trend in SO_X and NO_X emissions and cumulative proportion of established plots. Emission data from Schöpp et al. (2003a).

Plot size and corresponding tree numbers

We applied a thorough data checking procedure to ensure that the trees with growth measurements corresponded to the correct plot area. Using so-called Data accompanying reports ("DAR-Q forms") and plausibility checks we identified problems and obtained in some cases correct information directly from the responsible scientists. We came across a number of peculiarities, such as renumbering of trees between the two points of time.

In one country the observations were not assigned to tree numbers. In this case we developed an automatic routine for assigning the observations to arbitrary tree numbers, which allowed us to match measurements at the two points of time. First, for each plot all observations were sorted by tree species and diameter. If the number of trees were equal for the two points of time, the observations were matched by increasing diameter. In the case that the number of trees was higher at the first point of time, a number of trees were selected as lost trees. If a tree diameter at the first point of time was larger than the largest diameters at the second point of time (minus a 0.5 cm as a tolerance against random measurement errors), then these trees were labelled as lost trees. If none of the trees at the first point of time were larger, then trees marked as lost trees were selected evenly along the rank of diameters. It was vice versa for ingrowth trees, or any other new tree.

Growing period

For each plot the number of growing seasons was determined based on the dates of the measurements. All measurements were assigned to a measurement year, depending on the date of measurements, and each plot got by this a growth period in years. Almost all measurements were done outside the main growing season. Of a total of 726 dates of measurements, only six dates were in the period June 1 - August 1. For these six dates a fraction of a year was added or subtracted, based on the assumption that diameter growth is increasing linearly in the growing season. A majority of the plots (210) had at least five growing seasons, with a maximum of eight.

Correcting for diameter measurement devices

There are systematic differences between callipers and circumference bands, and both devices have been used. Based on the information about the tools used, as reported from the countries ("DAR-Q" forms), we found that at almost all plots the same method had been used at both measurements' points of time. Only on a few plots, different devices had been used. Here, calliper was used at the first point of time and circumference bands at the second time. For the tree species in question here (spruce) we made a correction of the diameter measurements at the second time by reducing the diameter values with 1.87%, based on measurements of 12,930 spruce trees (Bjørn Tveite, pers. comm.).

1.2.3 Estimating actual growth

Estimating tree volumes

We calculated actual volume increment based on diameter and height measurements on all trees within a plot of known area. Height was measured in 31% of the cases. First, we obtained the volume of these trees using the volume functions described in De Vries et al. (2003a) having diameter at breast height and tree height as input variables, as well as tree species and geographical location. These functions were elaborated within an EU-project on the basis of available functions in the literature, and reflect different form functions in different regions of Europe. Second, we used these trees to derive plot specific regression models of volume against basal area, which are known to be straight linear relationships. We derived these regression models using all available data, i.e. commonly for both years instead of regression models for each year. The advantages are that the random errors of the parameter estimates are smaller because the number of observations used is doubled and for 12% of the plots we had height data at one point in time only. More important; any systematic errors on the height measurements between the two points of time, due to changing field crews; changing measurement devices; or top breakage of trees during the years of our growing period, do not influence the estimates of volume growth. The average R^2 value in these 363 regressions were $R^2 = 0.97$. The volumes of all trees were estimated from these plot specific regression models, having the basal areas of all trees as input.

Many plots had a mix of tree species, i.e. up to 30% of the basal area for species other than the main species. Although we estimated the volume of all trees with height measurements taking into account each tree species, we did not distinguish between species for the estimation of tree volumes for trees without heights. This means, we estimated a plot specific regression to be used across species.

Removed trees and ingrowth trees

The volume growth of lost (removed) and new (ingrowth) trees was estimated from plot specific, linear regressions of volumes at the second point of time against volumes at the first point of time using trees that had diameter measurements at both points of time On average the R^2 value of these plot-specific regression models was 0.98. Lost trees are here trees with measurements only at the first point of time. The cause of this may be thinning operations; or eventually they were for some reason not measured at the second point of time. For these trees we firstly identified the most likely year of disappearance, and estimated their volume at this point of time. We set up a routine that searched the annual crown assessment files to find the last year where this tree was standing and alive. If eventually no crown assessments were available for the tree we set the last live year to be in the middle of the 5-year period. The volume of the tree at the point of time of its disappearance was estimated from the volume regressions, producing a growth value being a fraction of what the volume growth would have been if the tree had been alive throughout the growing period. The same procedure was used vice-versa for trees having a diameter measurement only at the end of the growing period. These are most likely small ingrowth trees, however, also trees that for some reason were not measured at the first point of time. The volume of these trees was estimated, using the same regression models as mentioned above.

1.2.4 Estimating expected growth

Here we calculated expected growth values by parameterizing volume growth models as a function of site productivity, stand age at breast height and stand density. The idea here is that expected growth should as far as possible represent growth rates (i.e. site productivity) before the major anthropogenic influences in recent decades. We computed several alternatives in order to obtain more robust results as we expected considerable residual variation. Hence, we calculated four alternative values of expected growth for each plot (Table 1.2). This was first done using country-reported class mid-point values for age and site productivity (Alternative 1), and second using accurate plot age and site productivity values from three different site productivity functions (alternatives 2a; 2b; 2c).

Table 1.2 Overview of four alternative model inputs for expected growth

Alternative	Site productivity	Age	Stand density
1	Yield class mid-point	Age-class mid-point	Reineke SDI
2a	Northern site index curves, input age and top height	Age	Reineke SDI
2b	Central site index curves, input age and top height	Age	Reineke SDI
2c	Southern site index curves, input age and top height	Age	Reineke SDI

Site productivity

The first step here was to obtain site productivity estimates for each plot. In alternative 1 we used the mid-point values of the yield classes as reported by the countries. These were class 1 (0.0-2.5 $m^3.ha^{-1}.yr^{-1}$, midpoint value: 1.59; class 2 (2.5-7.5 $m^3.ha^{-1}.yr^{-1}$, mid-point: 5.0); class 3 (7.5-12.5 $m^3.ha^{-1}.yr^{-1}$, mid-point:10.0); class 4 (17.5-22.5 $m^3.ha^{-1}.yr^{-1}$, mid-point: 20.0); and finally class 5 (>22.5 $m^3.ha^{-1}.yr^{-1}$, with the mid-point value used: 25.0).

However, a more sophisticated alternative was used in alternative 2. Here we derived a site productivity value from selected European site index curves, with input variables being age and top height. For each of our four tree species we selected three sets of site index curves: one from Northern Europe, one from central Europe, and one from Southern Europe (Table 1.3). Despite this geographical spread of the curve sets, we provided every plot with one site index value for each of these three curve sets (the alternatives 2a, 2b and 2c). The rationale here is that the various site index curves in Europe are largely influenced by random variations in the data used to obtain them, in addition to representing true geographical variations in growth. By selecting one northern, one central and one southern curve we ensure to make the results robust against random variations between the curves, and also to cover a range of different curves, over a gradient from northern, moist and cold climate to southern, dry and warm climate.

Table 1.3 Overview of selected sets of site index curves. For spruce, Germany (Assmann & Franz, 1963) we selected the alternatives: intermediate productivity level and optimal stand density. For spruce, Austria (Marschall, 1975) we selected the curves for the Weitra region.

Species	Region	Country	Reference
Spruce	Northern	Norway	Tveite and Braastad (1981)
	Central	Germany	Assmann and Franz (1963)
	Southern	Austria	Marschall (1975)
Pine	Northern	Sweden	Näslund (1947)
	Central	Austria	Marschall (1975)
	Southern	Spain	Madrigal *et al.* (1999)
Beech	Northern	Sweden	Hagberg and Matern (1975)
	Central	Switzerland	EAFV (1983)
	Southern	Spain	Madrigal et al. (1999)
Oak	Northern	Sweden	Hagberg and Matern (1975)
	Central	UK	Bradley et al. (1971)
	Southern	Spain	Barrio (2003)

We transformed the selected sets of site index curves into a two-dimensional raster of site productivity against age and top height with a 2-step modelling. First, we digitized points from published site index curves with high density and transformed these points into parameterized functions, and second, these functions were inter- and extrapolated into a raster. We defined the raster with age values from zero to 200 years (1 year resolution); with top height values from zero to 70m (0.1m resolution); and with site productivity values from 1 to 25 $m^3.ha^{-1}.yr^{-1}$ (Figure 1.3).

In the first step we used the following model (Schmidt, 1969):

$$HO = e^{a_0 + a_1 \ln age + a_2 \ln^2 age} \tag{1.1}$$

where *HO* is top height (m) and *age* is stand age at breast height given in years. The agreement between fitted and digitized site index curves was good to excellent, with model efficiency (Nash & Sutcliffe, 1970) exceeding 98% in all cases. The parameters a_0, a_1 and a_2 were estimated from a log-transformed version of the model, i.e. a second-order polynomial function. For observed growth curves, a_0 and a_2 are negative, whereas $a_1>0$. This model is suitable as it handles well two characteristic properties of site index curves, i.e. they are starting with age zero and at zero height, and contain an inflection point. A possible limitation of this function is that it exhibits a maximal height at age

$$age_{max} = e^{-\frac{a_1}{2a_2}} \tag{1.2}$$

contrary to site index curves, which are monotonically increasing and reach an asymptotic value at very high age. The maximum age in (Eq. 1.2) is, however, many hundreds to several thousand years for usual best fit parameter values. Only in cases where the observed height growth is already stagnant over many years, the maximum occurs at ages below 200 years. In these cases, extrapolation of the yield tables was limited to the age of maximum height. In addition, the function (Eq. 1.1) is suitable for extrapolation, which is needed because published curves in many cases do not cover the full range of productivities. The parameters were obtained by a nonlinear fit procedure (Levenberg-Marquardt method).

In the second step, we replaced site index codes with site productivity values, and smoothed this into a raster. In most site productivity curves we used, site index is given as an index value, such as a H_{100}. We replaced these index names to site productivity values in m^3.ha^{-1}.yr^{-1}. We obtained these site productivity values from tables associated with the curves, i.e. as mean annual production at the time when mean annual production culminates. We then interpolated and extrapolated these site productivity values. The relationship between height at a given age and productivity is very well reproduced by a quadratic polynomial. In some cases, the coefficient of the quadratic term was small while still being significant (i.e. an almost linear relationship). The obtained relationship has been used for interpolating to arbitrary productivities, and also to ascribe productivity to digitized curves where the conversion table was incomplete. Using the parametric fits, the height-productivity relation could then be used for any age. We tabulated the corresponding values within the raster given above. (Figure 1.3).

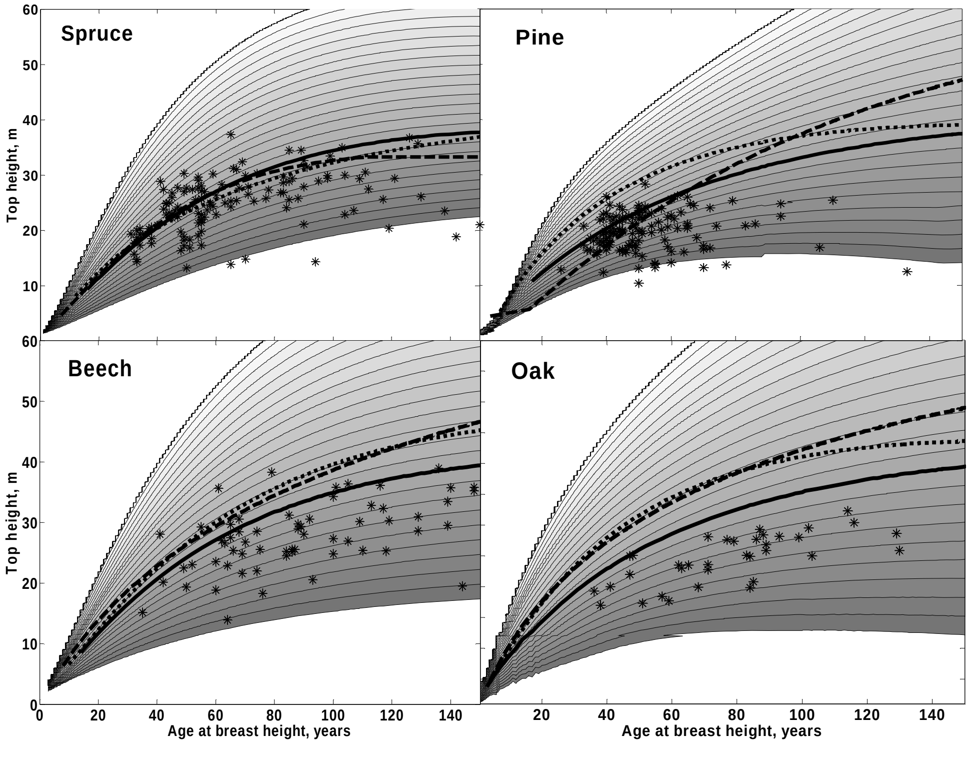

Figure 1.3 The interpolated set of central European site index curves. The greyscale indicates the site productivity level; thin black curves correspond to productivities from 1 to 25 m^3.ha^{-1}.yr^{-1} with a spacing of 1 m^3.ha^{-1}.yr^{-1}. Overlaid are northern curves (dotted lines) and southern curves (dashed lines), for the productivity level 10 m^3.ha^{-1}.yr^{-1}. The measured stands are indicated by asterisks.

Finally, some of the site index curves used total age at the ground as input variable, and we corrected these ages into breast height ages. The age corrections were derived from model (Eq. 1.1) by setting top height, *HO*, to 1.3 m, and they turned out to be varying from 6 to 15 years depending on site productivity.

With the input variables age and top height each plot obtained now a site productivity value from these site productivity rasters. For age, accurate assessments per plot were used (see below). Top height was estimated for each plot as the mean height of the 100 largest trees per hectare (by diameter) of the main tree species. Depending on the plot size and actually measured tree height the number of available top height trees varied. In some cases the number of trees with height measurements was fewer than four, and in those cases top height was set as the mean height of the three largest trees with height measurements. If no height data were available from the first point of time height measurements from the second point of time were used.

Age

In accordance with the assessment of site productivity in alternative 1, the plots were assigned to crude age classes, in which we used mid-point values of these classes. These were class 3 (41-60, mid-point 50); class 4 (61-80, mid-point 70); class 5 (81-100, mid-point 90); class 6 (101-120, mid-point 110); and finally class 7 (>120, and here we used the mid-point value 140).

In addition to stand age classes obtained from the database, we collated plot ages from each country for alternatives 2a-2c mostly by contacting the national experts. In a number of cases we found age data in national reports. Often we got age at the ground, or the year of establishment. We then subtracted around 10 years to get breast height age. The number of years to subtract was in some cases available from reports (e.g. Näslund, 1947). Plot ages were recalculated to age at breast height in 1995, i.e. at the beginning of the growing period.

Stand density

We employed Reineke's (1933) stand density index (SDI), later modified by Pretzsch and Biber (2005), defined as:

$$\mathrm{SDI} = \mathrm{N}*(25/\mathrm{D}_g)^b \qquad (1.3)]$$

where *SDI* is the modified Reineke's stand density index, *N* is the number of trees per ha, and D_g is the quadratic mean diameter at breast height, and *b* is an exponent depending on tree species being -1.664; -1.593; -1.789; and -1.424 for the tree species spruce, pine, beech and oak, respectively. This measure of stand density has the advantage for our study that it is a variable being orthogonal to age, contrary to other stand density measures.

Parameterizing expected growth functions

We used the present data to parameterize the volume growth functions, using a multiplicative model:

$$\mathrm{IV} = e^{\beta 0} * \mathrm{SITEPROD}^{\beta 1} * \mathrm{AGE}^{\beta 2} * \mathrm{SDI}^{\beta 3} \qquad (1.4)$$

where *IV* is mean annual volume increment ($m^3.ha^{-1}.yr^{-1}$); *SITEPROD* is a variable for site productivity ($m^3.ha^{-1}.yr^{-1}$), and *AGE* is stand age (yr). More details of the variables are given below. The parameters β_0 - β_3 were estimated using a log-transformed version of the model. Parameterizing the model on the data set itself implies that we can only detect relative variations in growth between plots. We can not detect eventual growth disturbances that have affected the entire European forest area in the same way. However, the relative residual of the model for a given plot and species reflects the impact of site-specific conditions as discussed below. From the functions each plot was provided with four alternative expected growth values, and then four alternative values for relative growth being the ratio between actual growth and expected growth. For the cases 2a-2c we also computed an average expected growth to average out possible differences between the three regional site index curves. Estimates from log-transformed models are known to have a bias when converted back to the non-logarithmic form. We corrected the obtained predicted growth values, using a fixed factor, λ, as described by Condes and Sterba (2005):

$$\lambda = \frac{\sum \mathrm{IV}_{\mathrm{observed}}}{\sum \mathrm{IV}_{\mathrm{predicted}}} \qquad (1.5)$$

As a consequence, the mean value of the model residuals vanish. In terms of relative growth, i.e. the ratio of estimated actual growth and predicted growth from Eq. (1.5), the average over all plots for a given species is 100%.

Correcting age for past suppression

In many cases the trees have suffered from suppression in their youth. In this case their age is higher than what the age would have been for trees of the same size when growing without suppression. Trees with earlier periods of suppression will lead to an underestimation of the site productivity. We used tree ring series from 49 plots in Norway and France, to estimate the difference between chronological age and physiological age. We compared the site productivity and expected growth estimations for these plots, in order to see how sensitive our methodological approach is to effects of past suppression.

The age correction was carried out using a method described in Tveite and Braastad (1981). Suppression turned out to have a very minor influence on the results. On the plots with age correction, the suppression period was on average 9% of the tree age at breast height, i.e. 8 years out of 87. The suppression period varied from 0 to 21% of the tree age. There was no clear difference between the tree species.The average suppression varied from 6 years for spruce up to 11 years for beech. The two age variables, chronological age and physiological age, were strongly correlated (r=0.99). Site productivity was calculated with the interpolated site index curves, as described above. Site productivity estimated with age correction was strongly correlated to site productivity estimated without age correction (r=0.99). The suppression caused an 8% underestimation of site productivity (on average), corresponding to 0.6 out of 7.1 $m^3.ha^{-1}.yr^{-1}$. We concluded to not carrying out any age correction due to suppression, firstly because the magnitude was small and secondly because the necessary data to do this were only available for a few plots.

1.2.5 Growth affecting factors

We selected one variable for each of the selected environmental factors assumed to influence growth, i.e. nitrogen deposition, acid or Sulphur deposition, summer drought, and summer temperature. For each variable we had at hand both measured data for some of the plots ('PLOT' data), as well as data from European wide data bases with estimated data for all plots ('GRID' data). For each of the variables we also defined a binary sensitivity variable, i.e. we made a sub-set of plots expected to being sensitive to the variable in question. The idea here is that a relationship between an environmental factor and forest growth should be clearer if we filter out plots that are sensitive to the actual type of stress. For example, in northern Norway forest growth is normally increased in a summer that is unusually dry, contrary to the response seen for most of Europe.

Nitrogen deposition

When applying the model to all 363 plots, nitrogen deposition was taken from the EMEP database, i.e. we used a 50 km x 50km grid averaged value for the period 1960-1990. The variable was defined as the sum of NH_4-N and NO_3-N, and given as kg per ha and year. For part of the plots (188) we also used plot measurements of total deposition of NH_4-N and NO_3-N for the period 1993-2000 as derived from both bulk deposition and throughfall, accounting for canopy exchange using a procedure described in De Vries et al. (2001). As sensitivity variable we used the C/N ratio in the organic layer. All plots with a C/N ratio above 25 were defined as the plots sensitive to N fertilizing effects.

Acid deposition

We used the variable *NETACID* as a variable describing the soil acidifying force of acid deposition. The variable was defined as

$$\mathrm{NETACID_{DEP}} = (\mathrm{SO_4} + \mathrm{NO_3} + \mathrm{NH_4} - \mathrm{Ca} - \mathrm{Mg} - \mathrm{K} - \mathrm{Na} + \mathrm{Cl})_{\mathrm{DEP}} \qquad (1.6)$$

where each variable is given as $keq.ha^{-1}.yr^{-1}$. As with N deposition, this variable was also directly taken from the EMEP grid data 1960-1990 (all 363 plots) and from bulk deposition and throughfall, accounting for canopy exchange, for part of the plots (188) for the period 1993-2000. The sensitive sub set of plots was here defined as plots with slow-weathering soils, i.e. soil types in the groups 1-4, being "haplic arenosols"; "other non calcareous arenosols"; "haplic podzols"; and finally "other podzols". These are soils with a low clay content, and are likely to be sensitive to acid deposition because of a slow weathering capacity and often a low base saturation. As another variable representing acid deposition we also used S deposition only, in $kg.ha^{-1}.yr^{-1}$.

Temperature and precipitation deviation

Here we used the deviation from long-term normal values. The variable used was mean temperature, and sum precipitation, for the months May to August for 1993-2000, deviating from the average 1961-90 values. As a sensitivity subset of plots that are likely to increase growth in response to increased temperature we used plots having a June mean temperature below 15°C. Andreassen et al. (2006) found in Norway that spruce plots with a 30-years' mean June temperature value below 12-13°C mostly reacted with increased growth when the summer weather was drier or warmer than normal, and vice versa. In our study very few sites, however, had mean June temperatures below 13°C, and in order to have a larger subset we set the sensitivity plots to those having a mean June temperature below 15°C. And using precipitation as a drought variable, we used the opposite criteria, i.e. plots having a mean June temperature above 15°C.

Relative drought

For drought stress we used a second variable describing drought given as values relative to the normal (30 years mean) drought stress at each site:

$$\text{Drought\_stress} = 100\% * \text{avg}(\text{PET}-\text{AET}) / \text{avg}(\text{PET\_norm}-\text{AET\_norm}) \qquad (1.7)$$

where PET and AET are potential evapotranspiration and actual evapotranspiration, respectively and PET_norm and AET_norm are 30 years average values (normals) derived for these variables (all in mm.yr^{-1}). PET and AET were derived from data in a 10'x10' grid from monthly temperature, precipitation, cloudiness, wind speed etc (Climatic research Unit dataset), using the WATBAL model (Starr, 1999)). In this model PET is calculated from the estimated global radiation and based on the relationship between air temperature and the ratio between evaporation and global radiation. The equation used is that by Jensen and Haise (1963); the so-called Alfalfa reference method, and is a further simplification of the Priestley-Taylor equation. It calculates the evaporative heat flux density, which is then converted into mm of PET using the latent heat of vaporization. A daily PET is calculated for the "representative day of the month" and then multiplied up to monthly values using the number of days in each month. A crop factor is used to convert this evapotranspiration to one for forests. AET is computed by comparing water supply and demand, taking into account water available in the soil profile.

PET and AET are averaged over the months May to August (assumed main growing season for stem growth) and over the years 1993-2000. The corresponding PET_norm and AET_norm are the 30 years average values from 1961-1990 using the same procedure as described for the the years 1993-2000. The precipitation data here is taken both from the European meteorological databases (grid), as well as from measurements at the plot. All temperature data from the grid were corrected for difference in elevation, using 0.6 degrees per 100 m. The sensitive subset of plots in the present study was set to plots having a mean June temperature above 15°C.

Measured versus modelled data for explanatory variables

The number of plots with plot measurements of meteorological data and deposition data was 245 and 187, respectively, out of the total 363 plots. For the deposition data there was a satisfactory correlation between the PLOT and the GRID data, with correlation coefficients ranging from 0.65 to 0.75. For the meteorological data the situation was less satisfactory: the correlations between PLOT and GRID were weaker or absent, and the 30-years long-term means were not available. While the agreement between PLOT and GRID data was high for precipitation, there was basically no agreement between PLOT and GRID data for the explanatory variable used: the precipitation and drought stress given as deviation from its long term mean value. For temperature no measured plot data were available. On this basis we decided to use both GRID and PLOT data in the analyses, and compare the results.

Statistical analyses

The statistical models were as follows, for simple regressions (Eq. 1.8) and the multivariate analysis-of-covariance (Eq. 1.10):

$$RG = \beta_0 + \beta_1 X_i + e \tag{1.8}$$

Where *RG* is relative growth (%) as defined after Eq. (1.5); β_0 is the intercept; β_1 is the slope; Xi is an explanatory variable, including N_{DEP}, $NETACID_{DEP}$, drought stress and temperature stress (deviations from the 1961-1990 normals) and e is the residual error. For the analysis of co-variance we initially started with the model:

$$RG = \beta_0 + \beta_{1i} + \beta_{2j} + (\beta_3 + \beta_{4i} + \beta_{5j} + \beta_{6ij})\, N_{DEP} + e \tag{1.9}$$

where $\beta_{0,}\, \beta_{1i}$, and β_{2j} are intercepts; and $\beta_3 .. \beta_6$ are slope parameters for the main effect of N deposition; including first- and second-order interactions between N deposition and the factors tree species (i=1,..,4) and sensitivity to N deposition (j=1,2). This analysis of co-variance model was done in a backward stepwise way, where the model was reduced step-by-step by removing non-significant effects. The tests applied here were sequential (Type I) F-tests. We applied equations similar to (Eq. 1.8) and (1.9) for each of the explanatory variables individually.

In a final approach we did an alternative one-step approach, where actual growth was regressed against both the site and stand factors, and the growth affecting factors simultaneously:

$$\ln(IV) = \beta_0 + \sum_i \beta_i^* X_i + e \tag{1.10}$$

where *IV* is mean annual volume increment ($m^3.ha^{-1}.yr^{-1}$). We log-transformed this into *ln(IV)* as the dependant variable in order to mitigate the problem with increasing residual variance with increasing growth values (heteroscedasticity). The other parameters are β_0 which is an intercept and β_i which are slope parameters for the explanatory variables being the site and stand factors (site productivity, stand density, age) and the environmental variable (deposition and meteorological variables).

1.3 Results

The approach for producing expected growth values was fairly successful in the sense that the parameters were mostly meaningful. Site productivity was the variable that most strongly and consistently explained growth, with fairly stable estimates across model alternatives and mostly highly significant (Table 1.4). For age, in most cases the parameter estimates were negative, as expected. However, except for pine, the effect of stand age was generally not significant. Stand density turned out to have little influence upon expected growth, with variable signs and mostly not significant. SDI was positively related in pine and spruce and negatively in beech and oak, but again, parameter estimates were often not significant. This may be due to more open pine and spruce sites at higher latitude. However, we kept all the three parameters in the models regardless of their statistical significance. The R^2-values obtained were between 18 and 40%, which is reasonably high considering that we use a European-wide data base. Many other factors have a large impact on forest growth, such as the later tested factors, but also, for example, insect caused tree defoliation. Models using the class values for site productivity had generally lower R^2 values than the models based on the more advanced alternatives with estimated site productivity from site index curves.

Table 1.4 Parameter estimates of estimated growth functions of the form $IV = e^{\beta 0} * SITEPROD^{\beta 1} * AGE^{\beta 2} * SDI^{\beta 3}$. *The* R^2 *value refers to the log-transformed version of the model. N is the number of observations. The results of the hypothesis testing of the effects are based on partial F-tests (type III tests), and are indicated with* $p<0.001$ *(***);* $p<0.01$ *(**);* $p<0.05$ *(*)*

Species	Alt		SITEPROD	AGE	SDI	N	R^2
		β_0	β_1	β_2	β_3		
Spruce	1 Class values	1.34	.61***	-0.27	.10	126	.20
	2a Northern SI	-1.45	.81***	-.27*	.11	131	.39
	2b Central SI	-.42	.41***	-.21	.13	127	.27
	2c Southern SI	-.39	.80***	.10	.07	127	.40
Pine	1 Class values	4.02	.22	-1.11***	.29**	123	.24
	2a Northern SI	2.41	.40**	-.59**	.14	130	.25
	2b Central SI	2.82	.27***	-.58**	.11	129	.28
	2c Southern SI	-1.11	.86***	.01	.14	130	.32
Beech	1 Class values	3.41	.43*	-.32	-.14	60	.19
	2a Northern SI	1.26	.86***	-.01	-.15*	65	.30
	2b Central SI	1.83	.67***	-.07	-.15*	65	.30
	2c Southern SI	.83	.88***	.10	-.17*	65	.30
Oak	1 Class values	4.94	.44	-0.69*	-.11	31	.24
	2a Northern SI	2.11	.94	-.11	-.24	36	.19
	2b Central SI	2.39	.76	-.14	-.24	36	.18
	2c Southern SI	.01	1.41*	.16	-.23	36	.23

An overview of the obtained data set and the site description variables is given in Table 1.5, while statistics for the explanatory variables for each species are given in Table 1.6.

Table 1.5 Overview of the obtained data set on growth: average and min-max. Here, all four site productivity alternatives are taken together.

Species	Actual growth (m^3.ha^{-1}.yr^{-1})	Expected growth (m^3.ha^{-1}.yr^{-1})	Relative growth, %	Site Prod (m^3.ha^{-1}.yr^{-1})	Age 1995 (yr)	SDI	HO (m)
Spruce	9.6	8.8	111	8.6	70	863	25
	0.0-28.0	1.3-15.6	0 – 418	0.5-16.7	31-186	133-1860	13-37
Pine	6.3	5.8	112	7.5	52	653	20
	0.8-13.8	0.9-9.3	19-363	0.5-14.0	26-133	87-1497	10-28
Beech	7.6	7.1	109	7.2	92	659	28
	1.6-22.8	2.7-12.0	21-301	2.2-13.6	35-161	58-2123	14-39
Oak	7.9	7.4	112	6.3	80	361	25
	0.5-14.1	3.5-14.8	12-221	3.8-8.8	36-180	59-1329	17-32

The results show an average growth increase of 9-12% (Table 1.5) at an average annual N deposition between approximately 20-25 kg N.ha^{-1}.yr^{-1} and an average temperature deviation between 0.5-1.0 °C and a relative increase in drought stress of 3-20 % (Table 1.6).

For all data sets N, S and acidic deposition were highly correlated with each other (Pearson's correlation coefficient ranged between 0.82 between S and N deposition and 0.99 between S and acidic deposition). N, S and acidic deposition increased from plots at low latitude up to approximate 52° northern latitude and then decreased again towards the most northern sites. Temperature deviation for May-August during 1993-2003 was in most cases positive and ranged between -0.4°C and 1.5°C. Temperature deviation showed a strong north-south gradient with highest positive deviation in the south and lowest in the north. For pine and spruce with its large number of plots in Scandinavia and Finland deposition and temperature deviation correlated therefore positively, while for beech no or slightly negative correlation were observed. Interestingly, drought and temperature deviation showed only small correlation (mostly below 0.5)

Table 1.6 Descriptive statistics for explanatory variables: average and min-max

Species	Nitrogen deposition (kg.ha^{-1}.yr^{-1})	Sulphur deposition (kg.ha^{-1}.yr^{-1})	Net Acid deposition (keq.ha^{-1}.yr^{-1})	Drought (%)	Δtemp (°C)
Spruce	18.7	32.5	3145	114	0.56
	1.7-39.2	2-129.7	179-10181	0-1275	-0.2-1.42
Pine	19.1	36.2	3413	120	0.49
	1.2-61.5	3.6-138.6	312-11920	58-362	-0.36-1.28
Beech	24.8	43.3	4142	103	0.94
	7.8-51.1	10.1-131.0	392-11311	17-199	0.15-1.40
Oak	24.4	38.9	3872	103	1.03
	9.9-54.4	16.3-132.8	1484-11932	57-199	0.13-1.46

Simple regressions

The simple regression analyses suggest a fertilizing effect of nitrogen deposition, i.e. a growth increase, for spruce and pine, while for beech and oak the results were less clear (Table 1.7). For spruce and pine this result was very consistent for the various model alternatives used. The N deposition variable modelled from EMEP (larger data set) had with one exception positive slopes and was for pine and spruce mostly significant with slopes around 1. This slope means that 1kg of nitrogen deposition corresponds to one percent increase in growth. For oak, a slope near 1.4% was found when using the grid data and neglecting the class values. N deposition measured on the plot had similar but lower slopes for spruce, pine and oak, and due to less available data the percentage growth change was less often significant. For beech, there was a consistent different sign between the use of modelled (grid) and measured (plot) N deposition data and the same was true for S deposition, but the signs were generally insignificant. S deposition and acidic deposition both had mostly positive slopes (significant for pine models). However, as said above, these two explanatory variables were highly correlated to nitrogen deposition.

Table 1.7 Overview of results of simple regression analyses for the four tree species and various alternatives for site index and age variables. The columns represent explanatory variables derived from official large-scale databases ("grid": EMEP and WMO), and as measured at the plots. Note that no temperature data were available from the plots. Bold face indicates statistical significance at the p <0.05 level. The values denote the percentage change in growth per kg N dep, per kg S dep, per keq acid dep, per mm.yr^{-1} *precipitation, per* ^{o}*C temperature change and per percent drought stress change*

Species	N dep.		S dep.		Net acid dep.		Prec. dev.		Temp. dev.	Drought dev.	
	grid		plot		grid		plot		grid	plot	
Spruce											
1 Class values	**2.02**	**1.48**	**0.51**	**0.78**	**0.01**	**0.01**	0.13	**-0.20**	**42**	**-0.23**	**0.13**
2a Northern SI	0.74	**0.43**	0.13	**0.01**	0.00	**0.00**	0.12	**-0.09**	**20**	0.02	**-0.14**
2b Central SI	0.84	0.46	0.13	-0.02	0.00	0.00	0.24	-0.22	**24**	**-0.18**	-0.14
2c Southern SI	**0.94**	**0.65**	0.23	0.35	0.00	**0.00**	0.06	-0.16	**22**	-0.01	-0.01
Pine											
1 Class values	**1.06**	0.47	**0.46**	0.59	**0.01**	0.01	0.14	0.54	**36**	**-0.23**	0.08
2a Northern SI	**1.15**	0.80	**0.45**	0.71	**0.01**	0.01	-0.07	0.63	**35**	**-0.26**	-0.06
2b Central SI	**0.92**	0.54	**0.39**	0.32	**0.00**	0.01	0.03	0.71	**24**	**-0.19**	-0.24
2c Southern SI	**1.02**	0.83	**0.40**	0.62	**0.00**	0.01	-0.05	**0.63**	**29**	**-0.17**	-0.20
Beech											
1 Class values	0.98	0.65	0.38	-0.91	0.00	0.02	-0.18	**0.36**	**38**	0.13	-0.33
2a Northern SI	0.29	-1.35	0.06	-0.98	0.00	0.00	0.03	**0.21**	28	-0.09	-0.02
2b Central SI	0.35	-1.28	0.07	-0.87	0.00	0.00	0.03	**0.20**	**29**	-0.09	-0.01
2c Southern SI	0.33	-1.33	0.08	-0.94	0.01	0.00	-0.01	**0.18**	28	-0.06	0.03
Oak											
1 Class values	-0.35	-2.87	-0.40	-1.50	0.00	0.02	-0.26	-0.53	-52	0.19	1.03
2a Northern SI	1.36	0.24	0.29	0.38	0.00	0.01	-0.38	0.42	-54	**0.50**	-0.18
2b Central SI	1.35	0.30	0.27	0.36	0.00	0.01	-0.38	0.38	-53	**0.49**	-0.13
2c Southern SI	**1.50**	0.13	0.34	0.43	0.01	0.01	-0.43	0.49	-56	**0.57**	-0.28

Signs for the parameter estimates for temperature deviation gave significant positive parameter estimates for pine and spruce and partially for beech, as expected, while oak had opposite estimates, but these estimates were not significant Estimates for drought were, as expected, generally negative for spruce pine and beech, but positive for oak, but here the estimates were less often significant (Table 1.7).

As *PLOT* and *GRID* deposition data showed correlation between 0.65 and 0.75 and the results were similar with more significant results for the larger data set we carried out all further analysis using the grid data only. However, we should be aware that correlation between modelled and measured precipitation was almost non-existent.

We repeated the analysis for sites considered to be either 'sensitive' for N deposition (high soil C/N ratio), for acidic deposition, temperature increase and drought. We used only the relative growth obtained from the site productivity classes, and the mean growth calculated as an average of all models based on estimated site index curves (Table 1.8). We restricted the analysis to data sets with at least 30 plots. Therefore mostly spruce and pine plots could be analyzed. On sites with high soil C/N ratios slopes were significant and steeper than when all sites had been considered. Even on sites regarded sensitive for acidic deposition no negative slopes were obtained. For sites assumed to be sensitive to increased temperature, i.e. having a normal June temperature below 15°C in the vegetation period, no clear tendencies were found. On sites sensitive to drought, i.e. having normal June temperatures above 15°C we found steeper negative slopes for the drought variable.

Table 1.8 Results of simple regression analyses with two alternatives for site index and age variables (1 class values, 2 mean site index curves and actual age) on all plots and sensitive plots only. The rows represent the tree species while the columns represent explanatory variables derived from official large-scale databases ("grid": EMEP and WMO). Only data sets with at least 30 plots were considered. Bold face indicates statistical significance at the $p < 0.05$ level. The values denote the percentage change in growth per kg N dep, per kg S dep, per keq acid dep, per °C temperature change and per percent drought stress change

Species	N dep.		S dep.		Net acid dep.		Temp. dev.		Drought dev.	
	all	sens	all	sens	all	sens	all	sens	all	sens
Spruce										
1 class values	**2.02**	**3.04**	**0.51**	**0.61**	**0.007**	**0.008**	**42**	**45**	**-0.25**	**-0.37**
2 site index	**0.94**	**1.28**	0.19	0.21	0.003	0.003	**24**	**26**	-0.01	**-0.26**
Pine										
1 class values	**1.06**	**1.23**	**0.45**	**0.35**	**0.005**	**0.004**	**36**	**39**	**-0.23**	-0.14
2 site index	**1.01**	**1.17**	**0.39**	**0.43**	**0.004**	**0.005**	**30**	**45**	**-0.19**	-0.12
Beech										
1 class values	0.99	-	0.38	-	0.004		**39**	25	0.13	-0.02
2 site index	0.52	-	0.13	-	0.001		28	17	-0.06	-0.07
Oak										
1 class values	-0.35	-	0.13	-	- 0.004		-53		0.19	
2 site index	**1.51**	-	-0.40	-	0.008		**-55**		**0.55**	**0.51**

Analysis of covariance

The analysis of covariance including one explaining variable and its first and second interaction with sensitivity and species significant relationships were found for N deposition and its interaction with the plot's sensitivity (C/N ratio) (Figure 1.4 and Table 1.9). The slopes were 1.85 and 0.14 for the sensitive and non-sensitive sites, respectively. No significant difference was found between tree species.

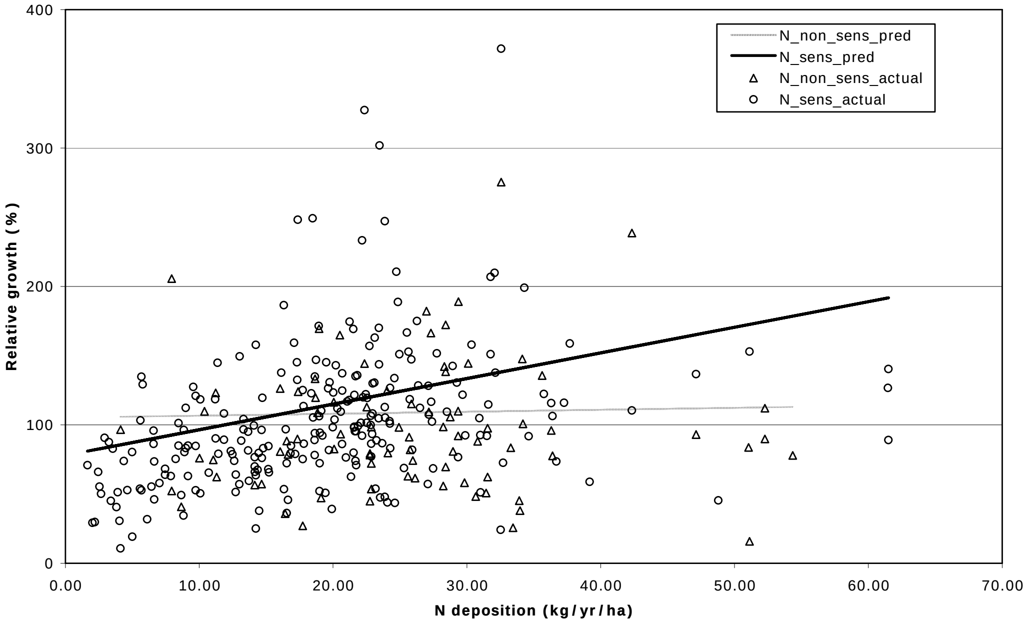

Figure 1.4 Relationships between nitrogen deposition and relative growth using the mean site index curve values. Regression lines represent the results of analyses of covariance (Table 1.9).

The covariance analyses for temperature deviation ended up with one common effect for all species, i.e. a common slope of 42, after the backward selection. This slope means that 1° increase in temperature corresponds to 42% increase in growth, which is unlikely to be a realistic parameter estimate for a temperature effect (see discussion). There was only a minor difference in intercepts between the species, which is an artefact from the type of analyses (Figure 1.5, Table 1.10).

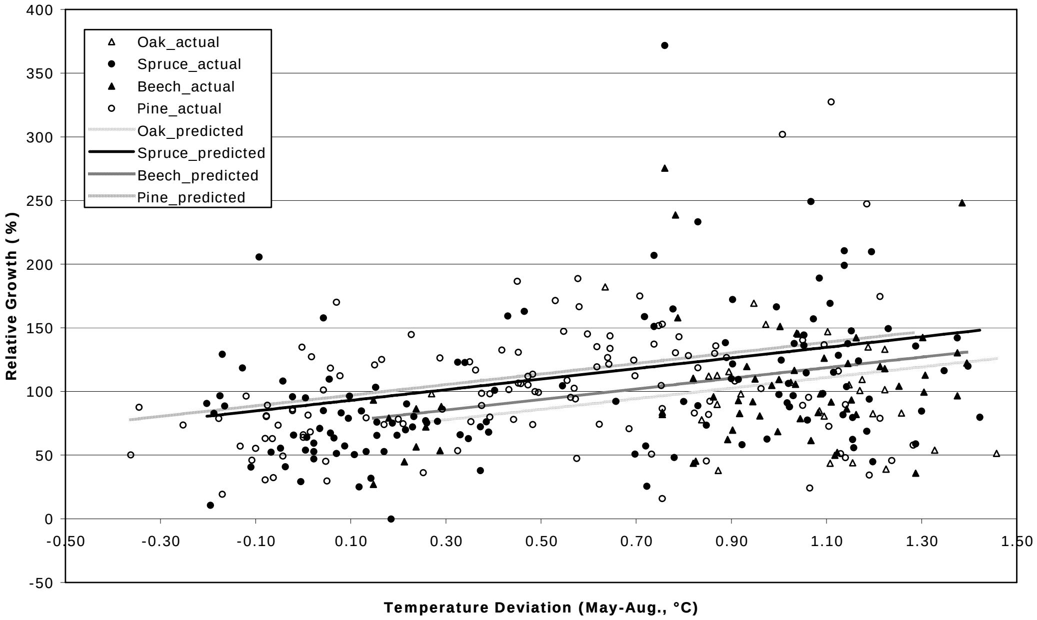

Figure 1.5 Relationships between relative growth and summer temperature deviation from the 1961-90 normal values. The regression lines represent the results of analyses of covariance (Table 1.10).

For drought, the covariance analyses gave less clear results. However, for sensitive sites (June temperature above 15°) of spruce and beech negative slopes were found, while for the non-sensitive sites no or positive slopes were found (Table 1.11).

Table 1.9 Analyses of variance for relationship between relative growth (alt 1, class mid-point) and N deposition (EMEP), and a co-variate being expected sensitivity to N deposition (C/N-ratio>25 in organic layer)

Source	DF	SS	MS	F	Pr > F
N_{DEP}	1	58726	58726	21.3	<.0001
sens_N	1	11262	11262	4.1	0.044
N_{DEP} * sens_N	1	19673	19673	7.1	0.008
Error	324	893353	2757		
Sum	327	983014			

Table 1.10 Analyses of variance for relationship between relative growth (alt 1, class mid-point) and temperature deviation from 30 years' normal value, May-August (WMO data) and tree species

Source	DF	SS	MS	F	Pr > F
ΔT	1	80445	80445	29.5	<.0001
species	3	25144	8381	3.1	0.028
Error	330	899844	2726		
Sum	334	1005433			

Table 1.11 Analyses of variance for relationship between relative growth (alt 1, class mid-point) and dryness (PET-AET) deviation from 30 years' normal value (ΔD), May-August (WMO data), as a second order interaction between ΔD and tree species and drought sensitivity

Source	DF	SS	MS	F	Pr > F
ΔD	1	35320	35320	12.1	0.0006
Error	333	970111	2913		
Corrected Total	334	1005433			

Multiple regression

Here we used actual growth and not relative growth values, i.e. we did a one-step modelling, as compared to the 2-step approaches above (Eq. 1.10). Having the log-transformed growth values, *ln(IV)*, as response variable we used a stepwise forward selection, followed by a stepwise backward selection procedure using the three site variables SDI, age, site productivity (either as class variable or the mean of the site index values) and using N deposition, temperature deviation and drought as explanatory variables (Table 1.12). The variables for S and acid deposition were discarded from the analyses because of their co-linearity with N deposition, as well as their inconsistent results in the simple regression analyses. Precipitation was also discarded due to its correlation with the drought variable. It turned out that most of the slope parameters got the sign as hypothesized: Age was frequently significant and always negative and site productivity when used positive. However, stand density got negative slope estimates.

When it comes to the environmental factors, the results became more complex: it was apparent that in the five years of investigation, N deposition and temperature deviation were strongly and positively correlated within the geographical range of spruce and pine distributions (Central to Northern Europe). The summer temperature in the actual period was clearly higher than normal in Central Europe, where also the N deposition is highest. Both N deposition and temperature deviation became lower with increasing latitude. For spruce, temperature deviation was the only explanatory variable that remained in the final model, but this may well be an artefact of the occasional relation between latitude and temperature deviation; a model with only N deposition was almost equally strong with respect to R^2 (not given in Table 1.12). For pine it was opposite: in both models N deposition was positively related to growth, but not to temperature. For spruce and pine we repeated the analysis for nitrogen sensitive sites only. On these sites N deposition became a significant predictor for both pine and spruce growth. For pine, there was a negative relationship between drought and growth. This means that where the summers were mostly drier than normal, this was associated with lower growth. For beech in both models temperature entered with a positive effect. N deposition was positively related to growth in oak sites, however, only in the model where we used the site productivity curves. Computed variance inflation factors were in all cases less than 3, indicating no over-parameterization of the model.

Table 1.12 Multivariate regression (stepwise forward/backward elimination) with parameter estimates and model adjusted R^2*. The results of the hypothesis testing of the effects are based on partial F-tests (type III tests;* $p<0.001$ *(***);* $p<0.01$ *(**);* $p<0.05$ *(*)). When multiplied by 100, the results give the percentage growth change per unit change of the environmental variable.*

Model	Site prod	age	SDI	N dep.	Temp. dev.	Drought dev.	Adj R^2	N
All plots								
Spruce-class	0.054***	-0.005**	-	-	0.524***		0.33	127
Spruce-mean SI	0.105***	-		-	0.371***		0.49	132
Pine-class	-	-0.017***	-	0.010*	-	-0.0032**	0.27	122
Pine-mean SI	0.078**	-0.010**	-	0.009*	-	-0.0019**	0.37	129
Beech-class	-	-0.005*	-	-	0.70***	-	0.26	57
Beech-mean SI	0.117***	-	-	-	0.36*	-	0.29	61
Oak-class	-	-0.009**	-	-	-	-	0.29	29
Oak-mean SI	0.198*	-	-0.007*	0.024*	-	-	0.18	34
N sensitive plots								
Spruce-class	0.039*	-0.004**		0.022**	0.32**	-	0.44	86
Spruce-mean SI	0.083***			0.024***	-	-	0.55	89
Pine-class	-	-0.017***	0.001*	0.013***	-	-0.002*	0.33	115
Pine-mean SI	0.098***	-0.009**	-	0.014***	-	-	0.40	121

1.4 Discussion

Impacts of N deposition

The major finding of this study was a positive relationship between higher than normal volume growth on one hand and nitrogen deposition and higher summer temperatures on the other hand, being most pronounced for spruce and pine. The results indicate a possible fertilizing effect of N deposition, and the parameters of the linear model suggest a 1% increase in site productivity per kg of N deposition for pine and spruce and of approximately 1.25 % for sensitive (N deficient) sites. A similar result was obtained by Laubhahn et al. (2007) in a multi-factor analysis with measured basal-area-increment of each individual tree as responding factor and factors related to tree size, tree competition, site fertility and environmental impacts (temperature change compared to long-term average, nitrogen and sulfur deposition) as influencing parameters. Nitrogen deposition effect for spruce and pine and for all species together varied around or slightly above, one unit. This means that for the stands used in this study (even-aged mostly single species stands ranging between 30 and 180 years in age) 1 kg of N-deposition per year corresponded roughly to a 1% increase in volume growth per year for the time period 1994-1999. This value is almost identical to the result obtained from a similar study on nationwide data-sets from Norway (level I and forest officers plots) (Solberg et al., 2004), but lower than the 4% estimated by Braun et al. (1999) for selected Swiss observation plots. For each of the four models in Table 1.7 and the models combining all three site-index curves (Table 1.8) we calculated the effect of 1 kg of N deposition on wood production by multiplying the mean measured volume growth per species (Table 1.5) with the estimated slope in the model and the mean wood density per species (De Vries et al., 2006b). Depending on the model 1 kg of N deposition corresponded to an increase of between 33 and 49 kg wood per year. Assuming a C content of 50% and using the value obtained for the model using the mean of the three site index curve models (38 kg) we estimate an increase in carbon fixation of 19 kg C per kg N.

This carbon to N fixation ratio is quite comparable to results obtained by Nadelhoffer et al. (1999b) who estimated that 1 kg of N deposition corresponded to an additional 25 kg C sequestration based on ^{15}N experiments. Rehfuess et al. (1999) presented results of simulations of 5 models on two forest sites showing a variation 15 - 25 kg C/kg N depending on the model used, which is in the same range. The ratio of 19 kg C per kg N for the selected level II plots seems also quite representative for Europe as a whole. De Vries et al. (2006b) found an average growth over Europe of all trees of 1729 kg $C.ha^{-1}.yr^{-1}$ for the period 1960-2000 and 1% increase would thus lead to a ratio of 17.3 kg C per kg N. The mean N deposition in this study was 20 $kg.ha^{-1}.yr^{-1}$, which would then correspond to an increased C sequestration near 300 $kg.ha^{-1}.yr^{-1}$, considering a reference background N deposition of 3-4 kg. For areas in Europe having the highest loads around 40-60 $kg.ha^{-1}.yr^{-1}$, this should mean roughly a 50% growth increase, but only if no detrimental effects would occur (Magill et al., 2004).

Below we will discuss whether conclusions on cause-effect relationships can be drawn from our findings. Tree growth is influenced by many factors (Dobbertin, 2005), and statistical relationships are not sufficient to infer cause-and-effect. The following discussion is structured around the five criteria that were proposed by the Committee on Biologic Markers of Air Pollution Damage in Trees for establishing cause-effect based on monitoring data (Anonymous, 1989): strong correlation; plausibility of mechanism; experimental replication; temporality; and weight of evidence.

Strong correlation

There should be a strong correlation between the causal agent and the measured effect, including the two concepts consistency and strength of correlation. The relationships we obtained between relative growth and nitrogen deposition for spruce and pine were weak concerning explained variance. Only up to 10% of the sum of squares was explained. However, they were strong in the sense that they produced parameter estimates indicating an effect of large magnitude, and also they were mostly statistically significant, which means that based on the residual variance estimates we obtained from the models, it is unlikely that these relationships could be due to random variations in the variables only. Also, the relationships were very consistent between spruce and pine, and for the various model alternatives with various alternatives for site productivity and age. In addition the slope of parameters increased on sites with a high C/N ratio in the upper soil layer, i.e. sites that we anticipated to be more sensitive to N deposition. Both simple regression analyses and the analyses of covariance gave similar statistical results, as did multiple regression analyses partly. The latter gave consistent significant results for pine using all plots and for spruce on the 'sensitive' sites only. This means that in one of the statistical models, N deposition was discarded in favour of temperature deviation. The co-linearity between N deposition and temperature deviation implies that the parameter estimates must be interpreted with care. However, because N deposition and temperature deviation were almost equally strong explanatory variables, and because the relationship with N was strong for the N sensitive plots, the data support the conclusion that there is a strong statistical relationship between growth and N deposition.

It is unlikely that much stronger relationships can be obtained in empirical studies such as the one presented here. We did most of our analyses in a two-step way, where growth was first modelled as a function of site productivity, age and stand density. Second, the residuals from this were modelled as a function of nitrogen deposition. The two steps had R^2 values around 20-40% and 3-10%, respectively. The multivariate analysis obtained adjusted R^2 values between 0.18 and 0.56 for spruce and pine. This is comparable to what has been obtained in controlled experiments. In experiments such as the Swedish fertilization trials around 1970-1980 Pettersson (1994) found the residual variation to be surprisingly high, although a number of explanatory variables were included in the models. He used a one-step model containing both the amount of added nitrogen as well as a number of stand and site variables and obtained an R^2-value of 44%. This demonstrates that a number of random, unknown effects are present.

We also found a strong temperature effect, with increasing relative growth on sites which experienced higher May to August temperature during the growth period (1993-2000) in comparison to the long-term average (1961-1990). For summer temperature deviation, the estimated parameters indicate a 2-4% growth increase for a 0.1°C temperature deviation. This implies that an increase in summer temperature of 1°C corresponds to 20-40 % increase in growth, which seems a high estimate for a temperature effect. In model simulations for comparable level II plots, Wamelink et al. (2007c) predicted a change in net primary productivity (NPP) of approximately -20-40% or -200-400 kg C for an increase in temperature of 1°C. In these model simulations, the predicted NPP changes are due to the interaction between temperature and drought stress affected by a change in both temperature and precipitation. Negative values are predicted only in the southern part of Europe (below a latitude of 52). The NPP change in the North (above a latitude of 52) ranged mostly between 20-40 % increase in growth for 1°C temperature increase, being comparable to these empirical results. In the simple regressions the temperature effect was significant for all models with pine and spruce and for half of the beech models. The analyses of covariance confirmed these results and in the multiple regressions for beech and spruce consistent significant results of temperature were obtained. For pine and spruce N deposition and temperature were correlated and thus a certain confounding effect may be expected.

In the simple regression drought was consistently negatively related to relative growth except for oak (assumed to be of highest drought resistance). The relationships were always significant for pine, in half of the cases for spruce, but never for beech. On drought sensitive sites the effect of drought stress on Norway spruce increased. In the multivariate analysis drought was only significant as a stress factor for pine as an interaction term with drought sensitive sites. We conclude that overall the drought effect was found to be less strong and less consistent among methods. The low correlation between modelled precipitation from the WMO grid values and precipitation measured at the plots suggests that there is considerable uncertainty in the precipitation data used here. S deposition and acidic deposition were not consistently related to stand growth. No hypothesized negative effect could be shown in the data.

Plausibility of mechanism

A plausible, biologic explanation of the mechanism of the observed association should be present. This is clearly the case for a growth increase as a response to N deposition. For large parts of Europe, the atmospheric deposition of nitrogen has increased from below 10 $kg.ha^{-1}.yr^{-1}$ before the industrialization to more than 30 $kg.ha^{-1}.yr^{-1}$ in the late 1980s in some parts of Europe. N is generally a factor that limits forest growth for large parts of the forest area in Europe, or at least this was the case prior to recent decades' anthropogenic deposition. Foliar analyses of various tree species have demonstrated that the N concentration is often in the deficiency range, or at least sub-optimal. A European wide survey of foliar chemistry revealed that most plots had an adequate status of nutrient concentrations, however, one third of all plots with the four tree species we study here had N values in the lowest class, i.e. N was deficient, while only 13% of the plots had a high or optimal concentration (Stefan et al., 1997). The thresholds commonly used are based on growth response, which means that growth is expected to increase when N is added to the forest ecosystem.

As hypothesized, there was an overall tendency of stronger relationship for the subset of plots that we a-priori expected to be more sensitive to N deposition, i.e. plots having high C/N ratios in the upper soil layer. Also, a few decades ago forest fertilization was common practice in forestry, and in almost all cases pure N fertilizers were used, such as NH_4NO_3. The amounts used correspond to average deposition rates in Europe. Typically, forest fertilization was 150 $kg.ha^{-1}$ applied every 7 years, which means about 20 $kg.ha^{-1}.yr^{-1}$. For Scots pine sites in central Europe a recent study on control plots of former fertilization experiments found increasing nitrogen concentrations in needles in parallel with increased nitrogen deposition, while in Northern Europe on sites with low nitrogen input no change in nitrogen concentrations was observed (Mellert et al., 2004).

When it comes to increased growth as a response to increases in summer temperature, the plausibility is less evident. On one hand a temperature increase may increase the length of the growing season. Hasenauer et al. (1999) found for the time period 1961-1990 a parallel increase in mean annual temperature, length of the growing season and growth in Austria. In temperate forests the growth during the potential vegetation period (determined by the seasonal global radiation budget) is limited by temperature (Kozlowski & Pallardy, 1996). Long-term phenological observations show for deciduous trees that leaf duration has increased by up to two weeks in Europe over the past thirty years due to increasing temperature (Menzel & Fabian, 1999). On the other hand, increased temperature may cause more drought problems, and this may outweigh the positive effects of temperature itself. One example is for White spruce in Alaska, where tree-ring series for the past 90 years show a strong decrease in growth with increasing temperature, and increasing drought may explain this (Barber et al., 2000). Another example is the reduced primary productivity observed in Europe in the very warm and dry summer 2003 (Ciais et al., 2005). Also, several studies found poor relations between leaf duration and stem growth (White & Nemani, 2003; Kaufmann et al., 2004; Jolly et al., 2005; Leuzinger et al., 2005). In the present study, the parameter estimate for a temperature effect indicated a 42% increase in growth for a one degree temperature increase. This is unlikely to be realistic. If we for example apply the functions developed by Nilsen & Larsson (1992), and recalculate the altitude differences to temperature differences (0.6°C.100 m^{-1}), we get 5-10% change in site productivity per 1°C. The temperature effect found is thus likely to mostly reflect the nitrogen fertilizing effect.

Most likely the effect of increased temperature is variable, depending on other factors such as water availability, and the effects may vary regionally (see also the model simulations of Wamelink et al. (2007c) on part of the Intensive monitoring plots). Changes in the intensity of drought stress may be a more important factor than temperature. Unfortunately, our drought stress variable is questionable, because local precipitation measured at some of the plots deviated considerably from precipitation obtained from the CRU. In Norway, Andreassen et al. (2006) studied tree-ring series from some 600 plots and found that unusually warm or dry summers caused increased growth in coastal, northern and mountainous areas, while the opposite was the case for the lowlands of southeast Norway. In the present study, temperature deviations from the long-term normal values were highest in central Europe, which is not the area where a positive effect is most likely. It is well established that tree stem growth is effected by the water availability during the growing season and years prior to it (Spiecker, 1990, 1995; Schweingruber, 1996). The severe drought during the temperature record-setting summer 2003 in Europe (Schär et al., 2004) also affected stem growth at long-term monitoring sites in Germany and Switzerland (Meining et al., 2004; Ciais et al., 2005; Jolly et al., 2005). Meining et al. (2004) report reduced stem diameter growth rates by an average of 50% in 2003 for all 10 spruce Level II sites in Baden-Württemberg. In Bavaria growth in 2003 for all seven Level II spruce sites was reduced in comparison to 2002 (Meining et al., 2004). For beech, growth reduction was also found at low altitude sites (510 to 780 m), but above 800 m beech showed no growth reduction. In Switzerland, tree growth 2003 in percent of growth in 2002 decreased with decreasing altitude. At low altitude (≤ 1200 m) tree growth was reduced in 2003 (on average by one third, Dobbertin, 2005) as compared to the wet year 2002, while the trees on plots above 1200 m a.s.l. exhibited increased stem growth (mean of 15%, Dobbertin, 2005) most likely due to increased temperature (Jolly et al., 2005). It can be concluded that temperature and drought related annual growth changes vary highly between sites and geographic locations. Altogether, the plausibility of temperature effects is uncertain.

Experimental replication (responsiveness)

The effect should be reproducible in a controlled experiment, or the effect should be removed by removing the causal agent. Beside, similar findings in other correlative studies on monitoring data would be valuable here. Many fertilization experiments have been carried out, and they normally show a clear response to nitrogen, while in most cases other elements give no response. The growth response to N fertilisation experiments is highly variable from site to site, but generally of the same or higher magnitude as we have found here (Pettersson, 1994; Persson et al., 1995; Nilsen, 2001; Nilsen & Abrahamsen, 2003). Other experimental studies with similar results are Spiecker (1990); Flückiger and Braun (1995); Joos (1997); Magill et al. (1997); and Wargo et al. (2002). The RECOGNITION study found that current height growth of young

Scots pine (*Pinus sylvestris*), common beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) is around 25% higher today than that of older trees in the past when they were of the same age (Kahle et al., 2005). Based on on a process-based forest growth model, another study concluded that forest growth has accelerated mainly due to nitrogen deposition (Milne & Van Oijen, 2005). Solberg et al. (2004) calculated 5-year basal area increment for Level I plots and other long-term observation plots ('officer plots') in Norway for Norway spruce and Scots pine and compared it with predicted increment from standard Norwegian growth models that use site index, stand age and stand density variables as input variables. They found that the actual growth in percent of the predicted growth was positively correlated with N deposition, suggesting a fertilizing effect of N, with the order of magnitude as found here, i.e. roughly one percent increase in growth per kg $N.ha^{-1}.yr^{-1}$.

We can not exclude the possibility that continued high N deposition in the long run may have negative effects such as declining growth or increased tree mortality. A long-term nitrogen fertilizer experiment (50 and 150 kg $N.ha^{-1}.yr^{-1}$) at the Harvard forest LTER site resulted in decreased growth and subsequent high mortality in red pine forests, while the mixed hardwood forests initially responded with increased growth (Magill et al., 1997). However, following a severe drought the mixed hardwood forest with high N treatment is now also experiencing high mortality rates and reduced biomass (Magill et al., 2004). It is unclear to us whether such effects may be present already in Europe, but we anticipate that this is unlikely to be the case for most parts of Europe as N deposition is mostly clearly below the doses applied in that experiment.

We could not obtain a fair test of the presence of effects of acid rain and soil acidification in the present study, because S and acid deposition are so strongly correlated to N deposition. However, it is clear that eventually such effects are clearly outweighed by the fertilizing effect of N, and also the deposition of acidic compounds has been strongly reduced to below critical loads for most regions during the last decades. Tveite et al. (1990) examined experimental Scots pine plots treated with artificial acid rain and/or lime in Norway. They found in the first 2 years stimulated stem growth with increasing acid loadings, but after five years growth declined. Liming resulted in positive effects 9 years after treatment.

Temporality

Causal agents and effects should vary synchronised, and the cause should precede its effect. This criterion is less easy to apply, because we are dealing partly with long-term aggregated effects as well as delayed effects. Also, we had at hand growth data for a five year period, and this crude temporal resolution is less suitable to establish temporality between any cause and its effect. We excluded very young plots and thus tried to derive a site productivity value which should be determined mainly in a period prior to the main N deposition. However, a majority of the plots were still less than 70 years old and thus had been subjected to increasing deposition rates. It would be best to have complete growth data for the entire stands from the period prior to anthropogenic deposition.

We cannot conclude here that this criterion is met, although we partly have fulfilled it, at least for the climate variables. We have purposely widened the climatic period to 2 years before the starting of the growth period to avoid the lag effect which is known to occur for example following drought.

Weight of evidence

Each of the criteria alone is not sufficient, but all the four criteria above should be met in order to establish the cause effect relationship. This criterion is reasonably met for the impact of N deposition on growth. Even though the results would have been more evident if the statistical relationships were stronger, there is a rather strong correlation between N deposition and growth of pine and spruce, specifically considering the type of study. Furthermore, the mechanism is plausible and there are experimental replication in terms of ^{15}N tracer experiments and N fertilizer experiments showing similar results. There is only a problem to prove the temporality criterion in this kind of study. For the temperature effect, the various criteria are not met so convincingly. The significance of the temperature effect is less and there is a confounding factor between temperature increase and N deposition increase.

In conclusion, we have found a very likely, but not absolutely convincing cause-effect relationship between N deposition and increased forest growth. Furthermore, a cause-effect relationship between increased temperature and increased growth is possible. Other effects are uncertain.

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2 The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical tree growth model

Abstract
In the climate change discussion, the possibility of carbon sequestration of forests plays an important role. Therefore, research on the effects of environmental changes on net primary productivity is interesting. In this study we investigated the influence of changing temperature, precipitation and deposition of sulphur and nitrogen compounds on forest growth. The data base consisted of 654 plots of the European intensive monitoring program (Level II plots) with 5-year growth data for the period 1994-1999. Among these 654 plots only 382 plots in 18 European countries met the requirements necessary to be used in our analysis. Our analysis was done for common beech (*Fagus sylvatica*), oak (*Quercus petraea* and *Q. robur*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). We developed an individual tree growth model with measured basal area increment of each individual tree as responding growth factor and tree size (diameter at breast height), tree competition (basal area of larger trees and stand density index), site factors (soil C/N ratio, temperature) and environmental factors (temperature change compared to long-term average, nitrogen and sulphur deposition) as influencing parameters. Using a mixed model approach, all models for the tree species show a high Goodness of fit with Pseudo-R^2 between 0.33 and 0.44. Diameter at breast height and basal area of larger trees were highly influential variables in all models. Increasing temperature shows a positive effect on growth for all species except Norway spruce. Nitrogen deposition shows a positive impact on growth for all four species. This influence was significant with $p<0.05$ for all species except common beech. For beech the effect was nearly significant ($p=0.077$). An increase of 1 kg N ha^{-1} yr^{-1} corresponds to an increase in basal area increment between 1.20 % and 1.49 % depending on species. Considering an average total carbon uptake for European forests near 1730 kg per hectare and year, this implies an estimated sequestration of approximately 21-26 kg carbon per kg nitrogen deposition.

2.1 Introduction

In the Kyoto Protocol governments agreed to reduce emissions of CO_2. They engaged themselves either to limiting the fossil fuel consumption or to increase the net C sequestration in terrestrial sinks through afforestation and land use or both. Especially mid-latitude forests like those in Europe play an important role in the net C sequestration of the biosphere (Kauppi et al., 1992; Nabuurs et al., 1997), In this respect, besides the changes in standing growing stock, the changes in net primary productivity seem to be important (Spiecker et al., 1996). A lot of environmental variables, as CO2, temperature, nitrogen deposition and others have been hypothesized to increase the net primary productivity (NPP) (Melillo et al., 1993; Friedlingstein et al., 1995; Holland et al., 1997; Hasenauer et al., 1999; Nadelhoffer et al., 1999b). As summarized in a review article (Hyvönen et al., 2007a), well documented responses on the NPP are an increased photosynthetic rate (main CO_2 response), an increase in the length of the growing season (main temperature response) and an increase in leaf area index (main N deposition response).

Since nitrogen often is the limiting nutrient in forests, nitrogen deposition is likely to increase productivity, thus increasing carbon sequestration by forests. Using a modelling approach, temperature has been claimed to be relatively unimportant, whereas the combination of CO_2 rise and elevated N deposition may account for a 15-20% increase in forest net primary productivity (Rehfuess et al., 1999). In this context, N deposition is claimed to be most important. Similar results were also obtained by Milne and Van Oijen, (2005). These authors showed that the main driver of increased forest growth in the 20th century has been increased nitrogen deposition, rather than increased CO_2 concentrations or climate change, using a process-based model. In an analysis of control plots in former fertilizer trials, combined with a retrospective analysis of height increment on selected intensive monitoring sites, Kahle et al. (2005) found an increased height growth of Scots pine, Norway spruce and common beech of around 25% as compared to 40 years ago. Combining these results with a process-based modelling approach using selected intensive monitoring sites for calibration and validation Karjalainen et al. (in press) also concluded that nitrogen deposition appears to be the main cause of the observed height growth increase. The number of sites used in the study was, however very limited.

In this contribution we tried to assess the combined effect of climate change (temperature and precipitation), acidification and eutrophication (in terms of sulphur and nitrogen deposition) on biomass growth and so also on carbon sequestration of forests, using an empirical model with measured basal area increment at tree level as responding factor. The model was applied by using data from the European intensive monitoring program (Level II plots). Increment data as well as data related to tree competition and soil data were available on all plots. The meteorological data and deposition data were recorded only at a part of plots.

In performing the multi-factor analyses, we tested the following hypotheses:
- Individual tree growth can be modelled on a European scale as depending on site factors and competition.
- Individual tree growth responds to changing climatic factors like precipitation and temperature.
- Individual tree increment also responds to nitrogen and sulphur deposition.

The way how we tested these hypotheses was to develop an individual tree growth model for basal area increment, depending on tree size (dbh), tree competition (stand density index, basal area of larger trees), and site factors like elevation, latitude, soil pH, and others. We added climate and deposition variables, which are assumed to describe environmental change and see if they contribute significantly to the model. If they do, their coefficients will describe the response of growth on these environmental change variables, for given site factors, tree size and competition.

Because basal area increment is highly correlated with biomass growth we used as a base concept Wykoff's (1990) basal area increment model. Having multilevel data, some on plot and others on tree level we had to upgrade this multiple regression model to a multilevel-mixed model. Mixed models have also been applied to this kind of data for example by Lappi et al. (1988), Hökkä et al. (1997), or Uzoh and Oliver (2006).

2.2 Locations and data assessment

2.2.1 Locations and plot selection

Overall we had data of 97773 individual trees (77 tree species) in 654 plots from 20 European countries available. All plots are located in subjectively selected stands by each country, in order to represent typical forest types and growing conditions. The plots are typically designed as a 0.25 ha homogenous and rectangular area (Haußmann & Lorenz, 2004). For nearly two thirds of all trees the diameter at breast height (dbh) at the beginning and the end of the investigation period, mainly 1995 to 2000, were measured

In a first step we had to exclude some plots and trees due to different reasons: fertilization, obviously errors in measurement, missing plot size or missing other necessary data (compare to Solberg et al., 2007, in this volume). Secondly we had to define criteria for tree species and plot selection to be able to get reliable models. At least 50 plots per species were needed, because we had stand and site variables per plot, and there should be (i) enough degrees of freedom left for the error term, and (ii) confounding of effects with locations should be avoided. For reliable results it is necessary to use only really measured increment data, and in some plots there were only a few trees where the dbh has been measured twice. Thus we defined the following criteria:

- The investigated species must have at least 20 measured individuals per plot.
- The basal area of the species must be higher than 10 % of the total plot's basal area.
- Although, due to inaccuracies in measurements negative increments could occur, we only used trees with positive increments.

The result was the selection of four tree species, Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), common beech (*Fagus sylvatica*), and oak (*Quercus robur and Quercus petraea*) in 382 plots in 18 countries for the growth model (Figure 2.1). In most of the plots only a few tree heights were measured and because of that we decided not to use tree height and volume in our model. Instead we used five year basal area increment, BAI as the growth variable. Mean values for the BAI were 46.7 cm², 57.8 cm², 81.4 cm², and 85.4 cm² for Scots pine, Norway spruce, common beech and oak, respectively. Information on the environmental variables is described later (section 2.2).

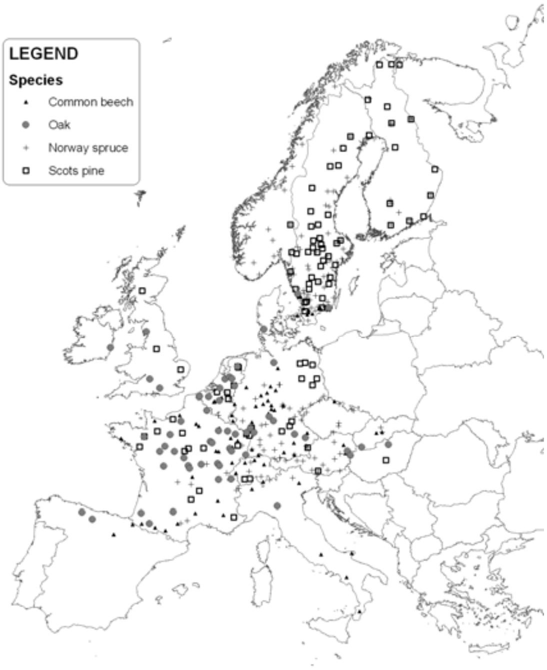

Figure 2.1 Distribution of the selected plots by species

In the map (Figure 2.1) it can be seen that Scots pine and Norway spruce grow from France to the north of Norway. Both broadleaves, oak and common beech were located mainly in central Europe up to the latitude of 57 degrees in the UK and in Denmark. A few plots of common beech can be found in the south of Italy.

In total 382 plots were selected: 152, 101, 87 and 61 plots for Norway spruce, Scots pine, common beech and oak, respectively. In some plots more than one selected species fulfilled all criteria and therefore the sum of the respective plots is 401 and thus larger than the total number of plots used. This numbers differs slightly from the selection results of Solberg et al. (2007) mainly caused by the use of different selection criteria, which were adapted to the respective research question. The much smaller number of plots for Scots pine in our study results from not using Solberg's (2007) automatic routine for assigning observations to arbitrary tree numbers of some Poland plots. Because of developing an individual tree model rather than a stand model we needed the exact assignment of trees from the first to the second measurement year for accurate information of increment of every single tree of a plot.

2.2.2 Data assessment and selection of predictor variables

Predictor variables

The various predictor variables used in explaining the 5 year basal area increment (forest growth) are tree characteristics, stand and site characteristics, meteorological characteristics and atmospheric deposition of major nutrients from the atmosphere, as summarized in Table 2.1. Table 2.1 is based on both the relevance of predictors and the availability of data. In all cases, use was made of the data that were available in the Intensive Monitoring database, except for temperature which was derived by interpolating data from nearby meteorological stations. The analyses were performed on plots where all information, mentioned in Table 2.1, was available, either directly measured or derived from external databases, as described below.

Tree characteristics

Included tree characteristics are related to tree size (tree diameter at breast height, dbh) and tree competition (basal area of larger trees, BAL), We transformed the dbh logarithmically and added the squared dbh as an additional independent variable, which effectively serves to prevent unlimited growth for large diameter trees according to natural conditions. Basal area of larger trees (BAL) is a competition parameter which we expected to be negatively correlated with growth. The less competition a tree experiences (BAL is low), the higher its increment is expected to be. As mentioned before, we did not use tree height due to too few measurements. Furthermore, we were not able to include crown ratio (ratio between crown length and tree height), as it is contained in the models of Wykoff (1990) and of Monserud and Sterba (1996) as it was only available in very few plots.

Table 2.1 Predictor variables used in the statistical analysis of individual tree growth

Predictor variables	Description
Tree characteristics	
- Diameter in breast height (dbh)	continuous; in cm
- Basal area of larger trees (BAL)	calculated for every tree per plot; m^2 ha^{-1}
Stand and site characteristics	
- Latitude	continuous; decimal degrees
- Longitude	continuous; decimal degrees
- Altitude	continuous; based on discrete intervals in meter
- Orientation	eight directions (1-8) plus "9" for plane surface
- Number of trees per hectare	counted data
- Stand density index (SDI)	calculated from number of trees/ha and dbh
- Available water capacity	continuous, values for the upper 50 cm; mm
- pH (CaCl2)	values of the mineral topsoil (0-20 cm) and organic layer
- Base saturation	values of the mineral topsoil (0-20 cm) and organic layer; percent
- C and N content (C/N ratio)	values of the humus layer and mineral topsoil (0-20 cm)
Climatic variables/water availability	
- Temperature T	annual average, Average in the growing season; °C
- Precipitation P	annual total, total in the growing season; mm
- Potential evapotranspiration (PET)	annual total, total in the growing season; mm
- Actual evapotranspiration (AET)	annual total, total in the growing season; mm
Deposition data / forest nutrition	
- Deposition of NO_x, NH_3, SO_x, Ca, Mg, K, Na, Cl	annual total: $kg.ha^{-1}.yr^{-1}$

Stand and site characteristics

Apart from position parameters like latitude, longitude, altitude and orientation, we included stand density index (SDI) as a plot competition parameter, according to Reineke (1933):

$$\mathrm{SDI} = \mathrm{N} \cdot \left(\frac{25}{\mathrm{dg}} \right)^{-1,605} \tag{2.1}$$

where N is the number of trees per ha and dg is the quadratic mean diameter at breast height. As for BAL on individual tree level, individual tree growth is expected to decrease with increasing tree density at stand level.

Furthermore, all relevant site variables influencing water and nutrient availability and soil acidity status and thereby forest growth, have been recorded at all plots (see Table 2.1) The C/N ratio is used as an indicator of N availability (high C/N is low availability) in connection with N deposition. Soil acidity (pH-$CaCl_2$) is expected to have a negative effect on forest growth, due to decreased nutrient availability at a lower pH and possibly root damage by dissolved Al and heavy metals. A comparable effect is expected for the base saturation. An increase in base saturation reduces Al concentrations and increases pH. For all soil properties, data are available for the humus (organic) layer and mineral topsoil (0-20 cm).

Climatic variables/water availability

Meteorological variables affecting forest growth are temperature (T) and precipitation (P), which both determine the potential evapotranspiration (PET) and actual evapotranspiration (AET). Increasing temperature leads to an increase in growth by lengthening of the growing season and an increase in the rate of photosynthesis during the growing season. For precipitation two kinds of effects can be expected. A positive effect may be expected on water limited sites. At very high precipitation sites, larger amounts of precipitation may cause a decreased nutrient availability by increased nutrient leaching, thus causing a negative effect on forest growth. On poorly drained soils high precipitation may lead to oxygen deficiency in the roots and thus again to a decrease in growth. Apart from the T, P, PET and AET during the five year period for which the increment data are available, two extra years in view of lag time in effects were included (1993-2000). Information on the previous 30 year average values (1960-1990) is used to gain insight in the deviation from a long term average. The hypothesis behind it is that the larger the deviation from the long term average, the larger the impact on growth.

Temperature has been only measured at some plots. The temperature data thus derived correlated very well with interpolated temperature data in an available meteorological dataset (De Vries et al., 2003a). This dataset includes data at a 10x10 km^2 grid for temperature, precipitation, cloudiness, wind etc. at a monthly interval for the period 1900-2000 (Climatic Research Unit (CRU) database). These derived data were thus used in our study.

For precipitation in the period 1993-2000, use was made of the results of bulk deposition monitoring for that period. Apart from the present values in the period 1993-2000, we calculated a 30 year long-term average value for the period, 1960-1990, which gives an impression of the average meteorological circumstances. For the long-term mean, use was made of precipitation data in the 10x10 km^2 dataset.

Potential evapotranspiration (PET) and actual evapotranspiration (AET) were derived from data in the 10x10 km grid from monthly temperature, precipitation, cloudiness, wind speed etc (CRU dataset), using the WATBAL (Starr, 1999) model. In this model PET is calculated from the estimated global radiation and based on the relationship between air temperature and the ratio between evaporation and global radiation. The equation used is that by Jensen & Haise (1963); the so-called Alfalfa reference method, and is a further simplification of the Priestly-Taylor equation. It actually calculates the evaporative heat flux density (Ep in WATBAL), which is then converted into mm of PET using the latent heat of vaporization (LH_Vap in WATBAL). Ep is calculated for the "representative day of the month" (the Julian day in the climate input file) and then multiplied up to monthly values using the number of days in each month. Ep is calculated from global radiation and air temperature, using coefficients found by Jensen & Haise (1963) based on an extensive set of measurements made in the western US on well watered alfalfa fields. A crop factor is used to convert this Ep to an Ep for forests. AET is computed by comparing water supply and -demand, taking into account water available in the soil profile. Both AET and PET were used as 30 year long-term and short time (1993-2000) parameter.

Deposition and forest nutrition

Deposition data included total deposition of NH_3, NO_x, SO_x, Ca, Mg, K, Na and Cl for the years 1993-2000, with total deposition computed from measured bulk deposition and throughfall at about 300 plots, using a canopy exchange approach described in De Vries et al. (2000). Since use of these total deposition data leads to a serious reduction in the number of plots, additional analysis was carried out using calculated total N deposition by EMEP for all the 382 plots where we have growth data. For comparison we calculated both, the growth model with measured deposition and the growth model with deposition from EMEP data. For this analysis we used only those plots where both datasets were available.

We checked whether there are different results when using modelled EMEP data and measured data for those plots. Since we had the largest number of plots for Norway spruce (152 EMEP and 111 measured) we compared the two datasets for this species first. Starting from this result we used the respective environmental data to find the best models for all species. However, having the best model for a species with EMEP data of all plots, we calculated the same model with those plots only, where measured data were available and checked for differences of the two datasets (EMEP, measured data) for the given model.

An increase in nitrogen availability is expected to increase forest growth, especially at sites where nitrogen is limiting forest growth. Parameters that give information on the availability are the atmospheric inputs of main nutrients (N, Ca, Mg and K).

Apart from this, soil acidification due to excess input of S and N over base cations may have a negative impact on forest growth. We used SO_x, Ndep (computed as the deposition of NO_x and NH_3) and NetAciddep (computed as the deposition of SO_x + N - Ca - Mg - K - Na + Cl), as deposition variables.

In Table 2.2 we give an overview of the variation of the finally used site factors and influencing environmental variables on forest growth (see chapter 2.4.2). Owing to the geographical distribution up to Scandinavia (see Figure 2.1 in chapter 2.2.1), the temperature on plots of both conifers was below that of beech and oak. In a few plots the annual average temperature during the investigation period was even below zero. The higher values of deposition on the broadleaves plots, especially on oak plots, in comparison to the plots of conifers reflect the current deposition patterns caused by emissions from industry, traffic and agriculture, being highest in Central Europe.

Table 2.2 Variation of all site factors and influencing environmental factors (climate and deposition) per tree species used in the final growth models (Eq. 2.6). Temp_9300_YrMean is average annual temperature between 1993 and 2000 [°C], CNRat_020 is C/N ratio in the upper 20 cm of soil, Ndep_9300_emep is average yearly deposition of nitrogen from EMEP between 1993 – 2000 [$kg.ha^{-1}.yr^{-1}$]

Tree species	N plots / trees	Minimum	Lower quartile	Median	Upper quartile	Maximum
Norway spruce	152 / 17608					
Temp_9300_YrMean		-1.8	3.9	6.2	7.5	10.3
CNRat_020		10.4	16.8	20.0	24.5	42.7
Ndep_9300_emep		1.5	6.9	16.5	24.0	33.8
Scots pine	101 / 11110					
Temp_9300_YrMean		-1.9	2.3	6.1	9.7	12.3
CNRat_020		9.1	17.9	21.0	25.9	36.3
Ndep_9300_emep		1.1	3.8	12.1	21.8	60.1
Common beech	87 / 7730					
Temp_9300_YrMean		4.6	7.2	8.5	9.4	14.3
CNRat_020		10.2	14.3	17.4	22.2	35.0
Ndep_9300_emep		11.1	18.7	23.1	17.9	60.0
Oak	61 / 3972					
Temp_9300_YrMean		6.7	9.0	10.4	11.7	14.9
CNRat_020		8.5	14.7	18.5	20.6	39.6
Ndep_9300_emep		12.7	17.4	22.5	32.7	60.0

Competition variables

In Table 2.3, the variation in the used tree competition variables, SDI and BAL at the time of the first measurement, are listed. Results show that oak and Scots pine stands have lower stand densities (lower SDI values) than the Norway spruce and common beech stands. The basal area of larger trees (BAL) is also much higher for Norway spruce and common beech than for the oak and Scots pine stands. This implies that the tree competition is strongest in Norway spruce and common beech stands.

Table 2.3 Variation of used tree competition variables per tree species. SDI is stand density index (Reineke, 1933, Eq. (1)), BAL is basal area of larger trees [$m^2\ ha^{-1}$] (Wykoff, 1990)

Tree species	N plots / trees	Minimum	Lower quartile	Median	Upper quartile	Maximum
Norway spruce	152 / 17608					
SDI		151	413	499	625	1593
BAL		0.0	13.8	23.3	34.6	123.9
Scots pine	101 / 11110					
SDI		118	271	373	504	1299
BAL		0.0	7.9	13.9	23.4	96.3
common beech	87 / 7730					
SDI		142	378	446	601	1593
BAL		0.0	13.3	22.5	30.3	123.9
oak	61 / 3972					
SDI		135	287	366	417	1040
BAL		0.0	7.0	12.3	18.0	69.7

2.2.3 Validation, correction and supplementation of data

To parameterize the model we used only measured increment data. The dependent variable, basal area increment was the result of two dbh measurements, one at the beginning and one at the end of the investigation period. The competition measures were those at the beginning of the investigation period, not already containing the resulting increment.

Unfortunately several trees seemed to have been measured only once, some at the end and others only at the beginning of the investigation period. Supposing that this was a numbering error, we tried to find out which tree at the second measurement could have been which tree at the first measurement. For every species and every plot separately, we calculated the theoretical first dbh of trees with only a second dbh, by subtracting the mean diameter increment from the second dbh. We set limits of ± 0.5 cm of the theoretical first dbh and sought for a tree which was only measured the first time with a dbh within this range. The final assignment of all fitting trees was done manually. The limits of ± 0.5 cm were chosen to avoid a negative increment of a tree because the lowest mean of diameter increment was 0.6 cm. Trees for which no matching diameters were found were not used in the final parameter estimation procedure.

Nevertheless, in order to describe the competition at the beginning of the investigation period correctly, we needed to calculate the first dbh of the remaining trees, when only the dbh of the second measurement was recorded. We thus derived a dbh-increment regression function based on the trees with two measurements with the dbh increment as the dependent variable and the dbh of the second measurement as independent variable. For trees which had only dbh-measurements at the second observation we inserted that dbh in the regression function, calculated the respective increment and then derived the first dbh by subtracting the increment from the second dbh. If for a species and the given diameter only a small growth could be expected, we set the first dbh to the second dbh. If there were not sufficient trees of a species in the plot with two dbh-measurements, we used similar species in the plot. We excluded trees with a dbh < 5 cm at the first observation, to avoid the problem of calculating a non existing first dbh of an ingrown tree. All calculations were made plot and species specific.

2.3 Methods

2.3.1 The growth model

We first checked whether volume increment is linearly related to basal area increment, which is used as response variable for the single tree growth model, because of many missing height data. We plotted volume increment of those trees, where dbh and height measurements were available for both observations over basal area increment (Figure 2.2). The R^2 of the linear regressions for the two conifers and oak were about 0.7 and for beech just 0.5. The dispersion was mainly reasoned by the methodical inaccuracy of height measurement. For example, Figure 2.2 shows the correlation for Scots pine. The arrow-marked outlier had two plausible dbh values but an unbelievable average height increment of 1.625 m per year. In general breast height diameter is a more reliable measurement than tree height, which is an additional reason to use basal area increment instead of volume increment in the analyses. Despite the uncertain tree height values (causing an $R^2 = 0.737$), the intercept of the respective regression is near zero (0.006), showing that volume increment is approximately proportional to basal area increment. This implies that percental changes in basal area increment in response to influencing parameters can be related to percental changes in volume increment and thereby in carbon sequestration.

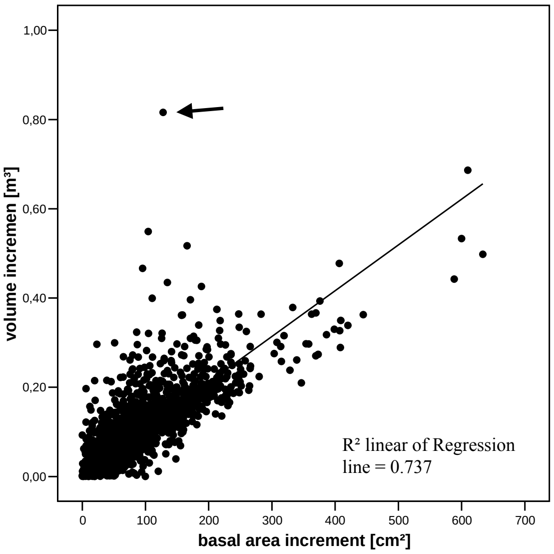

Figure 2.2 Correlation between basal area and volume increment of Scots pine calculated for such trees only, where dbh and height were measured twice, at the beginning and the end of the investigation period.

To parameterise the model we only used trees, where breast height diameters have been measured in both the first and second measurement year. As concept we used the model idea of Wykoff (1990) as it is written in Monserud and Sterba (1996):

$$\mathrm{lnBAI} = a + b^T \cdot \mathrm{SIZE} + c^T \cdot \mathrm{COMP} + d^T \cdot \mathrm{SITE} + e \qquad (2.2)$$

where BAI is the 5 year basal area increment, SIZE a vector of variables describing tree size, i.e. the natural logarithm of the dbh and dbh^2, COMP a vector describing tree competition, i.e. basal area of larger trees (BAL), number of trees per hectare and stand density index (SDI), and SITE a vector of different site descriptors, i.e. available water capacity, pH ($CaCl_2$), base saturation and C/N ratio, latitude, longitude, altitude, orientation, a the intercept, b, c and d are the vectors of the respective coefficients and e are the residuals. To take into account the hierarchical structure of our data (stand/site variables on plot level, size and competition variables on tree level) we used a mixed model approach with "plot" as the random effect u. Hence, we extended Wykoff's (1990) model to a multilevel-mixed model, as it was used with similar structured data for example by Lappi et al. (1988) and Hökkä et al. (1997). Further we added a site change (SITEC) vector and its coefficients f for describing environmental change in our model, including climatic variables (temperature, precipitation, potential evapotranspiration and actual evapotranspiration) and atmospheric deposition (SO_x, N and acidity) and their interactions with size- and competition variables. Thus, the final mixed model is:

$$\mathrm{lnBAI} = a + b^T \cdot \mathrm{SIZE} + c^T \cdot \mathrm{COMP} + d^T \cdot \mathrm{SITE} + f^T \cdot \mathrm{SITEC} + u + e \qquad (2.3)$$

with $\boldsymbol{b}$, the vector of the coefficients for the size-variables, $\boldsymbol{c}$, the vector of coefficients for the competition-variables, $\boldsymbol{d}$ the vector of coefficients for the site-variables, and $\boldsymbol{f}$ the vector of coefficients of the environmental change variables; $\boldsymbol{u}$ and $\boldsymbol{e}$ are the random effects of the plots and the trees respectively.

2.3.2 Parameter estimation

For estimating the coefficients in the vectors b, c, d and f of equation (2.3) we at first used multiple regression analysis with ln(BAI) as dependent variable. Starting with the size and competition parameters as independent variables we added and again deleted the SITE and SITEC parameters in order to finally have only parameters in the model, which behaved biologically reasonable and exhibited significant ($p \leq 0.05$) coefficients and variance inflation factors (VIF) <10, indicating tolerable collinearity between the independent variables (Montgomery & Peck, 1992). Then we used the restricted maximum likelihood (REML) method produced by the MIXED procedure in SPSS 12.0 with the plots as random effects. Since this procedure is not a least square method, the goodness of fit criterion is the -2 log likelihood (-2LL). In this procedure we started with those independent variables, which were in the final model of the multiple regression analysis and among them again deleted and added those which finally exhibited significant ($p \leq 0.05$) coefficients, while collinearity was already tested in the multiple regression analysis. Due to the hierarchic structure of the data (tree within plots), these estimates are the most appropriate ones. In order to get an idea of the impact of the random plot effect, we used the same procedure with the same variables to estimate the coefficients without a random plot effect, i.e. only with the fixed effects of the independent variables.

Finally, because the dependent variable in Equation 2.3 is the natural logarithm of the basal area increment, the estimates of the basal area increment itself are biased (Bradu & Mundlak, 1970). In order to correct for this bias, the multiplier, λ according to Condes and Sterba (2005) was used.

$$\lambda = \frac{\sum \mathrm{BAI}_{\mathrm{observed}}}{\sum \mathrm{BAI}_{\mathrm{predicted}}} \tag{2.4}$$

2.4 Results

2.4.1 Data selection - EMEP or measured environmental data

We started with the model for Norway spruce to check whether there are differences between environmental data based on EMEP or measured data. We started with the largest dataset (EMEP data) and finished with following equation for Norway spruce:

$$\begin{aligned} &\ln \mathrm{BAI} = a + b_1 \cdot \mathrm{ln\_dbh} + c_1 \cdot \mathrm{BALrel} + c_2 \cdot \mathrm{SDI} + d_1 \cdot \mathrm{CNRat\_020} \\ &+ f_1 \cdot \mathrm{Ndep9300} \end{aligned} \tag{2.5}$$

The explanations of the variables are given in Table 2.2 and Table 2.3. We calculated three models for comparison: I with measured deposition data on plots where measured deposition data were available, II with EMEP data on plots where measured deposition data were available and III with EMEP data on all plots (larger data set, see Table 2.4).

Table 2.4 Comparison of EMEP and measured data - results of mixed models: AIC is the Akaike information criterion, N-trees is the number of trees, N-plots, the number of plots, and a to f estimated coefficients of the model

Models	AIC	N - Trees	N – Plots	a	b_1	c_1	c_2	d_1	f_1
I	24245	13620	111	-0.873	1.737	-0.498	-0.00066	-0.0212	0.0141
II	24245	13620	111	-0.950	1.734	-0.502	-0.00068	-0.0198	0.0174
III	30693	17608	152	-0.875	1.720	-0.494	-0.00056	-0.0227	0.0126

All parameters were significant in all three models. The coefficients of the variables exhibited the same order of magnitude in all three models too. The quality of the models I and II with less plots and trees was equal and better than the quality of model III (see AIC-Akaike Information criteria). Owing to the similarity of models I and II and in order to have more plots, we decided to take the EMEP data and finished with the model III for Norway spruce. For the other species, we also use EMEP data only. Thus we were able to use a larger dataset, because we were not restricted to only those plots where deposition data were measured.

2.4.2 The Model

The following variables were influential on basal area increment (Eq. 2.3): In the vector SIZE, it was only the logarithm of the dbh and dbh². Regarding tree competition, both Reineke's (1933) stand density index (SDI) and the relative basal area of larger trees (BALrel), i.e. the ratio between the basal are of larger trees and the total basal area of a plot, appeared to be influential. As site parameter the C/N ratio in the upper 20 cm of the soil (CNrat_020), and the yearly mean temperature in the investigation period (Temp_9300_YrMean) showed an influence on growth.

To describe environmental change (SITEC vector) we added the differences in temperature between the long time measurements of the time span 1960 – 1990 and the investigation period 1991 – 2001 (Temp_change). It was computed as Temp_9300 – Temp_6100. The deposition of SO_x and Ndep in the investigation time is also part of the SITEC vector. To detect some relations between the variables we computed a lot of transformations and combinations of all factors. Only for Scots pine an interesting interaction between nitrogen deposition and competition became significant: Ndep · BALrel, which is the product of Ndep and BALrel. Finally, based on Equation 3 we developed the general model equation (2.6) with all these variables.

$$
\begin{aligned}
\ln \mathrm{BAI} = {} & a + b_1 \cdot \mathrm{ln\_dbh} + b_2 \cdot \mathrm{dbh}^2 + c_1 \cdot \mathrm{BALrel} + c_2 \cdot \mathrm{SDI} + d_1 \cdot \mathrm{CNRat\_020} \\
& + d_2 \cdot \mathrm{Temp\_9300\_YrMean} + f_1 \cdot \mathrm{Temp\_change} + f_2 \cdot \mathrm{Ndep9300} \\
& + f_3 \cdot \mathrm{Ndep\_BALrel}
\end{aligned} \tag{2.6}
$$

We parameterised four different models, one for each species, with different selections of parameters, depending on which of them proved to contribute significantly ($p \leq 0.05$) to the model and having a VIF<10. When there is no coefficient recorded, the respective variable was not significant and thus not used in the respective model (see Table 2.5). All the mentioned coefficients were significant at the 5% level in the mixed model approach, except f_2 for beech. However this coefficient was nearly significant (p=0.077). Only two out of ten variables (ln_d, BALrel) were significant in all models. As can be seen from Table 2.5, the coefficients for b_2, d_2, f_2 and g_1 are insignificant, for Norway Spruce, leading to Eq. 2.5 given before for this tree species.

Although the C/N ratio of the humus layer is a better predictor for N availability than the C/N ratio of the mineral topsoil, only the latter one was significant in the model for Norway spruce. The temperature in the investigation period was significant for Scots pine and oak. While Ndep deposition was significantly influential in the models of Norway spruce, Scots pine and oak as well as nearly significant in the common beech model, SO_x deposition was not significant for any species. As a climate change parameter the difference between long term temperature and the temperature in the investigation period showed a significant effect on growth of common beech. For Scots pine the model exhibited a significant interaction between competition and deposition (Ndep_BALrel = Ndep·BALrel).

Table 2.5 The estimated coefficients for the influencing factors that appeared to be significant ($p \leq 0.05$) in the models

Species	A (intercept)	b_1 (lndbh)	b_2 (dbh)	c_1 (BALrel)	c_2 (SDI)
Norway spruce	-0.87521	1.72013	-	-0.49441	-0.00056
Scots pine	-1.17577[1]	1.30008	-0.00031	-0.34301	-0.00066
Common beech	-3.82025	2.35728	-0.00012	-0.18252	-
oak	-2.77615	1.98750	-0.00024	-0.48240	-0.00062

Species	d_1 (CNrat)	d_2 (Temp)	f_1 Tempchange)	f_2 (Ndep)	f_3 (Ndep_BALrel)
Norway spruce	-0.02274	-	-	0.01256	-
Scots pine	-	0.05208	-	0.01480	-0.00836
Common beech	-	-	0.06184	0.01197[2]	-
Oak	-	0.07681	-	0.01332	-

[1] This coefficient is not significant p = 0.380.

[2] This coefficient is nearly significant at p =0.05 (p = 0.077).

2.4.3 Model validation

In absence of an independent data set, the validity of a model is usually described by different goodness of fit statistics and calculations, testing the reasonability of the model behaviour. In our case we used the Akaike Information Criterion (AIC), which is recommended for mixed models (Demidenko, 2004), and additionally the usual R^2 of the linear multiple regression and McFadden's (1979) Pseudo-R^2, which is calculated from the log-likelihood criterion, which results from the maximum likelihood parameter estimation procedure (see chapter 2.3.2).

$$\text{Pseudo-}R^2 = 1\text{-}(\log L_{MA}/\log L_{Mo}) \tag{2.7}$$

Where log L is the -2log likelihood, once for the model with the significant independent variables (MA) and once without any independent variable, i.e. assuming the dependent variable being sufficiently described by its mean (M0). For comparison of our models the R^2 of the multiple regression, the Pseudo-R^2 of the model calculated with the mixed procedure with no random effects, and the Pseudo-R^2 of the final mixed model with random and fixed effects are shown in Table 2.6.

Table 2.6 Quality of the models. AIC – Akaike Information criterion, R^2 - from multiple regression, Mf – mixed model with only fixed effects, Mm – mixed model with random and fixed effects, λ - bias correction

Species	AIC	R^2	Pseudo-R^2_{Mf}	Pseudo-R^2_{Mm}	λ
Norway spruce	30693.90	0.579	0.262	0.368	1.136
Scots pine	20972.85	0.369	0.173	0.333	1.150
common beech	14612.36	0.700	0.338	0.422	1.114
Oak	6430.40	0.678	0.382	0.424	1.096

The McFadden's (1979) Pseudo-R^2 is in general smaller than the R^2 of a multiple regression. Values between 0.2 and 0.4 already represent good fit (McFadden, 1979). To get an idea of the real meaning of the Pseudo-R^2 it is possible to compare the R^2 of the multiple regression and the Pseudo-R^2 of the mixed model with fixed effects.

Through all species models, adding the random plot variable led to an increase in Pseudo-R^2 which supports the use of a the mixed model approach.

Although the derived models are individual tree models, it is important to see how well the average growth per plot may be predicted. This is done in Figure 2.3, where the observed means of basal area increment per plot are plotted against the predictions for the four selected tree species. All models show very good predictions.

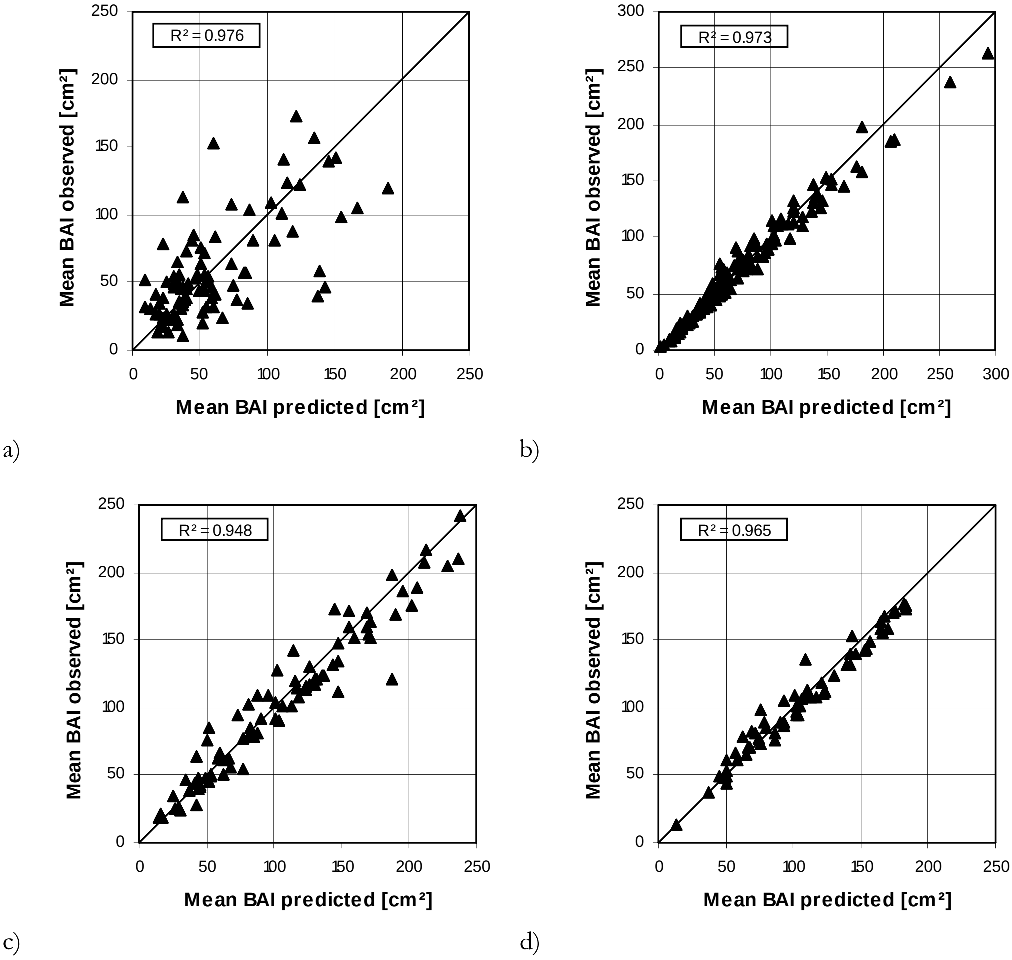

Figure 2.3 Observed means of basal area increment per plot against the bias-corrected predictions: a) Scots pine, b) Norway spruce, c) common beech, d) oak

2.5 Discussion

Model quality

Overall, our models showed good quality. The R^2 values of our models (Table 2.6) are quite similar in magnitude with comparable BAI-models of Monserud and Sterba (1996) for Austrian forests, Andreassen and Tomter (2003) for Norwegian forests, as well as those of Wykoff (personal communication, 1994, cited in Monserud and Sterba, 1996) for forests in the northern Rocky Mountains. Compared with

Monserud und Sterba (1996) even the ranking of the R^2 between the species was the same, highest in common beech and lowest in Scots pine.

Monserud and Sterba (1996) worked with eight species and resulted in R^2 ranges of 0.33 to 0.63. The R^2 of the models of Andreassen and Tomter (2003) ranges from 0.26 to 0.55 and the R^2 for Norway spruce and for Scots pine were 0.55 and 0.48, respectively. Although Wykoff (1990) worked with different species and in a quite different region the comparison is important due to the similarity of methods. The R^2 of his models ranged from 0.44 to 0.69 for 11 species. Although the goodness of fit of the common beech model was quite good (Psuedo-R^2_{Mm} = 0.422), the predictions against the observed data showed the highest variance (Figure 2.3c). This reflects high variance in the dataset. The model for Scots pine is the opposite example. Despite the Scots pine model was the most complex one, with seven variables included in the equation (Table 2.5), the smallest part of the variance could be explained by the model. Nevertheless, it showed the best prediction, having small variance in the dataset. The addition of the random plot variable to the models showed a smaller increase of goodness of fit of the two broadleaves which is maybe due to their narrower geographical distribution.

Impacts of stand and site characteristics and climate

The structure of all four models was considerably different. Only two out of ten variables (ln_d, BALrel) influence growth significantly over all tree species. These two variables and Ndep which is significant in three models and nearly significant for common beech are most influential for increment of the investigated tree species in Europe. For site and competition factors this is similar to findings of Monserud and Sterba (1996). The positive coefficient b_1 for the logarithmic dbh and the negative coefficient b_2 for dbh^2 reflect an increasing BAI with increasing age in young trees and a decrease in BAI with further increasing dbh (age) after a species specific culmination point. This is an expected behaviour of most growth models (Assmann, 1970). An increase in competition led to a decrease in increment which can be seen by the negative sign of BALrel and SDI in Table 2.5 in chapter 2.4.2, which seems to be logic and is also well known from silvicultural experience (Assmann, 1970).

Among the soil factors only the C/N ratio in the model of Norway spruce showed a significant effect on growth. The lower the C/N-ratio, the higher the nutrient status of the soil and this led to a significantly better growth of Norway spruce. The positive effect of the temperature increase in the investigation period (1995 – 2000), as compared to the long term period (1960 – 1990), on growth as a direct variable of climate change is only significant for common beech. No other computed direct variable of climate change between these two periods (e.g. precipitation change) was significant in any model. However for Scots pine and oak, at least the mean annual temperature of the investigation period showed an significant and positive influence on the basal area increment. For Norway spruce we could not detect any influence of the climate variables. The drought stress as it is defined by Solberg (2007), showed no significant effect in any model.

Impact of nitrogen deposition

The positive influence of N deposition on growth for all four species is a key finding in this study, in line with previous model studies (Rehfuess et al., 1999; Milne & Van Oijen, 2005) and experimental studies (Kahle et al., 2005; Karjalainen et al., in press). In Figure 2.4 all predictor variables except Ndep, were set to their mean, and BAI was calculated with the models described in Table 2.5. An almost equal increase of growth with increasing nitrogen deposition could be seen for all four tree species.

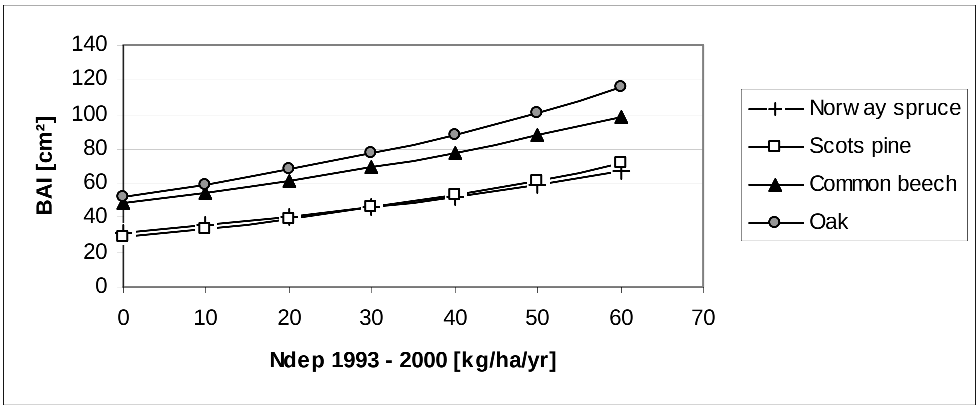

Figure 2.4 Basal area increment vs. average annual N deposition between the years 1993 and 2000, by species.

From the coefficient f_1 in our model, the relative increase in growth by 1 kg nitrogen deposition yr^{-1} ha^{-1} can be calculated from

$$\frac{BAI_{N+1}}{BAI_N} = \exp(f_1) \tag{2.7}$$

with BAI_N, basal area increment with Nitrogen deposition of N kg, BAI_{N+1}, basal area increment with nitrogen deposition being 1 kg higher, and f_1, the coefficient of our model as given in Table 2.5.

An increase in growth of 1.26 %, 1.49 %, 1.20 % and 1.34 % for Norway spruce, Scots pine, common beech, and oak, respectively results for an increase in N deposition by 1 kg. Because volume increment is approximately proportional to basal area increment (Figure 2.2), these percentages also hold for volume increment. Given a proportional relationship between the amount of carbon uptake and volume growth, the relative carbon gain per kg N deposition follows the same percentages. Our values are quiet similar to the result of Solberg et al. (2007), who found an equal increase of about 1 % for the conifers.

Referring to the total carbon uptake for European forests, given with 1729 kg carbon per hectare and year in De Vries et al. (2006b), the increase of carbon per kilogram nitrogen deposition can be estimated between 20.7 and 25.8 kg carbon per hectare and year, depending on tree species composition. This compares well with the 25 kg

C per kg N deposition as calculated by Nadelhoffer et al. (1999b) based on ^{15}N labelled tracer experiments in nine temperate forests indicating an average N retention fraction in stem wood of 0.05 and an average C/N ratio in stem wood of 500. The value is somewhat below the 33 kg as found by De Vries et al. (2006b), using a similar approach. It is also in line with results of simulations with three ecosystem models (Century, BGC and Hybrid), which estimated the average change in total carbon content of the ecosystem with the cumulative change in nitrogen deposition over 100 years at 20.1 kg C/kg N), with a standard deviation of 13.8 kg C/kg N (Levy et al., 2004). Similar results were also found in long-term (15-30 year) nitrogen-fertilizer trials in Sweden and Finland at rates of nitrogen addition below 50 kg $N.ha^{-1}.yr^{-1}$, indicating that this ratio seems rather robust (Högberg et al., 2006; Hyvönen et al., 2007b) Given the data, we could not prove a significant influence of SO_x on basal area increment during the investigation period.

Additionally, for Scots pine we were able to show a changing effect of deposition on BAI depending on competition (Figure 2.5). Trees with less competition (small BALrel) gain more from N deposition than highly competed trees. This unequal effect on growth will possibly lead to an increasing suppression of small trees in a given stand with increasing N deposition.

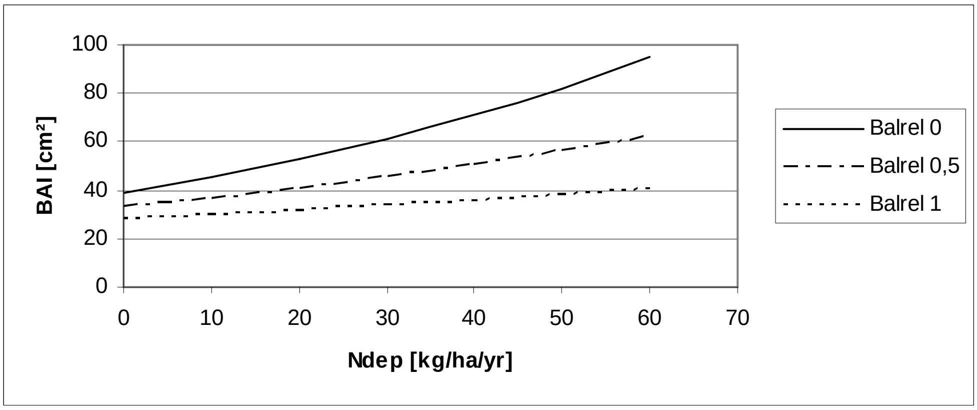

Figure 2.5 Interaction between competition and deposition for Scots pine. BAI is the basal area Increment, Ndep is average annual N deposition between the years 1993 and 2000, Balrel is the ratio between the basal are of larger trees and the total basal area of a plot.

2.6 Conclusions

To develop an individual growth model based on data on the plot level (e.g. temperature, soil) as well as on the individual tree level (e.g. dbh) a mixed model approach is necessary to take these different levels into account. Although many different variables were available, only three factors namely dbh as size factor, the competition factor BALrel and the nitrogen deposition seemed to have crucial influence on the increment of all investigated tree species. Apart from these factors, the models differed notably in structure. Out of all site factors only one soil factor, the C/N ratio and yearly mean temperature in the investigation period were significant for different species. The C/N ratio was only influential in the model for

Norway spruce. Mean annual temperature was positively related to the growth of oak and Scots pine. This positive relation of temperature with growth can be seen as an indirect sign of response by climate change. For common beech, the difference between the long term yearly mean temperature and the yearly mean temperature in the investigation period was significant in the model. The basal area increment of Norway spruce showed no response to temperature.

With the model for Scots pine it was possible to show an interesting interaction between competition, nitrogen deposition and basal area increment. Heavily competed trees gain less form nitrogen deposition than trees which are less strongly competed. Thus, nitrogen deposition will increase the competition within Scots pine stands.

Referring to the verbalised hypotheses we conclude that a strong relationship between basal area growth on the one side and tree size and competition on the other side was found in all investigated tree species. The only environmental-change factor affecting growth of all species was nitrogen deposition, while the role of other site factors differed by species. Evidence of an adverse effect of SO_x deposition on growth could not be proved by these data, while a positive effect of increasing temperature on growth could be proved for all species except Norway spruce. Keeping all other influential factors constant, the increase in growth by one additional kg nitrogen deposition varied between 1.2 % and 1.5 % depending on tree species, corresponding to a range of approximately 20-25 kg carbon sequestration per kg N deposition.

Acknowledgements

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The process based model SUMO

3 Vegetation succession as affected by decreasing nitrogen deposition, soil characteristics and site management: a modelling approach

Abstract

After many years of increasing nitrogen deposition, the deposition rates are now decreasing. A major question is if this will result in the expected positive effects on plant species diversity. Long-term experiments that investigate the effects of decreasing deposition are not available. Model simulations may yield insight in the possible effects of decreasing nitrogen deposition on the vegetation. Therefore we developed the vegetation succession model SUMO which is closely linked to the soil model SMART2. In SUMO the biomass development of five functional plant types is simulated as a function of nitrogen availability, light interception and management. The model simulates the change in biomass distribution over functional types during the succession from almost bare soil via grassland or heathland to various forest types.

The model was validated on three sites in the Netherlands and one site in the UK. The aboveground biomass of two grassland vegetation types was simulated properly, as well as the above ground biomass of heathlands during succession of sod removal. Some of the stages of forest succession were simulated less well, but the calculated biomass in the older stages agreed with the measured values.

To explore the long-term effect of a decrease in nitrogen deposition we applied the model to a heathland and a pine stand. In the heathland a major change was predicted as a result of decreasing nitrogen deposition in combination with turf stripping. The dominance of grasses changed into a dominance of dwarf shrubs, whereas at continuing high levels of nitrogen deposition grasses remained dominant. In contrast, the simulations indicated only very small effects of a decreasing N deposition in pine forests. This difference is due to the removal of excess nitrogen by management (turf stripping) in the heathland, whereas the more extensive management in the forest hardly removes any nitrogen from the system. The main conclusion from these examples is that a decrease of nitrogen deposition may retard succession, and consequently increase biodiversity in heathland but probably not in forest. The effects of declining N deposition depend on the amount of N that is removed from the system as a consequence of the various management regimes.

Key words: vegetation management, ammonium deposition, pollution, vegetation structure, nitrogen cycle

3.1 Introduction

High atmospheric deposition of sulphur and nitrogen has had an immense impact on vegetation composition and succession in the last century (Hogg et al., 1995; Lameire et al., 2000). Well-known examples are the succession of north-west European heathland dominated by *Erica tetralix* or *Calluna vulgaris* to monospecific stands of the grass *Molinia caerulea* (Berendse & Aerts, 1984; Aerts et al., 1990) and the change in species composition of the understory of forests (Van Dobben et al., 1999; Lameire et al., 2000). Simulation of the nutrient cycle and the competition between plant species can help to understand the processes behind changes, and can also provide insight into the most effective strategy to reduce human impact. An important driver for vegetation succession is the accumulation of organic matter (Van Andel et al., 1993; Olff et al., 1997; Van der Putten et al., 2000; Prach et al., 2001), which has a large impact on the soil and the plant community (Berendse et al., 1987; Knops et al., 2002), and even on the abundance of animal species (Olff et al., 1997; Van der Wal et al., 2000).

In Western Europe vegetation succession in 'natural' areas is strongly affected by management (Bakker, 1989; Uuttera et al., 1996; Van Diggelen et al., 1996; Buckley et al., 1997). Management intensity ranges from extensive, e.g. the regulation of grazers in forests by hunting, to intensive, e.g. the mowing of hay meadows several times a year. In areas with high levels of nitrogen deposition, vegetation management is often used to remove nitrogen from the system, and thus to counteract the negative effects of nitrogen deposition.This may be accomplished by e.g. turf stripping or grazing in heathland (Bokdam, 2001).

After decades of increasing nitrogen deposition (Burns, 2003; Fenn et al., 2003), deposition rates are now slightly decreasing at least in parts of North America and Western Europe (Wright et al., 2001; Kelly et al., 2002). The effects of decreasing nitrogen deposition, after years of high deposition are still unknown. Questions to be answered are: Will reduced nitrogen deposition change the rate of vegetation succession, and how do different management schemes interfere with the effect of the decreasing nitrogen input? Will reduced nitrogen input decrease the large nitrogen pool present in the vegetation and soil and prevent further leaching of nitrogen to the groundwater? Experiments that investigate the effect of decreasing deposition after years of excessive deposition are scarce and the long-term effects are still unknown.

Model simulation may be used in order to answer the questions addressed. Then models to be used should be able to simulate ecosystem development under unprecedented conditions. For this purpose a process model is most appropriate, while statistical or expert models are less suited since they are solely based on historical relationships (Verboom & Wamelink, 1999). As anthropogenic influence on the vegetation is not limited to a single vegetation type or an isolated area, the model should be able to simulate the influence of nitrogen deposition and management on succession in widely different vegetation types on a regional scale for a majority of the vegetation types.

Apart from management (in the broadest sense, i.e. including grazing) soil processes are among the most important factors that determine vegetation succession (Berendse, 1990; Van Wijnen & Bakker, 1999; Nierop et al., 2001). Therefore a vegetation succession model should include the simulation of soil processes, or be run in combination with a soil model. For the simulation of soil processes on a regional scale we used the model SMART2 (Kros et al., 1995; Kros, 2002). This model was built to simulate the effect of atmospheric deposition on soil processes, including soil N mineralization and soil acidity. It has for instance been used to calculate critical loads for nitrogen and acidity deposition on a national and European scale (De Vries et al., 1994; Van Dobben et al., 2006). However, in SMART2 the vegetation processes are mostly neglected. There is no interaction between soil and vegetation, and the vegetation development is simulated as either a steady state, or as a logistic growth curve. Only a very small number of vegetation types are distinguished, and vegetation succession is not simulated.

Over the years many vegetation models have been developed. Models like Century (Parton et al., 1987; Parton et al., 1993), NUCOM (Van Oene et al., 1999b), FORGRA, (Jorritsma et al., 1999), MASSIMO (Kaufmann, 2000; Schmid et al., 2006), FORSPACE (Kramer et al., 2003), NICHE (Koerselman et al., 1999), ForSAFE (Wallman et al., 2005) only simulate a single site or region, and only for one vegetation type (i.e. grassland, heathland, forest or dunes). The Century model was recently modified to be able to simulate forest as well (Kirschbaum & Paul, 2002) but only soil variables were validated. Although the Century model now is equipped for modelling grassland as well as forest, it is still unable to simulate the succession from grassland to forest. Changes in heathland can be simulated with the 'UK heathland' model (Terry et al., 2004). However, this model only simulates a few species and neglects natural succession towards forests. A variety of forest models exists with widely different aims, but these models do not simulate the development from or towards other vegetation types and mostly neglect the effects of the understory on the tree development (e.g. Bugmann et al., 1996; Jorritsma et al., 1999; Kaufmann, 2000; Smith et al., 2001; Porté & Bartelink, 2002; Kramer et al., 2003; Wallman et al., 2005). A model that is valid for all major vegetation types is required for the evaluation of the effects on biodiversity of nation-wide pollution abatement strategies. Although a number of GIS-based models exist that connect vegetation types to abiotic conditions (e.g. Runhaar et al., 1999; Münier et al., 2001; Nabuurs & Schelhaas, 2003) such models are either based on statistical relationships or on expert knowledge whereas dynamic processes are neglected. In such models new environmental conditions cannot be realistically dealt with. For the answering of the questions addressed in this paper a process model that is able to simulate vegetation responses in a changing environment is necessary. The JPL model (Sitch et al., 2003), also follows the modelling set up chosen here; it includes many vegetation types and functional types. JPL is a carbon driven model and does not include dynamic effects of nitrogen (limitation) on the growth. The combination of the GUESS-LPJ model (Hickler et al., 2003) uses a similar approach, but also here the effect of nitrogen on the growth is neglected.

For this purpose we developed the model SUMO (which is short for SUccession MOdel). In combination with SMART2 this model should be able to evaluate the effects of management and nitrogen deposition on plant competition and on the interaction between soil and vegetation. We used SUMO in combination with SMART2 to explore the effects of a decreasing nitrogen deposition on the vegetation to address the above mentioned questions.

SUMO was built as an extension to the already existing model SMART2 (Kros, 2002). SUMO is based on the same principles as the much more elaborate and plant species specific model NUCOM (Berendse, 1994b, a; Van Oene et al., 1999a; 1999b). Where NUCOM was built and tested for a specific area (the Veluwe in The Netherlands) to simulate the succession from bare soil to oak forest, SUMO is a more general model covering natural areas all over The Netherlands, where in principal many succession schemes are possible. Where NUCOM is a site specific model needing many input data, SUMO is a more general model applicable in many situations. SUMO needs only a limited number of site specific data. Although SUMO operates on the same principles as NUCOM it was totally rebuilt.

First we will give a short general description of SUMO and SMART2, and then we will describe each process in detail, including its parameterisation and validation.

3.2 Model description

SUMO is written in the computer language FORTRAN (Compaq Computer Corporation, 1999). It simulates the biomass and nitrogen dynamics in five functional plant types: herbs and grasses, dwarf shrubs, shrubs, pioneer trees, and climax trees. Each functional type is assumed to consist of three organs: root, stem, and leaf. The time step of the model is one year. In each time step the biomass of the five functional types is computed, based on the biomass in the previous time step, biomass growth and death in the present time step, and removal of biomass by management (Equation 1). The growth is in turn calculated on the basis of an assumed maximum growth, which is reduced by nitrogen availability (provided by SMART2) and light interception (Equation 2). The dead biomass (litter with nitrogen content) is returned to the relevant pools in SMART2.

SUMO distinguishes six vegetation types (grassland, heathland, reedland, shrub vegetation, salt marsh and forest). The model equations are parameterised for each combination of functional plant type and vegetation type. Much attention is given to the simulation of competition between the functional types. The competition for nitrogen and light is assumed to be the driving force for succession. The initial vegetation type is given as input to the model. Apart from biomass growth, SUMO also simulates height growth.

For the functional types herbs/grasses, dwarf shrubs, and shrubs, SUMO simulates the total biomass of all species. For the functional types pioneer tree and climax tree the biomass of a specific tree species is simulated. Each species is given its own set of parameters. The pool of tree species consists of Scots pine (*Pinus sylvestris*), larch

(*Larix decidua*), Douglas fir (*Pseudotsuga menziesii*), Norway spruce (*Picea abies*), birch (*Betula pendula* and *Betula pubescens*), ash (*Fraxinus excelsior*), alder (*Alnus glutinosa*), willow (*Salix alba* and *Salix cinerea*), poplar (*Populus spec.*), oak (*Quercus robur* and *Quercus petrea*), northern red oak (*Quercus rubra*) and beech (*Fagus sylvatica*). The dominant tree species included in the model are selected on the basis of the soil characteristics.

SUMO simulates the C and N fluxes. The nitrogen that becomes available through mineralization (simulated by SMART2) and atmospheric deposition is partitioned over the functional types and within each functional type over its organs, using fixed percentage distributions per functional type / vegetation type combination. Nitrogen reallocation before litterfall is also simulated.

The vegetation type may change during a model run. When the management (mowing) of grassland is stopped, succession to heathland or forest may occur. The vegetation type is determined on the basis of the biomass present in the five functional types. In grassland the vegetation type changes into forest if the stem biomass of the functional types shrubs, pioneer trees or climax trees exceeds a threshold value (Table 3.1). The pioneer tree, the climax tree and the forest type are selected on the basis of the soil type and the groundwater level present at the specific grid (Table 3.1). Table 3.1 gives a scheme of all possible succession pathways and the conditions for succession.

Table 3.1 Succession scheme for vegetation types with conditions under which succession takes place (msl = mean spring groundwater level in m below surface, SP = sand poor, SR = sand rich, SC = sand calcareous, CN = clay non-calcareous, CC = clay calcareous, PN = peat non calcareous and LN = loess non-calcareous), and tree species in the new vegetation. Succession will take place when the total stem biomass of the shrubs and trees is above 0.15 ton.ha^{-1}.

original type	new type	soil type	msl in -m	pioneer tree	climax tree
grassland	heathland				
grassland	natural forest	SP, SR, CN, CC, LN	< 0.3	alder	Ash
	pine forest	SP	≥ 0.3	birch	Pine
	natural forest	SR, LN	≥ 0.3	oak	Beech
	natural forest	SC		oak	Beech
	natural forest	CN, CC	≥ 0.3	alder	Poplar
	natural forest	PN	< 0.3	alder	Birch
	natural forest	PN	≥ 0.3	alder	Ash
heathland	natural forest	SP, CN, CC, LN	< 0.3	alder	Ash
	pine forest	SP, SR	≥ 0.3	birch	Pine
	natural forest	SR	< 0.3	birch	Oak
	natural forest	SC		oak	Beech
	natural forest	PN	< 0.3	alder	Birch
	natural forest	PN	≥ 0.3	alder	Ash
	natural forest	LN	≥ 0.3	oak	Beech
reedland	natural forest			alder	Ash
shrubland	natural forest			birch	Oak

The processes modelled in SUMO are based on the descriptions made by Berendse (1994b; 1994a), and are extensively described in Appendix 1.

3.3 Parameterisation

SUMO uses over 1000 different parameters (including the different parameters per organ for five functional types and for ten vegetation types). Almost all parameters are based on extensive literature research (references can be found in Wamelink et al., 2000a; Wamelink et al., 2000b and Appendix 1). The data from literature were stored in a database. The parameters were estimated from the database and used for test runs of SUMO using a test-set of vegetation types. Fine-tuning of the parameters took place until the model produced an acceptable outcome. Fine-tuning was always done within the range of the data found in literature (which was quite wide in some cases), but most of the parameters were left unchanged. Parameters that are fine-tuned are the maximum growth rate (A_{max} in Equation 2), light interception coefficient (k in Equation 3), minimum (N_{min} in Equation 6) and maximum nitrogen content (N_{max}). Maximum growth rate and light interception had to be fine-tuned because for these parameters data are scarce or absent. Parameters involved in the height of the functional type, the influence of moisture on the growth and management were never fine-tuned. The model does not need to be parameterized for different sites.

3.4 Validation

The simulation of biomass increment was validated using data collected at two grassland sites, a heathland site and a forest site. The nitrogen content of the leaves was validated on a set of forest stands.

The first grassland site is situated near Wageningen ($51^0$58' N, $5^0$39' E) and is part of a long-term field experiment started in 1958 on former agricultural land (Elberse et al., 1983). The soil type is clay with a regulated groundwater table suitable for agricultural use. The site is mown once a year and not fertilised. Every year the mown biomass was dried and weighed. The changes in aboveground biomass were simulated using site specific historical deposition data. Due to yearly differences in i.e. rainfall and temperature the measured biomass varies greatly between years, while the simulated biomass does not vary much among the years (Figure 3.1). But the slight decline in the simulated biomass is in agreement with the trend of the measured biomasses. The large difference for the first year is probably caused by the former agricultural use of the land, which has led to a relatively high measured biomass. The effects of former agricultural use of grassland or vegetation in general can not be simulated by SUMO. The decline in the measured and the simulated biomass is caused by the yearly removal of aboveground biomass, while fertilisation has stopped.

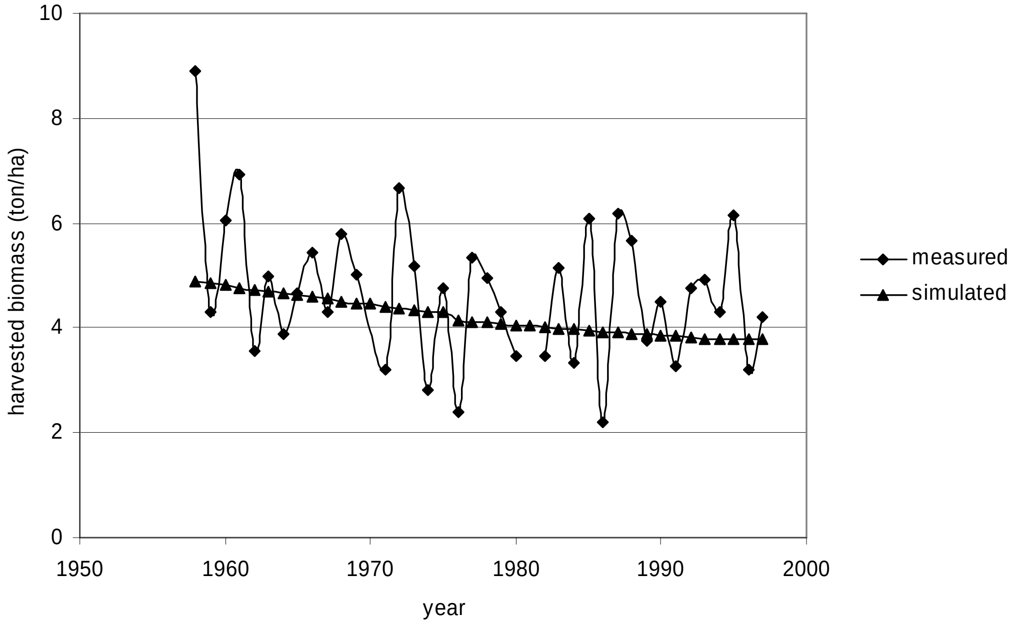

Figure 3.1 Measured and simulated aboveground biomass for a mown grassland site near Wageningen.

The second grassland site is the Parkgrass experimental site at Rothamstead in the UK. The site was mown twice a year and the harvested biomass was weighed and averaged over ten year periods. The experiment started around 1850 and continues until today. The site is extensively described by i.e. Lawes and Gilbert (1880), Cashen (1947), Thurston et al. (1976), Jenkinson et al. (1994). The site was probably extensively manured just after the start of the experiment, but this treatment stopped after a few years (Jenkinson et al., 1994). The model was initialised with an estimated amount of biomass (Appendix 2). The grassland was assumed to be mown once a year and grazed with a density of 2 sheep per hectare from 1850 until 1852, then mown twice a year till 1863 and manured with 25 $kg.ha^{-1}$ N from 1856 until 1863, and then mown once a year up to present. We used site specific data for sulphur and nitrogen deposition. Both S- and N-deposition increased steadily from the start of the experiment, but decreased in recent years, after c. 1980 and c. 1990, respectively (Appendix 2). The nitrogen deposition was more or less stable between 1900 and 1940, which is accounted for in the model run. The field data were retrieved from Dodd et al. (1994). The results show that the harvested biomass is fairly well simulated by SUMO (Figure 3.2).

Only the effect of the nitrogen deposition since approximately 1960 is slightly underestimated. But the reduction in biomass harvest in the early years due to exhaustion of the soil, the stabilisation of the harvest when the effect of N deposition compensates for the exhaustion, and the increase of the harvest later on due to the further raise of the deposition is simulated quite well. A part of the discrepancy between modelled and measured biomass may be caused by the changes in plant species composition under contemporary N inputs.

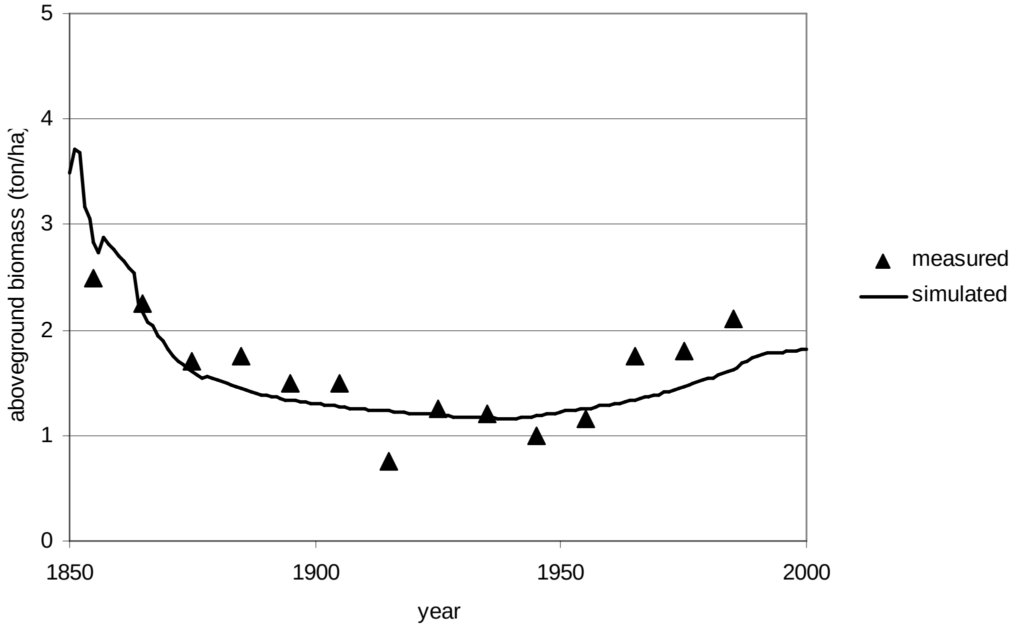

Figure 3.2 Measured and simulated biomass harvest for the Rothamstead experimental grassland site in the UK.

SUMO was validated for heathland on a site in the south of The Netherlands near Strabrecht ($51^0$23' N, $5^0$37' E, Appendix 2), which was studied by Berendse (1990). We compared the biomass in eight plots where turf stripping had taken place in different years. Turf stripping includes the removal of all biomass and the litter and humus layer down to the mineral soil layer after which succession starts on a bare substrate. Above and belowground biomass was harvested in 1984. SUMO was run for each site separately. The runs were started in the year of turf stripping, which differs for each site, and continued up to 1984 when the biomass was measured, using site specific information on soil type, deposition etc. Aboveground biomass simulated by SUMO was compared with the measured aboveground biomass. In general the aboveground biomass is simulated well, although it is overestimated for the plots were the turf was stripped 16 and 18 years before the field data collection (Figure 3.3). For the oldest plot the majority of the simulated biomass is present in grasses. In the field dwarf shrubs are only present as dead biomass in the litter layer in this plot. In all other plots almost all measured and simulated biomass is present in the functional type dwarf shrubs. The results are comparable to those found by Terry et al. (2004) for simulations of heathland development in the UK. They found that above 30 kg.ha^{-1}.y^{-1} nitrogen deposition the biomass of heath was replaced by biomass of grasses in the long term

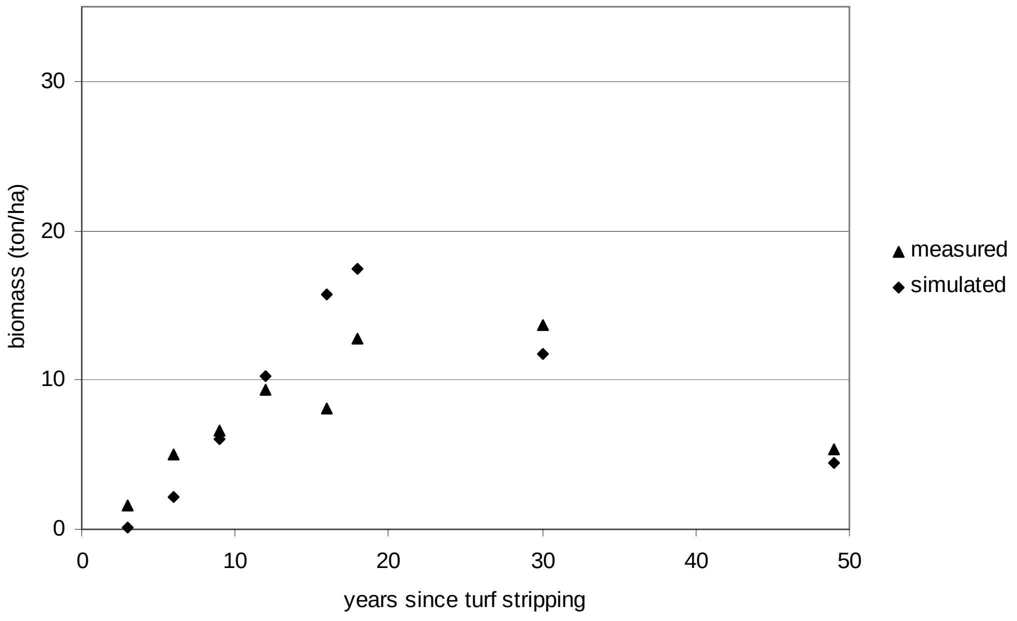

Figure 3.3 Simulated and measured aboveground biomass for a heathland near Strabrecht in The Netherlands. The simulated biomass is the result of separate independent simulations, starting at the moment of turf stripping, and continuing until the field survey.

The forest site that we used for validation is located in the north of The Netherlands near Sellingen ($52^0$57' N, $7^0$03' E, Appendix 2). Here small forest plots are situated on former agricultural land. This chronosequence consists of ten plots of 0, 14, 25, 32 and 89 years old in 1999 with two independent plots per successional age. At the beginning of each stage trees were planted. One of the 89-years old plots was cut before 1999 and therefore omitted. The remaining stages all have oak (*Quercus robur*) as the dominant tree species. The undergrowth is almost absent in some stages, while in other stages the understory is dominated by grasses. The 0-year stage that is still in agricultural use was used to initialise the simulation. The actual biomass of the trees was estimated on the basis of the diameter at breast height and the height. The above ground biomass of the herbs was harvested and weighed (Van Oene et al., 1999a; Wamelink et al., 2001). Historic deposition data were used for the simulation. The simulated values were compared with the measured biomass of the sites (Table 3.2 and Figure 3.4). Some of the successional stages are quite well simulated by SUMO; other successional stages are less well simulated. The simulated biomass in older forest is too low, but the biomass of other functional types is simulated quite well. An exception is the biomass of the pioneer trees in the 89-year-old stage and the biomass of the climax trees in the 25 and 32 year old stage. This difference is probably caused by the thinning regime in the past. Site specific data of the thinning regime are not available.

Table 3.2 Validation results for the chronosequence Sellingen. Figures are biomass in ton.ha^{-1} dry matter per functional type, measured in the field with (standard error) and simulated by SUMO.

age		herbs (s.e.)	dwarf shrubs (s.e.)	Shrubs (s.e.)	pioneer tree (s.e.)	climax tree (s.e.)
14	measured	0.81 (0.11)	0	0	0.02 (0.03)	28.13 (2.35)
	SUMO	0.79	0.11	0.64	0.64	26.50
25	measured	0.37 (0.16)	0	0	0.09 (0.09)	39.03 (0.72)
	SUMO	0.01	0.04	0.59	0.70	47.23
32	measured	0.14 (0.08)	0	0	0	66.96 (0.61)
	SUMO	0.01	0.02	0.58	0.73	48.95
89	measured	0.77	0	0	4.69	111.36
	SUMO	0.01	0.01	0.44	0.29	98.33

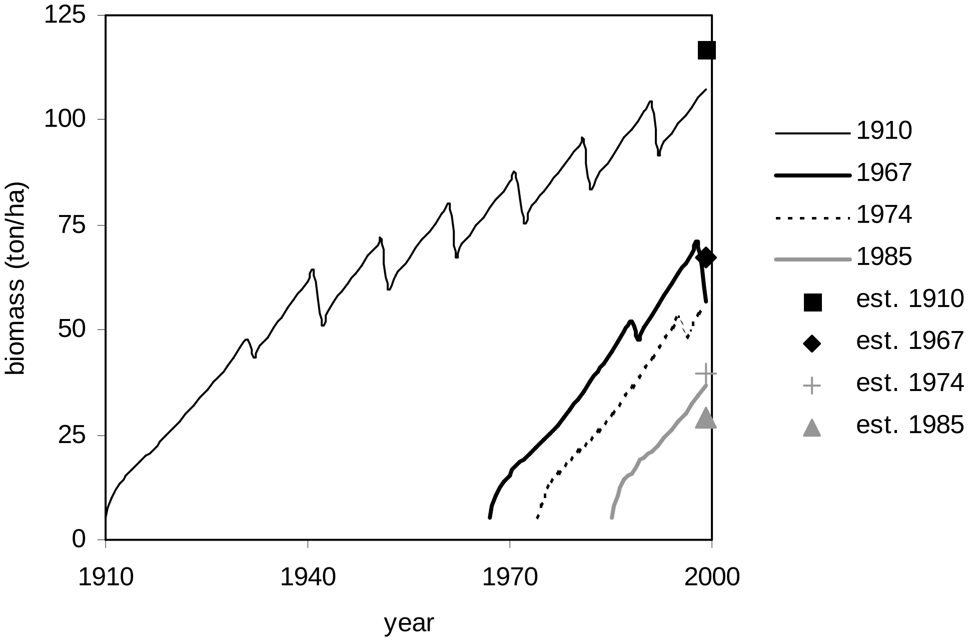

Figure 3.4 Simulated total biomass increment for four different successional stages at the Sellingen site. The forests where planted in 1910, 1967, 1974 and 1985 on former agricultural land. The biomass of the sites was estimated in 1999 (est. 1910, est. 1967, est. 1974 and est. 1985 giving the estimations for the respective plant years).

SUMO was also validated for the nitrogen concentration in the leaves of planted trees on 169 forest sites on all major soil types situated all over The Netherlands, The simulated N concentrations were regressed on the measured N contents ($R^2 = 39\%$, intercept = 2.1 ± 1.9 ($p = 0.27$), regression coefficient = 0.92 ± 0.09 ($p < 0.001$). When there is no difference between simulated and measured N content one would expect a regression coefficient of 1.0 and an intercept of 0.0. For both the values do not differ significantly ($p = 0.27$ for the intercept and $p = 0.34$ for the regression coefficient). The percentage explained variance indicates that the N contents of the leaves are simulated fairly well.

3.5 Analysis of the effect of decreasing nitrogen deposition

Using SMART2-SUMO we explored the effect of decreasing nitrogen deposition on the vegetation for three sites, a planted pine forest ('Zeesserveld', 52003' N, 6027' E, Appendix 3), a heathland ('Edesche heide', 52003' N, 5043' E, Appendix 3) and a grassland (near Renkum 51058' N, 5043' E, Appendix 3).

The three sites are nature reserves where the goal is to enhance or at least preserve biodiversity (Koop & Clerkx, 1995; Van Dobben et al., 2002b). In the forest the managers attempt to achieve this objective by cutting 10% of the pine biomass each 10 years, thereby promoting the development of oak and enhancing structural diversity. We initialised the simulation with measured tree biomass values, while the initial biomass of the other functional types was estimated from vegetation relevés. We simulated vegetation development for ten plots. Every 10 years 10% of the dominant trees were cut and the biomass removed. The presented results are the average of the ten plots. In the heathland it is attempted to preserve biodiversity by turf stripping each 30 years in order to prevent the dominance of grasses over heather. Here we also simulate vegetation development if only shrubs and trees would be removed from the heathland (to prevent succession). The initial biomass per functional type is the measured biomass in a heathland dominated by *Calluna vulgaris* (30 years old) or dominated by grasses (for the degraded stage of heathland, 50 years old). In the grassland the goal is to increase biodiversity by mowing once a year and removing of the mown biomass. The initial biomass is the measured biomass of a grassland site situated at the border of a brook valley and a forest on poor sandy dry soil. The grassland was till recently in agricultural use.

To be able to evaluate the effect of management combined with nitrogen deposition decrease we ran two deposition scenarios. The first scenario (1) combines the above-described management with a constant nitrogen deposition rate of 45 $kg.ha^{-1}.yr^{-1}$. The second scenario (2) has a linearly decreasing deposition rate, from 45 $kg.ha^{-1}.yr^{-1}$ in 2000 to 10 $kg.ha^{-1}.yr^{-1}$ in 2090. The models are initialised in the first ten years of the run (1990 - 2000) at a constant deposition of 45 $kg.ha^{-1}.yr^{-1}$.

In the simulation of the development of the forest site we observed a transition from pine to oak. At the end of the simulation period the vertical diversity is still low (Figure 3.5a and 3.5b for scenario 1 and 2, respectively).

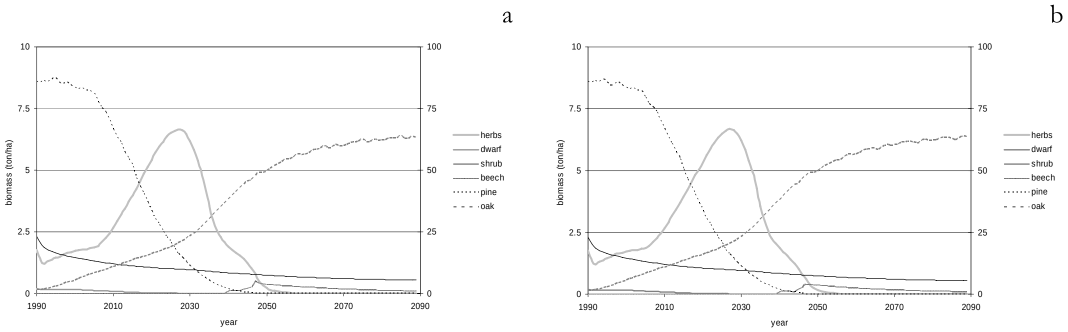

Figure 3.5 Simulated development of biomass per functional type in the 'Zeesserveld' pine forest under scenario 1 (a, constant deposition of 45 kg.ha^{-1}.yr^{-1}) and scenario 2 (b, decreasing deposition from 45 kg.ha^{-1}.yr^{-1} in 2000 to 10 kg.ha^{-1}.yr^{-1} in 2090). The right axis gives the biomass for pine and oak, the left axis for all other functional types.

During the transition phase from pine to oak the grasses/herbs become dominant. The shrubs steadily decrease and the dwarf shrubs almost vanish from the site. Around 2040 beech starts to appear, but this species becomes suppressed by oak. In the field beech is often observed to be able to grow under an almost closed oak canopy, which is not taken into account by the model. For this reason the biomass of beech is most likely underestimated. The end of the simulation period shows a dark forest with a strong dominance of oak and little undergrowth. Interestingly, a decreasing deposition has hardly any effect on these processes. This is caused by the relatively high soil N mineralization, despite the decreasing deposition. In the years that deposition rates were high, a large pool of nitrogen was built up in the forest, and this pool is depleted only very slowly, because harvesting of stem wood removes only little nitrogen from the system. The removal of biomass by cutting causes open spots where new tree species such as beech may get an opportunity to grow. In SUMO the biomass is just subtracted from the total biomass and no open spots will be present. This may partly explain why beech is suppressed by oak. This problem may be solved by modelling smaller grid cells, where thinning is achieved by removing all of the trees from some of the cells.

The results for the heathland are totally different from those for the forest (Figure 3.6a and 3.6b).

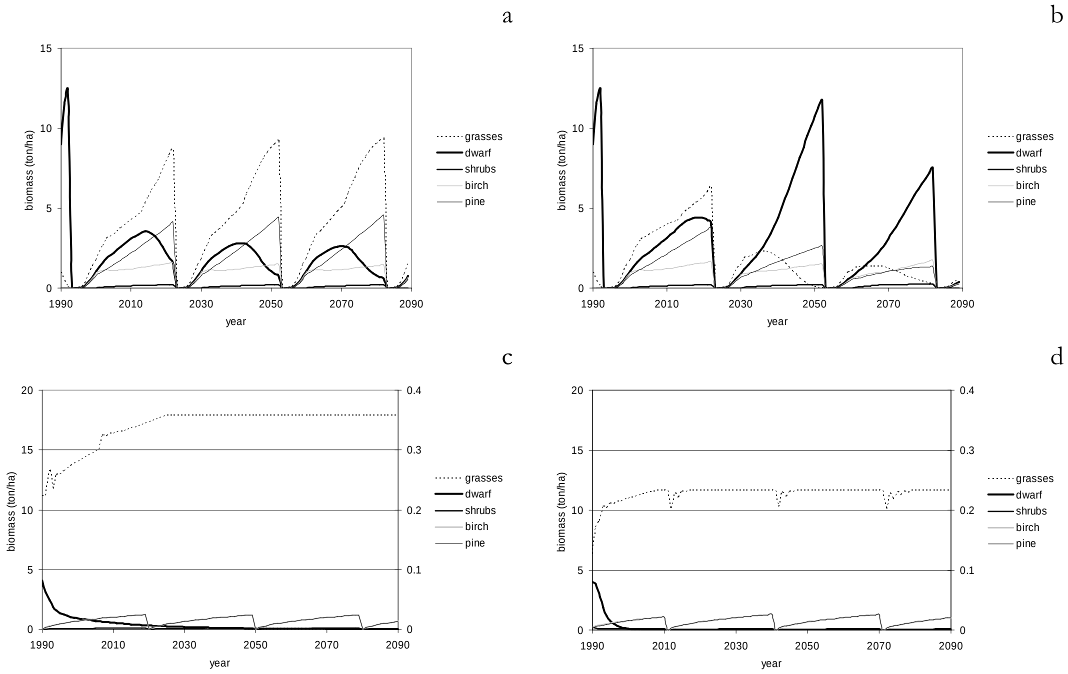

Figure 3.6 Simulated development of biomass per functional type in the 'Edesche Heide' heathland under scenario 1 (fig. a, constant deposition of 45 kg.ha^{-1}.yr^{-1}) and scenario 2 (fig. b, decreasing deposition from 45 kg.ha^{-1}.yr^{-1} in 2000 to 10 kg.ha^{-1}.yr^{-1} in 2090). Fig. c gives the simulation for scenario 1 of a degraded heathland, where only shrubs and trees are removed from the vegetation. Fig. d gives the simulation for scenario 2 combined with shrub and tree removal.

At a constant deposition of 45 kg.ha^{-1}.yr^{-1}, the grasses/herbs become dominant and the dwarf shrubs start to disappear at the end of the 30 year cutting cycle, and trees (birch and pine) are also becoming more dominant. However, when the deposition decreases the dwarf shrubs are more competitive and become the dominant functional type throughout the cutting cycle. Since with the turf stripping a lot of nitrogen is removed, the availability of nitrogen decreases and a different vegetation type evolves. The last cycle (Figure 3.6b) already indicates that when a 30 year cycle is maintained at low deposition, heather biomass will decrease and an open vegetation type may develop, that in term could even turn into blown sand. This is what actually has happened in historic times when heathland was over-exploited at low deposition rates (Gimingham, 1972). So if the objective is to maintain heathland, the management cycle has to be extensified. Figure 3.6c and 3.6d illustrate what would happen when only shrubs and trees are removed. With a constant deposition of 45 kg.ha^{-1}.yr^{-1} the heathland turns into a grassland and remain so (Figure 3.6c), and with a decreasing deposition turns into grassland, though with less biomass compared to the situation with high deposition (Figure 3.6d). The nitrogen pool in the vegetation and soil remains constant for a very long period. It is clear that if the excess nitrogen is not actively removed a return to a heathland is not likely to occur even when deposition drops.

A large difference between the two deposition scenarios is also simulated for the grassland (Figure 3.7). At a constant and high deposition the total biomass of the functional type grasses and herbs remains stable during the whole simulated period (Figure 3.7a), although quite a large amount of biomass and thus nitrogen is taken out of the system yearly. Only when the deposition decreases (Figure 3.7b) the total biomass decreases as well; almost all standing biomass is halved. The biomass of the other functional types than herbs and grasses is negligible.

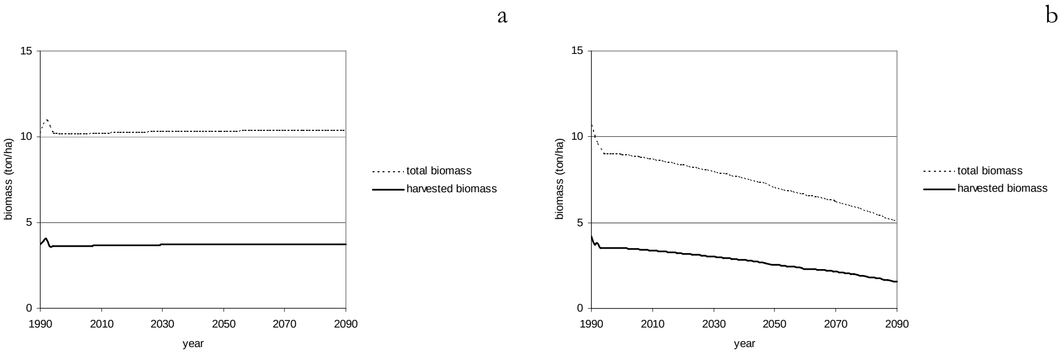

Figure 3.7 Simulated development of the total biomass and harvested biomass in a grassland near Renkum under scenario 1 (fig. a, constant deposition of 45 $kg.ha^{-1}.yr^{-1}$) and scenario 2 (fig. b, decreasing deposition from 45 $kg.ha^{-1}.yr^{-1}$ in 2000 to 10 $kg.ha^{-1}.yr^{-1}$ in 2090). The grassland is mown once a year, the biomass for the other for functional types than grasses and herbs is negligible.

3.6 Discussion

We simulated the long-term effect of a decrease in nitrogen deposition under the assumption that the model not only performs well under constant or increasing, but also under decreasing nitrogen deposition. The results for Rothamstead show that at least in grassland (in the earlier years of the experiment, see Figure 3.2) the effect of a decrease in nitrogen availability is simulated well and that in grassland that is mown yearly a drop in deposition rate will reduce the total biomass (Figure 3.7b). Mowing once a year alone is not sufficient to counteract the effect of deposition. Deposition must apparently decrease to reach a lower total biomass. These results do not agree with measurements in the field during the first years in other grassland sites, where the biomass dropped in the first years after fertilisation stopped (Berendse et al., 1992). Lower biomass production in former agricultural grassland is desirable because it is one of the requirements for the restoration of plant species diversity in grasslands (Al-Mufti et al., 1977; Grime, 1979; Schaffers, 2002; Marriott et al., 2004). At the simulated site the total biomass decreased from approximately 10 to 5 $ton.ha^{-1}$, which may lead to an increase in number of species from 25 to 35 (c.f. Schaffers, 2002), if other requirements are fulfilled, including sufficient seed dispersal.

For heathland the biomass distribution over the five functional types changes when nitrogen deposition decreases. Management is an important factor in heathland (Figure 3.6). It removes the excess nitrogen that has built up during the years of high nitrogen deposition. Turf stripping in combination with a drop in nitrogen deposition changes the dominance of the herbs and grasses into a dominance of dwarf shrubs. In natural heathland dominance of dwarf shrubs is strongly correlated with the occurrence of threatened plant species (Gimingham, 1972). If management would only aim at stopping succession by removing shrubs and trees, the soil nitrogen pool would increase even (see Figure 3.6d). By removing nitrogen from the system, management not only reduces the total biomass production but also changes the vegetation from dominated by herbs/grasses (e.g. *Molinia caerulea*) to dwarf shrubs (e.g. *Calluna vulgaris* or *Erica tetralix*). It is also clear from the scenario analyses that no increase in biodiversity can be expected if deposition rates do not change; in that case it will even be very difficult to maintain biodiversity at the present level. Moreover Figure 3.6c shows that when the deposition remains high and only shrubs and threes are removed, the biomass of herbs and grasses is not influenced by the removal of nitrogen from the system.

The effect of declining N deposition in forest is in strong contrast with the effect on heathland and grassland. In forest the differences between the two scenarios are negligible, and with 10% thinning every ten years no real increase in biodiversity can be expected even if deposition drops. Apparently the removal of nitrogen by thinning is too small to remove the excess nitrogen from atmospheric deposition.

Many processes were neglected in SUMO, but at least three of them are considered important enough to be incorporated in the model at a later stage. The first is the effect of moisture availability. The simulated sites are assumed not to be limited by water availability. However, especially in the light of the expected climate change and the associated changes in precipitation, the effect of water availability was incorporated in an updated SUMO version (see Wamelink et al., 2007c, this issue). Also missing in this first version of SUMO are the effects of phosphorus and base cations on the growth. Under natural circumstances, nitrogen availability is often limiting plant growth, which justifies the choice of basing the biomass growth on the nitrogen availability. However other elements like phosphorus, potassium, calcium and magnesium may also limit growth (Kooijman & Besse, 2002; Wassen et al., 2005). Therefore, the model cannot simulate situations where phosphorus or base cations are solely limiting the growth (see Wamelink et al., 2007c, this issue). The third is the production and decay of dead wood. Although the nitrogen content of dead wood is low, the total amount can be significant. Also, dead wood is considered as an important prerequisite for biodiversity in forest (Ohlson et al., 1997; Nilsson et al., 2001). However, the present version of SUMO was tested on sites where dead wood does not play a significant role.

SUMO does not simulate the effects of dispersion of seeds. It is assumed that each vegetation type will occur in any site with suitable abiotic conditions. When single species are important (here only the trees) this is an important limitation of the model. For the other functional types this is less serious since they consist of groups of many species.

The generally poor results of the simulations of the development of forest ecosystems may be due to the lack of sufficient data on the management of the validation sites. A more fundamental problem is that the shorter functional types (grasses and herbs and dwarfshrubs) are underestimated by SUMO during some of the successional stages. The same problem was also encountered by Smith et al.

(2001) when testing the GUESS-LPJ models. Here it also appeared to be difficult to simulate the biomass of grass when trees become the dominant functional types. This may be due to a too low simulated availability of light below the tree canopy. A shortcoming of both models is that the functional types compete for nitrogen in one homogeneous soil layer, while in reality the vertical distribution of the roots may differ among the various functional types so that they only partly compete for nitrogen. This problem may be solved by modelling the competition for nitrogen in different soil layers (cf. Berendse, 1979).

We conclude that SUMO can be used to evaluate scenarios of nitrogen deposition reduction after many years of high deposition rates with or without additional vegetation management. The model shows us that increased nitrogen input in the vegetation will lead to an accelerated increase of the amount of nitrogen in the ecosystem. When the input stops, the nitrogen will remain in the vegetation and litter layer for a long period. We predict that even after the nitrogen input from deposition has been reduced the vegetation will suffer long afterward, especially in forest ecosystems. Restoration of biodiversity is only possible by removing biomass or the soil top layer and thus nitrogen from the system. Vegetation management plays a crucial role in the restoration of vegetation after nitrogen deposition; it removes the excess nitrogen from the system. However, the high management intensity required to compensate for these high levels of N deposition can be costly (Wamelink et al., 2005).

Acknowledgements

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4 Effect of nitrogen deposition reduction on biodiversity and carbon sequestration

Abstract
Global warming and loss of biodiversity are among the most prominent environmental issues of our time. Large sums are spent to reduce their causes, the emission of CO_2 and nitrogen compounds. However, the results of such measures are potentially conflicting, as the reduction of nitrogen deposition may hamper carbon sequestration and thus increase global warming. Moreover it is uncertain whether a lower nitrogen deposition will lead to a higher biodiversity. In this study we forecast that a gradual decrease in nitrogen deposition from 40 to 10 kg $N.ha^{-1}.yr^{-1}$ in the next 25 years will cause a drop in the net carbon sequestration of forest in The Netherlands to 27% of the present amount, while biodiversity remains constant in forest, but may increase in heathland and grassland.

4.1 Introduction

Human activities have led to a worldwide decrease in biodiversity (Chapin et al., 1998; Swift et al., 1998; Smith et al., 2000; Dobson, 2005), often caused by land use change (Vitousek et al., 1997; Swift et al., 1998; Zebisch et al., 2004). Intensified land use caused an increase of reactive nitrogen in the atmosphere and soil in agricultural areas, but atmospheric reactive nitrogen also increased due to more intense traffic (Hogg et al., 1995) (Kelly et al., 2002) (Lameire et al., 2000; Wright et al., 2001; Tarasón et al., 2003). Moreover industrial activities have lead to an increase of CO_2 in the atmosphere, which may lead to higher temperatures causing an even higher pressure on biodiversity. Whether or not a higher CO_2 concentration will affect biodiversity directly still remains uncertain (Peterson & Melillo, 1985; Chapin et al., 2000; Smith et al., 2000; Malcom et al., 2002; Thomas et al., 2004). These global issues have been the subject of several international conferences where many countries have agreed on countermeasures to prevent further loss of biodiversity and to stop global warming (e.g. the Rio and Johannesburg conferences and the Kyoto conference leading to the Kyoto protocol). Main targets resulting from the conferences are to stop further decrease of biodiversity and to stop global warming. The latter may be reached by a reduction of CO_2 release into the atmosphere or by an increase of carbon sequestration. In areas that are densely populated or have an intensive agricultural use biodiversity may be enhanced by a reduction of the nitrogen release. These areas can be found mainly in Western Europe, e.g. England, Belgium, Denmark, Germany and the Netherlands, and some parts of the U.S.A. The policy goals, however, could be conflicting since a decrease in nitrogen deposition may negatively affect carbon sequestration. Experimental research has revealed a positive relation between N addition and growth, and thus carbon sequestration, in Scandinavian forests where nitrogen strongly limits growth (Tamm et al., 1999). The relation between N addition and biodiversity has also been experimentally tested (Bobbink & Roelofs, 1995; Bobbink et al., 1998; Thomas et al., 1999; Reich et al., 2001; Aerts et al., 2003) and showed that N addition leads to a decrease in biodiversity. However, research into the combined effect of nitrogen deposition on both carbon sequestration and biodiversity is scarce, especially on a regional scale (Reich et al., 2001; Huston & Marland, 2003).

Measures to reduce nitrogen emission have begun to take effect, and deposition has a downward trend at least in some areas (Kelly et al., 2002; Tarasón et al., 2003). But the deposition is still high; for instance the average deposition in Western Europe is approximately 18 kg N.ha^{-1}, whereas the estimated background deposition is approximately 3 kg N.ha^{-1} (Galloway et al., 1982; Galloway et al., 1984; De Vries, 1994; Tarasón & Schaug, 2000). Several sources claim that increased N deposition will enhance carbon sequestration, although the extent of this effect shows a great deal of variation (Peterson & Melillo, 1985; Schindler & Bayley, 1993; Townsend et al., 1996; Holland et al., 1997; Nadelhoffer et al., 1999b; Hungate et al., 2003), and some of these studies suggest that it is only of minor importance (Townsend et al., 1996; Nadelhoffer et al., 1999b). Although there is ample evidence that increased N deposition results in a decrease of floristic diversity, at least in grassland and heathland communities (Aerts et al., 1990; Bobbink et al., 1998; Roem & Berendse, 2000; Aerts et al., 2003; Stevens et al., 2004), it is not certain whether a decrease in deposition will also lead to an immediate return of lost species. This may depend on e.g. the presence of diaspores in the seed bank or in the neighbourhood for recolonisation. However, a decrease in N deposition will lead to improved environmental conditions for these species in terms of soil pH and N availability.

In view of the above, the big questions are (a) whether or not the biodiversity will improve after a decrease of nitrogen deposition and (b) how a decrease of nitrogen deposition will influence the carbon sequestration. To answer these questions, we explored the effect of nitrogen deposition on carbon sequestration in combination with its effect on potential floristic diversity by scenario analyses using the model chain SMART2-SUMO-NTM3 (Berendse, 1994b; Kros, 2002; Van Dobben et al., 2002b; Wamelink et al., 2003) on a regional scale. We choose floristic diversity because nitrogen deposition has a close effect on the occurrence of plant species; rare species tend to get locally extinct when deposition rates increases. The effects of climate change (raised temperature and carbon dioxide) on the growth of the vegetation are not included in this research.

4.2 Material and methods

Models

The SMART2 (Kros, 2002; Kros et al., 2002) model simulates soil processes, SUMO (Berendse, 1994b; Van Dobben et al., 2002b) simulates vegetation processes and succession, whereas NTM3 (Wamelink et al., 2003) predicts the 'potential floristic diversity' based on groundwater level, nitrogen availability and pH (the latter two simulated by SMART2). SMART2 and SUMO are dynamic process models that include complete nitrogen and carbon cycles, based on time steps of one year.

The model SMART2 (Kros, 2002; Kros et al., 2002) considers linked biotic and abiotic processes in the soil solution as well as in the solid phase. It represents the inorganic soil and two organic soil compartments. The model consists of a set of mass balance equations, describing the soil input-output relationships and rate-limited and equilibrium soil processes. The soil solution chemistry depends on the net element input from the atmosphere and groundwater, canopy interactions, geochemical interactions in the soil (CO_2 equilibria, weathering of carbonates, silicates and/or Al hydroxides, SO_4 sorption and cation exchange), and nutrient cycling (litterfall, mineralisation, root uptake, nitrification and denitrification). Nutrient uptake by the vegetation and litterfall (including the amount of dead roots and dead wood) are provided by SUMO. SMART2 delivers the nitrogen availability to SUMO as the sum of external N input and mineralisation. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and fixed depth.

Like SMART2, SUMO (Berendse, 1994b; Wamelink et al., 2005) is a process-oriented model that simulates vegetation succession and biomass production for time steps of one year. The biomass development is simulated for five functional types (FT), herbs and grasses (1), dwarf shrubs (2), shrubs (3), and two tree species (4 and 5). The five FT compete with each other for nitrogen (including nitrogen deposition), light, and moisture. Competition for nitrogen is based on the relative biomass present in the roots of the FT. Competition for light is simulated as a result of the height and the leaf biomass of the FT. Actual biomass growth of each FT is the result of a reduction of the maximum growth by moisture, nitrogen and light availability. The biomass can also be reduced as a result of management (mowing in grassland, sod cutting in heathland, thinning in forest). Mowing, sod cutting and thinning implies the removal of biomass and thus carbon and nitrogen from the system. SUMO requires information on soil type and groundwater level, the initial vegetation type and the management. Management is usually unknown and is therefore derived from the vegetation type. In this study grassland is mown once each year, sod cutting takes place in heathland every 30 years and in forest trees are thinned depending on the tree species and the biomass growth. The initial biomass (and nitrogen content) is derived per vegetation type and age class from a standard database containing biomass and nitrogen content for an average stand in The Netherlands. The model is initialised for 10 years to adjust the biomass and nitrogen content to the local circumstances.

NTM3 (Wamelink et al., 2003) is a regression model based on the criteria of the red list, i.e. the rarity, the temporal trend and the size of the distribution area of each species. It is a regression model that predicts the potential floristic diversity at given values of the soil characteristics nitrogen availability, soil pH and moisture availability. The nitrogen availability and soil pH are simulated by SMART2, the moisture availability as spring groundwater level is derived from a hydrological map. A nature conservation value (NCV) was assigned to the vascular plant species occurring in The Netherlands, based on the red list criteria, rarity, temporal trend and size of the distribution area (Mace & Stuart, 1994). The rarity was based on the occurrence of the species in the Dutch national 5km grid, and the trend is based on the change of occurrence of the species on the national grid between 1950 and 1990. The distribution area indicates the importance of the occurrence of the species in

The Netherlands for its total distribution area. Rare and decreasing species that have their major distribution in The Netherlands get a high value, common species get a low value or even a negative value when they are increasing (i.e. invasive species).

A data set containing 160,000 vegetation relevés was used as a training set to relate NCV to soil properties. As direct measurements of soil conditions are scarce, these conditions were estimated per relevé on the basis of the mean Ellenberg (Ellenberg et al., 1992) indicator values for moisture, pH and nutrient availability of the constituent species. The Ellenberg values were related to actual soil conditions using a separate training set of relevés where these conditions had been measured. A regression analysis using p-splines was used to smoothen the relationship between the soil characteristics and the NCV's of the species. The potential floristic diversity is predicted in an arbitrary scale, where values > 15 indicate a high probability of occurrence of red list species, and values < 12 indicate a low floristic diversity with a very low probability of occurrence of red list species. The lowest possible potential biodiversity is approximately 7 and the highest approximately 19. To account for differences in management, the model was calibrated four times, for heathland, for deciduous forest, for coniferous forest and for grassland. The model estimates the probability of occurrence for red list species at any given combination of groundwater level, nitrogen availability and pH, based on the assumption that sufficient recolonisation can take place if conditions improve. This is why we use the term *potential* floristic diversity.

Study area and scenarios

We used the Netherlands as study area because many data are available. We selected all 250m*250m grid cells with either deciduous forest (38707 cells), coniferous forest (109374 cells), unfertilised grassland (15362 cells) or heathland (558 cells) in the Netherlands. Information about the groundwater table, soil type, tree species and stand age per grid cell were used as input for the models. It covers all major soil types and groundwater tables in The Netherlands. The models were run for all stands with eight constant nitrogen deposition levels at 5, 10, 20, 30, 40, 50, 60 and 70 kg.ha^{-1}yr^{-1}. The simulations were run for 25 years using the system state in 2000 as starting point. The average net carbon sequestration in living biomass, litter and dead wood in forest was inspected in the last year of the 25 year period (2025). Potential floristic diversity was predicted for the end of this period in all vegetation types.

4.3 Results

Carbon sequestration

The simulated average net carbon sequestration (in living biomass, litter and dead wood) increases from approximately 0 and 0.4 ton.ha^{-1}.yr^{-1} to 1.1 and 2.2 ton.ha^{-1}.yr^{-1} for coniferous and deciduous forest respectively (Figure 4.1), between the lowest (5 kg.ha^{-1}.yr^{-1}) and the highest nitrogen deposition level (70 kg.ha^{-1}.yr^{-1}). We assumed that the effect of nitrogen deposition on the C-sequestration in grassland and heathland is negligible. The average simulated increase is 20-30 kg carbon per kg nitrogen deposition. The difference between deciduous and coniferous forest is caused in part by the difference in maximum growth rate. These figures are well in agreement with experimental results from Sweden (Tamm et al., 1999) with increases of 18 and 28 kg $C.kg^{-1}$ N depending on the site. The increase is also very similar to that estimated by Nadelhoffer et al. (1999b). They based their estimate on ^{15}N tracer experiments, showing that approximately 5% of the added N ends up in stem wood with an average C/N ratio of 500, leading to an assumed accumulation of 25 kg $C.kg^{-1}$ N if the C/N ratio remains constant.

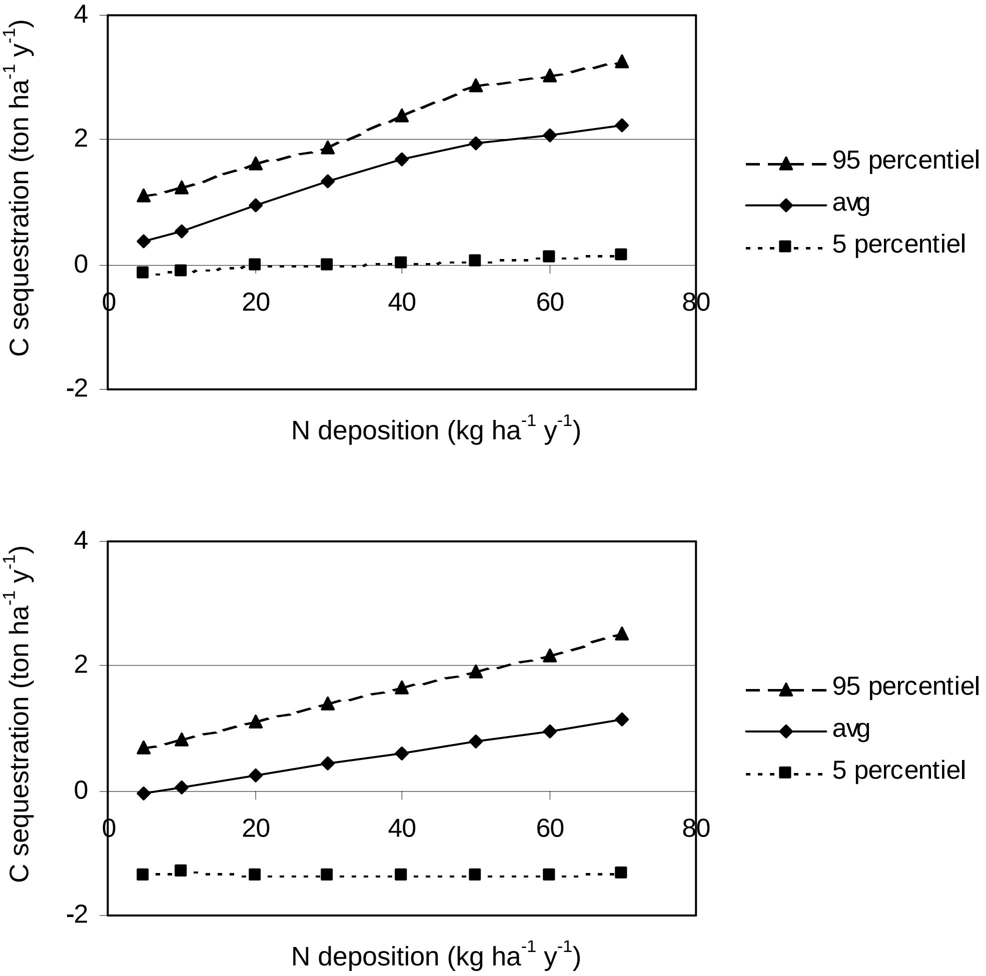

Figure 4.1 Simulation of the average carbon sequestration (living biomass + dead wood + litter) with its 5- and 95-percentile realised in deciduous (dec.) and coniferous (con.) forest at five nitrogen deposition levels for all forest in The Netherlands after 25 years.

In our results the variation is large for both coniferous and deciduous forest, caused by a wide variation in soil types, groundwater tables and age classes. Net emitters of carbon exist for both forest types (actually the older stands). Since Dutch forests are relatively young the amount of older stands will increase over time, especially because clearcutting is no longer practised. This may lead to a decrease in C sequestration over time. In deciduous forest the carbon sequestration levels off at higher nitrogen deposition levels, indicating that other factors besides nitrogen become growth limiting. Coniferous forests do not show such a decline. Field experiments show that in boreal areas nitrogen limitation of forest growth is becoming less important around a nitrogen addition of 60 kg.ha^{-1}.yr^{-1}, which agrees with our results for deciduous forest (Tamm et al., 1999).

Potential floristic diversity

The simulated potential floristic diversity decreases with increasing nitrogen deposition, the effect being most prominent for grassland followed by heathland and deciduous forest, whereas the effect is very limited in coniferous forest (Figure 4.2). The simulated large decrease in potential floristic diversity with nitrogen deposition in grassland, and to a lesser extent in heathland is in agreement with experiments as well as field surveys (Bobbink & Roelofs, 1995; Bobbink et al., 1998; Roem & Berendse, 2000; Aerts et al., 2003; Stevens et al., 2004), as is the impact on deciduous forest (Thomas et al., 1999; Van Dobben et al., 1999). Like for carbon sequestration, the variation in simulated potential floristic diversity is large. At low nitrogen deposition levels there are relatively many stands with high values, whereas at high nitrogen deposition levels many stands occur with very low values, as can be seen from the 5- and 95-percentile lines (Figure 4.2).

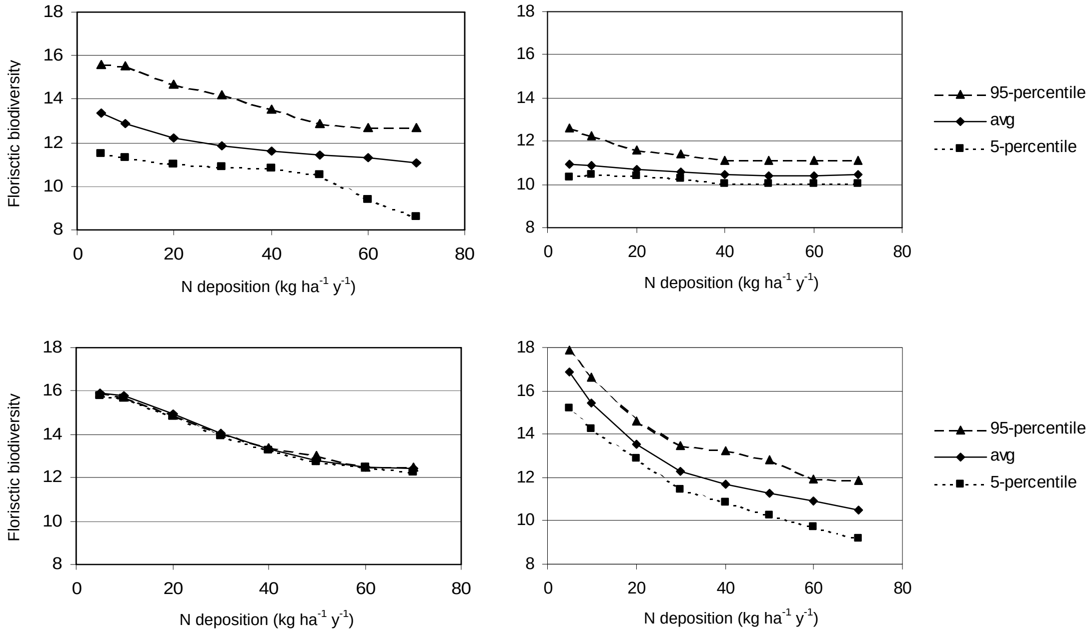

Figure 4.2 Prediction of the average potential floristic diversity with its 5- and 95-percentile for deciduous forest (top left), coniferous forest (top right), heathland (bottom left) and grassland (bottom right) in The Netherlands at eight nitrogen deposition levels after 25 years. The potential floristic diversity is predicted in an arbitrary scale, where values > 15 indicate a high floristic diversity with a high probability of occurrence of red list species, and values < 12 indicate a very low probability of occurrence of red list species.

In contrast to deciduous forest, the effect of nitrogen deposition on the potential floristic diversity is almost absent in coniferous forest (Figure 4.2) although the 95-

percentile indicates that a higher diversity may occur at very low nitrogen deposition levels. Most of the coniferous stands are plantations with only widespread and common species in their ground vegetation layer, although under conditions of very low nitrogen availability rare species may occur e.g. lichens (Van Dobben et al., 1999; Ericsson et al., 2005; Gustafsson et al., 2005).

The above results suggest that a decrease in nitrogen deposition will lead to a decrease in carbon sequestration. In order to make a more realistic prediction this observation was further explored in a scenario where nitrogen deposition gradually decreases from 40 kg.ha^{-1}.yr^{-1} N in 2000 to 10 kg.ha^{-1}.yr^{-1} N in 2025. The 40 kg.ha^{-1}.yr^{-1} N is approximately the average deposition in 2000 in The Netherlands and some other areas in western Europe (Tarasón et al., 2003). When a transition to more sustainable agriculture has been established a deposition of 10 kg.ha^{-1}.yr^{-1} N in 2025 may be achievable.

Table 4.1 shows the total net carbon sequestration in 2025 for the decreasing and for two of the constant nitrogen deposition scenarios. The results show that under the decreasing scenario carbon sequestration in 2025 will drop to approximately 27% of the sequestration at a constant deposition of 40 kg.ha^{-1}.yr^{-1}. Floristic diversity on the other hand will increase in deciduous forest (Table 4.1). The floristic diversity in coniferous forest increases just slightly, while the carbon sequestration drops dramatically, both in agreement with the results for the constant deposition levels. The largest increase in potential floristic diversity is predicted for heathland and grassland. This increase is much larger than for forest, although not as large that it reaches the floristic diversity for the constant low deposition. As Dutch forests are almost all plantations, the results are likely to be applicable to most plantation forests in temperate Europe (e.g. Germany, UK or Poland), but not to the semi-natural forests in the boreal region where floristic diversity may be more sensitive to nitrogen deposition because of the occurrence of the relatively sensitive bryophytes and lichens.

Table 4.1 Total carbon sequestration (living biomass + dead wood + litter) and average potential floristic diversity (in arbitrary units, cf. Figure 4.2) in the Netherlands after 25 years for three nitrogen deposition scenarios (N-dep.) and four vegetation types.

N-dep 2000	N-dep 2025	C sequestration (kton.y^{-1}) in 2025			Floristic diversity In 2025			
kg.ha^{-1}.yr^{-1}	kg.ha^{-1}.yr^{-1}	Deciduous forest	Coniferous forest	All forest	Deciduous forest	Coniferous forest	Grassland	heathland
10	10	17.9	-1.6	16.4	12.9	10.9	15.5	15.8
40	10	26.2	-1.9	24.2	12.5	10.8	14.2	15.2
40	40	56.7	30.5	87.3	11.6	10.5	11.7	13.3

4.4 Discussion

The presented simulations suggest that a decrease in nitrogen deposition may substantially increase floristic diversity in grassland and heathland, thus fulfilling Rio/Johannesburg requirements. However, this may also lead to a substantial decrease in carbon sequestration in both coniferous and deciduous forest, which would jeopardise the fulfilment of the Kyoto protocol. These results are probably applicable for large parts of Europe, where forests play a role in C-sequestration and important natural grasslands and heathlands are present, and nitrogen deposition is high at present. Forest fertilisation, as suggested by Oren et al. (2001), may compensate for the reduction in carbon sequestration but will also negatively affect floristic diversity, at least in deciduous forest where the potential gain in C sequestration is largest. The negative effect of reduced N deposition on C sequestration may be partly offset by a reduction in the emission of the greenhouse gas nitrous oxide. Taking the standard IPCC assumption that 1% of the deposition input is returning to the atmosphere as N_2O with a warming potential of 300 times that of CO_2, its effect would be equivalent to 3 kg $CO_2.ha^{-1}.yr^{-1}$, i.e. less than 1 kg $C.ha^{-1}.yr^{-1}$. Thus, this effect is likely to be very limited.

It is difficult to compare the importance of carbon-sequestration on the one hand and floristic diversity on the other hand, but in the end we believe that the good news of increased floristic diversity with decreasing nitrogen deposition outweighs the bad new of the decrease in carbon sequestration. This is especially true since the total contribution of carbon sequestration in existing forest is only a minor part of the total carbon that is released at the moment (Tarasón et al., 2003). Moreover, plantation of new, fertilised forest may compensate for the loss of carbon sequestration, financially stimulated by the government to fulfil the targets set in the Kyoto protocol.

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Process based modelling at the Intensive monitoring plots

5 Modelling soil carbon sequestration of intensively monitored in forest plots in Europe by three different approaches

Abstract
Information on soil carbon sequestration and its interaction with nitrogen availability is rather limited, since soil processes account for the most significant unknowns in the C and N cycles. In this paper we compare three completely different approaches to calculate carbon sequestration in forest soils. The first approach is the limit value concept, in which the soil carbon accumulation is estimated by multiplying the annual litterfall with the recalcitrant fraction of the decomposing plant litter, which depends on the nitrogen and calcium content in the litter. The second approach is the N balance method, where carbon sequestration is calculated from the nitrogen retention in the soil multiplied with the present soil C/N ratio in organic layer and mineral topsoil. The third approach is the dynamic SMART2 model in combination with an empirical approach to assess litterfall inputs. The comparison is done by first validating the methods at three chronosequences with measured C pools, two in Denmark and one in Sweden, and then application on 192 intensive monitoring plots located in the Northern and Western part of Europe. Considering all three chronosequences, the N balance method was generally most in accordance with the C pool measurements, although the SMART2 model was also quite consistent with the measurements at two chronosequences. The limit value approach generally overestimated the soil carbon sequestration. At the intensive monitoring plots, the limit value concept calculated the highest carbon sequestration, ranging from 160 to 978 kg ha^{-1} yr^{-1}, followed by the N balance method which ranged from 0 to 535 kg ha^{-1} yr^{-1}. With SMART2 we calculated the lowest carbon sequestration, from -30 to 254 kg ha^{-1} yr^{-1}. All the three approaches found lower carbon sequestration in Northern Europe (latitude above 60 degrees) compared to Central and Southern Europe (latitude from below 60 degrees. Considering the validation of the three approaches, the range in results from both the N balance method and SMART2 model seems most appropriate.

5.1 Introduction

Net primary production (NPP) of forests greatly depends on forest type, age, management, climate and nutrient availability. Increased net primary productivity (NPP), as observed in European forests (Spiecker et al., 1996) have been hypothesised to be due to increases in atmospheric CO_2 concentrations (e.g. Melillo et al., 1993; Friedlingstein et al., 1995), temperature (e.g. Myneni et al., 1997; Hasenauer et al., 1999) and nitrogen deposition (Holland et al., 1997; Nadelhoffer et al., 1999b). As summarized in a review article (Hyvönen et al., 2007a), well documented responses on the NPP are an increased photosynthetic rate (main CO_2 response), an increase in the length of the growing season (main temperature response) and an increase in leaf area index (main N deposition response). Using the process-based model EFM, Milne and van Oijen (2005) showed that the main driver of increased forest growth in the 20th century has been increased nitrogen deposition, rather than increased CO_2 concentrations or climate change. Similar results were also obtained by application of four process-based ecosystem models, EFIMOD, EFM, FinnFor, Q. Although the models differed greatly in structure and parameterisation, they all identified increasing nitrogen deposition as the major cause of observed changes in European forest growth during the twentieth century. However, future changes in forest growth are more likely to be caused by increasing atmospheric CO2 concentration and, especially in northern latitudes, by increasing temperature (Van Oijen et al., 2007). Similar results were obtained by Wamelink et al. (2007c), using the forest growth model SUMO, combined with the soil model SMART2 (Kros et al., 1995) and the hydrological model WATBAL (Starr, 1999) to predict the effects of a change in CO_2 concentration, climatic parameters (temperature and precipitation) and nitrogen deposition on carbon sequestration in 166 intensively monitored forest plots in Europe.

Since forest systems are generally nitrogen limited, nitrogen deposition increases forest growth and litterfall, which moves to the soil where it is only partially decomposed, thus increasing soil carbon sequestration. Recent experimental N fertilization results in Sweden and Finland (Högberg et al., 2006; Hyvönen et al., 2007b), investigating the impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe, showed an average response near 25 kg C/kg N depending on the site.

By far the largest amount of C stored in forests in the northern hemisphere is stored in the soil. Carbon fixed by photosynthesis ultimately While carbon sequestration in trees due to elevated growth is largely a transitory phenomenon, elevated soil carbon sinks could last for a much longer period, since below-ground carbon has much lower turnover times than above ground carbon or alternatively is stable. Thus, in the long term the soil is the ultimate sink or source of CO_2 for these ecosystems. Information on soil carbon sequestration and its interaction with nitrogen availability is, however, rather limited. Current hypotheses suggest that increased N deposition causes an increased rate of soil organic matter accumulation at least in two ways due to an increased leaf/needle biomass and litter production (e.g. Schulze et al., 2000) and a reduced decomposition of organic matter (Berg & Matzner, 1997; Harrison et al., 2000) The N-content of forest litter and humus might thus be an important indicator of the soil carbon sequestration rate. Soil processes account for the most significant unknowns in the C and N cycles.

The retention or sequestration in forest soils can be derived from repeated soil inventories. In the Swedish Forest Inventory, for example, monitoring of humus C increase is based on measurements of humus depth at a 5 year interval in which the samples analyzed for C. Long-term trends can thus be followed up. In the Netherlands humus C and soil C in the top 30 cm was measured in the period 1990-

2000 with a 5 year interval. Results thus obtained are presented in Leeters and de Vries (2001), but these results show that the change is hard to detect within a short period of time, considering the large present pools with the exception of the organic layer (see also De Vries et al., 2000). An alternative is the measurement of carbon stocks in chronosequences, being a series of forest stands planted in different years on similar soils in the same area (e.g Vesterdal et al., 2007). One can also estimate the net C sequestration in the soil from direct measurements of the carbon input to the soil by litterfall and root decay and carbon release by net mineralization. Such an approach, which was e.g. used by Schulze et al. (2000) is also hampered by the fact that the result is based on subtracting large numbers with relative high uncertainties. An empirical approach related to this principle is the limit value concept, in which the carbon release by net mineralization is equal to a maximum percentage (limit value) of the litterfall. Soil carbon accumulation is thus estimated by multiplying the annual litterfall with the recalcitrant fraction (the opposite of the limit value) of the decomposing plant litter (Berg et al., 1996; Berg & Meentemeyer, 2002)

A completely different approach to assess carbon sequestration is based on the principle that the potential C fixation response to elevated N deposition is restricted by the C-N stoichiometry of the forest ecosystem compartments. Because of the different C/N ratios, a lot more N is required to lock up C in soils than in woody biomass. This aspect is the rationale behind using information on the N immobilization in soils, in response to N deposition, to assess the related soil carbon sequestration by multiplying it with C/N ratio by which carbon is sequestered as compared to nitrogen. As a first approach, the present soil C/N ratio can be used. Examples of the use of this so-called N balance method are given by Nadelhoffer et al. (1999b) and De Vries et al. (2006b). By combining various tracer experiments, however, Nadelhoffer et al. (1999b) showed, that only a very small part of the added N (~5%) is stored in stem wood with a high C/N ratio (250-500) whereas most of the deposited N (~70%) is actually stored in soils with a much lower C/N ratio (10-30. De Vries et al. (2006b) used this approach to estimate net carbon (C) pool changes and long term C sequestration in trees and soils at more than 100 Intensively Monitored forest plots (Level II plots) and to scale up results to Europe based on data for more than 6000 forested plots in a systematic 16 km x 16 km grid (level I plots).

Finally, carbon sequestration in soil can also be based on a dynamic modelling exercise including the C cycle. Dynamic soil carbon models vary in complexity and input information they require (Powlson et al., 1996). Examples of process-oriented soil carbon models are CENTURY (Parton et al., 1987) and RothC (Coleman & Jenkinson, 1996), ANIMO (Groenendijk & Kroes, 1999) and CESAR (Vleeshouwers & Verhagen, 2002), most of them being developed for agricultural soil, although CENTURY and RothC for arable soils have also been applied to forest soils (e.g. Peng et al., 1998; Falloon et al., 2002). Examples of such models for forest ecosystems are the models in combination with SMART2 (Wamelink et al., 2007c), EFIMOD, EFM, FinnFor and Q (Van Oijen et al., 2007) and the Yasso soil model by Liski et al. (2002) in combination forest stand growth simulation models, such as CO2FIX (Masera et al., 2003) or the region-scale forestry model EFISCEN

(Karjalainen et al., 2002). Such models need to include both carbon inputs to the soil by litterfall and root decay and carbon release by net mineralization to allow the calculation of soil carbon sequestration.

This paper presents a quantification of carbon sequestration in the forest soils, using (i) the limit-value concept (ii) the N-balance method and (iii) the dynamic soil model SMART2, combined with a simple model describing N deposition effects on litterfall. The applicability of the various methods was first evaluated by comparing results obtained for soil carbon sequestration rates by these methods with measurements derived from three chronosequences. To gain more insight in soil carbon sequestration on a European wide scale, we then present an estimate of carbon sequestration rates in nearly 200 European forest soils that are part of the Pan-European "Programme for Intensive and Continuous Monitoring of Forest Ecosystems", carried out since 1994. The aim of this study is to evaluate the consistency of estimates of soil carbon sequestration rates by these three completely different approaches on a European wide scale as method to gain more insight in the reliability of such estimates.

5.2 Locations

5.2.1 Chronosequences in Sweden and Denmark

We made a comparison between the three calculation methods for carbon sequestration (the limit-value concept, the N-balance method and the SMART2 model) on three chronosequences in Sweden and Denmark where carbon stocks in the soil were measured. The term chronosequence is used for a series of forest stands planted in different subsequent years. All stands are planted on similar soils in the same area (preferably 1 km x 3 km). All stands in a chronosequence are exposed to the same climatic conditions and having experienced the same pollution regime. Apart from measurements of the C pool in the organic layer and mineral soil (up to 25 cm or the bottom of the AP horizon), the carbon pools in above ground biomass and the carbon input by litterfall were measured (Vesterdal et al., 2007). Furthermore, data were gathered on the water fluxes (Van der Salm et al., 2007b) and on the N deposition and N concentrations in soil solution, thus allowing the calculation of N budgets (Rosenqvist et al., 2007).

The field site of Tönnersjöheden in Sweden (56°40'N, 13°04'E) is an experimental forest area located 20 km from the city of Halmstad. Afforestation of land taken out of agriculture has been an ongoing large-scale change in land use during the 20th century, particularly over the last 50 years. Soils in the area are represented by till, glaciofluvial material, out-wash sand and peat. The soil type is Arenosol (FAO) developed on sandy glaciofluvial material. The soil contains a large amount of stones. Further-more, the soils are well drained with deep groundwater tables. The topography of the area is flat (elevation 50-65 m). The mean annual temperature is between 6.1 and 7.3°C and the mean annual precipitation is approximately 800-1050 mm. Surplus arable land has mainly been afforested with Norway spruce. Five stands were selected to represent a chronosequence of 90 years. Three of these stands were located within an area of 1x1 km, and the distance to the other two stands was approximately 4-6 km. It was verified for each stand that the former land use had been agriculture or pasture. No preparatory deep plowing was performed prior to afforestation.

Vestskoven in Denmark (55°41'N, 12°21'E) is an afforestation area located 15 km west of Copenhagen. In 1967 it was decided to establish an urban forest, and arable land has successively been bought up for afforestation over the years. The area presents a unique opportunity to study the influence of afforestation within the same soil type. The soils are nutrient-rich and moist Mollic Hapludalfs with a texture of sandy loam developed from calcareous till deposits. The topography in the area is flat (elevation 20-28 m). The climate is temperate with a mean annual temperature of 7.7°C and a mean annual precipitation of around 625 mm for the period 1960-1990. Seven stands of Norway spruce and seven stands of oak were selected to represent chronosequences of almost 30 years. The stands were located within an area of 1x3 km and it was verified for each stand that the land use had been agriculture (cropland) or horticulture for centuries until afforestation. The trees in all stands were planted directly following conventional tillage, i.e. soils were not disturbed by preparatory deep plowing. Weeds were controlled mechanically for about 3 years after planting by harrowing a couple of times during summer.

5.2.2 Intensive monitoring plots in Northwestern and Central Europe

We applied the limit-value concept, the N-balance method and the SMART2 model on selected plots of the "Programme for Intensive and Continuous Monitoring of Forest Ecosystems", carried out since 1994. This so-called level II Monitoring Programme includes approximately 860 permanent observation plots in 30 participating countries with data from: (i) mandatory surveys on a 1-10 yearly basis, carried out at all plots (crown condition, at least once a year; chemical composition of needles and leaves, at least every 2 years; soil chemistry, every 10 years; increment, every 5 years) and (ii) optional surveys on a daily to biweekly basis, carried out on a subset of plots (atmospheric deposition, soil solution chemistry and meteorology). In this study, the data were limited to plots which allowed the assessment of N budgets by including for atmospheric deposition, in terms of bulk deposition and throughfall, and soil solution chemistry data, mainly in the period 1995-2000. Furthermore, plots were excluded in which (i) soil solution is not sampled with tension lysimeters; (ii) reliable throughfall fluxes could be calculated and (iii) the soil type does not indicate the presence of ground water in the soil profile, since the hydrological simulations were made assuming free drainage. (see also De Vries et al., 2007b; Van der Salm et al., 2007a). This lead to a total number of 192 plots.

In Figure 5.1, a map of the 192 plots is presented for which these data are available and that were used in the various carbo sequetration methods to predict the impact of nitrogen deposition on soil carbon sequestration. The map shows that most plots are located in Northern Europe (Scandinavia), Western Europe (the British Isles, the Benelux, and France) and Central Europe (Germany). Only a few plots are found in the Mediterranean countries (2 in Spain and 2 in Italy). Most common tree species in the plots are Norway Spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Beech (*Fagus sylvatica*) and to a lesser extent Oak (Quercus robur and Quercus petraea; Table 5.1).

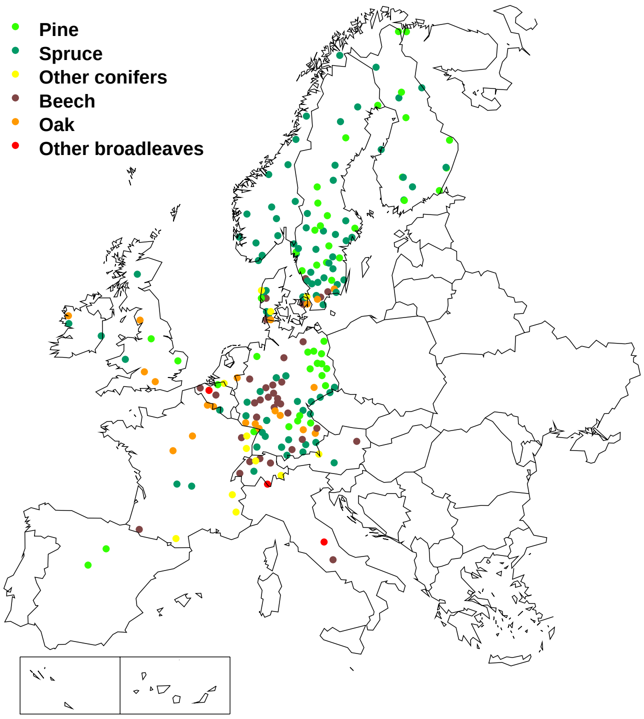


Figure 5.1 Locations of the Intensive Monitoring plots used for calibration and application the dynamic SMART2 model.

Table 5.1 Distribution of plots over combinations of tree species group

Species group	Species	Total
Spruce	Picea abies, Picea sitchensis	83
Scots pine	Pinus sylvestris	45
Other conifers	Abies alba, Pseudotsuga menziesii, Larix decidua, Pinus cembra, Pinus nigra	11
Standard Oak	Quercus petraea, Quercus robur	19
Beech	Fagus sylvatica	31
Other broadleaves	Quercus cerris, Fraxinus excelsior	3
Total		192

5.3 Modelling approach

We used three methods to calculate carbon sequestration. The SMART2 model is a dynamic process based model, whereas the limit value concept and the N balance method are empirical methods.

5.3.1 The three included process-based and empirical model approaches

The concepts to calculate carbon sequestration are the the limit value concept (Berg & McClaugherty, 2003), the N balance method (De Vries et al., 2006b) and the dynamic soil model SMART2 (Kros et al., 1995; De Vries et al., 2005).

Limit value concept

Tree foliar litter (and other litter species as well) almost never decomposes completely but leaves recalcitrant remains that vary in size with litter type and a range from 50% to 0% of stable remains have been found. The principle of the limit value concept is that soil carbon sequestration can be calculated by multiplying the annual litterfall by a recalcitrant fraction of the decomposing plant litter (e.g. Berg et al., 1996; Berg et al., 2001; Berg & McClaugherty, 2003). This so called recalcitrant fraction is based on the accumulated mass loss of litter in time that ultimately reaches a limit value (Berg & Eckbohm, 1991; Berg et al., 1996; Coûteaux et al., 1998). The limit value (*LimVal*) is defined as the maximum percentage of litter that will be decomposed. The recalcitrant fraction (rf) is thus related to the limit value according to rf = 1-*LimVal*/100. The C sequestration, according to the limit value concept ($Cseq_{LimVal}$) (kg ha^{-1} yr^{-1}) is thus calculated as:

$$\mathrm{Cseq_{LimVal}} = \frac{100 - \mathrm{LimVal}}{100} \cdot \mathrm{C_{litterfall}} \qquad (5.1)$$

where $C_{litter\ fall}$ is the amount of carbon in litter fall (kg ha^{-1} yr^{-1}). The model has been validated against measured values of C accumulation with up to 25 kg C per meter square during a period of 3000 years (Berg et al., 2001; Berg & Dise, 2004). The stability of the remains are thus valid for periods of millennia.

The capacity to store C varies with the chemical litter composition. More N-rich litter types having a larger recalcitrant fraction. The effect of N on the limit value is observed in the interval from 0.3 to 1.4 % N in the shed litter (Berg et al., 1999). That range includes most boreal and temperate foliar litter species.

N-balance method

The basic concept of the N-balance method is that carbon sequestration can be calculated from nitrogen retention in the soils, since carbon and nitrogen accumulation in organic matter occurs through the same mechanisms. Calculation of soil carbon sequestration in is based on the calculated nitrogen immobilisation (sequestration) in the soils, multiplied by the C/N ratio of the forest soils. N immobilisation (sequestration) is calculated as the difference of total N deposition minus N uptake and N leaching:

$$\mathrm{Nimmobilisation} = \mathrm{Ndeposition} - \mathrm{Nleaching} - \mathrm{Nuptake} \qquad (5.2)$$

This approach is based on the assumption that denitrification can be neglected in the organic layer and the mineral topsoil, where both N and C sequestration is assumed to occur. When multiplying the net N immobilisation rate with the C/N ratio, the variation of the C/N ratio with the depth of the soil profile was accounted for since is a large difference between C/N ratio in the organic layer (forest floor) and that in the mineral soil. Based on ^{15}N experiments (Tietema et al., 1998; Nadelhoffer et al., 1999b) we modelled the partitioning of N retention between forest floor and mineral soil as a function of the N input and the C/N ratio of the forest floor according to:

$$\mathrm{Cseq}_{\mathrm{Nbalance}} = \mathrm{N\ immobilisation} \cdot (\mathrm{fret}_{\mathrm{ff}} \cdot \mathrm{C/N}_{\mathrm{ff}} + (1 - \mathrm{fret}_{\mathrm{ff}}) \cdot \mathrm{C/N}_{\mathrm{ms}}) \tag{5.3}$$

where C/N_{ff} and C/N_{ms} are the C/N ratios of the forest floor and the mineral soil (up to a depth of 20 cm), and $fret_{ff}$ is the N retention fraction in the forest floor, being the ratio of the N retention in the forest floor and the N retention in the complete soil profile (forest floor and mineral soil to 20 cm). The N retention fraction in the forest floor was calculated as a function of the NH_4-fraction in the N input and the C/N ratio of the forest floor, as given by De Vries et al. (2006b).

SMART2 model

SMART2 (Kros et al., 1995) is a simple, single-layer soil acidification and nutrient cycling model. It includes the major hydrological and biogeochemical processes in the vegetation, litter and mineral soil. Crucial for the calculation of carbon sequestration in the soil by SMART2 is the litter fall rate and the decomposition rate, since the C sequestration rate is calculated as the difference between these two C fluxes, according to:

$$\mathrm{Cseq}_{\mathrm{SMART2}} = \mathrm{C}_{\mathrm{lf}}(\mathrm{t}) \cdot (1 - \mathrm{fr}_{\mathrm{mi,fl}}) - \mathrm{C}_{\mathrm{mi,lt}} \tag{5.4}$$

where C_{lf} is the carbon input by litterfall (kg ha^{-1} yr^{-1}), f_{mifl} is the mineralisation fraction of fresh litter (-), and $C_{mi,lt}$ is the mineralisation rate of carbon from the organic layer (kg ha^{-1} yr^{-1}). The litterfall rate is not simulated by SMART2 but needs to be assessed on the basis of measured data, empirical relationships or an external forest growth model, such as SUMO to which SMART2 has been coupled (Wamelink et al., 2007c). In this approach, use was made of the first two options (measured data at the chronosequences and empirical relationships at the intensive monitoring plots). Decomposition was modelled as a function of temperature and pH, which is dynamically simulated by SMART2. To assess pH, the model dynamically simulates changes in concentrations of major cations and anions (Al, Ca, Mg, K, Na, NH_4, NO_3, SO_4, HCO_3 and Cl) concentrations in the soil solution. In addition, it simulates changes in solid-phase characteristics connected to the acidification status, i.e. carbonate content, base saturation and amorphous Al precipitates. The model consists of a set of mass-balance equations, describing the soil input-output relationships, and a set of equations describing the rate-limited and equilibrium soil processes.

Comparison of principles of calculation of carbon sequestration by the three models

The limit value concept and the N-balance method are both methods that are typical applicable for a longer time perspective. It refers to the average carbon sequestration during a period of decades and results can deviate during shorter time periods due to impacts of e.g. climate on the carbon input by litterfall and the release by decomposition and thereby on the carbon sequestration. The modelling approach typically includes those variations and a comparison of results thus requires the calculation of a long time model average. Another aspect in which SMART2 differs fundamentally from the other two methods is that in the model all plots will in the long term reach a steady state, at which decomposition equals incoming litter fall, resulting in a carbon sequestration of zero when model input such as litter fall and growth are constant. In limit value concept, the calculated C accumulation never approaches zero as it equals the recalcitrant fraction of the litterfall input. This is in principle also the case when applying the N balance method as done in this study, where the N immobilisation is derived from the difference of measured or estimated N deposition, N uptake and N leaching at the chronosequences and the intensive monitoring plots. In a dynamic approach, however, the impact of N deposition on soil carbon sequestration may change in the future in view of the impact of N deposition on the N saturation in terms of a decline in soil C/N ratio and a related decrease in N immobilisation (increase in N leaching), thus ultimately causing zero carbon accumulation. This is likely to be hardly ever reached, as discussed further.

In the limit value concept and the SMART2 model, the calculated C pool changes in the soil are mainly driven by C pool changes in the vegetation and related changes in litterfall. In the N-balance method, calculated C pool changes are fully driven by the N deposition, together with the soil C/N ratio, which in turn affects N immobilisation. The crucial processes for the calculation of C sequestration by the three concepts are summarised in Table 5.2 and described in the following sections.

Table 5.2 Crucial processes and concepts for the calculation of carbon sequestration rates by SMART2, the limit value-approach and the N balance method.

Processes	Limit value	N balance	SMART2
C and N in litter fall	x[1]	-	x[1]
C decomposition	(x)[1]	-	x
N deposition	-	x	(x)[3]
N uptake	-	x	(x)[4]
N immobilization/leaching	-	x	(x)[4]

[1] N contents in litterfall affect the decomposition in the limit value approach, but C decomposition is not included as a process as such

[2] Both C and N fluxes by litter fall are included in SMART2. N fluxes by litter fall influence C sequestration indirectly by affecting the pH, which influences decomposition..

[3] N deposition affects N uptake and thereby soil pH and thus C sequestration.

[4] N uptake and N immobilization included in SMART2 influence C sequestration through soil pH.

In the model calculations, the various model inputs used for the limit value concept and the N balance method refer to the measuring period. For SMART2, however, it includes a calculation period, starting at the date of afforestation in case of the chronosequences and starting in 1880 at the intensive monitoring plots. Results were evaluated on the present carbon pool in the chronosequences or in the organic layer of the intensive monitoring plots (see section 5.4 on model calibration of SMART2). Since the chronosequences are located on formal agricultural area, we knew that the initial litter pool was zero at the time of planting. For the intensive monitoring plots, a period of 120 years (1880-2000) was used to give robust model results for the calibrated mineralisation rates.

5.3.2 Litter fall

Litter fall is the driving force of the calculation of carbon sequestration by SMART2 and by the limit-value concept. Litter fall is the largest natural inflow of organic material and nutrients to the forest floor and in most European forests it is dominated by that from the trees. Some large compilations have been published on litter fall. Liu et al. (2004) calculated litter fall for Eurasia and found separate patterns among the climatic zones; e.g. in the boreal zone the litter-fall rate was higher in coniferous as compared to deciduous forests. Meentemeyer et al. (1982) used data sets with nearly global coverage and related litter fall with AET, and other climatic variables. In a regional study for Fennoscandia, Berg & Meentemeyer (2001) related foliar litter fall to AET.

Chronosequences

At the investigated chronosequences, the amount of litter fall was based on measurements during a two year period in Denmark and a one year period in Sweden (Vesterdal et al., 2007). For the limit value concept, we directly used these values. For the SMART2 model, we needed litter fall for the period since afforestation. We fitted a logistic function, according to:

$$\mathrm{Am}_{\mathrm{lf}}(\mathrm{t}) = \frac{\mathrm{Am}_{\mathrm{lf,mx}}}{1+\exp(\mathrm{k}_{\mathrm{gl}} \cdot (\mathrm{t} - \frac{1}{3}\mathrm{t}_{½}))} \tag{5.5}$$

where $Am_{lf}(t)$ is the litterfall for the simulation year t (kg ha^{-1}) as derived for the year since afforestation for each of the chronosequences, $Am_{lf,mx}$ is the maximum rate of litter fall for a mature tree species (kg ha^{-1} yr^{1}), $t_{½}$ is the time at which half of the maximum biomass is reached (yr), and k_{gl} is a logistic growth rate constant characterising the speed with which growth increases. The values for $t_{½}$ and k_{gl} were derived from fitting the growth at the plots on the measurements (see section on growth), assuming that litterfall has a similar behaviour but a three times as low value for $t_{½}$ (see Eq. 5.5). The value of $Am_{lf,mx}$ was then fitted with Eq. (5.5) using the values for $Am_{lf}(t)$ since afforestation for each of the chronosequences.

Intensive monitoring plots

For the intensive monitoring plots, the maximum amount of litter fall ($Am_{lf\ mx}$), related to a mature tree species was calculated by regression functions derived from an independent database (Gundersen et al., 2006a). This data base consisted of 153 observations: 13 for deciduous forest, 67 for pine and 73 for spruce. The latitude in this dataset ranges from 37°12' to 69°45' N degrees with an average of 56°35'. The longitude ranges from -9°25' until 30°97' E with an average of 11°80'.

We used the following explanatory variables to calculate the amount of litter fall for pine and spruce: mean temperature period May to October (XT), Effective temperature sum (ETS), which is the temperature sum of temperatures above 0ºC the in period May to October), Precipitation - Potential evapotranspiration (Thornthwaite & Mather, 1957) for the period May to October (PES) and Latitude (LAT). For pine and spruce different combinations of the explanatory variables resulted in the best relationships, which had an R^2_{adj} of 0.44 and 0.49 respectively. For reasons of consistency, we decided to use the same model for both forest types and we selected the model with PES, ETS and LAT as explanatory variables, although the R^2_{adj} per tree type is a bit lower (0.43 for pine and 0.46 for spruce).

$$litter\ fall = Consant + a \cdot PES + b \cdot ETS + c \cdot LAT \tag{5.6}$$

The coefficients are given in Table 5.3. Since the amount of data for deciduous trees was too small to find reliable relations, we used literature values for leaf biomass and litter fall rate as presented in Table 5.4 (De Vries et al., 1990). Litter fall was calculated by multiplying leaf biomass and litter fall rate. The deciduous forest plots mainly occurred in the lower parts of Germany, Belgium and France, with comparable climatic circumstances and thus no strong climate influence on litter fall rates is likely in this region.

Table 5.3 Values for coefficients in regression functions for Scots pine and other conifers to calculate litter fall on level II plots.

Coefficient	Scots pine	Spruce (and other conifers)
Constant	2893	16619
A	-1.26	0.58
B	47.7	-5.4
C	-55.1	-225.0

Table 5.4 Leaf biomass and relative litter fall rates for different broad leaves

Tree type	Leaf biomass (kg ha^{-1})	Litter fall rate
Remaining broad leaves (Fraxinus excelsior)	3255	1
Beech (Fagus sylvatica)	3020	1
Oak (Quercus petraea, Quercus robur)	3490	1
Oak evergreen (Quercus Cerris)	2792	0.3

For the development of litterfall on the Level II plots, we used a logistic growth function, in a similar way as the stem growth, according to Eq. (5.5). The estimation of $Am_{lf,mx}$ for each plot was derived from the regression relation described in Eq. (5.6). In the limit value concept we used the 5 years average over the period 1995 - 2000. In the SMART2 model we used the yearly calculated litter fall according to Eq. (5.5) during the period 1950-2000.

5.3.3 Carbon decomposition

The decomposition of organic matter, which is a crucial process in the calculation of carbon sequestration in the limit-value concept and the SMART2 model, is estimated as described below.

Limit-value concept

In this approach, the limit value (*LimVal*), which is defined as the maximum percentage of litter that will be decomposed, is determined by factors that determine the degradation and modification of lignin, e.g. the initial litter N and Ca concentrations with a suppressing and stimulating effect on lignin degradation, respectively (e.g. Eriksson et al., 1990; Hatakka, 2001), according to:

$$LimVal = Constant - a \cdot ctN_{lf} + (b \cdot ctCa_{lv}) \tag{5.7}$$

where ctN_{lf} is the N content in litter fall (g kg^{-1}) and $ctCa_{lf}$ is the Ca content in litter fall (g kg^{-1}). The coefficients for three tree types are given in Table 5.5. The limit value data for other conifers were based on spruce, whereas the data for oak, beech and other broadleaves were all related to deciduous forests.

Table 5.5. Coefficients for calculation of the Limit value for Spruce, Pine and Deciduous forest.

Vegetation type	*Constant*	*a*	*b*	R^2
Spruce	96.17	3.499	0.424	77.5
Scots pine	65.28	0.215	2.652	75.7
Deciduous forests	94.55	2.096	0.048	26.2

SMART2 model

In SMART2 part of the incoming fresh litter is decomposed in the first year, while the remaining is transferred to the organic layer, as given in Eq (5.4). The decomposition of this pool is described by first-order kinetics (Van Veen, 1977):

$$C_{mi,lt} = k_{mi,lt} \cdot redT(t) \cdot redpH(t) \cdot AmC_{lt}(t) \tag{5.8}$$

where $k_{mi,lt}$ is the mineralisation rate constant of litter (yr^{-1}) at optimal temperature and pH, AmC_{lt} is the amount of carbon in the organic layer (kg ha^{-1}) and redT and redpH are reduction functions for temperature and pH, respectively. Mineralisation of organic matter in the mineral soil layers is not considered in SMART2, except for the mineralisation from root necro-mass, which is fed by root decay. The mineralisation rate constant $k_{mi,lt}$ was calibrated to the measured C pool in the organic layer. The nominal value was 0.05, but the calibrated values (see section 4) had a large variation with a median value of 0.044 and with a variation coefficient of 2.33.

Decomposition is reduced in SMART at low pH in a range between pH 2.5 and 6, according to:

$$rf_{mi,pH} = \begin{cases} 0 & for\ pH \le 2.5 \\ \dfrac{pH - 2.5}{2} & for\ 2.5 < pH < 3.5 \\ \dfrac{pH - 1}{5} & for\ 3.5 \le pH < 6 \\ 1 & for\ pH \ge 6 \end{cases} \tag{5.9}$$

Therefore, it is important to have good estimates of pH which is strongly affected by S and N deposition and by weathering of base cations, which is all included in SMART2. Besides a temperature effect was included on the decomposition rates according to (Kirschbaum & Paul, 2002), which we scaled to 10°C as reference temperature:

$$rf_T = e^{3.36\left(\frac{T-40}{T+31.79} - \frac{10-40}{10+41.79}\right)} \tag{5.10}$$

where rf_T is the reduction factor for temperature (-) and T is temperature (°C). The scaling to 10°C as a reference temperature yields that the reduction factor equals 1.0 at a temperature of 10°C.

The N-mineralisation rate, which strongly affects N concentrations in the soil solution, is reduced in SMART at low N contents (high C/N ratios) to account for immobilisation by microbes according to (Janssen, 1984). The dissimilation to assimilation ratio DA_{m0} was calibrated to the measured C:N ratio of litter. The nominal value was 5, the calibrated values had a median of 3.47 and a variation coefficient of 0.68. Even though this aspect is not so relevant for the calculation of the carbon sequestration, it has an influence through its effect on soil pH.

5.3.4 Growth

Both in SMART2 and the N balance method, growth is used for the calculation of soil C sequestration. In the N balance method, it refers to the measuring period, whereas for SMART2 it includes the whole calculation period starting at the data of afforestation in case of the chronosequences and in 1880 at the intensive monitoring plots.

N balance method

Growth data at the intensive monitoring plots were calculated from biometric observations, such as diameter at breast height (DBH), height and stem numbers to assess the amounts of above ground biomass in 1995 and 2000, as described in De Vries et al. (2003a) and summarized in De Vries et al. (2006b).

The N content in stems was assumed to vary with the N deposition, being higher in high deposition areas and lower in low deposition areas. This was based on the hypothesis that at a high N availability, a higher uptake takes place and that the additional N uptake is only partly leading to additional growth (C-pool change) and part is just leading to higher N contents (lower C/N ratios) in stem wood. Actually, the N content was assumed to range from 0.1 %, (C/N ratio of 500) the constant value used by Nadelhoffer et al. (1999b) in areas with a deposition below 1400 mol ha^{-1} yr^{-1} (approximately 20 $kg.ha^{-1}.yr^{-1}$) to 0.2 % (C/N ratio of 250) in areas above with a deposition above 4000 mol ha^{-1} yr^{-1} (approximately 60 kg ha^{-1} yr^{-1}). This relation is based on a variation of (stem wood) N contents between 0.1 and 0.2% (at a constant C content of 50%) in comparatively low deposition areas (Scandinavia) to high deposition areas (The Netherlands).

$$ctNst = b + 0.42 \cdot Ndep \cdot 0.0001 \tag{5.11}$$

where ctNst is N content in stems (%), *b* is a constant which is 0.05 for conifers and 0.1 for deciduous and *Ndep* is N deposition (mol ha^{-1} yr^{-1}). A similar relationship was used for the relation between N deposition and the N contents in branches.

SMART2 model

From the application of SMART2 on the intensive monitoring plots between 1880 and 2000 we used logistic growth functions to calculate growth rate with a rotation period of 100 years for all species except for the ‘other broadleaves’ for which we used 70 years. A rotation period of 100 years appears to be common practice in Europe for most tree species, except for particular broad-leaf species such as poplar and aspen (EFI, 2002). The calculated amounts of biomass in 1995 and 2000 for the intensive monitoring plots, as described in De Vries et al. (2003a), were used for fitting logistic growth curves according to:

$$\mathrm{Am}_{\mathrm{st}}(\mathrm{t}) = \frac{\mathrm{Am}_{\mathrm{st,mx}}}{1 + \exp(-\mathrm{k}_{\mathrm{gl}} \cdot (\mathrm{t} - \mathrm{t}_{1/2}))} \tag{5.12}$$

where $Am_{st}(t)$ is the biomass of stems and branches for the simulation year t (kg ha^{-1}) as measured for the years 1995 and 2000, $Am_{st,mx}$ the (maximum) amount of stem biomass for a mature tree (kg ha^{-1}), $t_{1/2}$ the half life-time (yr), and k_{gl} is the logistic growth-rate constant (yr^{-1}). Values for $Am_{st,mx,\ act}$, $t_{1/2}$ and k_{gl} were estimated for each site by a non-linear optimisation software. The actual growth rate as function of time, $G_{st}(t)$ (kg ha^{-1} y^{-1}) was derived through the derivate of the logistic growth function, according to:

$$\mathrm{G}_{\mathrm{st,act}}(\mathrm{t}) = \frac{\mathrm{k}_{\mathrm{gl}} \cdot \mathrm{Am}_{\mathrm{st,mx}} \exp\left(-\mathrm{k}_{\mathrm{gl}}(\mathrm{t} - \mathrm{t}_{1/2})\right)}{\left[1 + \exp\left(-\mathrm{k}_{\mathrm{gl}}(\mathrm{t} - \mathrm{t}_{1/2})\right)\right]^2} \tag{5.13}$$

where $G_{st,act}(t)$ is the actual growth for simulation year t (kg ha^{-1} yr^{-1}). By multiplying this growth with element contents, which are N deposition dependent in the case of N, the relevant annual net uptake is calculated.

5.3.5 N deposition

Total N deposition was used for the N balance method approach and the dynamic SMART2 model approach. In both methods, N deposition has an effect on net uptake due to the impact on the N content in stems and in branches, as described in the section on growth.

N balance method

For the N-balance method total N deposition refers to the measurement period of the chronosequences (2000-2003) and the intensive monitoring plots (1995-2000). The total N deposition (N_{td}) at the chronosequences was calculated as the sum of N in throughfall (N_{tf}), measured at each plot (Rosenqvist et al., 2007), an estimated N input by stemflow (N_{sf}) and an estimated above ground exchange (uptake) of inorganic nitrogen (N_{ce}). Stemflow flux was estimated from the annual through fall according to (Ivens, 1990):

$$N_{sf} = N_{tf} \cdot \alpha/(1-\alpha) \tag{5.14}$$

where α is an empirical value. For deciduous forest, α was set to 0.12 independent of age. For coniferous forests, the value of α was calculated as a function of stand age according to (Ivens, 1990)

$\alpha = 0.24$	age < 20
$\alpha = 0.31 - 0.0034 \cdot \text{age}$	20 < age < 90 (6.7)
$\alpha = 0.0$	age > 90

N exchange (Nce) was obtained by a relationship described by De Vries et al. (2001), using empirical relationships on throughfall, stemflow and independently measured total deposition, as reported by Johnson and Lindberg (1992) for 12 sites in the USA:

$$N_{ce} = 0.69 \cdot (N_{tf} + N_{sf}) + 91.9 \quad \text{for Ntf + Nsf} < 1000\ \text{mol}_c.\text{ha}^{-1}.\text{yr}^{-1} \tag{5.15}$$

Johnson and Lindberg (1992) made their measurements at sites situated in areas with relatively low N deposition with throughfall and stemflow fluxes of inorganic nitrogen ranging between 100 and 1000 $\text{mol}_c.\text{ha}^{-1}.\text{yr}^{-1}$. Equation (17) therefore can only be applied for this range of inorganic nitrogen fluxes, which appeared to be the case for the investigated chronosequences. In those rare cases where the N deposition exceeded this range an N exchange value of 780 $\text{mol}_c.\text{ha}^{-1}.\text{yr}^{-1}$ was used, being the calculated value for N exchange when the sum of Ntf and Nsf is 1000 $\text{mol}_c.\text{ha}^{-1}.\text{yr}^{-1}$. This occurred at the oldest age stadium in Tönnersjöheden and at the two oldest stadiums of the spruce chronosequence in Vestkoven. For the rest of the cases the sum of Ntf and Nsf ranged between 646 and 947 $\text{mol}_c.\text{ha}^{-1}.\text{yr}^{-1}$.

At the intensive monitoring plots, total N deposition, was calculated by a comparable approach but here the canopy exchange was derived by using data on both bulk deposition and throughfall of N (NH_4 and NO_3) and other major elements, such as

Cl, Ca, Mg, K and Na), based on a canopy exchange model described by De Vries et al. (2001).

SMART2 model

For the application of the SMART2 model, we used N depositions since the date of afforestation in case of the chronosequences (see age information in Table 5.6) and since 1880 on the intensive monitoring plots (see before). For these simulations, the trends in SO_2, NO_x and NH_3 deposition were derived using RAINS country emissions (Cofala & Syri, 1998b, a) and transfer matrices derived from the EMEP long-range transport model (Bartnicki et al., 2002) for 50 * 50 km EMEP grid cells for the period 1960 to 2000. These trend curves were scaled by the average computed total deposition (based on bulk and throughfall measurements as described above) for the period 1996-2000 so that the EMEP time series coincide with the plot-specific deposition for that period. Deposition trends between 1880 and 1960 were based on Schöpp et al. (2003b), by using one trend line for SO_2, NO_x and NH_3 independent of their location.

5.3.6 N immobilisation and N leaching

N immobilisation is used in the N balance method to calculate C sequestration. In this approach, N immobilisation is derived from the difference between calculated total N deposition, as described before, and the sum of N uptake (described also before) and N leaching (see also Eq. 5.2), as described in the next section. In the SMART2 model N immobilisation is also included, but this process does not affect C decomposition and thereby C sequestration.

For the chronosequences, the N leaching was derived by multiplying measured N concentration in the soil solution by the modelled water leaching with SWAP (see Van der Salm et al., 2007a). The N-uptake was calculated by multiplying the measured stem increase by the N content in stems, which was taken from Jacobsen et al. (2002).

For the intensive monitoring plots, N leaching is calculated in the N balance by multiplying the measured N concentrations in the soil solution with the calculated water leaching by the hydrological model WATBAL. For the water balance calculations within we used an existing simple water balance model WATBAL. WATBAL (Starr, 1999) is a monthly water balance model for forest soils based on the following water balance equation:

$$P = ET + R \pm \Delta SM \qquad (5.16)$$

Where P is precipitation (mm day^{-1}), ET is evapotranspiration (mm day^{-1}), R is soil water flux (mm day^{-1}) and ΔSM is Change in soil moisture storage (mm day^{-1}).

One of the main advantages of WATBAL is that the model uses input data which are either easily obtained or can be derived from other basic data using transfer functions. It uses relatively simple and readily available climate variables (e.g.

precipitation, air temperature and cloudiness) and the available water capacity (AWC) of the soil, which can be derived using transfer functions based on soil texture, bulk density, organic matter content or from the soil moisture curve. It handles sloping sites if the appropriate slope factors are given and snowmelt. Besides giving soil water flux values, all the components of the water balance are determined: potential and actual evapotranspiration, soil moisture, snow pack store and snowmelt, as well as global (direct and diffuse) radiation. Evapotranspiration is calculated using an estimation of global radiation using a reference crop equation adjusted by a crop (forest stand) coefficient to take into account the greater evapotranspiration from forests. WATBAL has been validated for several sites (Starr, 1999) were modelled global radiation is compared with measured global radiation from either on-site or a nearby weather station. In addition comparisons with measured soil water fluxes from in-situ (zero-tension) gravity lysimeters and soil moisture content measured with TDR probes are made.

5.4 Calibration of the SMART2 model

In order to calculate C sequestration, it is important to predict C pools adequately. Model inputs such as growth and litter fall are of great importance. We assume growth and litter fall as given values and did not calibrate them. Another important model input is the initial C pool of the litter layer. We decided to calibrate this initial pool, since measurements of the initial pools are not available. The main process in the SMART2 model that determines the C sequestration in the soil is mineralisation of the litter layer, with litter older than one year. Since the mineralisation is affected by pH, it is important to model the chemical composition of the soil solution adequately. Therefore we decided to calibrate C/N-ratio of the litter layer and Gapon exchange constants, which regulate the exchange of Al, H and base cations between the solid phase (exchange complex) and soil solution.

We did the calibration of the SMART2 model in four successive steps. First the initial litter pool at the beginning of the simulation run (1880) was calibrated to the measured present C pool of litter, considering that the initial litter pool was between zero and twice the measured C pool of litter. In the first step the nominal value of the mineralisation constant, being 0.05 yr^{-1}, was used. The second step was the calibration of the mineralisation constant, starting with the last value of initial litter pool. This was only done when the first step did not result in adequate values of the simulated C pools. Since there is a large uncertainty about the mineralisation rate constant, we varied it between 0.01 and 10 times the nominal value of the mineralisation rate constant. An example of the result of this calibration is given in Figure 5.2 for the intensive monitoring plots. The C pool of old litter was simulated well, which means that the calibration of initial litter pool and or mineralization rate constant succeeded. In Norway, the C pool of litter was not measured and we assumed a C pool of 3 kg m^{-2} for Scots pine and 3.5 kg m^{-2} for Norway spruce, the median values for the Swedish plots. It was necessary to calibrate the mineralization constant for most plots.

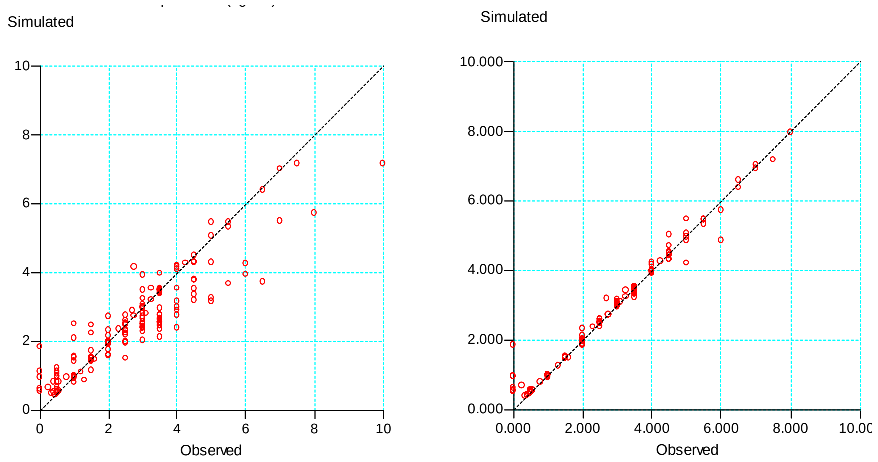


Figure 5.2 Simulated against observed C pool of the litter layer (kg m^{-2}), before (left) and after (right) calibration of initial C pool and mineralisation rate constant.

The third step was the calibration of the assimilation/dissimilation ratio of the decomposing microbes to the measured C:N ratio in litter. We varied the assimilation/dissimilation ratio between 1.5 and 10 using an initial value of 5. The result of this calibration for the intensive monitoring plots is given in Figure 5.3. The C:N ratio in old litter was simulated well too, although larger deviations were found. The range of dissimilation/assimilation ratio (D/A) was not always broad enough to meet the criterion. When the C:N ratio of litter was not reached the latest value of D/A was taken.

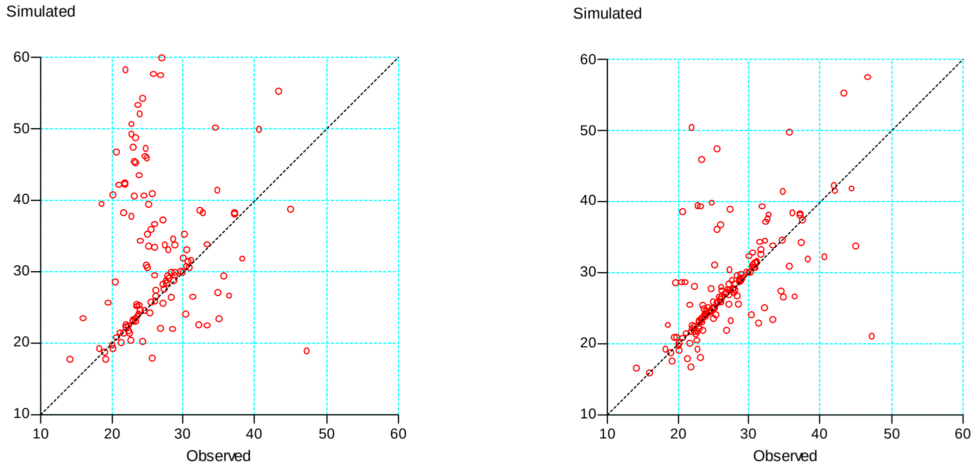


Figure 5.3 Simulated against observed C:N ratio of the litter layer, before (left) and after (right) calibration of the dissimilation assimilation ratio

Finally the Gapon exchange constants were calibrated to the measured base saturation, which is strongly related to the pH. The simulated pH before and after calibration did not differ much for the intensive monitoring plots (Figure 5.4). In general, the results agreed quite well with the observed values, especially between the values 4 and 5. Divergences had different causes. First, measurements were not always from the same depth as the model output. Second, some plots seem to have SO_4 weathering in the soil, which is not in the SMART2 model. At this plots the simulated pH was too high, whereas the SO_4 concentrations were too low. The plots with assumed SO_4 weathering were skipped.

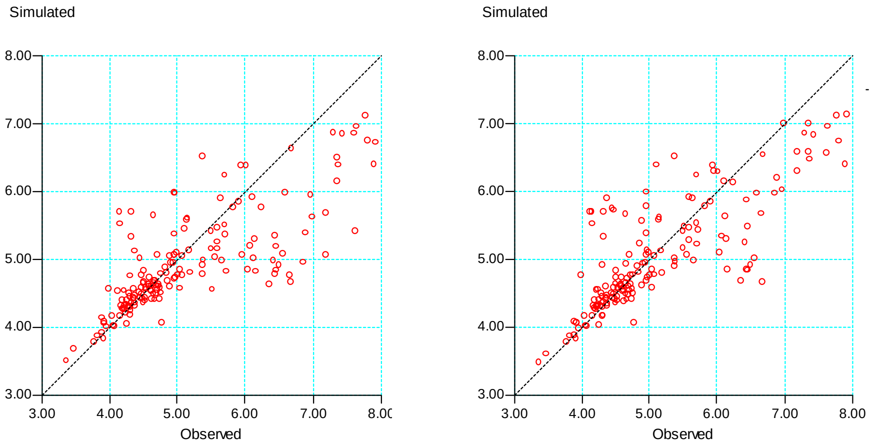


Figure 5.4 Simulated against observed pH, before (left) and after (right) calibration

We tested this procedure at the described chronosequences where, in contrast to the intensive monitoring plots, carbon sequestration, in a certain sense, is measured several times over a longer period. We did the calibration at the chronosequence as if we had just one measurement in time and chose therefore the measurements of the middle age stadium of each chronosequence, which were the 1967 measurements for Sweden, 1991 for the spruce site in Denmark and 1992 for the oak site in Denmark Afterwards we compared the simulated carbon sequestration for different times with the measured carbon sequestration at the corresponding age stadiums.

Since the chronosequences are located on formal agricultural area, we knew that the initial litter pool was zero so that we did not need to calibrate the initial litter pool. We thus started the procedure with the calibration of the mineralisation rate constant and then continued the calibration with the assimilation/dissimilation ratio and then the Gapon exchange constants. The calibrated mineralisation constants were 0.0005 yr^{-1} for both chronosequences planted with Norway spruce and 0.5 yr^{-1} for the one planted with oak.

5.5 Carbon sequestration estimates using SMART2, the limit-value approach and the N-balance method.

Results obtained for the chronosequences

We compared the three described methods on the chronosequences using as much as possible measured data from these locations (Table 5.6). For the limit value concept, we used the measured N and Ca contents in the litter fall and the measured litter fall in each age stadium. For the N balance method, we used the measured throughfall, stem wood increase and N concentration in the soil solution, to assess total N deposition N uptake and N leaching as described before.

Table 5.6 Used data for the calculation of the C sequestration with the limit value concept and the N balance method

Location	Age (yr)	N total deposition (kg ha^{-1})	N uptake (kg ha^{-1})	N leaching (kg ha^{-1})	C/N (-)		Litter fall (kg ha^{-1})	Content in litter fall (g kg^{-1})	
					ff	ms		N	Ca
Tönners-jöheden	19	19.2	7.6	0.2	27	15	905	11.5	4.15
	30	16.6	9.9	5.5	23	13	1390	11.5	4.15
	63	23.7	4.2	0.1	28	13	1170	11.5	4.15
	74	21.3	4.0	0.2	29	20	1055	11.5	4.15
	92	26.4	4.9	0.0	33	21	1310	11.5	4.15
Vestkoven Norway Spruce	11	19.7	7.6	0.	42.0	12.2.	202	11.9	5.4
	13	22.1	7.6	0.	42.0	12.2.	1219	8.9	4.0
	28	28.0	9.6	0.2	30.8	12.3	1745	10.7	4.8
	32	40.1	9.6	11.8	30.8	12.3	1657	9.8	4.4
Oak	8	17.6	8.8	3.2	25.8	11.2	1469	17.3	7.6
	13	15.7	8.8	0.1	25.8	11.2	2100	16.1	7.1
	22	18.6	9.7	7.2	35.2	11.7	2392	20.1	8.8
	24	19.8	9.7	11.6	35.2	11.7	2291	17.2	7.6
	31	19.5	10.2	10.7	34.1	10.9	2797	18.4	8.1

For the SMART2 model we used these data to derive those values since the time of afforestation (see before).The measured C sequestration per year (Table 5.7) was determined for each age stadium by dividing the total C pool of litter by the age of the site (Vesterdal et al., 2007).

Table 5.7 Measured and calculated carbon sequestration rates (kg ha^{-1} yr^{-1}) with the limit value concept, the N balance method and SMART2 at three chronosequences in Sweden and Denmark

Location	Species	Age (yr)	Carbon sequestration (kg ha^{-1} yr^{-1})			
			Measured	Limit value	N balance	SMART2
Tönnersjöheden	Norway spruce	19	258	381	334	247
		30	327	586	207	290
		63	352	493	319	412
		74	563	445	301	444
		92	609	552	285	480
		Average	422	491	289	375
Vestkoven	Norway spruce	11	347	87	397	81
		13	197	406	463	87
		28	320	685	450	131
		32	306	601	460	140
		average	293	445	443	110
	Oak	8	55	607	115	97
		13	112	816	136	134
		22	116	1127	47	92
		24	63	942	-43	82
		31	71	1220	-37	56
		Average	83	943	44	92

The results of the three methods were most consistent at Tönnersjöheden, the oldest chronosequence. The results of the three calculation methods agreed quite well with the measured C sequestration. At the older stadiums, all methods underestimated the carbon sequestration. At both Danish chronosequences, however, the results diverged considerably. At the Danish location planted with Norway spruce, both the limit value method and the N balance method overestimated the C sequestration, whereas SMART2 underestimated the C sequestration. At the oak chronosequence, the limit value method calculated a large overestimation of the sequestration. With the N balance method, the overestimation was smaller. With the N balance method we calculated two negative values at the two oldest stadium due to the relative high N leaching at those locations (Table 5.6). The SMART2 model results agreed very well with the measurements, which was also true for the trend in time of the sequestration, with a decrease at older age.

The results over al these chronosequences showed that the limit value approach leads to the largest calculated C sequestration, whereas the SMART2 model calculated the smallest C sequestration. Considering all three chronosequences, the N balance method was generally most in accordance with the C pool measurements, although the SMART model was also quite consistent with the measurements at two chronosequences. The limit value approach generally overestimated the soil carbon sequestration.

Results obtained for the intensive monitoring plots

The modelled C-sequestration rates in the soil has a large variation between plots but also between the various approaches to asses the soil carbon sequestration rate, as shown in Figure 5.5.

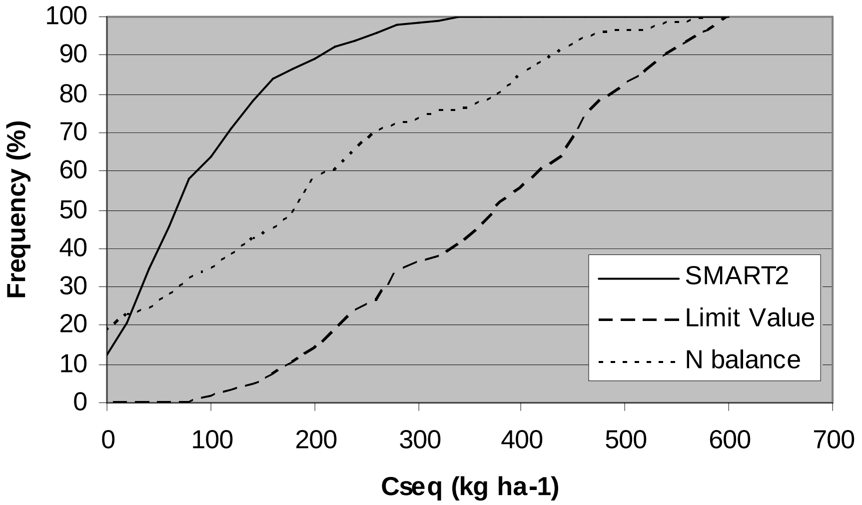


Figure 5.5 Cumulative frequency distribution of the average C sequestration from 1950-2000, calculated with SMART2, the limit value concept and the N balance method (kg m^{-2} yr^{-1}).

With the limit-value concept, the calculated carbon sequestration ranged from 160 - 978 kg ha^{-1} yr^{-1} with a median value of 446 kg C ha^{-1} yr^{-1} and with the N balance method, the results ranged from 0 - 535 kg ha^{-1} yr^{-1} with a median of 184 kg ha^{-1} yr^{-1}. With SMART2, we calculated a carbon sequestration between -30 and 254 kg ha^{-1} yr^{-1} with a median of 64 kg ha^{-1} yr^{-1}. The cause of low predicted values by has to be searched in the dynamic of the system. After a clear cut, which happens each 100 year in the SMART2 simulation, a lot of organic matter is decomposed, resulting in negative carbon sequestration. Taking the average over 50 years with a clear cut in that period leads to low average carbon sequestration values. For all three methods, the soil C sequestration rate was generally calculated to be lower in Northern Europe (latitude>60) that in Central and Southern in Europe, as shown in Table 5.8. In the N balance method, which is directly related to N deposition, there was on average a fourfold difference between Northern Europe and the rest of Europe, whereas the difference was approximately twofold for the Limit value concept and the SMART2 model. An overview of the geographic differences is given in Figure 5.6.

Table 5.8 Calculated carbon sequestration (kg ha^{-1} yr^{-1}) with the limit value concept, N balance method and SMART2 as a function of latitude. Median values are given with 5 and 95 percentile between brackets.

Latitude	Carbon sequestration (kg ha^{-1} yr^{-1})		
	Limit value concept	N balance method	SMART2 model
40-50	512 (153 - 996)	233 (0-532)	64 (-9 - 255)
50-60	455 (182 - 974)	193 (0-634)	70 (-37- 209)
60-70	291 (121 - 871)	54 (0-150)	39 (-11- 258)
All	446 (160 - 978)	184 (0 – 535)	64 (-30 - 254)

The large difference between the results of SMART2 and the limit-value approach is caused by difference in the decomposition concept. In the limit value concept, there is a recalcitrant fraction of the fresh litter fall that is not decomposed, which varied between 12% and 57%. In the SMART2 model, in principle all incoming litter fall is ultimately decomposed. This means that it is possible to reach a steady state where decomposition equals the litter fall, resulting in a C sequestration of zero. The empirical method is fundamentally different from the other two methods in that it focuses on N deposition impacts.

5.6 Discussion and conclusions

Plausibility of the derived carbon sequestration rates

The calculated C sequestration rates in the intensively monitored plots show large variations between the three described methods. The plausibility of the results can be evaluated against other literature results. Liski et al. (2002), using a modified version of the ForClim-D model (Perruchoud et al., 1999), later called the Yasso model (Liski et al., 2005), found an average rate in 1990 of 190 kg ha^{-1} yr^{-1} and of 305 kg ha^{-1} yr^{-1} in 2040, with a large variability, for the EU countries including Norway and Switzerland. Nabuurs and Schelhaas (2002) calculated a net carbon sequestration in soil for 16 typical forest types across Europe. The advancing mean of the net C sink of all forests was calculated to equal 110 kg.ha^{-1}.yr^{-1}.

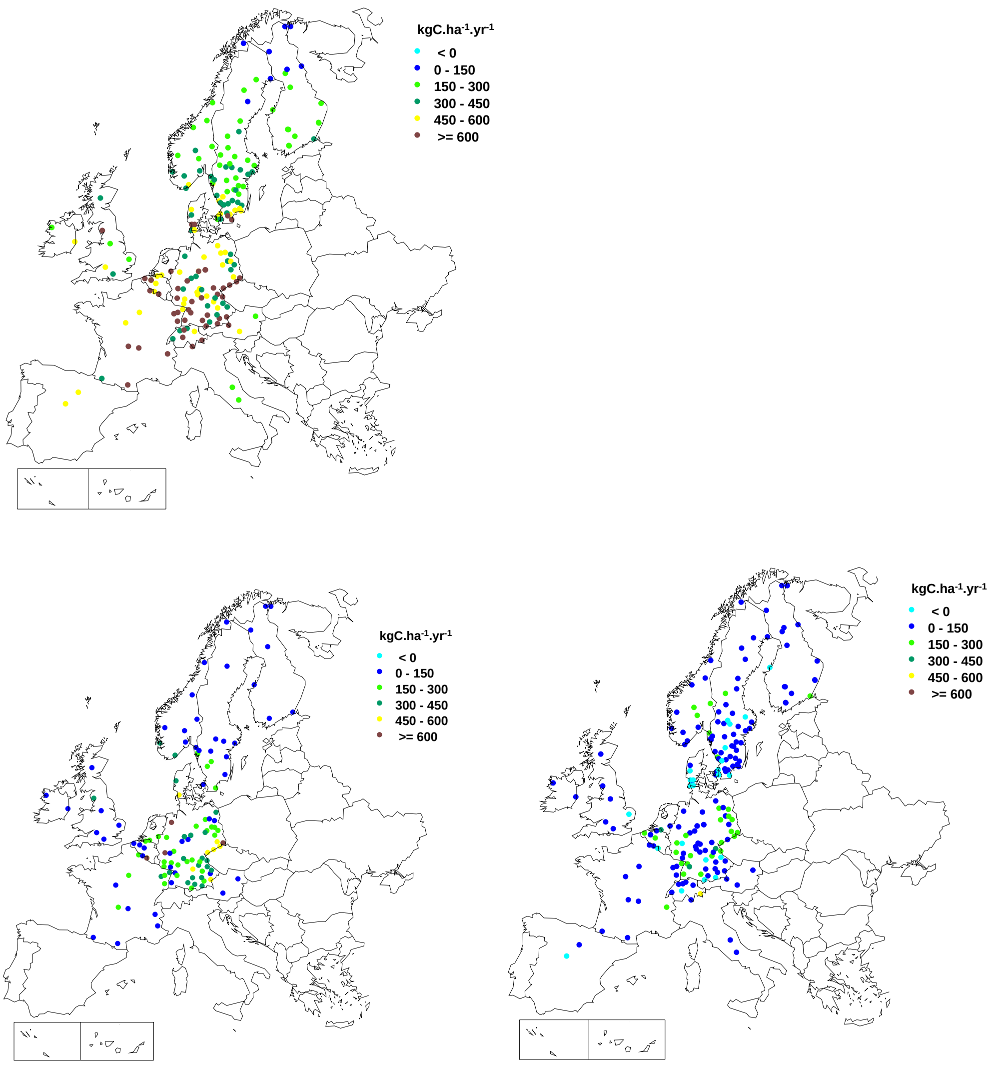


Figure 5.6 Carbon sequestration (kg ha^{-1} yr^{-1}) calculated with the limit value concept (top left), the N balance method (below left) and SMART2 (below right) at the investigated 192 intensive monitoring plots.

Results of the N balance method as applied by Nadelhoffer et al. (1999b) and De Vries et al. (2006b) lead to an average carbon response of 21 and 15 kg.ha^{-1}.yr^{-1}, respectively per kg N deposition. Hyvönen et al. (2007b) investigated the impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe (Sweden and Finland). They quantified the effects of fertiliser N on C stocks in trees and soils (organic layer +0–10 cm mineral soil) by analysing data from 15 long-term (14– 30 years) experiments in *Picea abies* and *Pinus sylvestris* stands in Sweden and Finland. Addition of a cumulative amount of N of 600– 1800 kg N ha^{-1} resulted in a mean increase of 11 kg C/kg N in soil, respectively. These results of 11-25 kgC/kgN can be used to derive a range in carbon sequestration rates by multiplying them with the additional N input on the intensive monitoring plots, compared to a background N deposition of 3 kg N. ha^{-1} yr^{-1}. The additional N input above 3 kg N. ha^{-1} yr^{-1}at the investigated plots ranged from 0.2 to 36 kg N ha^{-1} yr^{-1}, with a median of 13 kg N ha^{-1}

yr^{-1}. On average, this implies a range in carbon sequestration from 142 - 322 kg ha^{-1} yr^{-1}.

It seems in general that the results obtained with the N balance method at the intensive monitoring plots are most in line with literature data. The limit value concept generally calculates too high values, whereas the calculated soil carbon sequestration rates by SMART2 seem generally too low. The results of the application of the three methods to the chronosequences also showed that, in general, the N balance method corresponded best with the measured C sequestration. The limit value overestimated the C sequestration for some cases, whereas the SMART2 model sometimes underestimated the C sequestration. There is thus a need for improvement, as summarized below.

Uncertainties in litter fall in the limit value and SMART 2 model approach

The SMART2 model and the limit-value concept differ fundamentally from the empirical method. Both for SMART2 and the limit-value concept litter fall is a crucial input and an uncertainty in litter fall directly leads to uncertainty in C sequestration rates calculated with these methods. The empirical method just needs N input fluxes from deposition and N leaching fluxes, which are derived from measured soil solution concentrations and will thus have less uncertainty. Good estimates of litter fall are crucial for the calculation of C sequestration rates, using the SMART2 model and the limit-value concept. Since measured litter fall data were not available we used regression equations to estimate litter fall. Using these equations with an R^2 of 43% for pine and 48% for spruce, means a quite large uncertainty. An alternative is the use of SUMO, which calculates biomass production dependent on N availability (Wamelink et al., 2007c).

Uncertainties in the carbon to nitrogen sequestration ratio in the N balance method

The reliability of the soil carbon sequestration rates by N balance method relies on the accuracy of using present soil C/N ratios as a proxy for the ratio of C to N accumulation or sequestration, C/N_{seq}. Evidence of carbon accumulation in response to N addition has been presented by Evans et al. (2006) for two heathland N manipulation sites. The first site, Ruabon, is an upland (470 m) heath in North Wales dominated by heather (*Calluna vulgaris*). The manipulation experiment, established in 1989, includes a control treatment plus three N addition treatments of 40, 80 and 120 kg N.ha^{-1}.yr^{-1}, added monthly as finely sprinkled NH_4NO_3 solution. Measurements of soil C pools allowed to calculate changes in the C pools at given N inputs during the 11 year experiment, thus allowing to calculate the C/N sequestration ratio, as presented in Table 5.9. The results show remarkably clear soil carbon responses of to N addition, with values for C/N_{seq} being quite close to the C/N ratios of the soil.

Table 5.9 Estimated soil carbon sequestration per kg nitrogen addition and soil C/N ratios at the Ruabon heathland N manipulation site (after Evans et al., 2006).

N input in 11 year	Soil C pool	Change in soil C pool compared to ambient	C/Nseq	C/Nsoil
kg/ha	kg/ha	kg/ha	kg C/kg N	kg C/kg N
0	105360	-	-	33.4
440	120360	15000	34.1	31.9
880	125640	20280	23.0	31.2
1320	131880	26520	20.1	30.7

In applying the N balance method, one should be aware that the N immobilization rate may decrease with time due to N saturation, which is reflected in a lowering of the C/N constant, which is an important indicator for N leaching and N accumulation. There is, however, no clear evidence for an impact of N deposition on the soil C/N ratio. Dise et al. (1998a; 1998b) found significant relationships between the input flux of inorganic N and the N concentration of the forest floor, but no relationship between N input and the C/N ratio, supporting the hypothesis of carbon accumulation due to N fertilization on a regional scale. Furthermore, there are no clear long-term rising trends in inorganic N leaching (e.g. Monteith et al., 2000; Aber et al., 2002) which may also partly be caused by the limited effect of N deposition on the C/N ratio. When N deposition not only affects the N accumulation in litter but also the C accumulation from increased litter production and/or suppressed litter decomposition, such a limited impact is to be expected. As indicated by Evans et al. (2006), the change in organic soil C/N will be small, and N saturation will occur slowly when C/N_{seq} is high, since more of the N added to the system will be associated with increased C storage,. Inversely, where C/N_{seq} is low, C pool changes will be smaller, soil C/N will decrease more rapidly, and N saturation will occur faster.

Uncertainties in the SMART2 model simulation

Compared to SMART2, simulations by other soil models indicate a longer period before a steady state is reached (which anyhow only is reached in the case of undisturbed unmanaged forest soils). Judging from the shape of the curves, the dynamic soil carbon module Yasso used by Liski et al. (2002) seems to reach a steady state in the very long term, only. Masera et al. (2003) used the YASSO model by Liski et al. (2002) linked to the forest stand growth simulation model CO2FIX. This model seemed to reach the steady state after 200 years for a fir-beech stand and after 300 years for a spruce stand, which is longer than SMART2, where steady state is always reached within 100 years. This aspect can be improved by including the effect of a slower decomposable pool in SMART2.

At this moment, in SMART2, the decomposition is furthermore only affected by pH and temperature. The effects of soil moisture content and nitrogen content in litter on decomposition are not included in the model. The impact of soil moisture content on decomposition is included in most models, although the impact differs. For example, in the models ANIMO (Groenendijk & Kroes, 1999), CESAR (Vleeshouwers & Verhagen, 2002), GRASP (Cooksley et al., 1993), CENTURY

(Parton et al., 1987) and SNAP (Paul et al., 2002), decomposition is increasing with increasing moisture content, with a maximum above a certain moisture content, which stays constant at higher moisture contents. The models APSIM (Probert et al., 1998) and GrazPlan (Paul, 2001), however, use an optimum moisture content where the decomposition is at its maximum and where it decreases at lower and higher moisture content.

Including the impact of nitrogen contents in litter and decomposition is relevant, but also not trivial. In many experiments, a positive relation was found between N-content in fresh litter and decomposition (Vesterdal, 1999; Hobbie, 2000; Silver & Miya, 2001; Sariyildiz, 2003; Xu & Hirata, 2005), but there are also examples of experiments where the effect of N content on decomposition was not found (Melillo et al., 1982; Murphy et al., 1998; Fourqurean & Schrlau, 2003). There are some indications that N enrichment causes an decrease in decomposition, especially in the later stadium of decomposition (O'Connell, 1994; Berg & Matzner, 1997). Chertov and Komarov (1997) described a model of soil organic matter dynamics, called SOMM in which they incorporated the assumption that decomposition of fresh material is stimulated with increasing N content of the decomposing material and that decomposition of older litter is suppressed by increasing N content.

In summary, SMART2 can be improved by including the effect of a slower decomposable pool, with possibly a recalcitrant part, and accounting for the impact of moisture and N availability. Besides, effects of management during land-use history should be taken into account, since management aspects like thinning and clear-cut, affect the carbon-pool build-up rates and changes in the soil, and these were not included in the simulations.

6 Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on growth and carbon sequestration of Intensive Forest Monitoring plots in Europe

Abstract

We adjusted and applied the hydrological model WATBAL, the soil model SMART2 and the vegetation model SUMO to asses the effect of expected environmental changes in the period 1990 up to 2070 on the carbon accumulation in trees and soils of 166 European forest plots. Environmental changes included: (i) a raise in carbon dioxide concentration, (ii climate change, resulting in higher temperatures and changes in precipitation and (iii) a decrease in nitrogen deposition. The models were parameterized using measured soil and vegetation parameters and site-specific changes in temperature, precipitation and nitrogen deposition. The carbon dioxide concentration was assumed to rise uniformly across Europe. The results were compared to a reference scenario, consisting of a constant CO2 concentration and nitrogen deposition (data of 1990) while repeating the temperature and precipitation between 1960 and 1990 up to 2070.

The assumed rise in carbon dioxide concentration gives a rise in carbon accumulation all over Europe. Inversely, the assumed decrease in nitrogen deposition causes a decrease of carbon accumulation all over Europe and for all modelled tree species. Climate change leads to a predicted decrease in carbon accumulation in the South of Europe and an increase in the North. When the scenarios are combined an increase in biomass accumulation is predicted at most of the sites, with a raise in growth rate mostly between 0% and 100%. Only at a few sites in the south the carbon sequestration in trees is decreasing, due to an increased drought stress caused by a decrease in precipitation and an increase in temperature. An analysis of variance shows that climate change explains the major part of the variance, followed by the CO2 rise. The effect of the change in nitrogen deposition is relative small because of the relative small difference in nitrogen deposition and because soil and vegetation processes keep the nitrogen cycling relatively constant.

The predicted effects of a change in the investigated environmental variables on soil carbon sequestration are generally lower than on carbon sequestration by the trees but the magnitude is similar and also the dependence on location (latitude). As with trees, we predicted a net soil carbon release from at several sites in the south. Overall, we conclude that where nitrogen deposition was a major driver for a change in forest growth in the past, it is climate change and to a lesser extent CO2 change that will mainly determine forest growth in the future.

Key words: biomass, growth, carbon dioxide, climate change, nitrogen deposition, scenarios, forests, modelling, nutrient cycling, carbon sequestration.

6.1 Introduction

European forests play a major role in carbon sequestration (Kauppi et al., 1992; Nabuurs et al., 1997). It is of importance to arrive at reliable estimates of C sequestration in those forests since this may delay the rise in the atmospheric CO2 concentration with implications for the speed of climate change. However, there is no clear consensus in the literature as to which are the main environmental drivers behind forest carbon sequestration (Hyvönen et al., 2007a). For example, despite hundreds of papers that have now been published describing the responses of trees to elevated CO_2, including many reviews (e.g. Ceulemans & Mousseau, 1994; Curtis, 1996; Curtis & Wang, 1998; Saxe et al., 1998; Long et al., 2004; Nowak et al., 2004; Ainsworth & Long, 2005), there are still different views as to how forests will respond to future rising CO_2 levels. Interpreting the results from these studies is complex, as responses are confounded by the timescale of the studies, the stage of stand growth (expanding versus full canopy) and the relative availability of other resources, such as nutrients (Korner, 2006). Elevated CO_2 is expected to have little impact on forest growth by some –claiming nutrients (such as N or P) are always limiting – whereas others assume that greater carbon availability will lead to adaptations in assimilate allocation and root morphology that will increase access to nutrients sufficiently (Van Oijen et al., 2007).

Likewise, there is no clarity as to the environmental drivers that have been dominant in temperate forests over the past decades. Forest growth has increased in recent decades, as shown by studies of temperate forests in North America (Reddy et al., 1995) and Europe (Hunter & Schuck, 2002; Solberg et al., 2004). Some studies have suggested that in Europe the majority of forest growth increment can be accounted for by N deposition (Nellemann & Thomsen, 2001; Solberg et al., 2004; Van Oijen et al., 2004; Van Oijen & Jandl, 2004; Van Oijen et al., 2007) and very little by elevated CO_2 but this does not seem to apply in all regions and the issue requires further study. One way forward has been through modelling to simulate the long–term effects of, for example, elevated CO_2 on forest growth and plant–soil C dynamics (Medlyn et al., 2000; McMurtrie et al., 2001). Such studies have questioned the relevance of short–term experimentation in systems where longer-term biogeochemical feedbacks operate (Kirschbaum et al., 1994; Rastetter et al., 1997), but the long-term response of soils and trees to environmental change is not clear. For example, experiments with soil warming have produced results varying from sustained increase in respiration to gradual return to a base-rate. Similar contrasting results have been found for acclamatory response of trees to elevated CO_2 (Korner et al., 2005), and the effects of enhanced N-deposition have even been found to vary from detrimental to growth-enhancing (Schulze, 2000). The contradictory responses may be the result of differences between species or interactions between different environmental factors, but there are few empirical studies to build on.

One likely cause for the lack of consensus about the importance of different drivers of changes in forest growth has been the limited amount of data underlying each individual study. In the present study we aim to remedy the situation by using data from the largest current forest observation system in Europe, i.e. the Intensive

Monitoring plots (De Vries et al., 2003c). At over 200 European forest plots the soil processes are monitored as well as the biomass increment and the deposition rates according a standardised protocol. We used information from the plots to calibrate our models and subsequently applied the models for the plots to evaluate a combined carbon dioxide, climate and nitrogen deposition scenario.

Important questions with respect to carbon sequestration are related to the cause of the observed large CO_2 uptake in mid-latitude forests and the time period in which the terrestrial sink will become saturated (Houghton et al., 1998). If the large uptake is mainly due to elevated growth, it is likely that this is a short transitory phenomenon, whereas it could be a carbon sink for a long period if soil accumulation is the main cause, since below ground carbon has much higher turnover time than above ground carbon.

The past decades have seen increases in net primary productivity (NPP) (Spiecker et al., 1996), together with changes in forest management, influencing the standing growing stock (Nabuurs et al., 2001). Both changes may have influenced the forest carbon sink. It is thus important to have methods for a reliable quantification of the carbon sinks in forests, including the possible impacts of various environmental factors, such as changes in atmospheric CO_2 concentration, climate (temperature, precipitation) and nitrogen deposition, as discussed below.

Impacts of carbon dioxide concentrations: Increased forest productivity has been hypothesised to be due to increases in atmospheric CO2 concentration (e.g. Friedlingstein et al., 1995), temperature, (e.g. Myneni et al., 1997) and nitrogen deposition (e.g. Nadelhoffer et al., 1999b). Elevated CO2 may favour NPP as well as increase water use efficiency of trees. However, trees may adapt to changing CO2 concentrations and the effect may diminish soon (Magnani et al., 1998). Several recent studies reported effects of elevated CO2 on NPP in relatively long-term (5-8 years) Free-Air CO_2 Experiments (FACE). Loiseau and Soussana (2000) studied the effects of CO_2 in combination with temperature and nitrogen additions in a temperate grassland. They found an increase in the aboveground production of the grass sward. However, this increase was restricted by temperature and N availability. In four FACE experiments in temperate forested ecosystems Norby et al. (2005) found a clear increase in NPP due to elevated CO_2. Elevated CO_2 ($\approx$ 550 ppm) increased median NPP by 23%, which remarkably little variation across sites.

Impacts of climate: Higher temperature accelerates enzymatic processes and therefore biomass accumulation, unless other factors, such as water or nitrogen availability are limiting. However, at very high temperatures enzymatic activity will be hampered leading to growth reduction. Increasing temperature may also increase annual NPP by lengthening the growing season (Hasenauer & Monserud, 1997). Both effects are confounded and it is not easy to disentangle them in field studies.

Impacts of nitrogen deposition: Since nitrogen often is the limiting nutrient in forests, nitrogen deposition is likely to increase productivity, thus increasing carbon sequestration by forests. Furthermore an elevated carbon sequestration in the soil, due to an increased accumulation of soil organic matter in response to elevated N inputs, may play a role. By far the largest amount of C stored in forests in the northern hemisphere is stored in the soil. Carbon fixed by photosynthesis moves via litter to the soil, where it is only partially decomposed. Thus, over the long term the soil is a major sink or source of CO_2 for these ecosystems. As mentioned above, NPP and C sequestration are closely linked to the N cycle. Soil processes probably account for the most significant unknowns in the C and N cycle. Current hypotheses suggest that increased N deposition causes an increased rate of soil organic matter accumulation due to increased leaf/needle biomass and litter production (e.g. Schulze et al., 2000) and a reduced decomposition of organic matter (Berg & Matzner, 1997; Harrison et al., 2000; Hagedoorn et al., 2003). The N-content of forest litter and humus might thus be an important indicator of C-sequestration. Understanding the N cycle in semi-natural ecosystems may therefore be the key to understanding the long-term source or sink strength of soils for carbon. The basic assumption is that any additional N uptake or immobilisation because of enhanced N-deposition is reflected in carbon pool changes due to NPP or organic matter accumulation according to the C/N ratio of the tree or the soil (Nadelhoffer et al., 1999b).

Aim of the paper: Using various detailed modelling approaches, temperature has been claimed to be relatively unimportant, whereas the combination of CO_2 rise and elevated N deposition may account for a 15-20% increase in forest net primary productivity. In this context, N deposition is claimed to be most important (Rehfuess et al., 1999). These results are, however, based on model studies which: used only a small number of sites and did not include any European upscaling. Moreover, these studies were hampered by limited availability of data on forest growth across Europe to calibrate the models on. In this study we evaluate the combined effects of changes in carbon dioxide concentration, climatic variables (temperature and precipitation) and nitrogen deposition on forest NPP and related carbon sequestration by trees and soils using data from nearly two hundred Intensive Monitoring plots throughout the whole of Europe. This is done by a chain of process based models coupling the hydrological cycle, carbon cycle, nitrogen cycle and base cation/acidity cycle with NPP and carbon sequestration

6.2 Intensive Forest Monitoring plots

The combined effects of changes in carbon dioxide concentration, climatic parameters and nitrogen deposition on carbon sequestration were investigated by using data from selected plots of the "Programme for Intensive and Continuous Monitoring of Forest Ecosystems", carried out since 1994. This so-called level II Monitoring Programme includes approximately 860 permanent observation plots in 30 participating countries with data from: (i) mandatory surveys on a 1-10 yearly basis, carried out at all plots (crown condition, at least once a year; chemical composition of needles and leaves, at least every 2 years; soil chemistry, every 10 years; increment, every 5 years) and (ii) optional surveys on a daily to biweekly basis, carried out on a subset of plots (atmospheric deposition in terms of bulk deposition and throughfall, soil solution chemistry and meteorology). In this study, the data were limited to plots with two increment surveys, mainly in the period 1995-2000, in combination with soil solution chemistry data (see also Mol-Dijkstra et al., 2007). Furthermore, plots were excluded that (i) had been fertilized, (ii) had a growth period of less than three years and (iii) for other reasons, such as missing tree diameter or height information or obviously severe data errors (see also Laubhahn et al., 2007; Solberg et al., 2007). Furthermore, we did not use plots that were thinned during the measurement period for increment. This led to a total number of 166 plots. At these plots, information on all surveys was available with the exception of plot specific meteorological data, such as temperature and precipitation that were available at 112 plots only. For these data, use was also made of a meteorological database (see Section 6.3.3).

The countries involved in the program all used the relevant EC Regulations and manual of ICP Forests providing standard methods for the assessment of increment and the sampling and analysis of bulk precipitation, throughfall, stemflow, foliage, soils and soil solution. Through Data Accompanying Report Questionnaires the participating countries submitted information on the applied methods for most of the plots. More information on sampling equipment, sampling strategy, sample handling, analytical procedures and quality control is given in e.g. De Vries et al. (2000).

In Figure 6.1, a map of the 166 plots is presented for which these data are available and that were used in the dynamic model chain to predict the long-term impact of various scenario's on above and below ground carbon sequestration. The map shows that most plots are located in Northern Europe (Scandinavia), Western Europe (the British Isles, the Benelux, and France) and Central Europe (Germany), and only a few plots can be found in the Mediterranean countries (2 in Spain and 2 in Italy). Most common tree species in the plots are Norway Spruce (*Picea abies),* Scots pine (*Pinus sylvestris*), Beech (*Fagus sylvatica)* and to a lesser extent Oak *(Quercus robur and Quercus petraea;* Table 6.1). Information on the age class distribution is given in Table 6.2.

Table 6.1 Distribution of plots over tree species and species groups

Tree species	Nr of plots	Species group
Pinus sylvestris	41	Scots Pine
Picea abies	65	Spruce
Picea sitchensis	3	Spruce
Abies alba	4	Fir
Pseudotsuga menziesii	2	Fir
Pinus nigra	1	Mediterranean pine
Fagus sylvatica	28	Beech
Quercus petraea	8	Standard Oak
Quercus robur	11	Standard Oak
Quercus cerris	2	Oak other
Fraxinus excelsior	1	Remaining broadleaves
Total	166	

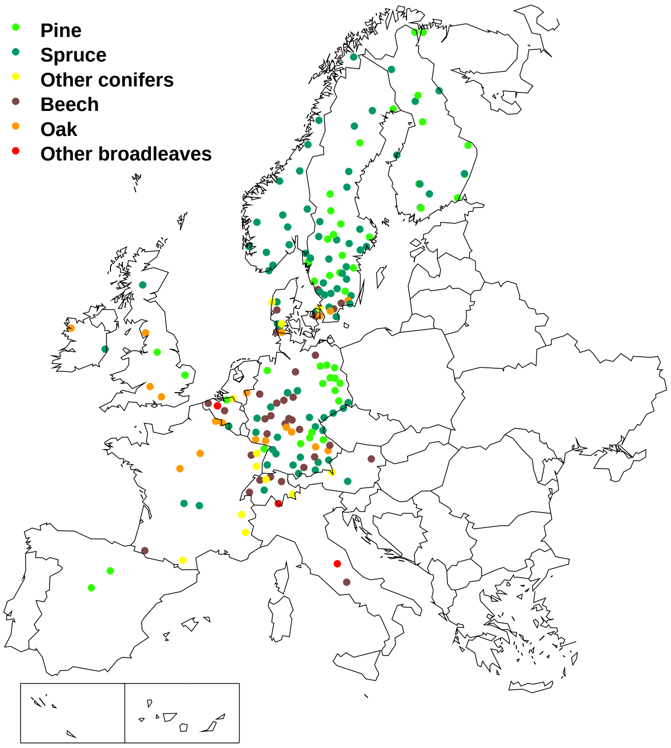


Figure 6.1 Locations of the Intensive Monitoring plots used for calibration and application of the dynamic SMART2 model.

Table 6.2 Distribution of plots over age classes

Age class	Number of plots
< 40	19
40 - 60	41
60 - 80	49
80-100	22
100-160	15
>160	10
Uneven aged	10
Total	166

6.3 The models involved

The integrated model chain is depicted in Figure 6.2. It consists of process based dynamic models predicting: (i) ecosystem succession, vegetation structure, forest NPP and carbon pool changes in the vegetation (SUMO), (ii) nutrient availability/fluxes, soil acidity and soil carbon sequestration (SMART2) and (iii) water availability/fluxes (WATBAL). A short description of process oriented models is as follows:

- SUMO (Wamelink et al., 2000a) is a mechanistic model predicting forest NPP while including understory, vegetation succession and vegetation structure.

Inputs are initial vegetation type, soil data from SMART2, management and grazing intensity. Outputs include forest NPP and carbon pool changes in the vegetation, foliar nutrition and vegetation structure.

- SMART2 (Kros et al., 1995) is a model for soil chemistry, including response to atmospheric deposition. Inputs are deposition and seepage fluxes of S, N, base cations and water, plant uptake, weathering, climate parameters and soil properties; outputs are soil chemistry (e.g. changes in N and C pools), soil solution chemistry and nutrient cycling fluxes.
- WATBAL (Starr, 1999) is a water balance model for forested stands/plots, calculating evapotranspiration, runoff and changes in soil moisture storage on a monthly basis. It uses relatively simple input data which are either directly available (e.g. monthly precipitation and air temperature) or which can be derived from other data using transfer functions and is therefore ideally suited to Intensive Monitoring plots and data.

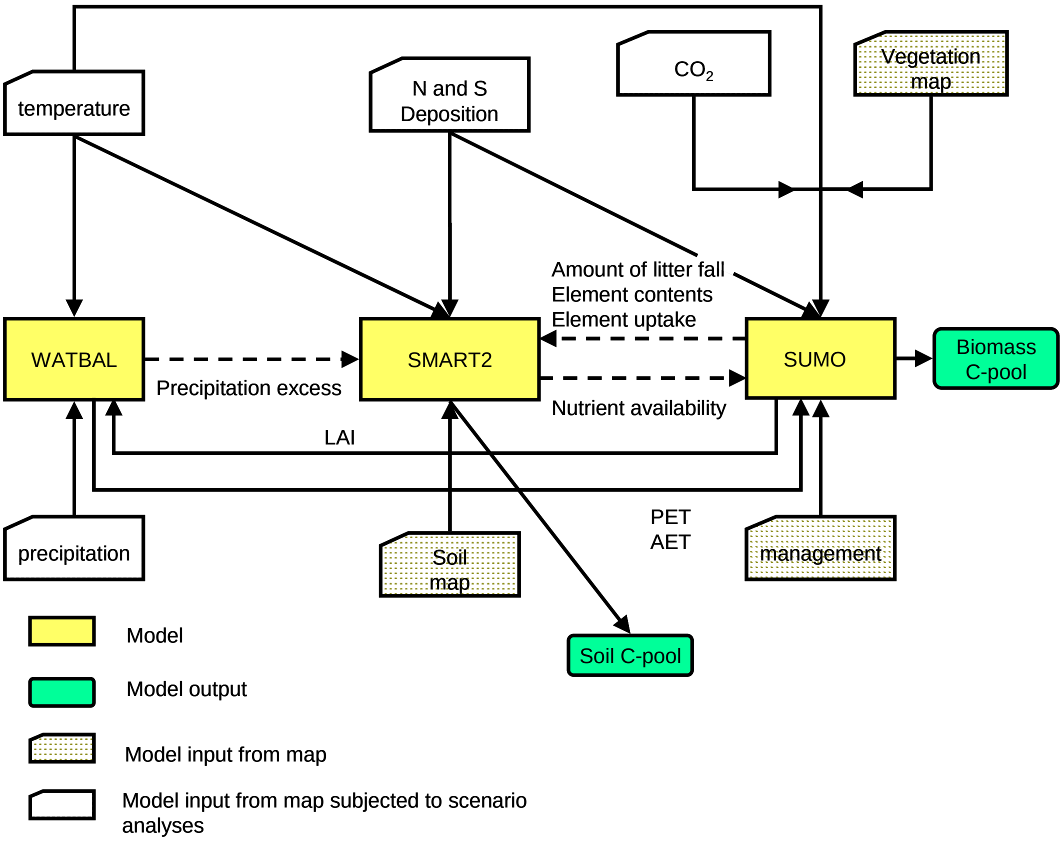


Figure 6.2. The integrated model chain SMART2-SUMO-WATBAL with the most important exchanged variables between the models and the most important input maps, partly subjected to scenarios.

The interaction of -SMART2-SUMO-WATBAL (SSW) is as follows: WATBAL provides SMART2 with information on water fluxes (precipitation excess) and SUMO with evapotranspiration (actual and potential) on a yearly basis. WATBAL needs info over the about LAI, which is provided by SUMO on a yearly basis, and which is translated into a monthly soil cover used in the water flux modelling. There is no feedback from SMART2 to WATBAL. SMART2 provides SUMO with the nutrient availability (N, Ca, Mg, and K) and the amount of nitrogen deposition interception by the canopy. SUMO provides SMART2 with nutrient uptake by the vegetation, litter amount including element contents and the vegetation type.

6.3.1 The SUMO model for forest growth

Model description

SUMO (Wamelink et al., 2000a; Wamelink et al., 2007a) is a dynamic growth and competition model. SUMO simulates the biomass, the biomass growth (NPP) and nutrient dynamics for five functional types; grasses/herbs, dwarf shrubs, shrubs, pioneer trees, and climax trees. The two tree functional types are simulated species specific. In this study, it is used exclusively to simulate forests. For each functional type biomass is partitioned over three organs: root, stem, and leaf. In each time step, of one year, biomass is computed from the biomass in the previous time step, NPP and death in the present time step, and removal of biomass by management. In this study, forest management, consisted of the removal of biomass (and thus nutrients) from the system, by thinning according an enforced thinning cycle. Once every ten years, an age and biomass dependent amount of biomass is removed from the system. The thinning cycle was only used for sites where in the field thinning is practiced.

Actual NPP is calculated using an assumed maximum NPP, which is rescaled for temperature and CO_2 concentration, and that is reduced by nutrient availability (provided by SMART2), water availability (provided by WATBAL) and light interception, according to:

$$\mathrm{NPPact}_t = \mathrm{NPPmax}(\mathrm{T}_{ref}, \mathrm{CO}_{2ref}) \cdot \mathrm{ST}_t \cdot \mathrm{SC}_t \cdot \mathrm{RI}_t \cdot \mathrm{RWav}_t \cdot \mathrm{RNav}_t \qquad 6.1$$

where NPPact_t is the actual growth ($kg.ha^{-1}.yr^{-1}$), $\mathrm{NPPmax}(\mathrm{T}_{ref},\mathrm{CO}_{2ref})$ is the maximum growth at a given reference temperature and CO_2 concentration (for the Netherlands, in $kg.ha^{-1}.yr^{-1}$), SC_t is a scaling factor for CO_2, ST_t is a scaling factor for the annual temperature, RI_t, RWav_t and RNav_t are reduction factors for the availability of light, water and nutrients (nitrogen, calcium, magnesium potassium), respectively. The original SUMO model only includes the effect of light, water and nitrogen limitations. Adaptations of SUMO for this study are the inclusion of effects of changes in CO_2 concentrations, temperature and base cation (calcium, magnesium potassium) availability on forest growth. The various functions are described below. The description of the original reduction functions is limited, since more information can be found in Wamelink et al. (2007a).

Inclusion of the effect of temperature change

The effect of temperature on forest growth was included in SUMO similar to the approach used in the Miami model (Chen & Lieth, 1993, formula 6.2):

$$\mathrm{NPPact(T)_t} = \mathrm{k(T_{ref})} \cdot \frac{1}{1 + \exp(1.315 - 0.119 * \mathrm{T_{a,t}})} \qquad 6.2$$

Where NPPact(T)$_t$ is the maximum NPP corrected for temperature effects (kg.ha^{-1}.yr^{-1}), k(T$_{ref}$) a species specific constant at a given reference temperature, replacing the overall value given 3000 by Lieth (kg.ha^{-1}.yr^{-1}), T$_{a,t}$ is the value of the yearly average temperature (-) of the location to be evaluated at time t. In SUMO, the reference temperature is the annual temperature for the Netherlands (T$_a$ = 10 ˚C).

k(Tref) is calculated from formula

$$\mathrm{k(T_{ref})} = \mathrm{NPPmax(T_{ref}, CO_{2ref})_t} \cdot \{1 + \exp(1.315 - 0.119 * \mathrm{T_{ref,t}})\} \qquad 6.3$$

Where T$_{ref,t}$ is the reference temperature.

Eq. (6.2) and Eq. (6.3) were combined for T$_{ref}$ = 10 ˚C, leading to:

$$\mathrm{NPPact(T)_t} = \mathrm{NPPmax(T_{ref}, CO_{2ref})_t} \cdot \frac{2.133}{1 + \exp(1.315 - 0.119 * \mathrm{T_{a,t}})} \qquad 6.4$$

The effect of temperature is related to the maximum NPP at a given reference temperature, according to (see Eq. 6.1):

$$\mathrm{NPPact(T)_t} = \mathrm{NPPmax(T_{ref}, CO_{2ref})} \cdot \mathrm{ST_t} \qquad 6.5$$

This leads to (combining Eq. 6.4 and Eq. 6.5)

$$\mathrm{ST_t} = \frac{2.133}{1 + \exp(1.315 - 0.119 * \mathrm{T_{a,t}})} \qquad 6.6$$

The values for the NPPmax(T$_{ref}$,CO$_{2ref}$) of the major tree species (*Picea abies*, *Pinus sylvestris*, *Fagus sylvatica* and *Quercus robur/Quercus petraea*) are 16, 20, 14, and 15 ton.ha^{-1}.yr^{-1}, respectively (see Table 6.5). Using these data implies that the effect of temperature ranges from ca. 0.5 ton.ha^{-1}.yr^{-1}.°C^{-1} to 1.5 ton^{-1}.ha^{-1}.yr^{-1}.°C^{-1} for these major tree species modelled by SUMO, as illustrated in Figure 6.3.

Chen and Lieth (1993), found an average temperature effect on growth of approximately 0.7 ton.ha^{-1}.yr^{-1} per °C, based on an NPP temperature relationship between -5 and +30°C, using different ecosystems of the world. This average increase is in line with data collected by Wamelink (2006) on net primary production and the corresponding yearly average temperature for forest all over the world (see Appendix 4). Based on this data set, Wamelink derived regression relations between T and NPP for the complete dataset, according to:

$$\mathrm{NPP} = 0.63\mathrm{T} + 9.3 \quad \mathrm{R}^2 = 0.16; \mathrm{N} = 129 \qquad 6.7$$

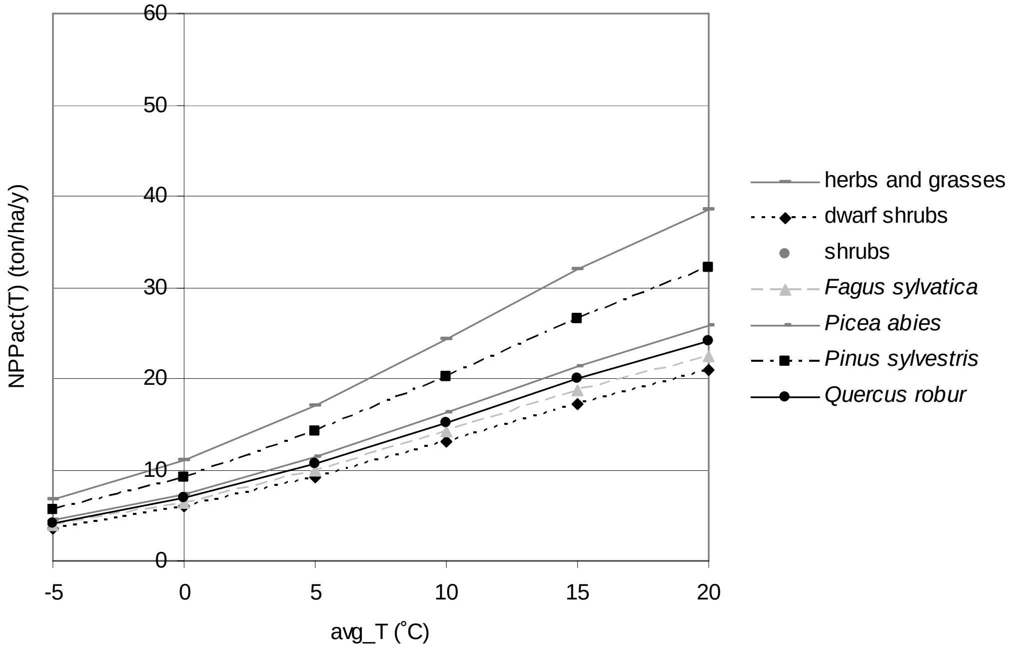


Figure 6.3 Effect of annual temperature (avg_T) on the maximum growth corrected for T (Eq. 6.4) for NPPAmax (T_{ref}) rates for the four main tree species in the study and the functional types herbs and grasses, dwarf shrubs and shrubs.

The low R^2 is due to the fact that temperature can not be viewed in isolation, but must be considered in combination with effects of tree species, tree age, climate zone, changing humidity, water availability and CO_2 concentration and in nutrient availability (see e.g. Kirschbaum, 2000b). The relation used in SUMO gives a NPP rise between approximately 0.5 ton.ha.yr.°C and 1.5 ton.ha.yr.°C, depending on the tree species. The average temperature effect on growth of approximately 0.6-0.7 ton.ha.yr.°C found by Wamelink (2006) and by Chen and Lieth (1993) is within the range of the middle of NPP raise simulated in SUMO, although at the lower end.

Inclusion of the effect of changes in CO_2 concentration

The rise of CO_2 concentration is assumed to work as a fertilizer as long as other variables are not limiting the growth. The effect of CO_2 concentration was built in SUMO with a scaling factor for CO_2, relative to the reference ambient CO_2 concentration, according to Gifford (1980):

$$SC = 1 + \beta \ln\left(\frac{C_a}{C_{a,0}}\right) \qquad 6.8$$

where C_a and $C_{a,0}$ are the CO_2 concentrations at ambient (elevated) and reference levels with the reference carbon dioxide level being set at 350 ppm and β is a dimensionless plant species dependent parameter quantifying the effect of CO_2 on growth. Since $C_{a,0}$ is a reference value before the rise in CO_2 concentration, it practically implies that the maximum growth is increased, depending on the CO_2 concentration in the scenario. The average value for β was estimated for each tree species based on the same relation between growth rate and CO_2 concentration according to Gifford (1980):

$$\beta = (\frac{G}{G_0} - 1) / \ln\left(\frac{C_a}{C_{a,0}}\right) \qquad 6.9$$

Where G and G_0 are the growth rates at ambient (elevated) and reference levels of carbon dioxide (C_a and $C_{a,0}$).

Inclusion of the effect of light

Light extinction corresponds with Lambert-Beer's law, with the extinction coefficient proportional to leaf biomass, according to:

$$RI_t = \sum_{c=1,5} \left[fI_{i,t,c-1} * \left(1 - e^{(-k_{i,j} * fBl_{i,t,c})} \right) \right] \qquad 6.10$$

Where RI_t is the reduction factor for light interception (Eq. 6.1), $fI_{i,t,c-1}$ is the fraction light remaining after interception in canopy layer c-1 Running from 1-4), $k_{i,j}$ is the light interception factor (functional type/tree species specific), $fBl_{i,t,c}$ is the fraction leaf biomass of functional type i in canopy layer c, and is the number of functional types present in a canopy layer.

The highest functional type catches light first, and functional types with leaves at equal height compete for light according to their leaf biomass. Therefore plant height is also explicitly simulated, dependent on biomass increment (see also Wamelink et al., 2007a).

Inclusion of the effect of water availability

The effect of water availability on the NPP (RWav, Eq. 6.1) is calculated as an empirical function of the difference between the actual evapotranspiration (AET in $m.yr^{-1}$) and potential evapotranspiration (PET in $m.yr^{-1}$) according to (Wamelink et al., 2004):

$$RWav_t = \frac{RW_{max}}{RW_{max} + \exp(-k_1 * (AET - k_2 * PET))} \qquad 6.11$$

Where $RWav_t$ is the reduction factor for water availability (-), RW_{max} is the maximum reduction set at 1 (-), k_1 set at 15 ($y.m^{-1}$) and k_2 set at 0.5 (-). The reduction of the NPP is 0.5 when AET = 0.5 PET. At AET = 0, the water reduction factor (and thus NPP) is near zero and at AET = PET, the reduction factor is near 1, implying no NPP reduction. For each location the PET was fixed. As a reference value for PET the average potential evapotranspiration over the period 1960-1990 was used. The actual evaporation and potential transpiration at each site was calculated by WATBAL as described in Section 6.2.3

The empirically derived reduction function was compared to data on the relation between water availability and tree growth (Van den Burg, 1987, see Figure 6.4). The reduction of the volume growth index due to the water availability capacity (AWC), i.e. the available water amount that can be stored in soil and is available for growing crops, of twelve tree species was compared to the reduction of the NPP as used by SUMO. For this comparison, we assumed that at AWC higher than 0.2 $m.yr^{-1}$ and AET higher than 0.6 $m.yr^{-1}$ there is no growth reduction, i.e. RWav = 1. Moreover, we assumed that the AWC has a comparable effect on NPP as AET. Consequently, a comparison was made based on rescaled (from 0 – 1) AET and AWC values (Figure 6.4). Results show that the empirical relation falls well within the range for the twelve different tree species and that the reduction function represents the average for the species quit well. However, the difference between the species is quit large; indicating that for individual species the fit is less good. In a future version of SUMO it would be advisable to model the effect of water availability on the growth functional type and tree species specific.

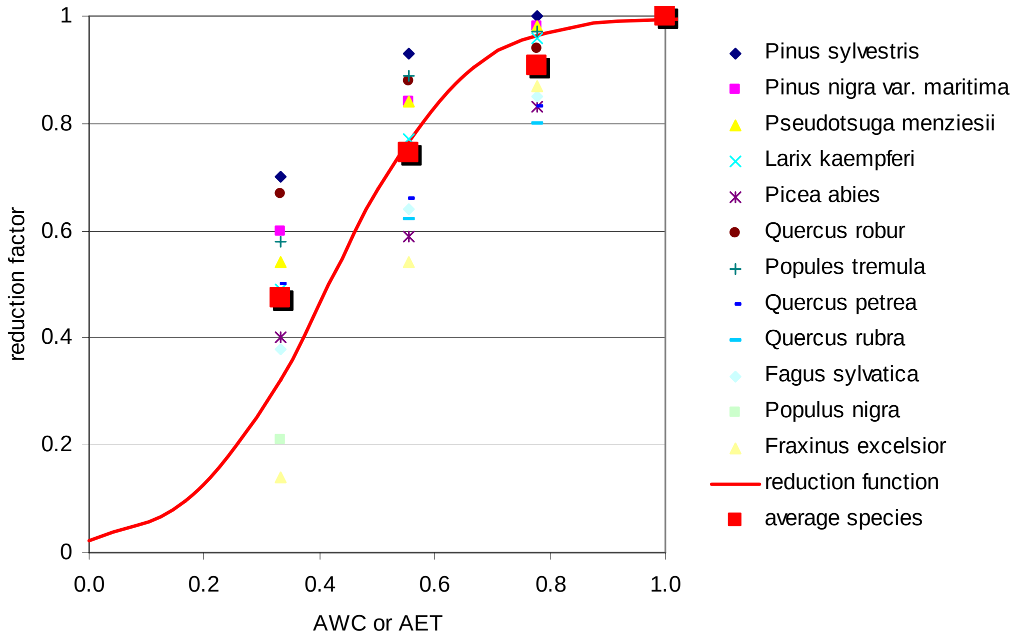


Figure 6.4 The reduction factor of NPP (RWav) calculated by SUMO based on AET compared to the reduction of available water capacity (AWC) on the volume growth index for several tree species (after Van den Burg, 1987). Both AWC and AET were rescaled from 0 till 1.

Inclusion of the effect of nutrient availability

The reduction factor for nutrient availability (RNav) is based on the availability of nitrogen, calcium, magnesium and potassium. We used Liebig's Law of the Minimum to model the effect of these four nutrients on NPP. The most limiting element per functional type determines the overall reduction factor. Disadvantage of this method is that co-limitation between elements is not accounted for. The limiting nutrient may vary from year to year and between the functional types.

In the original SUMO model, only carbon and nitrogen fluxes were simulated, in close interaction with SMART2. N uptake by the vegetation and N input by litterfall are provided by SUMO to SMART2, whereas SMART2 delivers the nitrogen availability to SUMO as the sum of external N input and mineralization. In SUMO, nitrogen comes from three sources: (i) root uptake from the soil, (ii) foliar uptake from the atmosphere and (iii) internal reallocation from one organ to another. The root uptake of soil nitrogen is calculated by SUMO, based on the nitrogen availability in the soil compartment (including the organic layer) simulated by SMART2, while taking into account the total foliar uptake and the internal reallocation. Nitrogen that is taken up by the roots of each functional type is assumed to be equal to the proportion of its root biomass in the total root biomass. Foliar uptake of atmospheric nitrogen for the whole canopy is calculated by SMART2, whereas the amount of nitrogen taken up by the canopy is distributed over the functional types by SUMO following the light interception. Within each functional type it is partitioned over its organs, using fixed percentage distributions per functional type/vegetation type combination. The uptake of nitrogen is limited by setting a maximum on the nitrogen content of the biomass; excess nitrogen remains in the soil and may be leached.

Since Mg, Ca and K are also important nutrients for the vegetation, which may limit the NPP, they were added to the SUMO model. The simulation of the fluxes follows that for nitrogen except that there is no reallocation for the cations. For the base cations there is one source: root uptake from the soil that is modelled in SUMO based on the base cation availability in the soil compartment (including the organic layer) simulated by SMART2.

6.3.2 The SMART2 model for soil chemistry

Model approach
In SMART2, part of the incoming litterfall is not decomposed in the first year and is transferred to the organic layer (L, F and H layer or complex of humus substances with undecomposed organic debris). The decomposition of this old litter pool is described by first-order kinetics (see e.g. Van Veen, 1977). The total release of C, N or BC (Ca, Mg or K) from the organic layer is calculated as:

$$X_{mi,lt} = f_{mi,fl,x} \cdot F_{lf} \cdot ctX_{lf} + k_{mi,ol,x} \cdot Am_{F} \cdot ctX_{ol} \qquad 6.12$$

Where X= C, N or BC (Ca, Mg or K), $f_{mi,1f,x}$ (-) is the actual decomposition fraction of the yearly total litterfall (fresh litter) of element X, F_{lf} is litterfall (kg.ha^{-1}.yr^{-1}), $k_{mi,ol,x}$ (yr^{-1}) is the decomposition rate constant of element X in the organic layer, Am_{ol} is the amount of organic layer or litter (kg.ha^{-1}) and ctX_{lf} and ctX_{F} are the contents of element X in litterfall and in the organic layer (mol$_c$.kg^{-1} or as %, see below!). At present, mineralisation of organic matter in the mineral soil layers is not considered in SMART2, except for the mineralisation from root necro-mass, which is fed by root decay and added to litterfall.

The actual decomposition fraction ($f_{mi,lf,x}$) and rate ($k_{mi,ol,x}$) for C (x=C) and N (x=N) and BC are calculated as maximum values multiplied with reductions functions for pH, moisture, temperature and N content in the decomposing material, according to:

$$f_{mi,lf,x} = f_{mi,max} \cdot rf_{mi,pH} \cdot rf_{mi,T} \cdot rf_{mi,lf,N} \cdot rf_{mi,CN,x} \quad 6.13$$

$$k_{mi,ol,x} = k_{mi,max} \cdot rf_{mi,pH} \cdot rf_{mi,T} \cdot rf_{mi,ol,N} \cdot rf_{mi,CN,x} \quad 6.14$$

where $f_{mi,\,max}$ and $k_{mi,max}$ are maximum values for the decomposition fraction for fresh litter (-) and the decomposition rate constant of older litter (yr^{-1}) respectively, $rf_{mi,pH}$, $rf_{mi,T}$, $rf_{mi,lf,N}$ and $rf_{mi,CN,x}$ are reduction factors for pH, T, N content and C:N respectively. For each reduction value the factor is always > 0 and generally < 1, but for temperature it can be > 1 (scaling factor).

The reduction function for pH and for the C/N ratio on N mineralization is described in (Tietema et al., 2002). The effect of temperature on the mineralization rate is based on a response function described by Kirschbaum (2000a) and Kirschbaum and Paul (2002) scaled to a reference temperature of 10°C (see Kros et al., 2007). Beyond the effect of N on decomposition, SMART2 also takes into account the effect of changes in the C:N on the ratio between N mobilization and immobilization. The reduction function for C/N ratio on N mineralization is described in (Tietema et al., 2002).

The original SMART2 model does not take into account an effect of N on C decomposition but only on the mineralization of N. In general, however, N addition increases decay rates for plant litter with low content of lignin, tannin, and other secondary compounds (Fog, 1988; Berg & Matzner, 1997; Berg & McClaugherty, 2003). Therefore the model was extended with a reduction function for N content of litter on mineralisation. The effect of N availability on decomposition is included in the SMART2 model in a comparable way as the model SOMM by (Smith et al., 1997). In this model of soil organic matter dynamics, they assumed that decomposition of fresh material is stimulated with increasing N content of the decomposing material and that decomposition of older litter is suppressed by increasing N content. SOMM is a three component model with fresh litter, a forest floor, which is divided in two sub-horizons F and H. We use the SOMM formulation to incorporate the N-effect on decomposition in the SMART2 model, while distinguishing between freshly fallen litter (< 1 year) and old (> 1 year) litter only. Contrary to the SOMM model, there is no very slowly decomposing organic pool available that decomposes independent from the N content.

Chertov and Komarov (1997) derived a k_1, the decomposition rate constant of fresh litter (L-layer), that is increasing with N-content, whereas k_2, the decomposition rate constant of older litter (F layer or complex of humus substances with undecomposed organic debris) is decreasing with N content, according to:

$$k_1 = 0.002 + 0.000909 \cdot \text{ash} + 0.00303 \cdot \text{ctN}_{\text{lf}} \quad \text{for } 0\% < \text{ctN}_{\text{lf}} < 3\% \tag{6.15}$$

$$k_2 = \begin{cases} 0.0008 \cdot \text{ctN}_{\text{ol}} \text{ for } \text{ctN}_{\text{ol}} \leq 0.5\% \\ 0.000456\text{-}0.000112 \cdot \text{ctN}_{\text{ol}} \text{ for } 0.5 < \text{ctN}_{\text{ol}} < 3\% \end{cases} \tag{6.16}$$

Based on these relations we derived N content related reduction functions by relating $f_{mi,1f,N}$ to k_1 and $k_{mi,ol,N}$ to k_2 while using a N content of 3% percent as a reference. Firstly, the following ash and/or N content related reduction values were calculated:

$$\text{rf}_{\text{mi,lf,N}}(\text{ash}, \text{ctN}_{\text{fl}}) = \frac{k_1(\text{ash}, \text{ctN}_{\text{fl}})}{k_1(\text{ash}, 3)} \tag{6.17}$$

$$\text{rf}_{\text{mi,ol,N}}(\text{ctN}_{\text{fl}}) = \frac{k_2(\text{ctN}_{\text{lt}})}{k_2(3)} \tag{6.18}$$

This was done for the ash range (0 < ash < 12%) and N content range (0< ctN < 3%) as indicated by Chertov and Komarov (1997). Subsequently, a linear regression relationship was fitted through the obtained values in case of $\text{rf}_{\text{mi,lf,N}}$ (Eq. 6.17), and directly solved for $\text{rf}_{\text{mi,ol,N}}$ (Eq. 6.18). This resulted in a decomposition fraction of freshly fallen litter (L-layer) that is increasing with N content according to:

$$\text{rf}_{\text{mi,lf,N}} = \begin{cases} 0.4254 + 0.1915 \cdot \text{ctN}_{\text{lf}} & \text{for } \text{ctN}_{\text{lf}} < 3 \\ 1 & \text{for } \text{ctN}_{\text{lf}} \geq 3 \end{cases} \tag{6.19}$$

whereas $k_{mi,ol,N}$, the decomposition rate constant of older litter (F layer or complex of humus substances with undecomposed organic debris) is decreasing with N content at N contents beyond 0.5%:

$$\text{rf}_{\text{mi,ol,N}} = \begin{cases} 2 \cdot \text{ctN}_{\text{ol}} & \text{for } \text{ctN}_{\text{ol}} < 0.5 \\ 1.14 - 0.28 \cdot \text{ctN}_{\text{ol}} & \text{for } 0.5 \leq \text{ctN}_{\text{ol}} < 3 \\ 0.3 & \text{for } \text{ctN}_{\text{ol}} \geq 3 \end{cases} \tag{6.20}$$

where ctN_{lf} is N content in freshly fallen litter (%) and ctN_{ol} is N content in old litter (%).At N contents above 3 it is assumed that the reduction value remains constant at the value for ctN_{ol}=3%, i.e. 0.3

6.3.3 The WATBAL model for soil hydrology

Model approach

For the water balance calculations within this project we to used the existing water balance model WATBAL. WATBAL (Starr, 1999) is a monthly water balance model for forest soils based on the following water balance equation for the rooting zone:

$$P = ET + R \pm \Delta SM \tag{6.21}$$

where P is Precipitation, ET is evapotranspiration, R is Soil water flux and ΔSM is change in soil water in the rooting zone (all in mm month^{-1}). One of the main advantages of WATBAL is that the model uses input data which are either easily obtained or can be derived from other basic data using transfer functions. It uses relatively simple and readily available climate variables (precipitation, air temperature and cloudiness) and the available water capacity (AWC) of the soil, which can be derived using transfer functions based on soil texture, bulk density, and organic matter content or from the soil moisture curve. It handles sloping sites if the appropriate slope factors are given and snowmelt. Besides giving soil water flux values, all the components of the water balance are determined: potential (PET) and actual evapotranspiration (AET), soil moisture, snow pack store and snowmelt, as well as global (direct and diffuse) radiation. Leaching fluxes are used in conjunction with predicted concentrations of compounds of interest in soil water by SMART2 to calculate leaching losses. WATBAL has been validated for several sites (Starr, 1999) with measured soil water fluxes from in-situ (zero-tension) gravity lysimeters and soil moisture content measured with TDR probes.

In this study, the actual and potential evapotranspiration calculated by WATBAL was used in SUMO to assess the effect of transpiration reduction (drought stress) on NPP. The monthly potential evapotranspiration (PET_m in mm) is calculated by WATBAL according to:

$$PET_m = PET_{pot} \cdot cf \cdot sc_m \tag{6.22}$$

where PET_{pot} is the monthly potential evapotranspiration (in mm) for a closed reference crop using the method of Thornthwaite, cf is a crop factor, used to scale the transpiration of a reference crop (alfalfa) to forests, taking into account the greater evapotranspiration from forests, and sc_m is the monthly soil cover. For all forest types, the crop factor is set to 1.6, irrespective of the succession stage of the forest (Starr, pers. comm.).

The distribution of the soil cover over the year is assumed to follow the variation in monthly LAI over the year, using the following relationships (see also Figure 6.5):

$$sc = \begin{cases} sc_{min} \text{ for } day < day_{lmin} \text{ or } day > day_{fmin} \\ sc_{max} \text{ for } day_{fmax} < day < day_{lmax} \\ sc_{min} + (sc_{max} - sc_{min}) \cdot \dfrac{(day - day_{lmin})}{(day_{fmax} - day_{lmin})} \text{ for } day_{lmin} < day < day_{fmax} \\ sc_{min} + (sc_{max} - sc_{min}) \cdot \dfrac{(day_{fmin} - day)}{(day_{fmin} - day_{lmax})} \text{ for } day_{lmax} < day < day_{fmin} \end{cases} \tag{6.23}$$

where sc_{min} is minimum soil cover, sc_{max} is maximum soil cover, day_{lmin} and day_{fmin} is last day in spring and first day in autumn, respectively, where soil cover is at its minimum ($sc = sc_{min}$), whereas day_{fmax} and day_{lmax} is first day in spring and last day in autumn, respectively, where soil cover is at its maximum ($sc = sc_{max}$).

For very few plots, the stem density is so low that the canopy will not close in any month of the year. For those plots, the maximum canopy closure was computed using a relation between stem diameter and canopy closure (the area occupied by the crowns divided by the plot area) according to (Nagel, 1999):

$$\mathrm{cc} = \max\left(1, \frac{(\mathrm{a} + \mathrm{b} \cdot \mathrm{DBH})^2 \cdot 0.25 \cdot \pi \cdot \mathrm{ntrees} \cdot 10^{-4}}{\mathrm{plot\ size}}\right) \qquad 6.24$$

in which cc is the canopy closure, a (m) and b (m) are constants and DBH is the diameter at breast height (m), ntrees is the tree density (ha^{-1}). Parameters for a and b are listed in Table 6.3.

Table 6.3 Parameters used to calculate the canopy closure (based on Nagel, 1999).

Tree species	a	b
Oak	1.411	0.154
Beech	1.389	0.181
Spruce	0.842	0.110
Pine	0.714	0.133

The actual monthly evapotranspiration is determined by the interception evaporation (Ei), which is directly related with the leaf area index (LAI) and the evapotranspiration. The LAI is calculated in SUMO from the yearly standing biomass of the foliage according to:

$$\mathrm{LAI}_y = \begin{cases} 0.5 \cdot \mathrm{Bl}_y & \text{for} \quad \text{Needle forest} \\ \mathrm{Bl}_y & \text{for} \quad \text{Deciduous forest} \end{cases} \qquad 6.25$$

Where Bl_y is annual leaf biomass of the trees ($\mathrm{ton.ha}^{-1}$) and LAI_y is the annual average LAI. The evapotranspiration of soil water may take place at the potential rate (PET) or at a reduced rate, the actual evapotranspiration (AET), depending on a relationship determined by the soil water storage (SM) and the available water capacity (AWC) in the rooting zone. Evapotranspiration can only take place from the rooting zone; losses from the soil beyond the rooting zone only take place through drainage. If precipitation (+snowmelt) is in excess of PET, then the excess goes to fill the storage capacity of the soil. If the AWC is filled then any further excess of precipitation (+snowmelt) goes to form drainage, i.e., the soil water flux from the soil layer in question. The actual and potential monthly evapotranspiration were summed to yearly values for use in SUMO to derive its impact on forest NPP as described earlier.

6.4 The model application

6.4.1 Model parameterization

WATBAL parameters determining soil cover

The seasonal trajectory of LAI as compared to its maximum value is given in 5. Data are based on various authors (after Ogink-Hendriks, 1995; Bartelink et al., 1997; Gond et al., 1999; Lefèvre et al., 2000; Gielen & Ceulemans, 2001; Mussche et al., 2001; Van Dobben et al., 2002a; Simpson et al., 2003; Bonten & Brus, 2006; Holst et al., 2007). The results showed very little effect of tree species on the distribution of LAI/LAI max over the year. Because the yearly computed PET value proved to be rather insensitive to the exact timing of the various leaf development stages (PET in spring and fall is determined by the meteorological conditions in those periods, rather than the soil cover), average values for each stage were derived from Figure 6.5. The value of the minimum soil cover (sc_{min}) was set to 0 for deciduous trees and to 0.2 for conifers and evergreen broadleaved trees and the maximum value (sc_{max}) was set to 1. Values of day_{fmin} and day_{lmin} were set at day 100 and day 300, while day_{fmax} and day_{lmax} were set at day 130 and day 280, respectively, irrespective of tree species (see Figure 6.5).

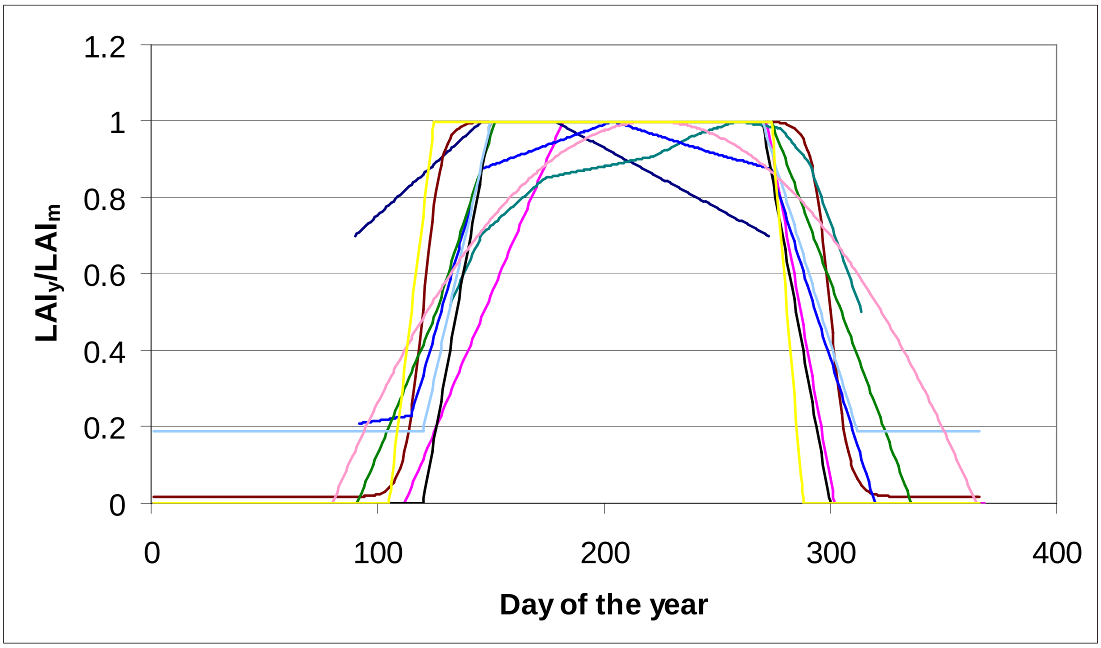


Figure 6.5 Seasonal distribution of LAI over the year, used as a surrogate for the distribution of soil cover over the year for poplar, oak and beech and two modeled curves for deciduous forest (after Ogink-Hendriks, 1995; Bartelink et al., 1997; Gond et al., 1999; Lefevre et al., 2000; Gielen & Ceulemans, 2001; Mussche et al., 2001; Van Dobben et al., 2002a; Simpson et al., 2003; Bonten & Brus, 2006; Holst et al., 2007).

Other WATBAL input parameters

Because WATBAL is a simple water balance model, it has only a limited number of input parameters. Available water capacity for WATBAL was estimated as function of soil type and texture class according to Batjes (1996) who provides texture class dependent AWC values for all FAO soil types based on an extensive literature review. Critical soil water parameters: AWC ratios (the ratio between actual soil water content and AWC at which transpiration is reduced) were computed as a function of soil texture according to the standard WATBAL procedure.

SUMO model parameters describing impacts of CO_2, temperature and nutrients

Here we describe the assessment of model parameters in SUMO describing impacts of CO_2 (β), temperature (NPP at a reference temperature of 10°C and nutrients (minimum and maximum foliar nutrient contents). Results for all tree species included in SUMO are given in Appendix 5 (see also Appendix 6). In this section we limit the results to the tree species occurring at the investigated Intensive Monitoring plots.

β values, which determine the impact of CO_2 on NPP, were derived from literature data on experiments with information on growth rates at elevated and reference levels of carbon dioxide (Lincoln et al., 1984; Bhagsari & Brown, 1986; Hollinger, 1987; Radoglou & Jarvis, 1990; Bazzaz et al., 1993; Poorter, 1993; Kittel et al., 1995; Lee & Jarvis, 1995; Hättenschwiler & Körner, 1996; Norby et al., 1999; Broadmeadow & Jackson, 2000; Laitat et al., 2000; Hättenschwiler, 2001; Calfapietra et al., 2003; Silva et al., 2004; Kettunen et al., 2006), while using Eq. (6.3). The original data used per tree species used in SUMO can be found in Appendix 5 and 6). Data thus derived for the tree species included in this study are given in Table 6.4.

Table 6.4 Values of β per species used in the SUMO model to describe the effect of CO_2 concentration on forest growth, based on literature data, while using Eq. 6.3 (see Appendix 6).

species	average	Standard deviation	n
all species	0.53	-	125
avg C3 trees	0.59	-	39
Avg wild plants	0.50	-	50
Abies alba	0.45	0.55	4
Fagus sylvatica	1.01	0.82	5
Fraxinus excelsior	0.41	-	1
Larix decidua	0.18	-	1
Picea abies	0.27	0.28	4
Picea sitchensis	0.32	0.30	3
Pinus sylvestris	0.30	-	1
Pseudotsuga menziesii	0.04	-	1
Quercus petrea	1.08	-	1
Quercus robur	0.51	0.18	4

The β values are not available for all species in SUMO. In these cases β is either the value for a species in the same family or the average value for C3 trees (see Table 6.5). The value for shrubs is the overall value for trees and the value for dwarf shrubs and grasses and herbs is the value for all species. This implies that dwarf shrubs and grasses and herbs will benefit in the same way from a raise in carbon dioxide concentration.

Values of NPPmax(T_{ref}, CO_{2ref}), which determine the impact of temperature on growth, were derived from literature and expert judgment. The literature data included growth experiments of tree species (mostly pot-experiments), field experiments where biomass growth was measured by harvesting or estimated by indirect from measurements (published and unpublished data) and values from other models. A problem with field estimates is that it merely reflects the actual growth as a result of growth limiting factors as nutrient availability, water availability etc. That is why the NPPmax values often need to be adjusted in the parameterisation process. For grasses and herbs and Larix, the values were adjusted from the original settings described by Wamelink et al. (2007a) as a result of the calibration process described in Section 6.3.2. Data were derived from Ogaya et al. (2003), Bauer et al. (Bauer et al., 2000), Augusto et al. (2002), Hagen-Thorn et al. (2004), Reichle (1981), Schenk et al. (1995), Prins et al. (1988), Miller et al. (1980), Meeuwsen and Rottier (1984), Malindo et al. (1990), Jans et al. (1994), Heil and Bobbink (1993), Finer (1989), Elberse and Berendse (1993), Dyck and Bement (1972), Dijkstra (1990), Diemont and Oude Voshaar (1994), Diemont (1994), Conijn (1991), Berendse (1994a), Berendse and Aerts (1984), Berendse et al. (1987), Berendse et al. (1994), Aerts and Berendse (1988) and Aerts and Heil (1993).

Table 6.5 Values of NPPmax(T_{ref} = 10°C) per functional type/species used in SUMO to describe the effect of temperature on forest NPP. For grasses and herbs and Larix, the NPPs were changed in the parameterization (denoted as ‘).

Species/functional type	NPP_{max} ($ton.ha^{-1}.yr^{-1}$)
Grasses and herbs	14‘
Dwarf shrubs	13
shrubs	15
Picea abies	19
Pinus sylvestris	16
Picea sitchensis	28
Pinus nigra	23
Abies alba	23
Pseudotsuga menziesii	23
Larix decidua	18‘
Quercus petrea	19
Quercus robur	19
Fagus sylvatica	28
Quercus cerris	10
Fraxinus excelsior	28

Minimum and maximum values for N, Ca, Mg and K, needed in SUMO to assess the foliar contents and derive the impact of nutrient limitation, are based on literature research. The values for maximum and minimum content of the elements per organ are given in Table 6.6.

Table 6.6 Minimum and maximum element contents per functional type and tree species

functional type/tree species	N_{min}	N_{max}	K_{min}	K_{max}	Mg_{min}	Mg_{max}	Ca_{min}	Ca_{max}
Grasses and herbs	0.011	0.025	0.005	0.01	0.001	0.003	0.003	0.015
Dwarf shrubs	0.0085	0.023	0.004	0.009	0.001	0.003	0.002	0.014
Shrubs	0.0085	0.023	0.005	0.01	0.001	0.003	0.003	0.015
Picea abies	0.01	0.0163	0.001	0.0083	0.0006	0.0018	0.0023	0.0105
Pinus sylvestris	0.009	0.0193	0.001	0.0076	0.0006	0.0018	0.0016	0.0069
Picea sitchensis	0.005	0.0201	0.001	0.0108	0.0006	0.0014	0.0022	0.007
Pinus nigra	0.007	0.0193	0.001	0.0076	0.0006	0.0018	0.0016	0.0069
Abies alba	0.008	0.0161	0.00005	0.0087	0.0007	0.003	0.005	0.0163
Pseudotsuga menziesii	0.008	0.025	0.001	0.0114	0.0005	0.0022	0.004	0.0058
Larix decidua	0.005	0.02	0.001	0.0075	0.0011	0.002	0.0048	0.0178
Quercus petrea	0.008	0.0224	0.001	0.00139	0.0009	0.0025	0.0045	0.0125
Quercus robur	0.009	0.025	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Fagus sylvatica	0.01	0.025	0.0005	0.0128	0.0008	0.0031	0.005	0.0177
Quercus cerris	0.008	0.0229	0.001	0.0116	0.001	0.0029	0.0006	0.00137
Fraxinus excelsior	0.008	0.023	0.001	0.0142	0.0012	0.0035	0.0046	0.0158

SUMO uses an overall content for all organs, which is mostly best represented by the contents in the leaves. The minimum and maximum content are defined as the 5 and 95 percentile of the contents found in the literature (Duvigneaud & Denaeyer-De Smet, 1970; Van den Burg, 1985, 1989; De Vries et al., 1990; Di Stefano et al., 1997; Medlyn & Jarvis, 1999; Kytoviita et al., 2001; Cutini, 2002; André & Ponette, 2003; Komarov et al., 2003; Tausz et al., 2004; Puértolas et al., 2005; Streck et al., 2007). The values are subject to parameterization i.e. some of the values were adjusted as a result of the calibration process described in 6.3.2. However, element contents were kept within the range of measured values.

Site parameters
For the actual runs on the sites SMART2 was parameterised per plot (for the parameterisation see Mol-Dijkstra et al., 2007). The derivation of the soil parameters is described by De Vries et al. (2003c). Most important soil parameters are the cation change capacity (CEC), the base saturation, and the exchange (or selectivity) constants describing cation exchange and weathering rates since these parameters determine the long term behaviour of the soils. CEC and exchangeable cations were directly derived from measurements. The exchange constants were calibrated and the weathering rates were estimated from the budget (the average of the differences between deposition and leaching corrected for base cation uptake) of the respective elements. Furthermore, parameters that determine nitrogen immobilisation, denitrification and nitrification were estimated (De Vries et al., 2003c). The immobilisation is dependent of the C to N ratio in the mineral soil, denitrification is derived by a function of texture and gley class and nitrification was computed from the measurements of different N fluxes.

6.4.2 Model calibration

We calibrated the SUMO model for the sites using measured site-specific data for soil and vegetation and verified the WATBAL results. The SMART2 model was not calibrated, we used the values as described in section 6.3.1.

WATBAL

The reliability of the water fluxes was checked by comparing the leaching of chloride (Cl) and sodium (Na) against the deposition for those Intensive Monitoring plots where these two elements were measured in the soil solution. Both chloride and sodium can be considered as tracers (Cl) or nearly tracers (Na), i.e. the (long-term average) leaching computed from the modelled downward water flux and the measured concentration should match the deposition. The measurements of Na and Cl in deposition and soil solution thus allow checking whether the hydrology is modelled accurately.

Figure 6.6 shows the deposition-leaching relations for Cl and Na for plots with at least 2 years of measurements. As can be seen, the average slope for Cl is close to the perfect 1, indicating that there is no overall bias in the hydrological model. However, the graphs also show that there are several plots with rather unbalanced inputs and outputs. In the case of Na this could partly be explained by weathering. Part of the plots where chloride leaching is higher than chloride deposition are located close to the sea, which may cause imbalances in the budget due to sea-salt input on the soil that is not collected in the deposition samplers.

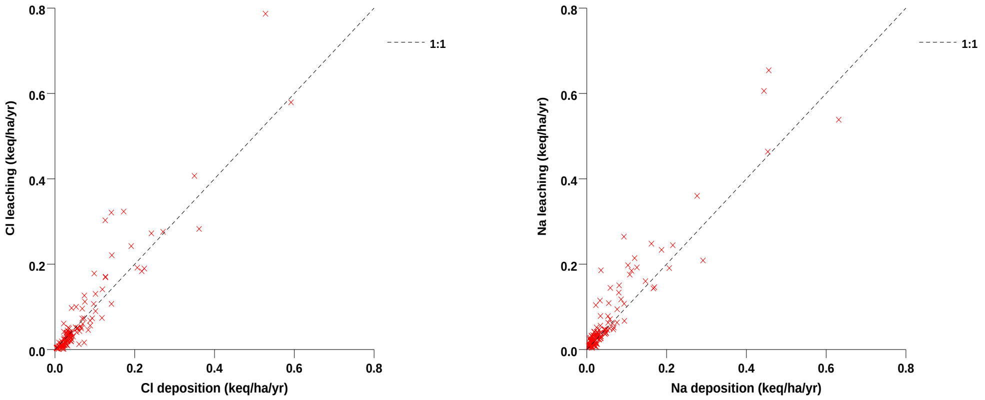


Figure 6.6 Cl and Na input-output (deposition-leaching) relationships

SUMO: SUMO was calibrated for this project on the standing biomass and biomass increment at the sites. SMART2-SUMO was run from the planting date for each plot to simulate woody biomass of the trees for the years in which measurements are available. Out of the 166 sites, 153 plots with reliable biomass measurements were available for at least one year. From the biomass the NPP was calculated, when measurements for two years were available. Furthermore, 4 plots were omitted because they had a negative growth in the measured period (most likely due to management), leading to 120 plots where model calibration took place for biomass growth, 149 plots were used for the calibration of the biomass.

The calibration was not done per site, but per species over all sites. This method is in line with the way SUMO is set up and it gives the possibility to use the data set as a check on the performance of the model, though the data are not independent and the check can thus not be regarded as a validation. Consequently, the modelled NPP does not match exactly the growth at each site. Calibration took place by adjusting model parameters within the range of measured values reported in the literature for the maximum NPP, light interception and minimum and maximum N-content to reasonably match the field data. These parameters were the most sensitive ones as shown by sensitivity analysis of SUMO (G.W.W. Wamelink, pers. comm.).

Figure 6.7 shows the relation between measured and simulated biomass. The results include both years from a plot, although they are not independent. Ideally, the regression line (in grey) would not differ significantly from the y=x line (in black). Although the simulated NPP looks adequate the regression coefficient differs significantly from 1.0 and the intercept differs significantly from 0 ($y = 0.7644x + 71.106$; $R^2 = 0.61$). The simulations of the NPP over the measured period are less good (Figure 6.8)

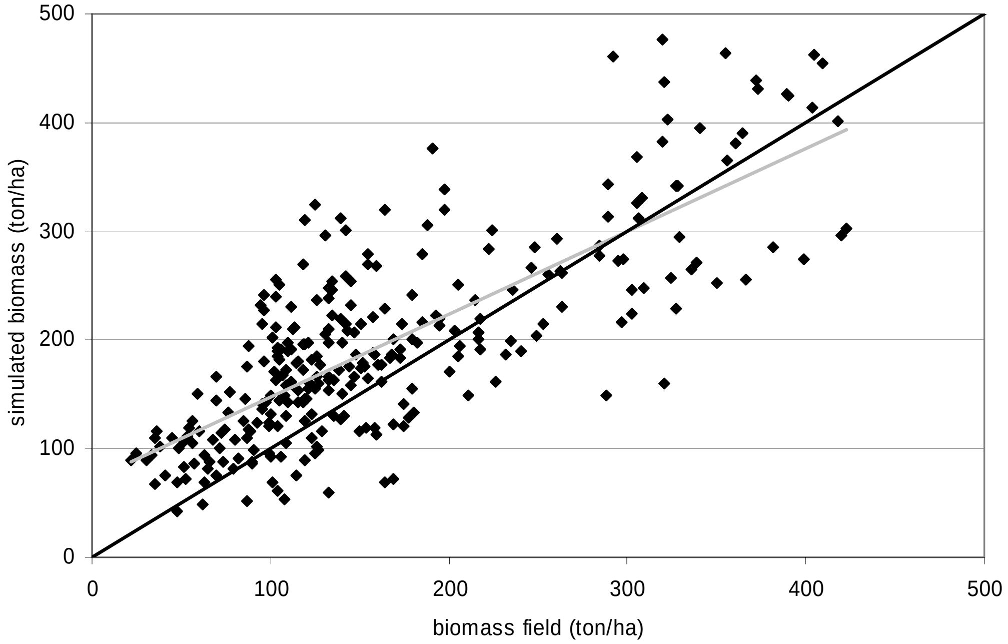


Figure 6.7 Relation between field measurements and simulated biomass for 149 intensive monitoring forest plots in Europe. Most of the plots have two measurements of biomass, which are both included in combination with the simulated biomass. The black line shows the y=x line, the grey line the regression line.

Here also the regression coefficient differs significantly from 1 and the intercept differs significantly from 0 ($= 0.4969x + 4.436$; $R^2 = 0.6482$). However, we judged the results to be good enough for application of SMART2-SUMO for the plots.

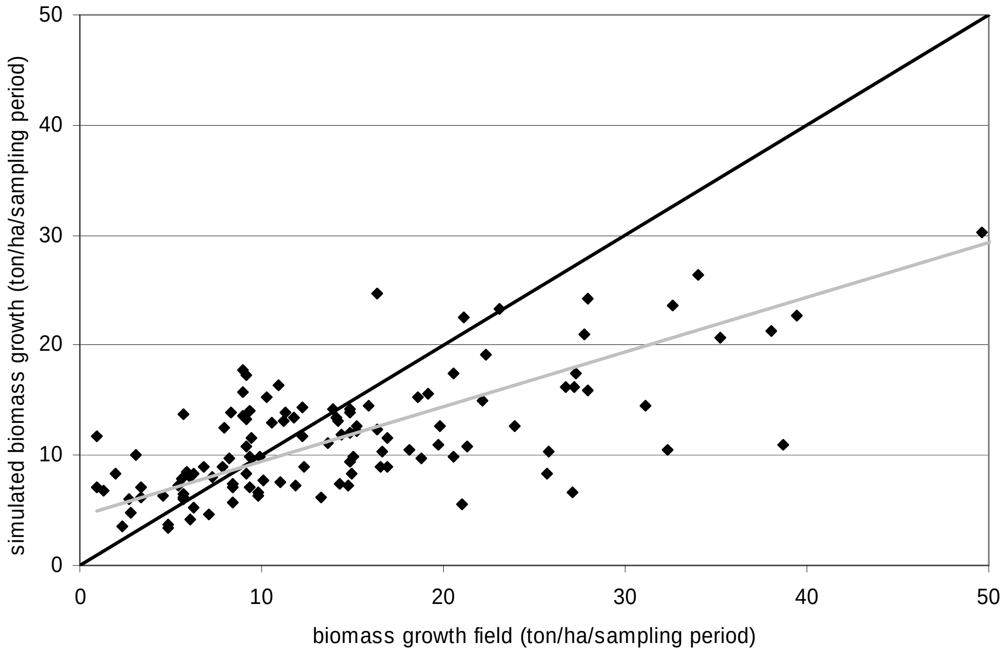


Figure 6.8 Relation between field measurements and simulated biomass grwoth for 120 intensive monitoring forest plots in Europe. Most of the plots have two measurements of biomass, which are both included in combination with the simulated biomass. The black line shows the y=x line, the grey line the regression line.

6.4.3 Scenario analyses

To assess the separate effects of an increase of carbon dioxide, climate change and nitrogen deposition change and the combined effect of all three factors on biomass accumulation in European forest, we applied the models WATBAL, SMART2 and SUMO for the period 1990-2070 by comparing various scenarios with a reference run. The scenarios for increase of carbon dioxide, climate change and nitrogen deposition change were applied using site-specific estimates of the change in climatic parameters (precipitation and temperature) and nitrogen deposition. Only for the carbon dioxide scenario we applied a common trajectory of increasing carbon dioxide concentration. Four scenarios and a reference scenario were constructed, as summarized below.

(1) A CO_2 scenario. This scenario is identical for all the simulated plots and is based on an extrapolation of the times series of observed CO_2 concentrations from Mauna Loa Observatory (Keeling et al., 2005). Figure 6.9 shows the CO_2 scenario constructed. The predicted CO_2 concentration in 2070 is 536.61 ppm CO_2). This scenario was compared to a constant CO_2 concentration assuming constant CO_2 after 1990 (a value of 339.47 ppm CO_2).

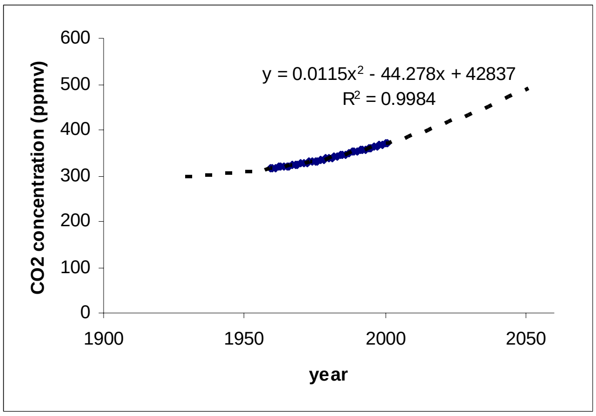


Figure 6.9 Constructed CO_2 scenario. Thick part of line is the measurement period.

(2) A climate scenario, including temperature change and precipitation change for the period 2000 – 2100 according to the IPCC A2 scenario evaluated with the HADCM3 model (Mitchell & Jones, 2005, Figure 6.10A and Figure 6.10B). Climate data were assigned to the plot based on the location of the plot in the meteo data grid. For temperature this follows the HADCM3 model, for precipitation the site specific percentage was also based on the bulk deposition at the sites. This scenario was compared with a scenario with no change in temperature and precipitation after 1990: to account for variations in meteorology, the constant scenario after the year 1990 consists of repetitions of the data from the period 1960-1990.

(3) A nitrogen deposition scenario. The trends in SO_2, NO_x and NH_3 deposition were derived using RAINS country emissions based historic data and emission projections from the Gothenburg protocol (Cofala & Syri, 1998b, a) and transfer matrices derived from the EMEP long-range transport model (Bartnicki et al., 2002) for 1960 to 2010. After 2010 deposition is assumed constant. These trend curves on a 50×50 km grid were scaled by the average computed total deposition (based on bulk and throughfall measurements) at the plot for the period 1996-2000 so that the EMEP time series coincide with the plot-specific deposition for that period This scenario was compared with a scenario where the nitrogen deposition remains constant after 1990 at the level of 1990 (Figure 6.10C).

(4) The fourth scenario is a combination of the previous three scenarios, so a change in CO_2 concentration, climate and N-deposition. This scenario was compared to the combination of the constant CO_2, climate and N deposition scenario.

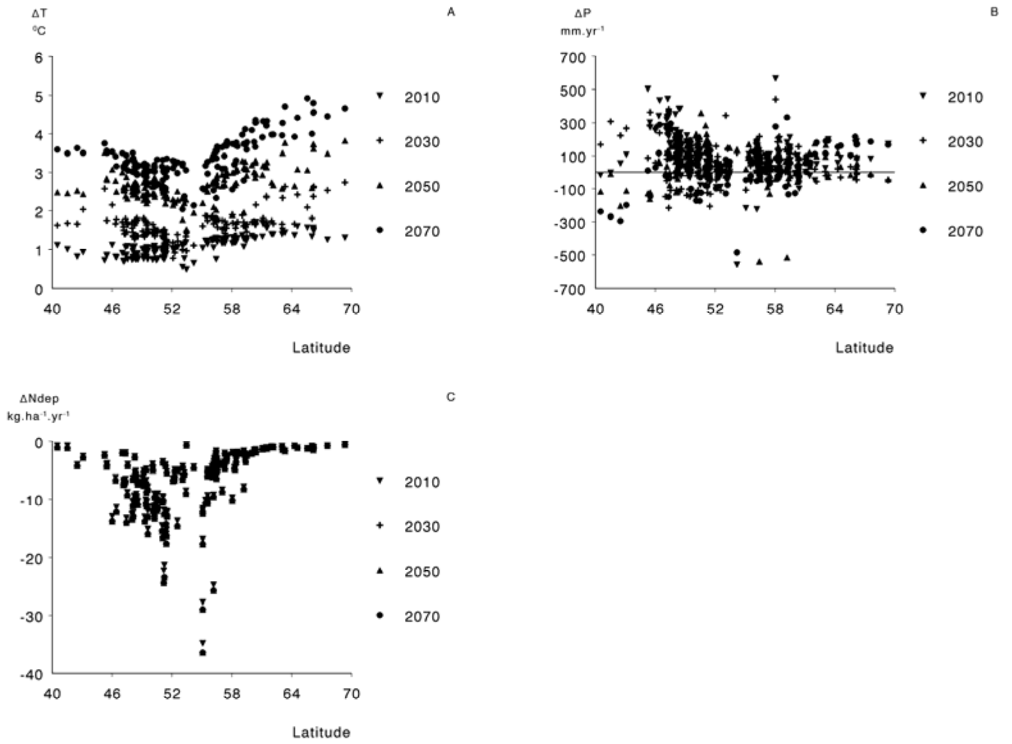


Figure 6.10 Difference in temperature (A), and precipitation (B) and nitrogen deposition (C) between the reference run and the climate change scenario and N deposition scenario respectively in 2010, 2030, 2050 and 2070 as a function of latitude.

A summary of the effect of the various scenarios on on N deposition, temperature and precipitation in 2010 and 2070, as compared to 1990, per latitude classis given in Table 6.7.

Table 6.7 Summary of the average effect of various scenarios on N deposition, temperature and precipitation in 2010 and 2070, as compared to 1990, per latitude class.

Latitude	ΔN (kg N.ha^{-1}.yr^{-1})		ΔT (°C.yr^{-1})		ΔP (mm.yr^{-1})	
	2010	2070	2010	2070	2010	2070
40-50	-7.5	-8.0	0.9	3.2	179	74
50-60	-7.8	-8.3	1.1	3.1	21	12
60-70	-1.2	-1.2	1.5	4.3	56	97

Model runs were carried out for each plot separately. Model results of carbon sequestration in trees and soil were compared for 1990 and 2070 for four different scenarios. Runs were carried out for seven age classes (0-20, 20-39, 40-59, 60-79, 80-99, 100-160 and >160 years). The runs were started in the planting year of the class averages, i.e. in 1960 for the class 20-39 year for the 1990 results, or in 1940 for the class 100-160 year for the 2070 results.

The models were applied on all sites, including different tree species, age classes, soil types and different climate zones, for each scenario separately and for the combined scenario. The results were compared to the reference scenario. The model runs were started at the planting date of the forest and used the historical local climate, carbon dioxide and nitrogen deposition until 1990. The historical local climate, carbon dioxide and nitrogen deposition were based on the measurements at the sites and then extrapolated back in time using the local trends. Model runs for trees that were 130 years old in 1990 were started in 1860 and the run onwards till 2070.

Model runs were carried out per age class to be able to link the results with EFISCAN, which calculates the future biomass surface covering for all the involved countries. Since all age classes are present in the countries it was necessary to run all age classes for the level 2 plots to feed EFISCAN with sufficient information.

The results from SUMO were transferred to EFISCEN for further modelling. We only used the woody biomass of the tree species from SUMO for this. Although SUMO simulates biomass for all the tree organs (so including leaves and roots) it does not distinguish between stem and branches, which is necessary for the more detailed version of EFISCEN. Although a factor could have been used to split up the biomass of the wood to stem and branches, it would not have any influence on the results and was therefore omitted. EFISCEN uses different 'tree species' then SUMO. Therefore the results from SUMO had to be translated into EFISCEN tree types (see Pussinen et al., 2007).

6.5 Results

6.5.1 Responses for six example sites

As an example the site specific scenarios (and results) are given for six sites for precipitation, temperature and nitrogen deposition carbon dioxide; two in Sweden, two in the UK and two in Germany, representing three climate zones in Europe namely Boreal, Atlantic and Central (Figure 6.11a-g). Scenarios are site specific (except for carbon dioxide).

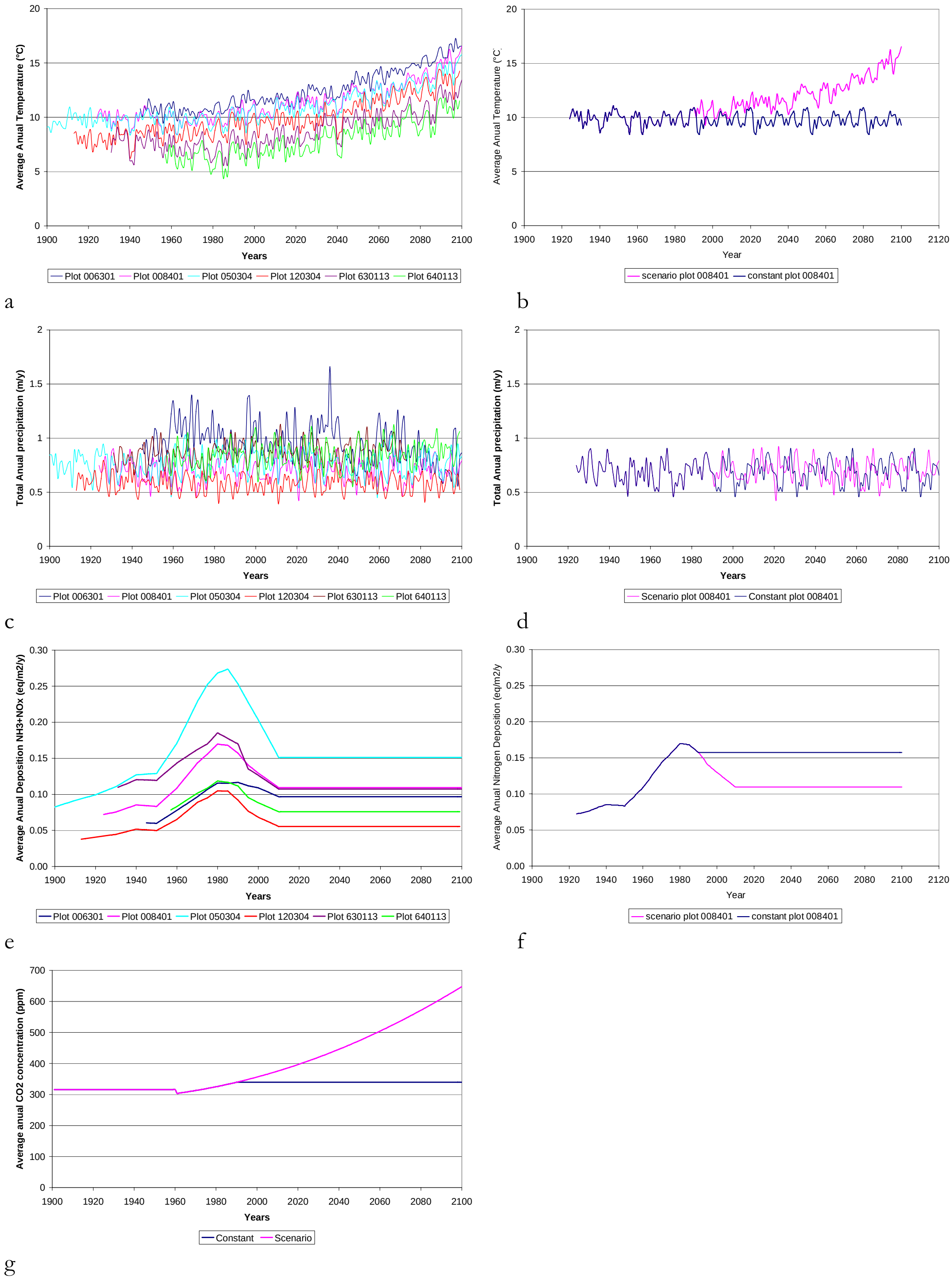
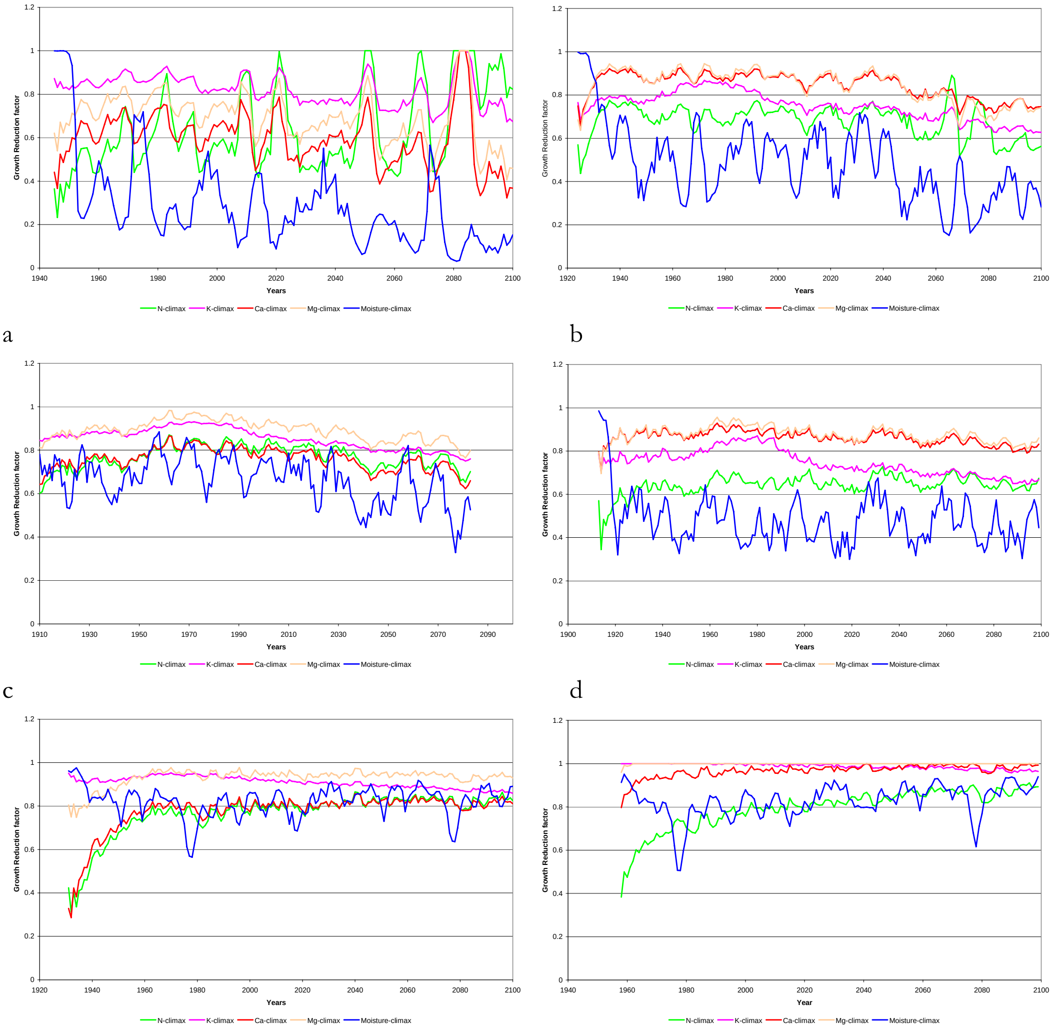


Figure 6.11 Scenarios for six European sites for temperature, precipitation, nitrogen deposition and carbon dioxide. The carbon dioxide scenario is equal for all sites. (a), (c) and (e) give the scenarios for the six sites according the Gothenborg protocol, (b), (d) and (f) give the Gothenburg scenario compared to the 'constant' scenario for one site (Fagus sylvatica in Sweden). With plot 006301: Pinus sylvestris in Sweden: 008401: Fagus sylvatica in Sweden, 050304: Pinus sylvestris in the UK, 120304: Fagus sylvatica in the UK, 630113: Pinus sylvestris in Germany and 640113: Fagus sylvatica in Germany.

The NPP reduction factors ($RWav_t$, $RNav_t$ from formula 6.1, including all the reduction factors for nutrient availability) for the six example sites for the climax tree (*Fagus sylvatica* and *Pinus sylvestris*) are changing in time as a result of the combined scenario (Figure 6.12). For all the results described below we must keep in mind that it reflects the site specific circumstances and that is difficult to distinguish between tree species and countries. The most limiting factor on the NPP also changes in time, as well as there are differences between the sites and tree species. The moist reduction factor directly follows the scenario on precipitation for the sites (Figure 6.12). For the nutrients, in most cases nitrogen is the limiting factor, though for some sites and some moments during the simulations Ca becomes the limiting factor. When looking at the three countries, the difference in growth reduction by moisture shortage is most striking. In Sweden the water shortage is quite large, while in Germany it most of the time only minor. In Germany also the nutrient limitation of the growth is less than in the other countries. There are also differences between the tree species visible, although less striking. The biomass growth for the sites reflects the NPP reduction functions (Figure 6.13). Effects of the four scenarios are visualised as well, which cause (after 1990) differences in NPP. The differences between the base scenario and the N-deposition scenario are very small for the selected sites. The effect of climate change (moist and T) gives for all three countries and two tree species in some years a lower NPP. A rise in CO_2 always gives a higher NPP. The combined scenario gives for Sweden (both pine and beech) and for the UK (pine) in some periods a lower NPP than the base scenario. This seems mostly caused by the climate scenario. However, for most periods in Sweden and the UK and Germany the NPP is higher for the combined scenario than for the base scenario.

The yearly changes in NPP and differences due to the scenarios result in different amounts of standing biomass at the sites (Figure 6.14). For the German sites all scenarios causes a higher standing biomass for all years, with the highest biomass for the combined scenario. For the pine stand in Sweden the climate scenario is that stressful, that besides the climate scenario also the combined scenario causes a lower standing biomass in 2100 than for the base scenario. For two of the sites the climate scenario causes a lower biomass for the combined scenario than for the scenario with the highest standing biomass (CO_2 scenario). Forest management causes the decrease in biomass that is visible every 10 years. For these six examples only one site shows a lower standing biomass as a result of the expected climate change.



a

b

c

d

e

f

Figure 6.12 Reduction functions for water and nutrient availability as a result of the combined scenarios for two different climax tree species (Pinus sylvestris, fig. A, C and E) and Fagus sylvatica, fig. B, D and F) and three countries (Sweden fig. A and B, UK fig. C and D and Germany fig. E and F). A value of 1.00 implies no reduction of the NPP and a value of 0 is the maximum reduction (no NPP).

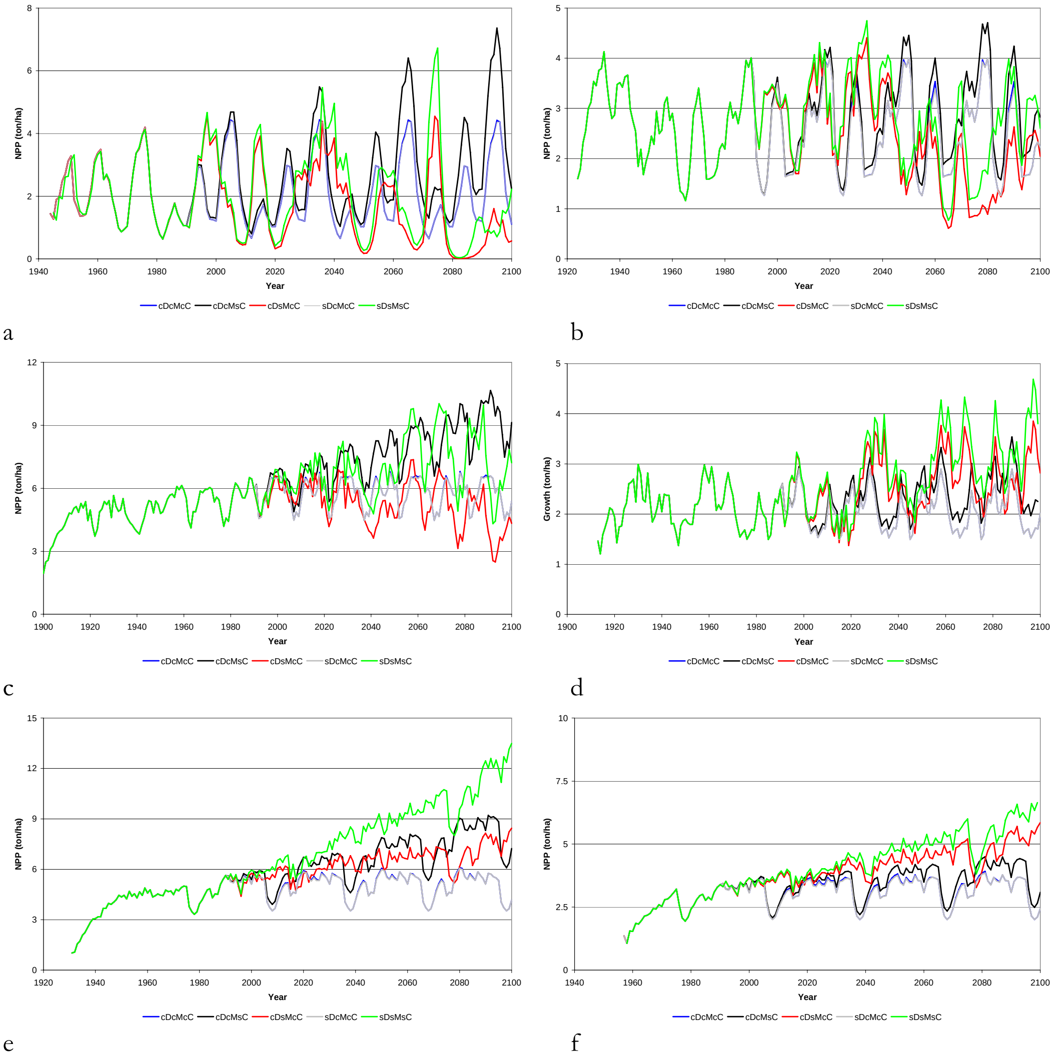


Figure 6.13 NPP as a result of five different scenarios for two different climax tree species (Pinus sylvestris, fig. a, c and e) and Fagus sylvatica, fig. b, d and f) and three countries (Sweden fig. a and b, UK fig. c and d and Germany fig. e and f). With cDcMcC; constant N-deposition, constant climate and constant CO$_2$, cDcMsC; constant N-deposition, constant climate and elevated CO$_2$, cDsMcC; constant N-deposition, changing climate and constant CO$_2$, sDcMcC; decreasing N-deposition, constant climate and constant CO$_2$, sDsMsC; decreasing N-deposition, changing climate and elevated CO$_2$.

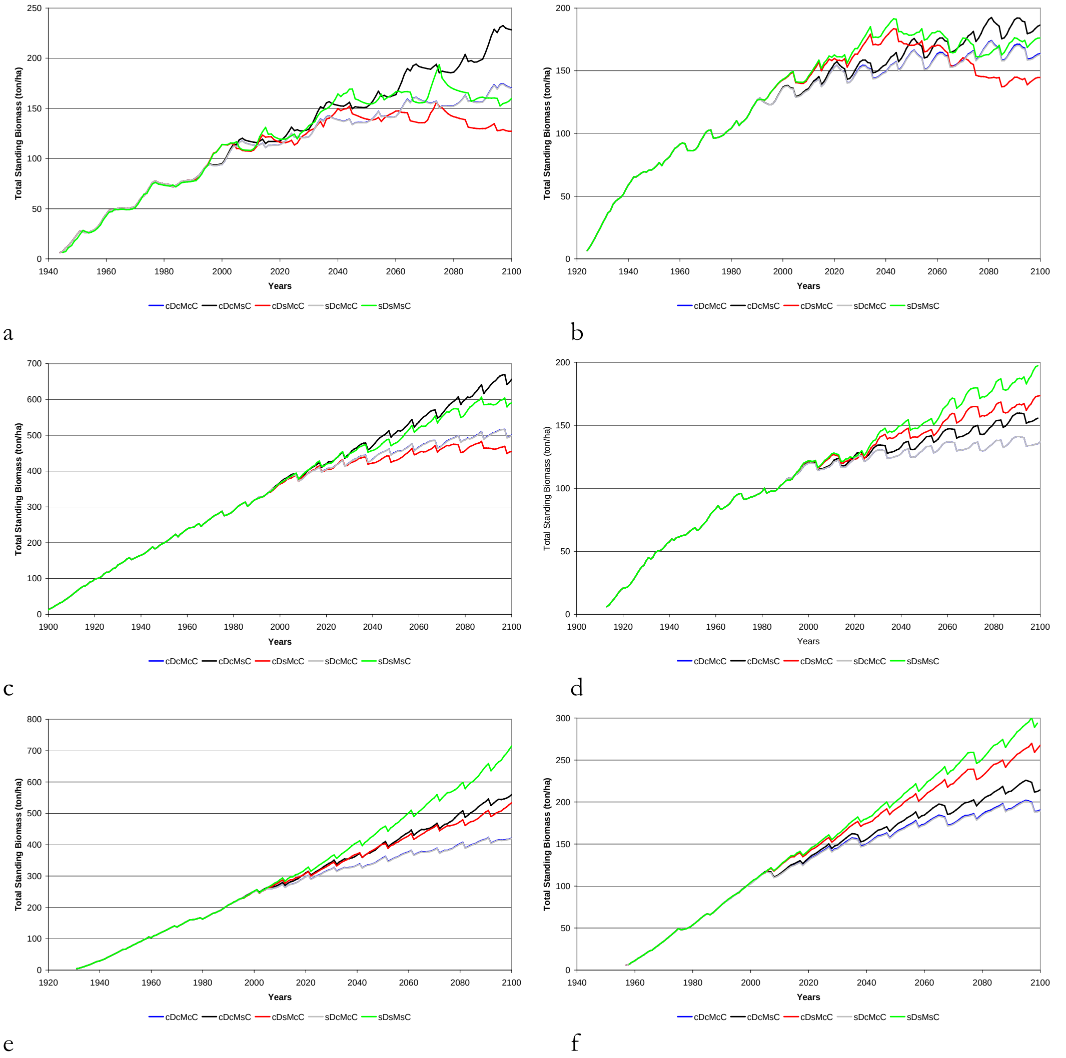


Figure 6.14 Total biomass as a result of five different for two different climax tree species (Pinus sylvestris, fig. a, c and e) and Fagus sylvatica, fig. b, d and f) and three countries (Sweden fig. a and b, UK fig. c and d and Germany fig. e and f). With cDcMcC; constant N-deposition, constant climate and constant CO_2*, cDcMsC; constant N-deposition, constant climate and elevated* CO_2*, cDsMcC; constant N-deposition, changing climate and constant* CO_2*, sDcMcC; decreasing N-deposition, constant climate and constant* CO_2*, sDsMsC; decreasing N-deposition, changing climate and elevated* CO_2*.*

6.5.2 Relative impacts of CO_2, climate and N deposition on carbon sequestration by trees and soil

6.5.2.1 Impacts of all combined environmental changes

The simulated impact of all combined environmental changes (CO_2, climate and N deposition) on the carbon sequestration by trees, soil and the total carbon sequestration, including all plots (averaging for all latitudes, tree species and tree ages) is given in Figure 6.15. Background information on the carbon sequestration per latitude can be found in Appendix 7.

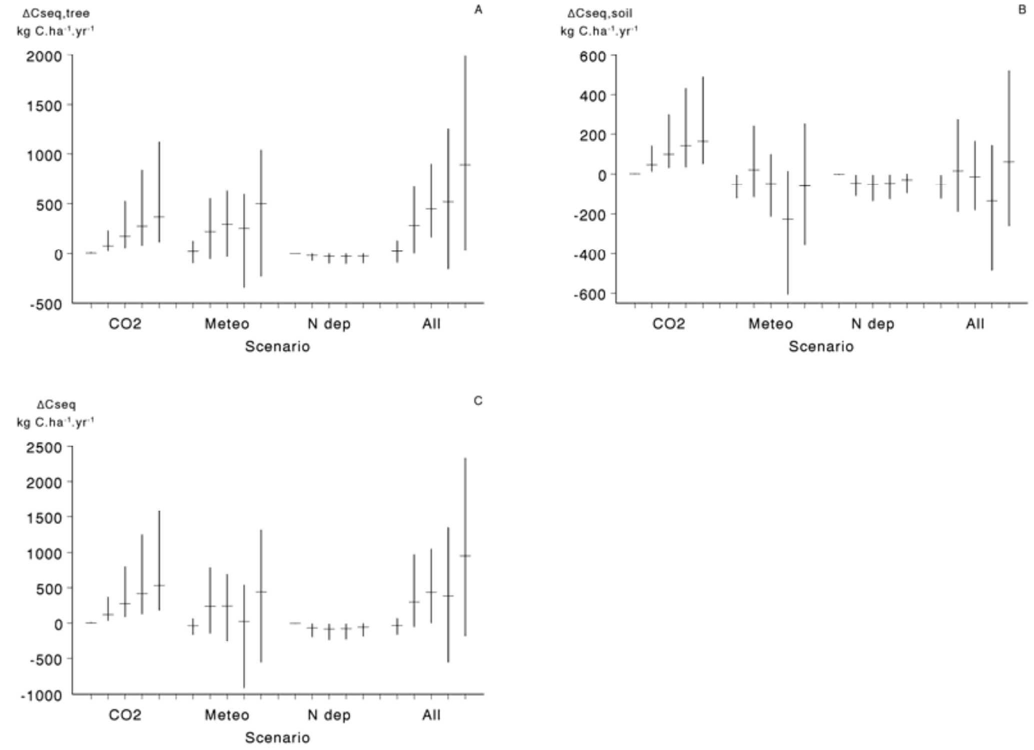


Figure 6.15 The average carbon sequestration for the four scenarios (CO_2,, Climate; Meteo, N deposition; N dep and the combined scenario; all) compared to the carbon sequestration in 1990. Given are the average (horizontal line) and the standard error (vertical line) for the years 1990, 2010, 2030, 2050 and 2070 for the trees (fig. a), the soil (fig. b) and the total of trees and soil (fig. c).

The carbon sequestration in the trees increases in time for the CO_2 scenario and the combined scenario (Figure 6.15A). In general the climate scenario also gives an increase, though the increase is smaller in 2050 than in 2030. The N deposition scenario causes as small negative effect on the carbon sequestration, the expected decrease in N deposition causes a relative small decrease in carbon sequestration. The variation in carbon sequestration in the trees is quite large over the examined plots. For the climate scenario and the combined scenario there are also plots were the carbon sequestration decreases. Where the carbon sequestration for the trees gives in general a positive response on the scenarios (except N dep) the carbon sequestration in the soil gives for many plots a negative effect (Figure 6.15B). The CO_2 scenario gives for all years a larger carbon sequestration, increasing over the years. However, the climate scenario gives in general a negative effect on the carbon sequestration; the average sequestration is lower for all years except in 2010. As for the trees there is a negative effect of the N deposition scenario on the carbon sequestration in the soil; a lower N deposition causes a lower carbon sequestration. The strong negative effect of the climate scenario influences also strongly the carbon sequestration of the combined scenario causing negative average carbon sequestrations for some years. This implies that at least in some years, the relative dry years, a net release of carbon from the soil can be expected. When the effects of the scenarios on carbon sequestration on trees and soil are viewed together than, on average there, is a positive (Figure 6.15C) effect of the carbon sequestration present, except for the N deposition scenario. However, for the climate scenario and the combined scenario many plots are expected to release carbon at least in some periods (dry years). The strong negative effect of the climate scenario on the carbon sequestration in the soil is dimmed by the effect of the trees, which is in most cases stronger than the effect on the soil. We conclude that in general the expected changes in climate, CO_2 concentration and nitrogen deposition will give a higher carbon sequestration in large parts of the European forest, despite the lower N deposition and the periodic lower water availability.

A comparison per latitude class shows that a negative carbon sequestration mainly occurs at the latitudes from 40 – 50 in the soil (Table 6.8). On average the carbon sequestration is positive for all latitude groups. The amount of carbon sequestrated is highest from the latitude 50 -60. The total yearly sequestration ranges from 483 till 1240 kg $C.ha^{-1}.yr^{-1}$. Most sites show an increase of NPP between 0 and 100%, however large differences are present between the sites. Some sites have in 1990 almost no growth; therefore a small absolute NPP increase gives already a strong relative effect on the carbon sequestration.

Table 6.8 Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the combined scenario per latitude class.

Latitude	ΔCseq, tree		ΔCseq, soil		ΔCseq, tot	
	(kg $C.ha^{-1}.yr^{-1}$)	(%)	(kg $C.ha^{-1}.yr^{-1}$)	(%)	(kg $C.ha^{-1}.yr^{-1}$)	(%)
40-50	604	36	-120	466*	483	20
50-60	1072	75	167	188	1240	87
60-70	824	85	41	13	865	67

* This value is positive because of one outlier where the change in C-sequestration is approximately 24000% (for this site there is no sequestration under the reference scenario and an absolute small increase in carbon sequestration).

6.5.2.2 Response on species level

The effects of the combined scenarios on the species are quite large, they all show a positive reaction; the biomass accumulation increases in average for all tree species and for all the age classes (Table 6.9). For some species the total effect on the NPP is larger than the effect of the sum of the separate scenarios. The effect of the scenarios differs per tree species. A higher CO_2 concentration increases NPP of all species, although huge differences are present, varying from app. 2% for *Pseudotsuga menziesii* till over 80% for *Quercus cerris*. The average climate response is for most species positive. *Quercus petrea* shows a clear negative response on climate change; *Abies alba* shows a minor negative response. The response of the species is a combined effect for changes in temperature and precipitation. The drop in nitrogen deposition gives for all species a relative small decrease in biomass accumulation. From this we conclude that in general all species will show a positive growth response for the examined plots.

Table 6.9 Changes in NPP simulated by SMART2-SUMO-WATBAL for 2070 for four scenarios (averages of 2065-2074) per tree species.

Tree species	n	Combined, %	CO_2 response, %	Climate response, %	Deposition response, %
Picea abies	76	57.9	12.5	44.1	-1.9
Pinus sylvestris	43	69.7	17.8	50.1	-0.9
Picea sitchensis	4	37.4	12.7	26.3	-2.5
Pinus nigra	1	109.8	64.7	36.1	-0.8
Abies alba	6	16.3	18.1	-1.9	-1.2
Pseudotsuga menziesii	2	54.2	1.8	55.7	-2.5
Larix decidua	1	43.1	8.0	35.9	-3.0
Quercus petraea	8	5.4	28.3	-15.4	-0.1
Quercus robur	12	58.0	27.4	27.9	-0.7
Fagus sylvatica	31	69.1	47.0	18.0	-1.2
Quercus cerris	2	127.9	81.3	61.5	-3.5
Fraxinus excelsior	1	42.5	20.3	20.1	-0.4

6.5.2.3 Response per country

As for the average responses for the individual tree species the response per country of the combined scenarios varies largely; from almost absent (France, 0.8%) till almost doubling of the NPP (Finland, 91.4%). On average, the Nordic countries show a quite large increase in NPP, though the two plots in Italy also show a very large increase. This effect seems mostly be caused by the CO_2 effect, which is far higher than for the other countries (Table 6.10). The effect of the climate scenario alone gives a quite large negative effect on the NPP in France and the largest positive effect in the Nordic countries. The effect of the N-deposition decrease is relative small for all countries.

Table 6.10 Changes in NPP simulated by SMART2-SUMO-WATBAL for 2070 for four scenarios (averages of 2065-2074) per country

Country	Number of plots	Average response 2070, %	CO_2 response, %	climate response, %	Deposition response, %
France	14	0.8	24.6	-17.5	-0.9
Belgium	8	48.1	31.4	14.6	-0.8
Germany	56	43.9	23.8	20.1	-1.6
Italy	2	86.2	80.9	26.2	-0.3
United Kingdom	6	26.3	19.0	8.0	-0.7
Ireland	2	29.2	15.8	13.3	-1.4
Denmark	11	86.7	23.7	57.1	-2.2
Spain	2	18.8	4.2	14.2	0.0
Sweden	46	88.5	19.1	64.2	-1.0
Austria	2	64.4	30.8	29.3	-0.8
Finland	16	91.4	17.3	72.3	-1.7
Norway	15	56.3	12.5	42.3	-1.2
Switzerland	7	49.6	33.8	16.3	-3.4

6.5.3 The impact of CO_2 change on carbon sequestration by trees and soil

Results show that raise in CO_2 concentration leads to a higher biomass NPP at all latitudes (Table 6.11, Appendix 7). The differences in CO_2 sequestration are caused by the different tree species. The effect of CO_2 is largest below the 57th latitude, but this also is a species effect. More specifically, we predict an increase in carbon sequestration by trees of approximately 1.0 kg C per ppm CO_2 at latitude >57 and a variation between 1-7 kg C per ppm CO_2 below this latitude (See Appendix 7 Figure A7.1B). For soil, the increase in carbon sequestration of approximately 0.5 kg C per ppm CO_2 at latitude >57 and a variation between 1-3 kg C per ppm CO_2 below this latitude, leading to a total predicted increase of 1-10 kg C per ppm CO_2. Considering the predicted CO_2 increase of 197 ppm CO_2 between 1990 and 2070, this implies a predicted large increase in CO_2 sequestration up to 1400 kg C for trees and up to 600 kg C for the soil implying a total sequestration up to 2000 kg C.

Table 6.11 Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the CO_2 scenario solely per latitude class.

Latitude	ΔCseq (kg $C.ha^{-1}.yr^{-1}$)			ΔCseq/ΔCO_2 (kg $C.ha^{-1}.yr^{-1}.ppm\ CO_2^{-1}$)		
	tree	soil	total	tree	soil	total
40-50	425	165	590	2.2	0.84	3.0
50-60	397	186	583	2.0	0.95	3.0
60-70	158	85	242	0.81	0.43	1.2

Above latitude 57, the NPP raise is near 150- 200 kg C, which implies an NPP raise of approximately 15% in 2070 and below latitude 57 it is generally above 300-400 kg C implying an NPP raise above 30% (Table 6.12, Appendix 7).

Table 6.12 Summary of the relative carbon sequestration of European forest in 2070 compared to the reference run for the CO_2 scenario solely per latitude class.

Latitude	%ΔCseq			%ΔCseq/%ΔCO_2		
	tree	soil	total	tree	soil	total
40-50	26	769	31	0.13	3.9	0.16
50-60	24	123	33	0.12	0.63	0.17
60-70	16	27	19	0.08	0.14	0.10

6.5.4 The impact of temperature change and of water availability

The temperature raise has a significant effect on the NPP (Table 6.13, Appendix 7). Where the effect of CO_2 is always positive, here also negative effects are present, especially for the soil. For some Southern plots the total carbon sequestration decreases. For the latitude groups the carbon sequestration ranges from -5 till 206 kg $C.ha^{-1}.yr^{-1}.°C^{-1}$ (Table 6.13) or -1.5 till 16% (Table 6.14). For all plots in the North the carbon sequestration increases. The NPP changes are due to the interaction between temperature and precipitation and the influence of them on the available water for trees. The three outliers are sites in mountainous areas where without climate change the NPP of the trees is almost zero. Higher temperatures give a NPP change and trees start to grow (approximately 1 $ton.ha^{-1}.yr^{-1}$), resulting in a large NPP change. On average the NPP change is larger in the North than in the South.

Table 6.13 Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the temperature scenario solely per latitude class.

Latitude	ΔCseq (kg $C.ha^{-1}.yr^{-1}$)			ΔCseq/ΔT (kg $C.ha^{-1}.yr^{-1}.°C^{-1}$)		
	tree	soil	total	tree	soil	total
40-50	193	-214	-21	61	-67	-5.1
50-60	632	17	649	202	4.0	206
60-70	636	-30	606	149	-7.6	142

Table 6.14 Summary of the relative carbon sequestration of European forest in 2070 compared to the reference run for the CO_2 scenario solely per latitude class.

Latitude	%ΔCseq			%ΔCseq/%Δ°C		
	tree	soil	total	tree	soil	total
40-50	13	-23	-4.8	3.8	-7.4	-1.5
50-60	48	77	52	15	23	16
60-70	67	-8.8	48	15	-2.2	11

6.5.5 The impact of nitrogen deposition on carbon sequestration by trees and soil

The drop in N-deposition levels influences the biomass accumulation in general in a negative way and is relative small compared to the effects of the CO_2 and climate scenarios (Table 6.15, Table 6.16, and Appendix 7). This effect is visible at all latitudes and ranges between mostly in a decrease between 0–150 kg C for both trees and soil which is equal to a decrease in NPP of 0-10%.

Table 6.15 Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the N-deposition scenario solely per latitude class.

Latitude	ΔCseq (kg $C.ha^{-1}.yr^{-1}$)			ΔCseq/ΔN (kg $C.ha^{-1}.yr^{-1}.kg\ N^{-1}$)		
	tree	soil	total	tree	soil	total
40-50	-32	-35	-67	3.6	5.0	8.6
50-60	-25	-31	-56	3.1	4.2	7.3
60-70	-13	-13	-26	12	11	24

The decrease ranges mostly between 0–50 kg C (giving a NPP decrease between 0-3%). This effect is due to the predicted decrease in N deposition compared to the reference run. The absolute effect is largest in the Southern countries and smallest Nordic countries. However, when expressed per kg N change the effect is largest in the Nordic countries. The ratio in C sequestration per kg N deposition that ranges mostly between 1-15 kg C per kg N for above ground biomass with some values going up to 25 kg C per kg N at latitude >60. In the soil the variation is comparable. Here the ratio in C sequestration per kg N deposition ranges mostly between 1-20 kg C per kg N with some values going up to 30 kg C/kg N. A few sites show an increase in NPP despite the lower N deposition implying a negative C sequestration per kg N deposition. The effect of N deposition on C sequestration is largest between the 45th and 55th latitude. Here countries like the UK, The Netherlands, Belgium and Germany are situated, all with a current high nitrogen deposition. In these areas the decrease in nitrogen on forests is highest, thus causing the largest effect.

Table 6.16 Summary of the relative carbon sequestration of European forest in 2070 compared to the reference run for the N-deposition scenario solely per latitude class.

Latitude	%ΔCseq			%ΔCseq/%ΔNdep		
	tree	soil	total	tree	soil	total
40-50	-1.4	-43	-2.5	0.15	4.6	0.30
50-60	-1.3	-18	-2.6	0.18	2.7	0.38
60-70	-1.5	-3.7	-2.0	1.4	3.3	1.9

6.6 Discussion and conclusion

Based on the model simulations we expect that there will be effects of climate change on the carbon sequestration in European forest. The raise of the CO_2 concentration will have a positive effect on the carbon sequestration, the expected decrease in nitrogen deposition a relative small negative effect. The effect of the climate scenario is more complicated, where temperature raise alone seem to have a positive effect. However, the change in precipitation can have a positive as well as a negative effect. The negative effect is most pregnant in France, where a negative carbon sequestration is expected. The separate scenarios cause in general an increase in carbon sequestration for the combined scenario in the 190 simulated forests (except for France). Due to the variation in temperature and precipitation the sequestration differs sometimes largely between the years; in some years we expect only a minor carbon sequestration or even a general carbon releases. The effect of the scenarios is approximately three times as a high on the carbon sequestration in trees than in the soil. Moreover, the negative effect on the carbon sequestration of the climate (precipitation) scenario is much higher in the soil. In many years there will be a net carbon loss from the soil. Together with the negative effect of the decreasing N deposition it also causes a release of carbon from the soil for the combined scenario. The rise in carbon sequestration caused by the rise in CO_2 concentration can not compensate for the negative effects. Since the effects on the trees species are much larger than in the soil and the effects of the combined scenario are more positive for the carbon sequestration the overall effect of the carbon release from the soil is limited. In most cases the trees will compensate. However we expect that the carbon storage in the soil will decrease at least till 2070 due to the expected climate change and change in nitrogen deposition. This may also affect the occurrence of species direct or indirect dependend on the soil circumstances and therefore influence the biodiversity in the forests.

The effects of the scenarios largely depend on the tree species present at the simulated plots. When the goal is to store as much carbon as possible, based on this study, we can recommend planting *Pinus nigra* and *Quercus cerris* were appropriate, since they show the highest positive relative response to the expected climate change and change in nitrogen deposition. However, local circumstances may lead to another choice.

Assigning the relative impacts by multiple regression

From the results it is clear that there is an effect of combined scenario on the biomass growth and thus carbon sequestration in trees and soil. The different scenarios sometimes seem to strengthen each other and some evidence of interaction is present. However, also contrary effects are present. To investigate the effect of the separate scenarios on the combined scenario we carried out a multiple regression of the NPP response for the combined scenario with the NPP responses of the individual scenarios as explanatory variables. There is a highly significant relation between the NPP response of the CO_2 scenario and the climate scenario and the NPP response for the combined scenario (Table 6.17).

Table 6.17 Regression analyses of the NPP changes of the combined scenario with the NPP changes of the individual scenarios as explanatory variables. The accumulated analysis of variance is shown, with degrees of freedom (d.f.), sum of squares (s.s.), mean of squares (m.s.), variance ratio (v.r.), F probability (F pr.) and the parameter estimates, standard error (s.e.) and t probability (t pr.).

	d.f.	s.s.	m.s.	v.r.	F pr.
Regression	7	660357	94336.68	2361.95	<.001
Residual	182	7269	39.94		
Total	189	667626	3532.41		

Percentage variance accounted for 98.9

*** Estimates of parameters ***

	estimate	s.e.	t(182)	t pr.
Constant	-1.95	1.69	-1.16	0.248
C2070	0.9776	0.0539	18.15	<.001
D2070	-0.071	0.949	-0.07	0.941
M2070	1.2022	0.0297	40.43	<.001
C2070.D2070	-0.0668	0.0374	-1.79	0.076
C2070.M2070	-0.003226	0.00052	-6.2	<.001
D2070.M2070	0.0905	0.0255	3.54	<.001
C2070.D2070.M2070	-0.001668	0.000622	-2.68	0.008

There is no significant relation between NPP changes of the combined scenario and the deposition scenario, indicating that the influence of N-deposition on the result of the combined scenario is minimal. The interactions between the CO_2 scenario and the climate scenario and between the deposition and climate scenario are highly significant, as is the three-way interaction. Together the three scenarios (including the interaction terms) explain almost all variance (98.9%). To complete the analyses, each combination of scenarios and each single scenario were used to explain the results of the combined scenario. The percentages of explained variance are given in Table 6.18. By far the largest portion of variance is explained by the climate scenario. The raise of the CO_2 concentration also explains a major part of the variance. Though some interactions are significant, they do not contribute much to the explanation of the variance. From this very simple sensitivity analyses it can be concluded that the model results for the combined scenario seem to be most sensitive for the climate scenario and in a lesser way for the CO_2 scenario. The interactions play a minor role and the sensitivity for the deposition scenario is negligible.

Table 6.18 Explained variances for regression analyses of the overall scenario as explained variable and with the individual scenarios as explanatory variables (including interactions when appropriate).

Explaining variables (including interaction)	Explained variance (%)
C2070, D2070, M2070	98.9
C2070, D2070	26.4
C2070, M2070	98.7
M2070, D2070	92.3
M2070	91.9
C2070	26.9
D2070	0.8

After the regression and variance analysis using the scenario results we used the same statistical techniques to investigate the relative importance of the reduction factors in SUMO and the scenarios. Table 6.19 gives the results for the comparison of the combined scenario and the standard scenario for the year 2070.

Table 6.19 Results of a regression analysis, and an analysis of variance for the combined scenario for carbon sequestration in 2070. The total variance accounted for is 83.1%. Tested are the difference between standard scenario and combined scenario. Only significant parameters are shown, parameters included in the analysis are the nitrogen reduction factor of SUMO (N), the calcium reduction factor in SUMO (Ca), the magnesium reduction factor in SUMO (Mg), the potassium reduction factor in SUMO (n.s.), the moisture reduction factor in SUMO (moist), the tree species (split up in species group for the regression, but as tree for analysis of variance), the precipitation (n.s.), the temperature (n.s.) and the nitrogen deposition (n.s.).

fitted parameter	estimate	s.e.	t(152)	t. pob	%a.v.	∑ % a.v.
constant	819.8	47.6	17.23			
N	-1984.	396.	-5.01	0.000	2.6	2.6
CA	4531.	952.	4.76	0.000	2.4	5.0
Mg	2018.	832.	2.42	0.017	0.5	5.5
Moist	2403.	219.	10.96	0.000	13.0	18.5
trees				0.000	54.5	73.0
spruce	47.9	42.4	1.13			
fir	281.3	91.0	3.09			
Mediterranean pine	585.	210.	2.78			
beech	1138.0	54.7	20.79			
oak	143.5	60.1	2.39			
oak other	-207.	161.	-1.28			
remaining broadleaves	664.	208.	3.19			

Almost all reduction factors of SUMO contribute significantly to the end result. Only the potassium reduction function is not significant, indicating that in general the sites are not limited by potassium. From the reduction functions the moist reduction function is the most important indicating that most sites are more limited by moisture availability than by nutrient availability. The sites that are limited by nutrients are mostly limited by nitrogen and calcium. The latter could indicate an effect of the (ongoing) acidification of at least some sites. The scenarios represented by precipitation, temperature and nitrogen deposition do not contribute significantly directly to the end result (CO_2 could not be included, since there are no differences between the sites). This indicates probably that the scenario parameters are confounded with the reduction factors. Most of the variance is explained by the tree species. This means that the choice of the planted tree species can make quite a large difference on the future carbon sequestration.

Impacts of CO_2 and temperature

From the simulations it appears that the NPP is at least partly limited by the current CO_2 concentration (app. 350 ppm). Results show an increase in carbon sequestration by trees up to 1400 kg C for trees and up to 600 kg C for soil implying a total sequestration up to 2000 kg C for a predicted CO_2 increase of 197 ppm CO_2 between 1990 and 2070. The amount of C-sequestration varies largely between the tree species. When trees are planted for C-sequestration purposes Pinus nigra and Quercus cerris are the most appropriate species, also because the combined effect with climate change gives the highest increase in carbon sequestration. From our results there is no evidence that the effect of an increased C-sequestration due to elevated CO_2 levels is only temporary.

Impacts of climate change on carbon sequestration

In this study we did not include an interaction between CO_2 and temperature. A global modelling study of the combined effect of CO_2 and temperature on C sequestration in terrestrial ecosystems with LPJ (Scholze et al., 2006) showed a strong interaction between CO_2 increase and temperature increase. By including this interaction, their model study showed a CO_2 net sink for the 1980s and 1990s and in future predictions this sink persisted throughout the 21st century at a temperature increase < 2°C, the. However, at a 2–3°C increase, the sink increased up to 2050 followed by a decline. For > 3°C increase, the sink increases (but less strongly), then declines to zero but with large uncertainty. This result implies a substantial risk that terrestrial uptake of anthropogenic CO_2 will cease if global warming is > 3°C. This negative feedback of temperature increase on CO_2 fertilization is not included in this study.

Impacts of N deposition on carbon sequestration

We choose to set 1990 as the year to which the simulations were compared, since this was the starting year of the scenarios. Since nitrogen deposition has slightly decreased since 2000 (Kelly et al., 2002; Tarasón et al., 2003) and is expected to decrease further a negative carbon sequestration response is found as a result. However, this ignores effect of the rise of the nitrogen deposition since 1950. If the nitrogen deposition effects would have been compared with say 1950 a strong positive effect would have been visible (c.f. Wamelink et al., 2007a). Interesting is the relative small reaction of the carbon sequestration on the decrease in nitrogen deposition. It ranges mostly between 1 kg C/kg N till 15 kg C/kg N with values going up till 25 for trees and 20 for soil. Compared to earlier results by Wamelink et al. (2007a) for The Netherlands this is a relative low range. They found an average simulated increase was 20-30 kg carbon per kg nitrogen deposition. Results from field measurements, other model runs and theoretical calculations give similar results

(Table 6.20), except Currie et al. (2004) who found a carbon sequestration of 5 kg C/kg N, which is within the range found in this research. Our results indicate that a decrease in nitrogen deposition will not result in a similar decrease in carbon sequestration as was found for the increase in carbon sequestration by increasing nitrogen deposition. We argue that a deposition decreases not automatically leads to a decrease in nitrogen availability for the vegetation and thus a lower NPP and carbon sequestration. The build up N-pool is not decreasing as rapidly as it was built up due to the nitrogen deposition. A decrease in N-pool can only be expected as a result of either the harvest of trees or by leaching to the groundwater. Moreover, the present nitrogen pool may also be diluted over the newly formed biomass, thus giving a relative high NPP and carbon sequestration at a lower N-content.

Table 6.20 Estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in forest at various scales.

Scale of application	Carbon sequestration (kg C/kg N)		Approach	Author
	Above ground	Below ground		
Global average	25	21	Extrapolation of ^{15}N experimental data with world average data	Nadelhoffer et al. (1999b)
European Average	33	15	Extrapolation of ^{15}N experimental data with site specific data at approximately 6000 plots in Europe	De Vries et al. (2006b)
Dutch average	20-30	-	Range in results of model simulations	Wamelink et al. (2007a)
Forest in Sweden	18-28	-	Range in results from fertilizer experiments	Tamm et al. (1999)
Two forest sites	15-25	-	Range in results of model simulations	Rehfuess et al. (1999)
Europe	15-38	-	Multivariate relation between measured growth increase of nearly 400 level 2 plots and influencing factors	Solberg et al. (2007) Laubhahn et al. (2007)
Harvard forest USA	5	-	model runs for red pine forest and mixed hardwoods	Currie et al. (2004)

Unlike previous studies, such as those by Van Oijen and Jandl (2004), the effect of N deposition is on average much smaller than the effect of the change in CO_2 and climate. This is because the change in N deposition compared to the reference run is small compared to the expected changes in CO_2 and climate.

Aspects not included in the simulations

In simulating the impacts of environmental change on forest NPP and carbon sequestration it has to be realized that several influencing aspects have not been accounted for. More specifically, the following effects were not taken into account

- The impact of temperature change on the length of the growing season, mainly by an earlier start of the growing season. This aspect can not be included in SUMO, which simulates the various processes at an annual time step. In principle the assessed impacts of temperature on NPP, as assessed by Wamelink (2006) masks the effect of both a direct effect of temperature on NPP and an indirect effect by lengthening the growing season and this effect is within the range of the temperature effect simulated by SUMO.

- The impact of P availability on nutrient limitation by P, even though P fluxes can be simulated by SMART2 and SUMO. The reason for this is that we did encounter problems parameterising P on a European scale. The effect is most likely small, since at most sites the growth is still limited by nitrogen despite the nitrogen deposition (Tamm et al., 1999).
- The impact of moisture on the decomposition of organic matter. Most likely, this impact is small. Very wet or dry circumstances, that may cause a strong reduction of decomposition rates, do not occur at the examined plots

Generalizations for European forests based on the Intensive monitoring data

7 Impacts of nitrogen deposition on carbon sequestration by forests in Europe

Abstract

An estimate of net carbon (C) pool changes and long term C sequestration in trees and soils was made at more than 100 Intensively Monitored forest plots (Level II plots) and scaled up to Europe based on data for more than 6000 forested plots in a systematic 16km x 16 km grid (level I plots). Carbon pool changes in trees at the Level II plots were based on repeated forest growth surveys At the level I plots, an estimate of the mean annual C pool changes was derived from stand age and available site quality characteristics. Carbon sequestration, being equal to the long term C pool changes accounting for CO_2 emissions due to harvest and forest fires, was assumed 33% of the overall C pool changes by growth. Carbon sequestration in the soil were based on calculated nitrogen (N) retention (N deposition minus net N uptake minus N leaching) rates in soils, multiplied by the C/N ratio of the forest soils, using measured data only (level II plots) or a combination of measurements and model calculations (Level I plots). Net C sequestration by forests in Europe (both trees and soil) was estimated at 0.117 Gton.yr^{-1}, with the C sequestration in stem wood being approximately 4 times as high (0.094 Gton.yr^{-1}) as the C sequestration in the soil (0.023 Gton.yr^{-1}). The European average impact of an additional N input on the net C sequestration is estimated at approximately 25 kg C per kg N for both tree wood and soil. The contribution of an average additional N deposition on European forests of 2.8 kg.ha^{-1}.yr^{-1} in the period 1960-200 is estimated at 0.0118 Gton.yr^{-1}, being equal to 10% of the net C sequestration in both trees and soil in that period (0.117 Gton.yr^{-1}). The C sequestration in trees increased from Northern to Central Europe, whereas the C sequestration in soil is high in Central Europe and low in Northern and Southern Europe. The result of this study implies that the impact of forest management on tree growth is most important in explaining the C pool changes in European forests.

7.1 Introduction

Measurements of atmospheric CO_2 indicate that from the estimated 7.1 Gton C released by man (5.5. fossil fuel and 1.6 from land use change and deforestation) only 3.4 Gton is found back in the atmosphere. From this, an estimated 1.5-2.0 Gton is being absorbed by the oceans (Bousquet et al., 1999). The remaining 1.5-2.0 Gton would be global terrestrial uptake (Ciais et al., 1995) but this estimate is also commonly referred to as the missing sink. In this context it is of importance to arrive at reliable estimates of CO_2 sequestration in forests, considered to be most responsible for the terrestrial uptake of CO_2. Furthermore, in the Kyoto Protocol governments agreed to reduce emissions of CO_2 either by limiting fossil fuel consumption or by increasing net C sequestration in terrestrial sinks through afforestation and land use change or both. Even though increasing net C sequestration is still limited to strictly defined cases of afforestation and land use change, it has been advocated (IGBP Terrestrial Carbon Working Group, Steffen et al., 1998) to use a full carbon budget, including all potential terrestrial sinks over a sufficiently long time period, to be accounted for in international CO_2 emission reductions. This requires methods for reliable quantification of these C sinks.

Important questions with respect to C sequestration are related to the cause of the large uptake of the mid-latitude forests and the time period in which the terrestrial sink will be saturated (Houghton et al., 1998). European forests have a role in net C sequestration of the biosphere (i.e.Kauppi et al., 1992; Nabuurs et al., 1997). Apart from changes in standing growing stock (influenced by forest management), changes in net primary productivity may also play a role in this respect (Spiecker et al., 1996). Increased net primary productivity has been hypothesised to be due to increases in atmospheric CO_2 concentrations (e.g. Melillo et al., 1993; Friedlingstein et al., 1995), nitrogen deposition (Holland et al., 1997; Nadelhoffer et al., 1999b) and temperature, increasing the growing season (e.g. Myneni et al., 1997). Increase in CO_2-concentrations on the other hand may favour growth as well as increase water use efficiency of trees. However, trees may adapt to changing CO_2-concentrations and the effect may diminish soon (Tognetti et al., 2000). Using a modelling approach, temperature has been claimed to be relatively unimportant, whereas the combination of CO_2 rise and elevated N deposition may account for a 15-20% increase in forest net primary productivity (Rehfuess et al., 1999). In this context, N deposition is claimed to be most important (Rehfuess et al., 1999). The remaining explanation would then be the impact of forest management.

Furthermore an elevated C sequestration in the soil, due to an increased accumulation of soil organic matter in response to elevated N inputs, may play a role. By far the largest amount of C stored in forests in the northern hemisphere is stored in the soil. Part of the carbon fixed by photosynthesis ultimately moves via litter fall to the soil, where it is only partially decomposed. Thus, over the long term the soil is the ultimate sink or source of CO_2 for these ecosystems. Soil processes account for the most significant unknowns in the C and N cycle and their interactions. For example, chronic N additions to temperate forest soils in the US have been shown to cause an initial increase in soil respiration, but continued additions for more than a decade resulted in a reduction in soil respiration of more than 40% (Bowden et al., 2004). Current hypotheses suggest that increased N deposition causes an increased rate of soil organic matter accumulation through (i) an increased leaf/needle biomass and litter production (e.g. Schulze et al., 2000) and (ii) a reduced decomposition of organic matter, depending on the stage of humus formation (Berg & Matzner, 1997; Harrison et al., 2000; Hagedoorn et al., 2003). This is based on the assumption that (part of) the additional N is taken up by plants/trees (or their mycorrhizal symbionts and transported to the plants) to facilitate additional photosynthesis to form new biomass Fixing of additional C does, however, not occur when the additional N deposition is completely immobilized in the soil by abiotic or even biotic processes (Davidson et al., 2003) and thus does not become available to plants. Understanding the N cycle in semi-natural ecosystems is therefore the key to understanding the long-term source or sink strength of soils for carbon.

Since nitrogen often is the limiting nutrient in forests, nitrogen deposition may increase wood production and accumulation of soil organic matter, thus increasing C sequestration into the forest. Earlier estimates suggested that this mechanism could take up one third of the global CO_2 emission from fossil fuel (or 2 x 10^{15} $g.yr^{-1}$) if most of the deposition nitrogen was taken up by trees and used to form new woody biomass (Holland et al., 1997). The assumption that the trees get all (or nearly all) of the N from deposition, and that N will be sequestered in the soil only after it cycled through leaf, root, and wood tissues, is however not true. The true potential for elevated N deposition to increase C accumulation in both below and above ground sinks appears to be much more limited. Recent data on the distribution of deposition nitrogen between trees and soil (Nadelhoffer et al., 1999b), however, suggest that a large part of the nitrogen is accumulated in the soil at low C/N ratio (10-40) and not in the trees at high C/N ratio (200-500). Thus the increase in nitrogen deposition may cause a much smaller additional CO_2 sequestration in forests (0.25 x 10^{15} $g.yr^{-1}$). This issue is a matter of ongoing scientific debate (e.g. Jenkinson et al., 1999; Schindler, 1999; Sievering, 1999). When C sequestration is mainly due to elevated tree growth, it is a more transitory phenomenon than when soil C accumulation is the main cause, since below ground carbon has lower turnover times than above ground carbon.

There is quite some information available on C and N sequestration in forest ecosystems in response to changes in N deposition, but the uncertainty is high and insight in the response on a European wide scale is presently still limited. This paper presents an estimate of C sequestration by European forest and forest soils and of the impact of nitrogen deposition on these sequestration rates, making use of available data from two Pan-European Forest Monitoring Programmes. The "Programme for Intensive and Continuous Monitoring of Forest Ecosystems", carried out since 1994 is used to derive relationships between N deposition and C sequestration. Approximately 860 permanent observation plots, with more than 500 plots with atmospheric deposition data, have been selected in 30 participating countries (the so-called level II Monitoring Programme). Upscaling of results is enabled by a European Monitoring Programme on air pollution impacts since 1986, in which several forest and soil condition characteristics are monitored at a systematic 16 km x 16 km grid at more than 6000 plots throughout the whole of Europe (the so-called level I Monitoring Programme, e.g. UN/ECE & EC, 2001) For these plots, relevant site and soil characteristics and modelled N deposition estimates are available. The results are put into perspective by first presenting an overview of results on the C sink of forests in Europe.

7.2 Assessment of the terrestrial carbon sink: an overview of methods and results

Up to now, several studies have been carried out, to assess carbon sequestration in forests in Europe, but a direct comparison is hampered because of the measurement of different carbon sink terms. First of all, there is a difference in the assessment of the so-called net ecosystem productivity (NEP) or net ecosystem exchange (NEE), and the net biome production (NBP). Even though NEE has been used to describe both instantaneous and time integrated values of net carbon exchange between ecosystems and the atmosphere and NEP typically refers to a time integrated value, both terms are an indication for the total uptake of CO_2 by photosynthesis, corrected for plant and soil respiration. NBP equals the NEP corrected for CO_2 emissions due to harvest and forest fires. The latter term is critical with respect to carbon sequestration (long-term carbon storage) in forests since an aggrading forest may temporarily sequester large carbon amounts, but part of it is re-emitted to the atmosphere after logging. In this paper we focus on the sequestration in forests (trees)and forest soils, not accounting for the C that continues to exist after harvest in organic form such as wood products or in landfills or as bioenergy that offsets fossil fuel emissions. This aspect is further mentioned in the discussion section.

An overview of various estimates of the carbon sequestration in Europe, focusing on different ecosystem compartments and using different methods is given in Table 7.1. Apart from a distinction in the type of flux and the forest compartment, a differentiation has been made in the quality of the upscaling methods, going from individual sites to the European scale. A systematic discussion related to the various approaches and results is given below.

Inverse modelling: This is the main approach used up to now to assess C sinks on a regional scale, since it includes regionally distributed data and models. Those models, however, do not differentiate between forests and other land use types. Studies using global inversion models indicate that a significant portion of the net uptake of the terrestrial biosphere occurs at northern mid-latitude forest regions (Ciais et al., 1995; Fan et al., 1998; Bousquet et al., 1999). Bousquet et al. (1999) estimated a carbon sink of 0.3 Gton C.yr^{-1} for Europe using a global inversion model including data on regional CO_2 emissions and tropospheric CO_2 concentrations. Similarly, Bousquet et al. (1999) estimated a C sink in North Asia of 1.5 Gton C.yr^{-1} and of 0.5 Gton C.yr^{-1} in the Northern United States and Canada. In the Arctic and tropical Asia a net release of respectively 0.2 and 0.8 Gton C.yr^{-1} was estimated.

NEE/NEP estimates of whole forests or trees from CO_2 net flux and tree growth measurements

An NEP estimate related to forests only is based on direct measurement of the net CO_2 exchange flux to the forest ecosystem at seventeen so-called EUROFLUX sites along a transect from North Sweden to Central Italy (Valentini et al., 2000). Tree species included were Norway spruce and beech. Results indicate that most forests act as sinks at present, and sequester CO_2 at an average rate of 3.03 ton.ha^{-1}.yr^{-1}.

Table 7.1 Overview of different estimates of carbon sequestration on a European wide scale.

Type of C flux	Compartment	Method	Estimated sink Gton.yr^{-1}	Upscaling method	Reference
NBP landscape					
NBP	Landscape	Inversion modelling	0.30	Good	Bousquet et al. (1999)
NEE/NEP Whole forest/trees					
NEE	Whole forest	CO_2 net flux measurements	0.47	Neural networks	Papale and Valentini (2003)
			0.25	Forest maps	Martin et al. (1998)
NEP	Total above-ground biomass	Tree growth measurements	0.42[1]	Multiply with forested area	Schulze et al. (2000)
NBP whole forest/trees					
NBP	Trees (stem wood)	Repeated forest Inventories	0.10	Country inventory data	(Kauppi et al., 1992) (Nabuurs et al., 1997)
NBP	Trees (stem wood)	Modelling forest growth	0.06-0.10[2]	Country inventory data	Liski et al. (2002)
NEP contribution	Trees (above-ground biomass)	N retention	0.039[3]	World average values	After Nadelhoffer et al. (1999b)
NBP forest soil					
NBP	Forest soil (below-ground biomass)	Carbon soil input minus carbon mineralization	0.14[1]	Multiply with forested area	Schulze et al. (2000)
NBP	Forest soil (below-ground biomass)	Modelling forest growth and decomposition	0.031-0.049[2]	Country inventory data	Liski et al. (2002)
NBP	Forest soil (below-ground biomass)	N retention	0.034[3]	World average values	After Nadelhoffer et al. (1999b)

[1] The estimates derived by Schulze et al. (2000) were slightly lower based on a forested area in Europe of 149 million ha, but the estimates were scaled to an area of 162 million ha, used in this study

[2] These estimates were originally limited to the EU + Norway and Switzerland (approximately 138 million ha) but results were scaled to the European forested area, excluding most of Russia (approximately 162 million ha)

[3] These estimates were originally global but were scaled to the European N deposition on forests of 1.54 Mton.yr^{-1}. Actually, the estimate by Nadelhoffer et al. (1999b) for carbon sequestration in trees refers to the contribution of N deposition to NEP by trees and not to the total NEP by forest growth.

Scaling these results to the level of the continent remains, difficult. Recently, Papale and Valentini (2003), used the net CO_2 exchange flux collected in the EUROFLUX network at sixteen of these sites to train a neural network to provide spatial (1 x 1km) estimates of carbon fluxes of European forests. By using this approach, they estimated the total NEE to equal 0.47 Gton C.yr^{-1}. This is almost equal to an estimate that can be derived by simply multiplying the average net CO_2 exchange flux of 3.03 ton.ha^{-1}.yr^{-1} with the forested area 149 million ha of forests, which is generally used as an estimate for forests in Europe excluding Russia (Nabuurs et al., 1997), that would lead to an NEE of 0.45 Gton C.yr^{-1}. Earlier, Martin et al. (1998), estimated that only between 0.17 and 0.31 Gton C.yr^{-1} was sequestered by European forest in 1997, using an upscaling technique with forest maps, based on net CO_2 exchange fluxes ecosystem at eleven EUROFLUX sites. In both approaches, on an aerial basis the net sequestration was largest in Central Europe and lowest in Northern Europe, with Southern Europe in between.

At 11 forest sites, two of them overlapping with the Euroflux sites (so called Canif sites), the current carbon sequestration by tree growth or NEP (by trees), based on process studies and inventories, was estimated to equal 2.64 ton.ha^{-1}.yr^{-1} (Schulze et al., 2000). Schulze et al. (2000) multiplied this value by 149 million ha of forests, to estimate an NEP of 0.39 Gton C.yr^{-1} for Europe. Using a forested area of 162 million ha, applied in this study, it would lead to a sink of 0.42 Gton C.yr^{-1}. Apart from the still relatively poor upscaling procedures, it should be noted that data on the present sequestration in the trees by uptake (and the same holds for the present CO_2 exchange) do overestimate the net carbon sink, as this approach does not account for C release after disturbances (NEE or NEP is larger than NBP).

NBP assessments for trees from repeated forest inventories and modelling forest growth

The net increase in carbon in forests (NBP) can be derived from repeated forest inventories. Such data do account for the losses due to forest growth or forest fires as it only includes the increase of C in the standing tree biomass. Available data indicate an increase in the period between 1970-1990 of 25% (Kauppi et al., 1992) leading to a net NBP in trees of approximately 0.1 Gton C.yr^{-1}. A similar value was obtained by Nabuurs et al. (1997), using much more detailed information on forest inventories in most countries within Europe.

Liski et al. (2002) gave an estimate of the net carbon sequestration in trees based on a dynamic modelling exercises, using data on stem wood volumes from forest resource information over Europe. The growth of branches, foliage and roots is included by an additional allocation of dry matter increment, relative to the known stem wood increment data. The model was applied to the EU countries including Norway and Switzerland. The net carbon sequestration in trees was estimated at 390-600 kg.ha^{-1}.yr^{-1} in 1990 and at 440-510 kg.ha^{-1}.yr^{-1} in 2040. Considering the forested area of the included countries (138 million ha) this leads to a net carbon sequestration of 0.054-0.082 Gton.yr^{-1} in 1990 and of 0.062-0.070 Gton.yr^{-1} in 2040. Assuming that the average carbon sequestration is equal in the forests that are not considered, the net carbon sequestration equals 0.063-0.0972 Gton.yr^{-1} in 1990 and of 0.071-0.083 Gton.yr^{-1} in 2040 for a forested area of 162 million ha used in this study.

A comparable model was used by Nabuurs and Schelhaas (2002) who calculated the net carbon sequestration in trees for 16 typical forest types across Europe. The advancing mean of the net sink of all forests was calculated to equal 800 kg.ha^{-1}.yr^{-1}. Multiplication of this amount by the European forested area is not allowed, since the calculations are just meant to give indicative values for representative forest types. If one, however, simply multiplies this average value with a forested area of 162 million ha, it would lead to a net carbon sequestration of 0.13 Gton.yr^{-1}.

NEP assessments for soil from carbon cycling measurements and modelling soil C dynamics

As with CO_2 sequestration in tree biomass, the retention or sequestration in forest soils can be derived from repeated soil inventories, but those data are hardly available. In this context, retention stands for the change in soil C (or N) pool, being equal to the difference in input by litterfall and root decay and the net decomposition or mineralization (mineralization minus immobilisation). An example of results thus obtained is presented in Leeters and de Vries (2001), but the results show that the change is hard to detect within a short period of time, considering the large present pools with the possible exception of the organic layer (see also De Vries et al., 2000). One can also estimate the net C sequestration in the soil from direct measurements of the carbon input to the soil by litterfall and root decay and carbon release by net mineralization, but this approach is again hampered by the fact that the result is based on subtracting large numbers with relative high uncertainties. Such an approach was used by Schulze et al. (2000) at eleven "Canif" sites, mentioned above. These authors estimated an average C accumulation in soils of 0.86 ton $C.yr^{-1}$. By simply multiplying this figure with 149 million ha of forests, they calculated a sink of 0.128 Gton $C.yr^{-1}$ at the European scale. Using a forested area of 162 million ha, as consistently applied in this study, it would lead to a sink of 0.139 Gton $C.yr^{-1}$.

Apart from net carbon sequestration in trees, Liski et al. (2002) also gave an estimate of the net carbon sequestration in soil, based on the dynamic modelling exercise described before for the EU countries including Norway and Switzerland. The net carbon sequestration in soil was estimated at 190 $kg.ha^{-1}.yr^{-1}$ in 1990 and at 305 $kg.ha^{-1}.yr^{-1}$ in 2040. Considering the forested area of the included countries (138 million ha) this leads to a net carbon sequestration of 0.026 $Gton.yr^{-1}$ in 1990 and of 0.043 $Gton.yr^{-1}$ in 2040. Assuming that the average carbon sequestration is equal in the forests that are not considered, the net carbon sequestration equals 0.031 $Gton.yr^{-1}$ in 1990 and of 0.049 $Gton.yr^{-1}$ in 2040 for a forested area of 162 million ha. Their findings only refer to aboveground wood biomass and not to total ecosystem sequestration. Nabuurs and Schelhaas (2002) also calculated the net carbon sequestration in soil for 16 typical forest types across Europe. The advancing mean of the net C sink of all forests was calculated to equal 110 $kg.ha^{-1}.yr^{-1}$.

Carbon sequestration derived from N retention

A completely different approach compared to all the former approaches is related to the possibility to assess C sequestration from N uptake by trees and N in soils in response to N deposition. First estimates based on this approach suggested that this mechanism could take up one third of the global CO_2 emission from fossil fuel (or 2 Gton $C.yr^{-1}$), being equal to the missing carbon sink (Holland et al., 1997). In this approach most of the deposition nitrogen was assumed to be taken up by trees to form new woody biomass. The assumption was that carbon and nitrogen accumulate in organic matter at the same relative rates through the same mechanisms. This means that nitrogen saturated forests with low nitrogen retention will have nearly no CO_2 sequestration in the soil.

Recent data on the distribution of deposition nitrogen between trees and soil, however, suggest that a large part of the nitrogen is accumulated in the soil at a low carbon to nitrogen ratio and not in the trees at a high carbon to nitrogen ratio. These results are based on the short-term fate (1-3 yr) of ^{15}N labelled tracer experiments in nine temperate forests (Nadelhoffer et al., 1999b). Using a total world N deposition estimate of 5.1 Mton.yr^{-1}, average N retention fractions in stem wood (0.05) and in the soil compartment (0.7) and averages values for the C/N ratio in stem wood (500) and forest soils (30), these authors thus came to a ten times lower global estimate, than estimated by Holland et al. (1997). In Table 7.1 the estimates by Nadelhoffer et al. (1999b) have been scaled to an estimated N deposition for Europe of 1.7 Mton.yr^{-1}. The results suggest that the sinks in forest trees and forest soils are of equal magnitude.

This estimate by Nadelhoffer et al. (1999b) of the C sequestration gave rise to statements about the ”mysterious” missing carbon sink (Schindler, 1999), since it would imply that forest are not responsible for the net uptake of the missing 1.5-2.0 Gton of CO_2 in the atmosphere. According to various authors (Jenkinson et al., 1999; Sievering, 1999), the above-ground carbon sequestration is likely to be underestimated by Nadelhoffer et al. (1999b) since the authors neglected the effect of direct foliar uptake. The repeated forest inventory data by Kauppi et al. (1992) and Nabuurs et al. (1997) for Europe, leading to a net NBP in trees of approximately 0.1 Gton C.yr^{-1} would indeed be a strong indication for an underestimate. The problem in this discussion, however, is that Nadelhoffer et al. (1999b) focused in principle on the additional C sequestration in response to N deposition and not on the total sequestration, as discussed further below.

7.3 Methods used in this study

Calculation of carbon sequestration in trees at Intensive Monitoring plots

The long term C sequestration (NBP) in stem wood at intensive Monitoring plots was calculated on the basis of: (i) periodic annual increment, allowing the calculation of carbon pool changes (net ecosystem production or NEP) and (ii) the assumption that NBP equals 33% of the NEP. This percentage is based on an estimated average NBP/NEP ratio for Europe, showing an average net increase in standing forest biomass of 33% of the growth since 67 % is removed by harvesting or forest fires (Nabuurs & Schelhaas, 2003).

At the intensive Monitoring plots, information on periodic annual increment has become available because of a first re-measurement of the trees, five years after installation. Repeated data on tree diameter (at breast height) and tree height at the Intensive Monitoring plots were used to calculate standing wood volume and changes therein (Dobbertin, 2000). By multiplying single tree volume with wood densities and tree carbon contents, an estimate for the carbon pool stored in the stem was derived and extrapolated to carbon pools per hectare.

In performing calculations the following data were used:

- Measurements: Diameter at breast height and tree height, soil thickness (volume) and soil carbon contents.
- Estimates: Form factors (to derive tree volume from diameter at breast height and tree height), stem wood density and carbon contents in stem wood (close to 50%).

Stem wood volume of each individual tree (V in m^3) was calculated as a function of the diameter at breast height (d, or dbh, in cm) and tree height (TH or h in m). The calculations were done for (clusters of) major tree species, while distinguishing between coppice forests and high forests. Two different type of volume equations were used to calculate the volume of each individual tree as a function of diameter and height:

A direct relationship between V and (d) and (h), according to some type of polynomial relationship, according to:

$$\begin{aligned} V = a + b_1 d + b_2 h + b_3 dh + b_4 d^2 + b_5 h^2 + b_6 d^2 h + b_7 dh^2 + b_8 d^2 h^2 + b_9 d^3 \\ + b_{10} d^3 h + b_{11} d^3 h^2 + b_{12}/h \end{aligned} \tag{7.1}$$

An indirect relationship between V and (d) and (h), according to the multiplication:

$$V = \sum_{i=1}^{N} d_i^{\,2} \frac{\pi}{4} \cdot h_i \cdot f(d_i, h_i) \tag{7.2}$$

where:

V = volume (m^3)

d = diameter at breast height (cm)

h = tree height (m)

f = an individual tree form factor equation

In situations where height data are missing, they were calculated from species and plot specific height curves, the parameters of which were calculated from the sample for which height and dbh were measured, according to (Prodan, 1965):

$$h - 1.30 = \frac{d^2}{\alpha_0 + \alpha_1 \cdot d + \alpha_2 \cdot d^2} \tag{7.3}$$

The form factor f was mostly calculated as (Pollanschütz, 1974; Schieler, 1988):

$$f = b_1 + b_2 \ln{}^2 d + \frac{b_3}{h} + \frac{b_4}{d} + \frac{b_5}{d^2} + \frac{b_6}{dh} + \frac{b_7}{d^2 h} \tag{7.4}$$

For some species, the coefficients were estimated separately for trees with d (dbh) < 10.4 cm and d (dbh) > 10.4 cm in a way that for dbh = 10.4 cm both equations resulted in the same form factor (Pollanschütz, 1974; Schieler, 1988) Equation (7.4) has also been used for Swiss pine, Black pine and the so called "subsidiary broadleaves" in the high forest system, while being valid for dbh > 5 cm (Schieler, 1988). Actually, 5 cm was the minimum diameter for tree to be included in the Intensive Monitoring plots. An overview of the type of equations that were used as a function of tree species and geographic region and the various coefficients that were used in the direct volume equation and in the form factor equation are given in De Vries et al. (2003a).

Carbon pools in trees in stem wood were calculated by multiplying stem wood volumes ($m^3.ha^{-1}$) with stem wood density ($kg.m^{-3}$) and an assumed C content of 50% in stem wood. ($kg\ C.kg^{-1}$). Data on stem wood density per tree species that were used are presented in Table 7.2. Most data were derived from Wagenfuhr and Schreiber (1989), with data for a few species being based on Wiselius (1994). For the Eucalyptus, use was made of data in (Ilic et al., 2000).

Calculation of carbon sequestration in soils at Intensive Monitoring plots

An estimate of net C sequestration in Intensive Monitoring plots was based on the calculated nitrogen retention (sequestration) in the soils, multiplied by the C/N ratio of the forest soils, distinguishing between the organic layer and mineral soil. The basic assumption is that CO_2 sequestration can be calculated from nitrogen retention in the soils since carbon and nitrogen accumulation in organic matter occurs through the same mechanisms and that the C/N ratio does not change in time. Another assumption is that denitrification can be neglected in the organic layer and the mineral topsoil, where both N and C sequestration is assumed to occur. The reliability of both assumptions is evaluated in the discussion section. N retention (sequestration) was thus calculated as:

$$\text{N retention} = \text{N deposition} - \text{N net uptake} - \text{N leaching} \tag{7.5}$$

For many of the Intensive Monitoring plots the N fluxes in Eq. (7.5) can be estimated based on methods described in de Vries et al. (2001). Figure 7.1 shows the calculated N budget (N deposition minus N leaching) and net N uptake (N uptake needed for growth) for these plots, thus allowing the calculation of N retention. This included the plots with information on: (i) both bulk deposition and throughfall of N, thus allowing the calculation of total N deposition, and (ii) soil solution chemistry, thus allowing the calculation of N leaching. Such budgets were only available for 124 plots, due to the limited availability of soil solution chemistry data. The budgets are an update of those described in De Vries et al. (2001) by including two additional years (the period 1995-2000). The plots were located in Belgium, France, Denmark, Germany, UK, Ireland, Norway, Sweden, Finland and Austria (Figure 7.1).

Table 7.2 Stem wood densities per tree species that were used to calculate carbon pools in trees

Tree species Group	Included tree species	Wood density (kg.m^{-3})
Salix	Salix alba, Salix caprea, Salix cinerea, Salix eleagnos, Salix fragilis, Salix sp.	330
Thuja	Thuja sp.	350
Cedrus	Cedrus atlantica, Cedrus deodara	400
Abies/Populus	Abies alba, Abies borisii-regis, Abies cephalonica, Abies grandis, Abies nordmanniana, Abies pinsapo, Abies procera, Pinus radiata, Pinus strobus, Populus alba, Populus canescens, Populus hybrides, Populus nigra, Populus tremula,	410
Picea	Picea abies, Picea omorika	400
Picea sitchensis	Picea sitchensis	350
Tsuga	Tsuga sp.	440
Other conifers	Cupressus lusitanica, Cupressus sempervirens, Juniperus communis, Juniperus oxycedrus, Juniperus phoenicea, Juniperus sabina, Juniperus thurifera, Taxus baccata, Chamaecyparis lawsoniana, Other conifers	450[1]
Pseudotsuga	Pseudotsuga menziesii	470
Pinus/Tilia	Pinus brutia, Pinus canariensis, Pinus cembra, Pinus contorta, Pinus halepensis, Pinus heldreichii, Pinus leucodermis, Pinus mugo, Pinus nigra, Pinus pinaster, Pinus pinea, Pinus sylvestris, Pinus uncinata, Tilia cordata, Tilia platyphyllos,	490
Alnus	Alnus cordata, Alnus glutinosa, Alnus incana, Alnus viridis	510
Prunus/Larix	Prunus avium, Prunus dulcis, Prunus padus, Prunus serotina, Larix decidua, Larix kaempferi	550
Juglans	Juglans nigra, Juglans regia	560
Olea/Platanus	Olea europaea, Platanus orientalis	580
Acer	Acer campestre, Acer monspessulanum, Acer opalus, Acer platanoides, Castanea sativa	590
Other broadleaves	Buxus sempervirens, Ilex aquifolium, Tamarix africana, Arbutus unedo, Arbutus andrachne, Ceratonia siliqua, Cercis siliquastrum, Erica arborea, Erica scoparia, Erica manipuliflora, Phillyrea latifolia, Phillyrea angustifolia, Pistacia lentiscus, Pistacia terebinthus, Rhamnus oleoides, Rhamnus alaternus, Betula tortuosa, Ceratonia siliqua (same as 75), Crataegus monogyna, Other broadleaves	595[1]
Betula	Betula pendula, Betula pubescens	610
Acer/Ulmus	Acer pseudoplatanus, Ulmus glabra, Ulmus laevis, Ulmus minor	640
Fraxinus/ Quercus	Fraxinus angustifolia, Fraxinus excelsior, Fraxinus ornus, Quercus cerris, Quercus coccifera, Quercus faginea, Quercus frainetto, Quercus fruticosa, Quercus ilex, Quercus macrolepsis, Quercus petraea, Quercus pubescens, Quercus pyrenaica, Quercus robur, Quercus rotundifolia, Quercus rubra, Quercus suber, Quercus trojana	600
Fagus	Fagus moesiaca, Fagus orientalis, Fagus sylvatica	680
Eucalyptus	Eucalyptus sp., Malus domestica, Pyrus communis, Laurus nobilis, Myrtus communis	700
Sorbus	Sorbus aria, Sorbus aucuparia, Sorbus domestica, Sorbus torminalis	730
Robinia pseudacacia	Robinia pseudacacia	740
Carpinus	Carpinus betulus, Carpinus orientalis, Corylus avellana, Ostrya carpinifolia	790

[1] Stem densities for the considered other conifers and other broadleaves have been set at the average of all species

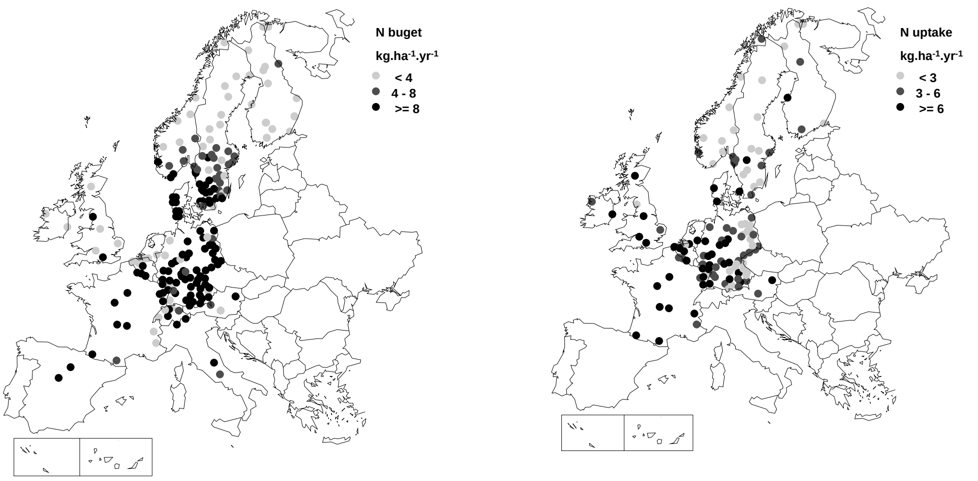


Figure 7.1 Nitrogen budget (N deposition minus N leaching; left) and N uptake (right) at the 121 Intensive Monitoring plots (kgN.ha^{-1}.yr^{-1}) that were used for the calculation of carbon sequestration in soils.

The net N uptake was derived by multiplying changes in standing biomass, in terms of stem wood, from repeated growth surveys in the period 1995-2000 with deposition dependent N contents in biomass. The uptake in branch wood was thus neglected. In nearly all cases total N retention (equal to N uptake and soil N retention) is larger than uptake implying that N is retained in the soil. The results show that both net N uptake and total N retention systematically increases going from Northern to Southern Europe (Figure 7.1).

In multiplying the soil N retention with the C/N ratio, the variation of the C/N ratio with the depth of the soil profile must be accounted for. Especially there is often a large difference between C/N ratio in the organic layer and in the mineral soil. The retention of N in those layers is dependent on the transport of the mineral N input down the profile. From experiments simulating increased nitrogen deposition it is shown that nitrate is much more mobile than ammonium (Nadelhoffer et al., 1995; Emmett et al., 1998) and some transport of nitrate down the profile even occur at sites with high C/N in the organic layer (Gundersen & Rasmussen, 1995; Moldan et al., 1998).

The fate of deposition N in forest soils has been studied by nitrogen tracer (^{15}N) techniques. For example, Nadelhoffer et al. (1999a) added labelled nitrate and ammonium by spraying an NH_4NO_3 solution monthly in the growing season to simulate N deposition of 58 kg.ha^{-1}.yr^{-1}. Results of the experiment are shown in Table 7.3. Most of the retained ammonium (80%) was found in the organic layer, whereas the retention of nitrate was about equal in the organic layer and the first 20 cm of the mineral soil. The retention of both N compounds was slightly higher in the red pine stand, which had a higher C/N ratio than the oak stand. This indicates that at higher C/N ratio, which determines the sink strength of the organic layer, less N is transported down to the mineral soil.

Table 7.3 The fraction of added N (ammonium or nitrate) retained in the forest floor relative to the total soil N retention of the compound in both the forest floor and the mineral soil (0-20 cm) in two stands at Harvard Forest, USA. (Nadelhoffer et al., 1999b).

Forest stand	N Labelling	Fraction N retained in the forest floor
Red Pine	Ammonium	0.82
(C/N = 26)	Nitrate	0.58
Oak	Ammonium	0.78
(C/N = 23)	Nitrate	0.52

Within the NITREX project, Tietema et al. (1998) performed ^{15}N tracer studies with various combinations of input levels (current deposition and simulated increase or decrease of deposition) and dominating N compounds (NH_4-fractions from 0.1 to 0.8). Based on the fate of N added over one year, 40 to 75 % of soil N retention occurred in the organic layer. These retention fractions in the organic layer are lower than those obtained Nadelhoffer et al. (1999a), whose results may have been overestimated due to lack of sampling of lower mineral soil. The lowest percentages were found at the highest nitrate depositions rates (lowest NH_4-fraction). In nitrifying soils (lower C/N ratio soils) labelled NH_4 may over time be transformed to nitrate and leached down the profile, which makes the interpretation of these numbers difficult. Based on these results, we modelled the partitioning of N retention between organic layer and mineral soil as a function of the N input and the C/N ratio of the organic layer according to:

$$\text{C sequestration} = \text{N retention} \cdot (\text{fret}_{\text{ol}} \cdot \text{C/N}_{\text{ol}} + (1 - \text{fret}_{\text{ol}}) \cdot \text{C/N}_{\text{ms}}) \tag{6}$$

Where C/N_{ol} and C/N_{ms} are the C/N ratios of the organic layer and the mineral soil (up to a depth of 20 cm), and $fret_{ol}$ is the N retention fraction in the organic layer, being the ratio of the N retention in the organic layer and the N retention in the complete soil profile (organic layer and mineral soil). The N retention fraction in the organic layer was calculated as a function of the NH_4-fraction in the N input and the C/N ratio of the organic layer, by multiplication of two factors t and r according to:

$$\text{fret}_{\text{ol}} = \text{t} \cdot \text{r} \tag{7}$$

With t and r are being values depending upon the NH_4-fraction in the N input and the C/N ratio of the organic layer, according to:

$$\begin{array}{ll} \text{t} = 0.5 & \text{if NH}_4 \text{ fraction} < 0.5 \\ \text{t} = \text{NH}_4 \text{ fraction} & \text{if } 0.5 < \text{NH}_4 \text{ fraction} < 0.75 \\ \text{t} = 0.75 & \text{if NH}_4 \text{ fraction} > 0.75 \end{array} \tag{8}$$

$$\begin{array}{ll} \text{r} = 1.0 & \text{if C/N ratio} < 20 \\ \text{r} = 1.0 + 0.033 \cdot (\text{C/N ratio - 20}) & \text{if } 20 < \text{C/N ratio} < 30 \\ \text{r} = 1.33 & \text{if C/N ratio} > 30 \end{array} \tag{9}$$

A comparison of calculated N retention fractions in the organic layer for sites and treatments included in Tietema et al. (1998) and the observed partitioning from the tracer experiments is presented in Figure 7.2A. The figure shows a reasonable comparison, but the simple relationships may give a slight overestimation of the fraction of N retained in the organic layer. Values for the N retention fraction in the organic layer thus calculated for the intensive monitoring plots considered are presented in Figure 7.2. In general the N retention fraction is higher than 50%. The C/N ratio of both organic layer and the mineral topsoil for the intensive monitoring plots is given in Figure 7.3. The figure shows that generally, the C/N ratios of the organic layer are much higher than in the mineral soil. Specifically in the Nordic countries the difference can be large with C/N ratios in the organic layer often being higher than 35 and in the mineral layer varying between 20-30 (compare Figure 7.3 left and right).

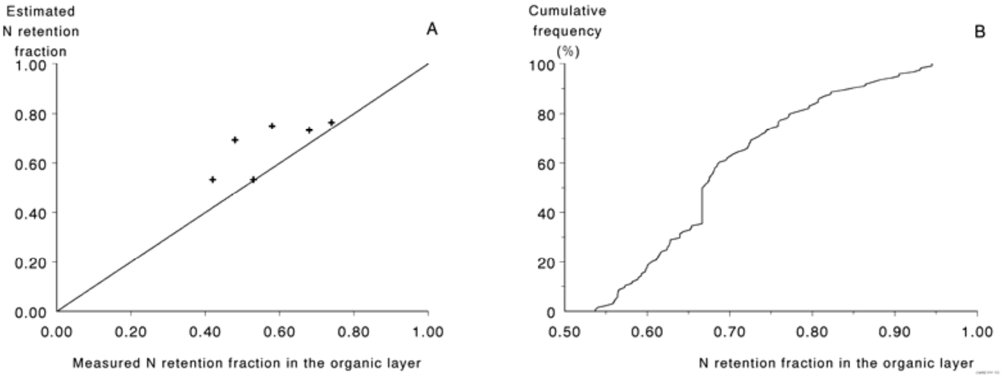


Figure 7.2 Comparison of predicted and measured N retention fractions in the organic layer of six forest plots (A) and predicted N retention fractions in the forest floor of the 121 Intensive Monitoring plots (B)

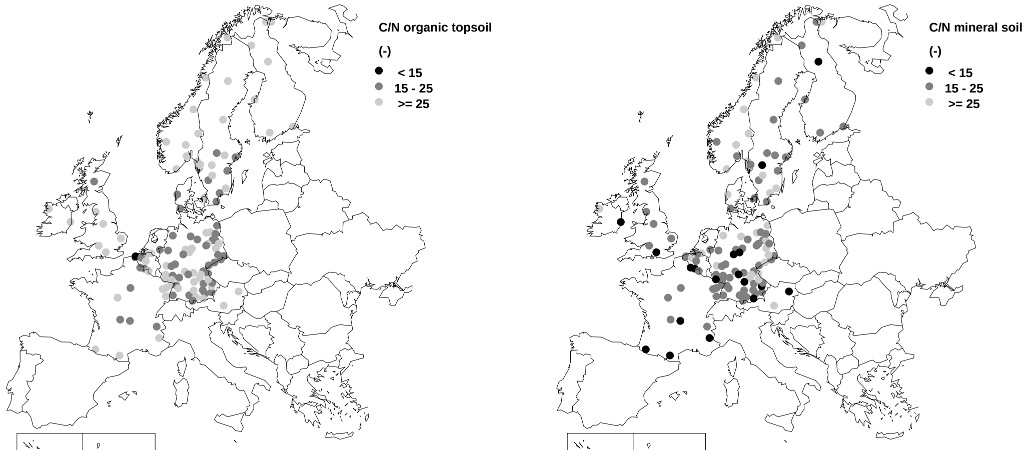


Figure 7.3 C/N ratios in the organic layer (left) and mineral topsoil (right) at the 121 Intensive Monitoring plots that were used for the calculation of carbon sequestration in soils.

Extrapolation of carbon sequestration to the European forested area

In order to scale up results to the European scale, an estimate of net C sequestration was made for more than 6000 forest soils, located in a systematic grid of 16 km x 16 km (level I plots), being representative for approximately 1.62 million km^2 for Forests in Europe, including part of Russia (each plot represents approximately 256 km^2). The assumed representative forest area of each grid cell in a country was scaled to the total forested area in each country given in the Annexes of the executive reports of ICP forests.

An estimate of mean annual increment and related C pool changes (NEP) in stem wood of forests at all level I plots was derived from stand age and available site quality characteristics, using forest yield tables that are available since the sixties and early seventies to estimate the mean forest growth (Klap et al., 1997), using a C content of 50%. This estimate was assumed to equal the baseline growth assuming 1960 as a reference year. As with the level II plots, the net C sink (NBP) in stem wood was calculated by assuming that NBP equals 33% of the NEP.

As with the Intensive Monitoring plots, the calculation of C sequestration in soils was based on calculated nitrogen retention in the soils, multiplied by the C/N ratio of the organic layer and mineral topsoil (see Eq. 7.6). N retention (sequestration) was now calculated as a fraction of the N deposition corrected for N uptake, according to:

$$\text{N retention} = \text{frN}_{\text{ret}} \cdot (\text{N deposition - net N uptake}) \tag{7.10}$$

In the calculation use was made of site specific estimates for the more than 6000 forest soils in a systematic grid of 16 km x 16 km (level I) of the:

- N (NH_4, NO_3) deposition: EDACS model estimates.
- Net N uptake: yield estimates as a function of stand age and site quality as described in Klap et al. (1997) multiplied by deposition dependent N contents in biomass.
- Total N retention fraction frN_{ret} related to measured C/N ratios of the forest soil (partly extrapolations).

An overview of the calculated N deposition in 1960 and 2000 is given in Figure 7.4.

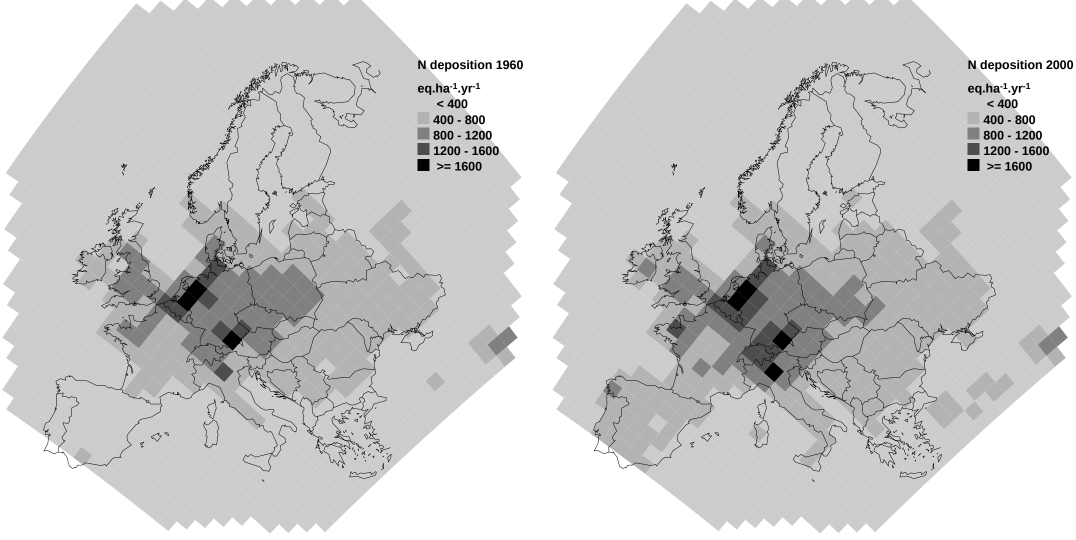


Figure 7.4 N deposition (mol N.ha^{-1}.yr^{-1}) over Europe for the years 1960, 1990 and 2000 as calculated by EMEP. Those data were allocated to the approximately 6000 level I plots based on a direct overlay

Results show the large increase in N deposition in that period. Actually, N deposition was at its peak near 1990 and decreased continually since then. The data for 1960 were used to calculate the reference carbon sequestration in the soil. The data for the period 1960-2000 (data at 5 year intervals that were linearly interpolated) were used to assess the contribution of elevated N deposition in that period on the increase in carbon pools in both standing biomass (tree wood) and in soil in that period, compared to the reference year 1960. The calculation approach is described in the following section.

The fraction frN_{ret} was calculated as a function of the C/N ratio, using presently available results on this relationship given in Dise et al. (1998a; 1998b) and Gundersen et al. (1998). This relationship was derived by plotting the relation between N retention/N deposition and C/N ratios in the organic layer in more than 30 forest conifer plots are presented in Figure 7.5A.

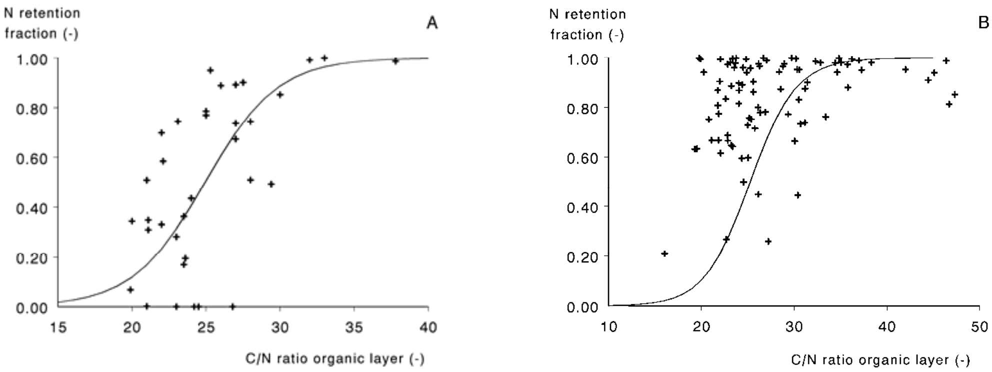


Figure 7.5 Relationship between N retention fraction and C/N ratios in the organic layer. The left graph refers to 34 forest plots of mainly conifers using ECOFEE-data from Gundersen et al. (1998) with N input being throughfall of N and N output referring to nitrate only (A). The right graph refers to 121 Intensive Monitoring plots with available data on total N deposition and N leaching (B).

Based on these data, Gundersen et al. (1998) presented a range in retention fractions as a function of the N status of the ecosystem, including C/N ratios, as given in Table 7.4.

Table 7.4 An overview of ranges in N retention fractions as a function of the N status of the ecosystem based on results from Gundersen et al. (1998; 2006b) and De Vries et al. (2001).

Nitrogen status	Low (N limited)	Intermediate	High (N saturated)
Input (kg N.ha^{-1}.yr^{-1})	0-15	15-40	40-100
Needle N%	< 1.4	1.4-1.7	1.7-2.5
Soil N flux density (litterfall + throughfall) (kg N.ha^{-1}.yr^{-1})	< 60	60-80	>80
C/N ratio (g C.g N^{-1})	> 30	25-30 or 20-30[1]	< 25 or <20[1]
Proportion of input retained (%)	>90	40-100	0-70

[1] the first criterion is based on Gundersen et al. (1998) and the second on De Vries et al. (2001).

Using the average fractions at each C/N ratio, a logistic function of the N retention fraction as a function of C/N ratio was derived from the data in Figure 7.5A as:

$$frN_{ret} = \frac{1}{1 + \alpha \cdot e^{(\beta \cdot (CN - 25))^{\gamma}}} \tag{7.11}$$

where $\alpha = 0.95$, $\beta = 0.4$ and $\gamma = 1.05$.

The reliability of the suggested N retention fractions as a function of C/N ratio is only partly substantiated by the results of the Intensive Monitoring plots as presented in Figure 7.5 B. The results show indeed that N retention is nearly complete (above 90%) at C/N ratios above 30-35 and very low at low C/N ratios (below 20) but in between it is highly variable. On average, the N retention fraction is near 80%, being close to the value of 70% used by Nadelhoffer et al. (1999b). However, the Intensive Monitoring data include many sites with low input and low C/N (e.g. boreal forests in Scandinavia) that exhibit full retention simply because the input is low as illustrated in Dise et al. (1998b). In general, however, the results for the Intensive Monitoring plots indicate that the N retention may be underestimated when using Eq. (7.11). On the other hand, this underestimation may be compensated by the fact that the differences between net N input (N deposition minus net N uptake) and N leaching is all retained in the soil, whereas part may be denitrified (see also discussion).

Assessing nitrogen deposition effects on carbon sequestration by European forests

The methodology used to calculate the impact of elevated nitrogen deposition on carbon sequestration by European forests is inspired by the approach of Nadelhoffer et al. (1999b). These authors assessed additional C sequestration on a global scale from additional N uptake by trees and N retention in soils in response to N deposition. Actually, the paper is sometimes rather unclear whether it derives the additional carbon sequestration due to N deposition, above the C sequestration due to 'normal' forest growth, or whether it calculates the total C sequestration using N retention as the indicator. This ambiguity is also partly reflected in the reactions on the paper debate (e.g. Jenkinson et al., 1999; Schindler, 1999; Sievering, 1999) and follows from the calculation. The estimate by Nadelhoffer et al. (1999b) was based on the assumption of (i) a constant N uptake fraction of 0.05 and a constant N retention fraction of 0.70, based on short-term (1-3 year) ^{15}N labelled tracer experiments in 9 temperate forests, and (ii) an average C/N ratio in stem wood of 500 and in forest soils of 30. Using this approach, an additional N deposition of 1 kg.ha^{-1}.yr^{-1} leads to a C sequestration of 46 kg.ha^{-1}.yr^{-1}, of which 25 kg.ha^{-1}.yr^{-1} is retained in stem wood (0.05 x 500) and 21 kg.ha^{-1}.yr^{-1} in soil (0.7 x 30). These results suggests that C sequestration in forest trees and in forest soils in response to additional N deposition is of equal magnitude. Using an estimate for the present total world N deposition, Nadelhoffer et al. (1999b) show that the contribution of N deposition to net carbon sequestration is limited,

Apart from the rough generalisation, the confusing aspect in this approach is that the present total world N deposition is used, whereas the paper discusses the possible impact of elevated N deposition. The 'unaffected' growth figures should be related to a certain N deposition as well. This implies that one should discuss the impact with reference to the increase in carbon pool in trees in the last decades, as presented by Kauppi et al. (1992) and Nabuurs et al. (1997). Those authors estimated a net increase in the C pool in trees in Europe of approximately 0.1 Gton C.yr^{-1} in the period 1970-1990. This implies that one has to estimate what the impact of increased N deposition in that period is on the C sequestration. In this study we used this approach but we extended the period to 1960-2000, assuming that the net C pool change in trees in that period is also 0.1 Gton C.yr^{-1}.

An overview of all the differences between our approach and those used by Nadelhoffer et al. (1999b) is presented in Table 7.5.

Table 7.5 Overview of differences between the approach used by Nadelhoffer et al. (1999b) and in this study to calculate the impacts of N deposition on carbon sequestration.

Nadelhoffer et al. (1999b)	Our approach
Reference N deposition is negligible	Reference N deposition is 1960
Constant average N deposition	Spatially distributed and time dependent N deposition$^{1)}$
N uptake fraction is constant	N uptake fraction is f(N deposition)
Soil N retention fraction is constant	Soil N retention fraction is f(C/N ratio humus layer/soil, NH_4/NO_3 in deposition)
C/N ratio tree is constant	C/N ratio tree varies in space and time as f(N deposition$_{x,t}$)$^{1)}$
C/N ratio soil is constant in space and time	C/N ratio organic and mineral layer varies in space$^{2)}$

1) Based on calculated EMEP N deposition

2) Based on the measured C/N ratio data at approximately 6000 forested plots

First of all, we used 1960 as the reference for N deposition (this leads to 'reference' growth) and calculated what the additional N deposition was in the period 1960-2000 compared to that reference year. Nadelhoffer et al. (1999b) implicitly assumed that the reference N deposition is negligible. Unlike those authors we included the spatial differences in N deposition on the plots (EMEP estimates). Furthermore, we assumed that the additional N uptake due to N deposition (uptake fraction) is a function of the N deposition, with values being higher in low deposition areas, because of N deficiencies, and lower in high deposition areas. Actually, the uptake fraction was assumed to vary from 10% in areas below 300 $mol.ha^{-1}.yr^{-1}$ (approximately 5 $kg.ha^{-1}.yr^{-1}$) to 5% (the constant value used by Nadelhoffer et al. (1999b) in areas above 1500 $mol.ha^{-1}.yr^{-1}$ (approximately 20 $kg.ha^{-1}.yr^{-1}$). Similarly, the N retention fraction was assumed to be a function of the C/N ratio of the organic layer and the NH_4/NO_3 ratio in deposition, as described in Eq. (7.6) - (7.9), and not a constant of 70%.

Similar to the uptake fraction, the C/N ratios in trees were assumed to vary with the N deposition, values being higher in low deposition areas and lower in high deposition areas. This was based on the idea that luxury consumption takes place at a high N availability, meaning that the additional N uptake is only partly leading to additional growth (C pool change) since part is just leading to higher N contents (lower C/N ratios) in stem wood. Actually, the C/N ratio was assumed to vary from 500 (the constant value used by Nadelhoffer et al. (1999b) in areas below 1500 $mol.ha^{-1}.yr^{-1}$ (approximately 20 $kg.ha^{-1}.yr^{-1}$) to 250 in areas above 5000 $mol.ha^{-1}.yr^{-1}$ (approximately 70 $kg.ha^{-1}.yr^{-1}$). This relation is based on a variation of N contents between 0.1 and 0.2% (at a constant C content of 50%) in comparatively low deposition areas (Scandinavia) to high deposition areas (The Netherlands). For the C/N ratio in the organic layer and mineral layer, we used the measured values at all Level I plots, instead of using a constant value of 30.

The above described methodological approach is presented below in mathematical terms. First the N sequestration in the tree is calculated from the additional N input in the period 1960-2000 and the related C sequestration is calculated by multiplication with an N deposition dependent C/N ratio in the tree according to:

$$N_{seqtree}(extra) = \sum_{t=1960}^{t=2000}(Ndep_{(t)} - Ndep_{(1960)}).fr_{up_{(t)}} \tag{7.12}$$

$$C_{seqtree}(extra)_{(t)} = N_{seqtree}(extra)_{(t)} \cdot \frac{C}{N} tree_{(t)} \tag{7.13}$$

with the uptake fraction by stem wood being dependent on N deposition according to:

$$fr_{up_{(t)}} = 0.10 - 0.05 \cdot \frac{(Ndep_{(t)} - 300)}{1200} \tag{7.14}$$

for 300< Ndep < 1500, with $frup_{(t)}$ = 0.1 if = Ndep < 300 and $frup_{(t)}$ = 0.05 if = Ndep > 1500

and with the C/N ratio in the tree being dependent on N deposition according to:

$$\frac{C}{N} tree_{(t)} = 500 - 250 \cdot \frac{(Ndep_{(t)} - 1500)}{5000} \tag{7.15}$$

for 1500< Ndep< 5000, with $C/N_{(t)}$ = 500 if = Ndep < 1500 and $C/N_{(t)}$ = 250 if = Ndep > 5000

Then, the N retention (sequestration) in the soil is calculated from the additional N input (N deposition in a given year minus the N deposition in 1960, corrected for the additional N uptake due to this increased N availability) for the period 1960-2000, multiplied with the N retention fraction, according to (see Eq. 7.6):

$$N_{retsoil}(extra) = \sum_{t=1960}^{t=2000}(\delta Ndep_{(t)} - \delta Nup_{(t)}) \cdot frN_{im} \tag{7.16}$$

with frN_{ret} being calculated according to Eq. (7.11). Finally, the related C sequestration in the soil is calculated by multiplication of the calculated N retention with the C/N ratio in the soil (organic and mineral layer), according to:

$$C_{seqsoil}(extra)_{(t)} = N_{imsoil}(extra)_{(t)} \cdot f(CN_{soil}) \tag{7.17}$$

with f (CN_{soil}) being equal to the description given in Eq. (7.6) and estimated based on the simple model described in Eq. (7.7)- (7.9).

7.4 Results

Carbon sequestration in trees and soils at Intensive Monitoring plots

The estimated long-term annual carbon sequestration in trees and in soils at the 121 Intensive Monitoring plots is shown in Figure 7.6.

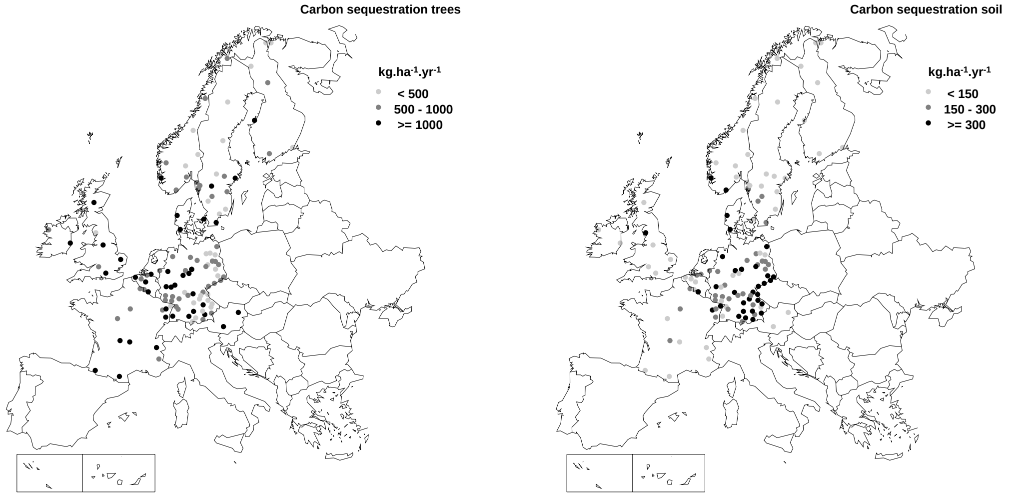


Figure 7.6 Calculated carbon sequestration (kgC.ha^{-1}.yr^{-1}) in trees (left) and soils (right) at the 121 Intensive Monitoring plots for the year 2000

The carbon sequestration (long-term carbon pool changes) in trees (Figure 7.6A) is assumed equal to one third of the current carbon pool change due to forest growth in the last five years, to account for harvesting and forest fires as mentioned before. As expected, the carbon sequestration in trees increases going from Northern to Central Europe. In Northern Europe the calculated C sequestration rate was generally below 500 kg.ha^{-1}.yr^{-1} (related to an annual growth rate < 3 m^3.ha^{-1}.yr^{-1}, being equal to a net increase of < 1 m^3.ha^{-1}.yr^{-1}). In Central Europe, the calculated carbon sequestration rate was mostly above 500 and in many cases even above 1000 kg.ha^{-1}.yr^{-1} (related to an annual growth rate of > 6 m^3.ha^{-1}.yr^{-1}).

The results show that the carbon sequestration rates in the soil (Figure 7.6B) are generally 2-3 times as low as the estimated carbon sequestration rates in tree wood. Values vary mostly from 100-500 kg.ha^{-1}.yr^{-1}. In line with the calculation procedure, the calculated changes in the soil carbon pool follow the N deposition pattern, being high in Central Europe (mostly > 300 kg.ha^{-1}.yr^{-1}) and low in Northern and Southern Europe (mostly below 150 kg.ha^{-1}.yr^{-1}; Figure 7.6B). Interestingly, however, the same kind of pattern is found by Papale and Valentini (2003), presenting spatial (1 x 1 km) estimates of carbon fluxes of European forests based on the net CO_2 exchange flux (NEE) collected at sixteen of sites in the EUROFLUX network, using neural networks for the spatial extrapolation.

Carbon sequestration in trees and soils on the European scale in response to nitrogen deposition

Estimated nitrogen and carbon fluxes in European forests and forest soils for the reference year 1960 and the period 1960-2000 are given in Table 7.6.

Table 7.6 Estimated nitrogen and carbon fluxes in European forests and forest soils for the reference year 1960 and the period 1960-2000.

Element	Type of flux	Flux ($Mton.yr^{-1}$)		Flux ($kg.ha^{-1}.yr^{-1}$)	
		1960	1960-2000	1960	1960-2000
Nitrogen	Deposition	1.54	1.99	9.5	12.3
	Net uptake	0.56	0.59	3.46	3.65
	Sequestration tree[1]	0.19	0.20	1.15	1.22
	Sequestration soil	0.54	0.76	3.33	4.69
Carbon	Net uptake	266	281	1636	1729
	Sequestration tree[1]	89	94	545	576
	Sequestration soil	16.5	23.2	101	143

[1] N and C Sequestration by trees (NBP) equals 1/3 of the net uptake by forest growth (NEP)

Results are given both in $Mton.yr^{-1}$, considering 162 million hectare of European forests, and in $kg.ha^{-1}.yr^{-1}$ (being the average value for this forested area). The estimate for both the N and C uptake due to forest growth for the reference year 1960 was based on the use of standard forest yield tables, related to available site quality characteristics for each level I plot, while correcting for stand age. The estimate during the period 1960-2000 includes the additional average growth due to elevated N deposition compared to 1960, as described before. Table 7.6 also includes an assessment of the net C sink corrected for CO_2 emissions due to harvest and forest fires (the net biome production or NBP) assuming that the latter value equals 33% of the NEP.

Note that the ratio between net N uptake to N deposition for the reference year 1960 is much higher than the additional N uptake in response to additional N deposition. In the discussion about the paper of Nadelhoffer et al. (1999b), (Jenkinson et al., 1999; Sievering, 1999), the neglect to make this distinction has led to confusion. In the reference situation, the total estimated N uptake was 0.56 $Mton.yr^{-1}$ at an estimated total deposition of 1.54 $Mton.yr^{-1}$. This would imply an uptake percentage of 36% if one would relate N uptake to N deposition only. However, such a direct comparison is dangerous since the N may come from other sources as well. The calculated average additional N uptake in the period 1960-2000 was however only 0.029 $Mton.yr^{-1}$ at an additional N input of 0.45 $Mton.yr^{-1}$, implying an average uptake percentage of 6.4%. This is close to the value of 5% for the additional N uptake related to N deposition used by Nadelhoffer et al. (1999b). The calculated average C/N ratio in tree wood (net C uptake/net N uptake) is near 475 being also close to the value of 500 used by Nadelhoffer et al. (1999b).

The calculated carbon pool change in stem wood due to forest growth equals 266 (reference year 1960) – 281 (1960-2000) $Mton.yr^{-1}$. The impact of the additional N input (on average 0.45 $Mton.yr^{-1}$ in the period 1960-2000) is thus 15 $Mton.yr^{-1}$, being equal to 33.3 kg C per kg N. This is 25% higher than the estimate of Nadelhoffer et al. (1999b) who assumed an additional C pool change of 25 kg C per kg N. Considering an average extra N deposition of 2.8 $kg.ha^{-1}.yr^{-1}$ in the period 1960-2000 (12.3 kg $N.ha^{-1}.yr^{-1}$) compared to 1960 (9.5 kg $N.ha^{-1}.yr^{-1}$), this implies an extra average C pool change of 93 $kg.ha^{-1}.yr^{-1}$ This is exactly the calculated mean C pool change in stem wood in the period 1960-2000 (1729 $kg.ha^{-1}.yr^{-1}$) compared to 1960

(1636-kg.ha^{-1}.yr^{-1}) (see Table 7.6). Assuming that NBP is 33% of the NEP, leads to a mean net C sequestration rate of 545 (reference year 1960) – 576 (1960-2000) kg.ha^{-1}.yr^{-1}. The impact of the additional N input on the net C sequestration is thus 31 kg C at an additional N input of 2.8 kg.ha^{-1}.yr^{-1}, being equal to 11.1 kg C per kg N (Table 7.6).

The calculated soil C sequestration rate for the period 1960-2000 was lower than the results derived by the Nadelhoffer et al. (1999b) approach (0.023 vs. 0.034 Gton.yr^{-1}; compare Table 7.1 and Table 7.6). This is to be expected since these authors assumed a constant low net uptake (5%) and a constant high soil accumulation of 70% in the forest soil. Using the assumption that all the net incoming N is retained (total retention, no leaching) gave an estimate (0.042 Gton.yr^{-1}) that is slightly higher than the estimate by Nadelhoffer et al. (1999b). The ratio between the estimated C sequestration in the tree and the soil for the period 1960-2000 is 4.1 (94/23). This is higher than the ratio between trees and soil for the intensive monitoring plots, where this ratio was near 3. This is due to the higher N input on the intensive monitoring plots.

The impact of the additional N input on the net soil C sequestration per hectare is 42 kg C (143-101) at an annual additional N input per hectare of 2.8 kg N, being equal to 15 kg C per kg N (Table 7.6). This is 30% lower than the estimate of Nadelhoffer et al. (1999b) who assumed an additional soil C pool change of 21 kg C per kg N, based on an average N retention fraction of 0.7 and a C/N ratio of 30. The calculated average C/N ratio in the soil (net soil C sequestration/net soil N sequestration) was near 30, being almost equal to the value used by Nadelhoffer et al. (1999b). This seems high but the major reason for this is that a large part of the N input is immobilised in the humus layer with relatively high C/N ratios, specifically in the Nordic countries, where a large part of the European forests is located. The reason for the difference is thus the lower calculated N retention fraction (on average near 0.5). This value may, however, be an underestimate, considering the N retention in the Intensive Monitoring plots (see before).

The additional C uptake in trees of approximately 15 Mton.yr^{-1} in the last 40 years is only 5.3% of the total C uptake of 281 Mton.yr^{-1}. Similarly the C sequestration in trees of approximately 5 Mton.yr^{-1} is only 5.3% of the total C sequestration of 94 Mton.yr^{-1}. For soil the impact is larger, namely 29% (6.7/23.2) which is due to the fact that soil C sequestration is directly related to N retention. Overall the impact of N deposition on the total C sequestration by trees and soils is estimated near 10% (11.8/117; see Table 7.6).

The estimated carbon sequestration in tree wood (the net biome production or NBP) and in soil as a function of the geographic region is given in Table 7.7.

Table 7.7 Estimated net carbon sink (NBP) in European forests, due to an increase in standing biomass (NBP, being 33% of the NEP), and European forest soil for the reference year 1960 and the period 1960-2000.

Region	Area Million ha	Csequestration tree (Mton.yr^{-1})		Csequestration tree (kg.ha^{-1}.yr^{-1})	
		1960	1960-2000	1960	1960-2000
Tree					
Northern Europe (>52)	83	38	40	454	478
Central Europe (44-52)	51	35	37	679	717
Southern Europe (<44)	28	16	17	577	613
Total/Average	162	89	94	545	576
Soil					
Northern Europe (>52)	83	7.7	10.4	92	126
Central Europe (44-52)	51	8.0	10.9	157	214
Southern Europe (<44)	28	0.8	1.9	28	68
Total/Average	162	16.5	23.2	101	143

The results show that despite the fact that the productivity of forests is much higher in Central Europe (and also in Southern Europe) compared to the Northern part, the total sequestration in tree wood is highest in the North because of the large forested area in this region. In the soil, however, the largest sequestration is calculated in Central Europe since soil C sequestration largely depends on N deposition, being highest in this region.

The geographic variation in carbon sequestration in trees and soils is further illustrated in Figure 7.7.

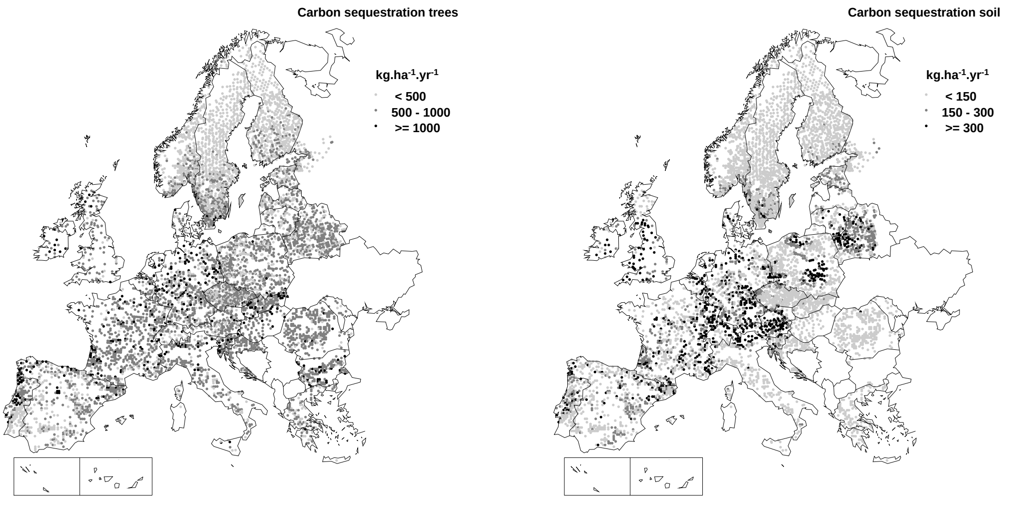


Figure 7.7 Calculated average carbon sequestration (kgC.ha^{-1}.yr^{-1}) in trees and soil for the period 1960-2000 at more than 6000 level I plots in Europe using the standard run.

As with the level I plots, the carbon sequestration in tree wood is generally low (<500 kg.ha^{-1}.yr^{-1}) in Northern (cold climate) and Southern Europe (water stress) and moderate to high in Central Europe. The pattern in forest soil carbon sequestration general follows the pattern of N deposition over Europe. It shows that C sequestration is small in Northern Europe, where the N input is low and nearly all incoming N is retained by the vegetation, and higher in Central and Eastern Europe where the N input is larger. This can, however, be a slight overestimate since part of the N accumulation may occur as a dilution of the C/N ratio at high deposition. The finding that C sequestration is negligible in northern boreal forest is in line with results from Martin et al. (1998) based on flux measurements for CO_2.

7.5 Discussion and conclusions

Comparison of calculated carbon pool changes in trees with literature values

As with the carbon pools in standing biomass, the carbon pool changes at Intensive Monitoring plots are low in Northern and Southern Europe and moderate to high in Central Europe. The median carbon pool change in living trees at all plots equals 2175 $kg.ha^{-1}.yr^{-1}$ with an overall variation of approximately 400 (evergreen oak) - 4500 $kg.ha^{-1}.yr^{-1}$ (fir). This is close to the maximum sequestration rates calculated by Nabuurs and Schelhaas (2002) after approximately 40 years for sixteen typical European forest types over Europe. These authors calculated an overall average value of 2980 $kg.ha^{-1}.yr^{-1}$ varying between 1150 and 4100 $kg.ha^{-1}.yr^{-1}$, depending on the tree species. This result implies that the carbon pool changes at most plots are likely near their maximum. This is in line with the age class of the trees, which are mostly in the range of 40-60 years.

The average carbon pool change at all Level I plots due to forest growth equals approximately 1650 $kg.ha^{-1}.yr^{-1}$, being only 2/3 of that measured at all Intensive monitoring plots during a five year period. Apart from the fact that the Intensive Monitoring plots are not representative for the whole of Europe, this difference is due to the fact that the calculated growth rates for the level I plots are average values over the total rotation period. For a total forested area in Europe of 162 million ha, the calculated carbon pool change in stem wood due to forest growth (NEP) equals approximately 0.28 $Gton.yr^{-1}$.

Results of the NEP appear to be comparable to those based on CO_2 exchange fluxes (NEE) derived by Martin et al. (1998) based on the Euroflux sites (0.28 $Gton.yr^{-1}$), but the value is less (nearly twice as low) than the NEE value derived by Papale and Valentini (2003) from net CO_2 exchange fluxes collected at sixteen EUROFLUX sites. These fluxes do, however, include sequestration by trees and soil. The values are also twice as low as the NEP value derived from carbon flux data in forest at eleven “Canif” sites along a North –south transect through Europe (Schulze et al., 2000); compare Table 7.1). This illustrates that a simple extrapolation of results at a limited number of plots is highly questionable.

Assuming that NBP is 33% of the NEP, gives results close to 0.1$Gton.yr^{-1}$, being the estimate derived from repeated forest inventories (Kauppi et al., 1992; Nabuurs et al., 1997). Using a forested area of 162 million ha, the mean net carbon sequestration rate in tree stem wood is approximately 550 $kg.ha^{-1}.yr^{-1}$. This is close to net carbon sequestration rates in trees calculated by Liski et al. (2002) based on a dynamic modelling exercise, as described before. These authors calculated a net carbon sequestration in trees was 390-600 kg.ha^{-1}.yr^{-1} in 1990. Upscaling their results to a forested area of 162 million ha, also gives results for the NBP near 0.1 Gton.yr^{-1} (see Table 7.1). The average value is approximately half the average value of 800 kg.ha^{-1}.yr^{-1} obtained by Nabuurs and Schelhaas (2002) for 16 typical forest types across Europe, but it is in a comparable order of magnitude.

Comparison of calculated carbon sequestration estimates in soil with literature values

The calculated net carbon sequestration in the soil of approximately 0.016 Gton.yr^{-1}, being equal to an average accumulation of 70 kg.ha^{-1}.yr^{-1}, is 10 times lower than the value derived by Schulze et al. (2000) based on the C retention in eleven sites (0.13-0.17 Gton.yr^{-1}). The latter estimate is likely to be an overestimate, as it would imply that the C/N ratio of European forest soils is strongly increasing. There are no indications that this is the case. To the reverse, it is more likely that C/N ratios are decreasing, especially in areas with an elevated N deposition. This result thus illustrates that it is dangerous to make estimates on a European scale based on a limited number of plots using a simple upscaling procedure.

The estimated average soil C sequestration rate of 143 kg.ha^{-1}.yr^{-1} for the period 1960-2000 is in line with the value of 190 kg.ha^{-1}.yr^{-1} in 1990 derived by Liski et al. (2002), based on the dynamic modelling exercise described before. Even though this leads to higher values on a European scale, the difference (see also Table 7.1) is by far not so large as with Schulze et al. (2000). Furthermore, the results are in line with the net carbon sequestration in soil for 16 typical forest types across Europe derived by Nabuurs and Schelhaas (2002), equal to 110 kg.ha^{-1}.yr^{-1}.

The conclusion that net sequestration potential of the below ground carbon in the soil, which has much lower turnover times than above ground carbon, is only small in forests is also in line with field data, showing that soil C sequestration is even small after afforestation on arable fields (Vesterdal et al., 2002). This implies that the terrestrial carbon sink can only be viewed as "buying variable time to address the most significant perturbation of the carbon cycle: fossil fuel emissions" (Steffen et al., 1998).

Impacts of nitrogen deposition on carbon sequestration

The basic assumption for carbon pool changes in both tree and soil was that the additional N uptake or soil N retention is reflected in carbon pool changes due to growth or soil organic matter accumulation, according to the C/N ratio of the tree or the soil, respectively. The calculation focused on C sequestration in the soil from N retention assuming that nitrogen retained in the soil form organic matter with a constant carbon to nitrogen ratio. Most likely, the estimate constitutes an upper limit since nitrogen deposition tends to decrease the carbon to nitrogen ratio over time.

The conclusion that the increase in forest growth in trees is very small, about 5% only, seems contradictory with a generic more sophisticated modelling approach, in which the combination of CO_2 rise and elevated N deposition was estimated to account for a 15-20% increase in forest net primary productivity (Rehfuess et al., 1999). In that study, model predictions were made of carbon sequestration in view of changes in climatic variables, temperature and precipitation, CO_2 concentrations and nitrogen deposition. Results showed that the impact of temperature was much less important than that of CO_2, whereas N deposition was claimed to be most important (Rehfuess et al., 1999, last ref recognition). This contradiction is however due to the upscaling of the model to the European scale. The net impact of additional N deposition on forest growth was estimated at approximately 15 to 25 kg C per kg N by the various sophisticated forest growth models, being slightly lower than the result of the model applied in this study (near 35 kg C per kg N). It implies that in Central European areas with a large additional N input (e.g. of 10 to 20 $kg.ha^{-1}.yr^{-1}$), the impact is large but not in Northern and Southern Europe, where the additional N input is generally low. Considering an overall average additional N input of 2.8 $kg.ha^{-1}.yr^{-1}$ the impact of this additional N deposition is still limited.

The predicted impact of N deposition in high deposition areas might even be overestimated. A positive effect can indeed be expected in areas where forest growth is limited by N availability, but a continuous high input of N may lead to a situation where other growth factors, such as other nutrients and water, become limiting for the growth of forest. The relation between water shortage and N surplus can be explained by the fact that a high N input favours growth of canopy biomass, whereas root growth may be relatively unaffected (shown only for seedlings). The increase in canopy biomass will lead to a higher demand for water and therefore to an increased risk of water shortage (drought). It also causes an increased demand of base cation nutrients (Ca, Mg, K) whereas the availability of these cations can be reduced by increased dissolved levels of NH_4 and/or Al (induced by NO_3 and SO_4). This effect may reduce the fertilising effect of high N deposition.

Uncertainties in the impact of nitrogen deposition on carbon sequestration in European forests

There are various uncertainties in the calculated impact of N deposition on net carbon sequestration related to: (i) the assumptions made, including the assumed constant C/N ratio and negligible denitrification, (ii) the neglect of the occurrence of forest disturbances, of off-site C sequestration in e.g. hardwood products and of lag times between changes in N deposition and C sequestration and (iii) the uncertainty in the parameterization. These aspects are all discussed below.

Invariable C/N ratio: The assumption of a constant C/N ratio is based on the assumption that C increases at the same rate as N, induced by an increased litter production and a reduced decomposition of organic matter in response to N input. As mentioned before, the assumption of an additional C input by litterfall is only true when trees use part of the N from deposition to form biomass and that this N will be sequestered in the soil after it cycled through leaf and root tissues. When, however, the N that is immobilized in the soil, without cycling through the system, then it does not support C sequestration and would instead result in lowering the soil C/N ratio.

Testing the hypothesis is difficult since there are few sites at which C/N ratios have measured by repeated sampling over time. Furthermore, the large pools in C and N, compared to the possible annual changes, in combination with the inherent variability in those pools make it difficult to accurately quantify changes in soil C and N pools in time, even when these are measured (De Vries et al., 2000). For example, data on changes in C and N pools in more than 100 Dutch forest soils in response to a decrease in N deposition in the period 1990-1995 indicate an increase in C/N ratio in the organic layer but a decrease in the mineral topsoil (Leeters & de Vries, 2001). However, considering that spatial variability in the C and N pools, the time period is too small to draw any conclusion about a statistically significant change in time. A notable example of long term data on changes in soil C/N ratio are data from Rothamsted, such as the Rothamsted Park Grass control plots (Dodd et al., 1994). These data show hardly any variation over more than a 100 year period.

Furthermore, data on N leaching and soil C/N under different addition levels are available from plot-scale N manipulation studies. Results of more than 10 years of nitrogen addition to the NITREX catchment at Gardsjon, show no change in C/N ratio (Moldan, pers. comm.), although the nitrate transport down the profile increased (Gundersen & Rasmussen, 1995; Moldan et al., 1998). Inversely, Evans et al. (2006) observed decreases in C/N ratio at two moorland pools under three treatment levels, but they also observed an increase in C storage as a consequence of N deposition, which slowed down the rate of C/N change. In summary, even though the assumption of a constant C/N ratio is not really verified, it is clear that ecosystem carbon accumulation is constrained by nitrogen availability (e.g. Townsend et al., 1996; Hungate et al., 2003). The uncertainty in the long–term response due to this assumption can be assessed by assuming changes in C/N ratio occurring in the soil, within reliable boundaries, as illustrated further below.

Neglecting denitrification: The assumption that denitrification (the conversion of nitrate to N_2 or other gaseous forms, such as NO and N_2O) under anaerobic conditions is negligible is not really warranted by literature data. If nitrate and a dissolved organic carbon (C) substrate are available, denitrification is of importance in anoxic wet forests (high ground water table) and in the riparian zone along forest streams (Lowrance, 1992; Ashby et al., 1998; Konohira et al., 2001). However, in most well drained and well-aerated forest soils, denitrification losses are < 2 kg $N.ha^{-1}.yr^{-1}$ and in conifers often < 0.5 kg $N.ha^{-1}.yr^{-1}$ (Persson et al., 2000; Oura et al., 2001). In acid forest soils, large part of the N loss occurs through the release of N_2O. Recently, Denier van der Gon and Bleeker (2005) compiled the literature on N_2O emissions from forests in Europe (mainly Germany, but also Finland, Sweden, Denmark, UK, Belgium and Austria) and in North America (US and Canada). Their results show that measured annual N_2O fluxes range from 0.2 to 4.0 kg N_2O-$N.ha^{-1}.yr^{-1}$ but the values mostly stayed below 1.5 kg N_2O-$N.ha^{-1}.yr^{-1}$. Application of the PnET-N-DNDC model to European forest soils, covering almost entire Europe, lead to an estimated average N_2O emission from of 0.58 kg $N.ha^{-1}.yr^{-1}$ (Kesik et al., 2005). Considering an estimated additional average N sequestration in soil of 4.69 kg $N.ha^{-1}.yr^{-1}$ the possible overestimation of the N retention and thereby the C sequestration is probably 10-20%. This may compensate for the possible underestimation of the N retention, since the N retention fraction might be overestimated when considering the results obtained from the Intensive Monitoring plots (see before).

Forest disturbances: Information on effects of disturbances on the productivity of forest ecosystems, either natural as a consequence of e.g. fire, wind, pest or diseases, or managed such as forest logging, has been achieved by the use of chronosequences of forest stands at different ages. Results show that disturbances decrease photosynthetic capacity, completely in the case of logging, and typically converts a forest from a carbon sink into a carbon source (see also Hymus & Valentini, 2006). The time required for a stand to become C neutral and ultimately sequester C after the initial disturbance depends on the type and intensity of the disturbance and on post disturbance management for evergreen forests (Thornton et al., 2002). Periods generally vary between 10 - 12 years but periods near 25 have also been found (Hymus & Valentini, 2006).

Incomplete carbon accounting: In this study we assume that wood which is harvested and removed from a site is ultimately released as CO_2 into the atmosphere. We thus only account for the C sequestered in standing biomass. However, often harvested wood can reside in solid wood products, recycled products or landfills for centuries. A sometimes large fraction of harvested wood is also used for energy production. Results show that increases in off-site C sequestration can be sizable, perhaps matching increases in on-site C sequestration (e.g. Pacala et al., 2001). If N deposition accelerates forest growth, the potential for the off-site C sequestration (storage in products or in landfills, bioenergy offsets of fossil fuel emissions) is thus increased. This aspect implies that the overall impact of N deposition on C sequestration is most likely underestimated.

Lag times between changes in N deposition and C sequestration: The observed increase in growth in forests following 1960 may partly relate to elevated N deposition before that year due to lag effects. Because the soil is a large reservoir of N, especially in so-called 'N saturated forest soils', decreases or increases in atmospheric N deposition may not cause direct changes in forest growth and it may take up to a decade before effects are to be seen on productivity in case of modest annual N additions. However, the overall effect on a 40 year period is likely to be small and the uncertainty is likely to be insignificant compared to the uncertainties in the calculation method. Furthermore, age-related decline will diminish the potential of forests to respond to additional inputs of N, but this holds also for the C sequestration without additional N deposition and the relative contribution of additional inputs of N on C pool changes in forests may not change with time.

Uncertainty in the parameterization: There is clear uncertainty in the various uptake and retention fractions used in the study. The short-term nature of most ^{15}N referred to by Nadelhoffer et al. (1999b) may have caused an underestimation of the N uptake by trees. Furthermore, the assumed N retention fraction in soil may be an overestimate in low N deposition areas where N leaching is generally negligible and N retention thus near 100%. Similarly, there also uncertainties in the C/N ratio of the tree and the soil. To gain insight in the impact of those uncertainties on the impact of N deposition on additional carbon sequestration in tree and soil, we compared results obtained with Eq. (7.12)-(7.17) using the standard parameterization (standard run) and alternative assumptions regarding the parameters determining N retention (Table 7.8). Using the standard run leads to an additional C sequestration in trees and soils of approximately 11.8 Mton.yr^{-1} in the last 40 years.

Table 7.8 Overview of the additional C sequestration in view of elevated N deposition in the period 1960-2000 compared to the annual net carbon sequestration in 1960 (Mton.yr^{-1}).

Variation	Assumptions	Extra C sequestration 1960-2000 (Mton.yr^{-1})	
		Tree	Soil
1 This study: standard		5.1	6.7
- Uptake fraction	N dependent 5-10%[1]		
- Retention fraction	N dependent 0-100%[1]		
- C/N ratio tree	N dependent 250-500[1]		
- C/N ratio soil	Site dependent[1]		
2 This study alternatives			
- Uptake fraction	Constant 5%[2]	3.3	6.6
- Uptake fraction	Constant 10%[2]	6.6	6.2
- Retention fraction	Constant 70%[2]	4.9	7.3
- Retention fraction	Constant 100%[2]	4.9	10.6
C/N ratio tree	Constant 500[2]	4.8	6.4
C/N ratio tree	Constant 400[2]	3.8	6.4
C/N ratio soil	Constant 30[2]	4.9	11.4
C/N ratio soil	Constant 25[2]	4.9	5.4
3 Nadelhoffer standard	Constant fractions and C/N ratios[3]	3.3	9.2
4 Nadelhoffer alternative	Adapted constant fractions and C/N ratios[4]	5.2	10.3

[1] The variation in fractions and C/N ratios depends amongst others on N deposition as described in the main text

[2] This variation implies that all other parameters are standard according to variation 1

[3] The standard Nadelhoffer calculation includes constant fractions for tree uptake (5%) and soil retention (70%) and constant C/N ratios in tree (500) and soil (30)

[4] The alternative Nadelhoffer calculation includes adapted constant fractions for tree uptake (10%) and soil retention (100%) and constant C/N ratios in tree (400) and soil (25)

The sensitivity analyses showed that the contribution varies between approximately 10 and 16 Mton.yr^{-1} implying a potential contribution of N deposition to the carbon sequestration near 120 Mton.yr^{-1} of 8-14 %. The additional carbon sequestration in the soil is approximately 57% of the amount sequestered in the tree when using the standard run with a variation between approximately 50-70% for the various alternatives. Using the standard Nadelhoffer approach, the additional sequestration in tree (3.3 Mton.yr^{-1}) is about one third of that in soil (9.2 Mton.yr^{-1}). This seems deviating form the results by Nadelhoffer et al. (1999b) who assumed a nearly equal C pool change. However, their results relate to the total NEP, whereas the results presented in Table 7.8 refer to the NBP, which is assumed 1/3 of the NEP. Despite the possible uncertainties, the soil C sequestration derived is generally lower that estimates given in the literature based on measured C cycling fluxes (see discussion presented before).

Conclusions and outlook

Based on soil data collected at the Level I and Level II monitoring plots and modelled nitrogen deposition data, an estimate of CO_2 sequestration for European forests, divided in trees and soils, could be made. Furthermore, the contribution of N deposition to forest growth and soil carbon sequestration could be assessed. Using the above mentioned approach, the following conclusions can be drawn:

- Carbon sequestration in stem wood is on average approximately 4 times as high (0.094 $Gton.yr^{-1}$) as the C sequestration in the soil (0.023 $Gton.yr^{-1}$). As expected the changes in the carbon pool in tree due to forest growth increase going from Northern to Central Europe. The calculated changes in the carbon pool in soil do follow the N deposition pattern being high in Central Europe and low in Northern and Southern Europe. This follows from results at both level I and level II plots.
- Net increases in the carbon pool by forests in Europe (both trees and soil) are in the range of 0.10-0.15 $Gton.yr^{-1}$, being an important part (about 50%) of the terrestrial carbon sink in Europe, derived from atmospheric inversion models. The results furthermore show that the C sequestration by forest is mainly due to a net increase in forest growth, since the longer term C sequestration in the soil is limited.
- The contribution of additional N deposition to the net sequestration of carbon in trees and soil in the period 1960-2000 is approximately 11.8 $Mton.yr^{-1}$ (5.1 $Mton.yr^{-1}$ in tree wood and 6.7 $Mton.yr^{-1}$ in soil), being near 10% of the total carbon sequestration in that period (approximately 117 $Mton.yr^{-1}$).

Although the general conclusions are robust, there is a substantial uncertainty in the various estimates due to the assumptions made, the complexity of the processes involved and the large diversity of forests on a European scale. In future estimates, more emphasis should be given to a more accurate estimate of N retention, accounting for denitrification, impacts of forest disturbances and inclusion of a complete C budget including off-site C sequestration. Furthermore, the impact of N deposition on the exchange of other greenhouse gases than carbon dioxide (CO_2), specifically nitrous oxide (N_2O) and methane (CH_4), has to be taken into account. First estimates of this impact on European forests on the overall global warming potential (in kg CO_2 equivalents) indicate, however, that the increase of N_2O emissions in response to elevated N inputs is much lower than the increase in vegetation CO_2 sink, whereas the impact on the (decrease in) soil CH_4 sink. is comparatively negligible (De Vries et al., 2006a).

Despite these uncertainties, the results of this study imply that the impact of forest management on tree growth is most important in explaining the carbon pool changes in forest in Europe. The increase in carbon pools in trees is mainly due to the fact that forests in Europe are aggrading because the removal by harvesting and forest fires is less than the net growth. A further contribution to C sequestration on the forest area may come from earlier and recent afforestations on fields or grasslands. Effects of such land use change are not included in the calculations. On these areas the build up of C stock in trees may be substantial but still a transitory phenomenon lasting a forest generation.

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8 Modelling long term impacts of environmental change on mid- and high-latitude European forests and options for adaptive forest management

Abstract
The process based model SMART2-SUMO-WATBAL was applied to 166 intensive monitoring forest plots of mid and high latitude Europe to evaluate the effects of expected future changes in carbon dioxide concentration, temperature, precipitation and nitrogen deposition on forest growth (net annual increment. These results were used in the large scale forest scenario model EFISCEN (European Forest Information SCENario model) to upscale impacts of environmental change and to combine these results with adapted forest management. Because of the few plots available, Mediterranean countries were excluded from the analyses. Results are presented for 23 European countries, representing 109 million hectares of forests.

We predict significant impacts of environmental change on mid and high latitude European forests. Under a no climate change scenario, an increased fellings scenario caused an increase in fellings from approximately 3.8 - 5.3 m^3.ha^{-1}.yr^{-1} from in 2000 to 2010, to reach a stable growing stock volume between 170 and 180 m^3.ha^{-1}. In 2100 it was thus possible to cut 50% more under intensive management than current felling level. Climate change increased this possibility to 90% (from 3.8 to 7.2 m^3.ha^{-1}.yr^{-1}). The growing stock in 2100 increased to 279 m^3.ha^{-1} under base felling level and no environmental change, but under environmental change, the rise was up to 381 m^3.ha^{-1} in 2100. The average carbon stock of whole tree biomass was 72 Mg.ha^{-1} carbon in 2005 and it increased to a predicted 104 Mg.ha^{-1} carbon in 2100 under no environmental change and base fellings. Environmental change enhanced the build up of carbon stocks to up to 143 Mg.ha^{-1} carbon in 2100. An average 35-40% higher increment is thus foreseen for 2100 compared to a no environmental change scenario (both under base fellings). The largest relative growth rate change is foreseen for the Nordic countries, with up to 75% growth increase. The impact of environmental change on C stock change in trees is as significant as the impact of forest management. The impact of environmental change on C removals is however minimal, compared to forest management.

Keywords: European forests, Carbon, NPP, adaptation, forest management, mitigation

8.1 Introduction

The IPCC in its Fourth assessment report states that forests may be impacted detrimentally by climate change, eventually leading to widespread carbon losses (Fischlin et al., 2007). The IPCC also confirms that in some cases productivity increases may be found, but that overall uncertainty is very high. Regional differences may be very large, but current understanding is too limited to specify regionally adapted management responses. Overall, the evidence for the IPCC statements is based on few studies only that range from (FACE) experiments to dynamic global vegetation models (DGVM). Thus, the uncertainty behind these rather bold statements on widespread decline and disturbances is very large. Regional studies taking into account the specific regional circumstances are therefore needed.

European forests have been intensively managed for timber production for a long time. Most of these forests were established in the beginning of the 20th century, often on degraded sites. On these sites, foresters usually applied a regular planting, thinning and clear cutting regime in even aged monospecies forest stands. The forest owners stimulated growth through site improvement or selection of fast growing provenances. Partly because of this, the total stemwood volume increment has increased from around 400 million $m^3.yr^{-1}$ in the 1950's to over 800 million $m^3.yr^{-1}$ around 2000 (UNECE).

For decades the main emphasis has been on timber production. This is indirectly shown by the fact that European forests comprise only 4% of the world's forests but provide 13% of the current global fellings of wood (Pajuoja, 1995; UN-ECE/FAO, 2000). Also, the European forest sector's output is about a quarter of the current world industrial production of forest products, accounting for almost 30% in wood panels and paper and paperboard (Mery et al., 1999). However, forest management is changing towards a multi-functional management in which nature conservation plays an equally large role as wood production (Peck, 1998; Farrell et al., 2000; Hüttl et al., 2000; Müller, 2000). The growing stock of European forests is increasing due to significantly higher net annual increment than felling (UN-ECE/FAO, 2000). European forest area is slightly expanding with some 0.5 million $ha.yr^{-1}$ even though scattered deforestation occurs. Storm damages have been relatively small, i.e. have not exceeded annual fellings. However, locally storm damages and forest fires cause large impact on forests but not at the European scale. The area of primary forests is very small with just few hundred thousands of hectares. Biological diversity is declining, to a large extent caused by influences from outside the forest sector, e.g. eutrophication, habitat fragmentation, deposition, drainage, tourism, and urban sprawl. Through the establishment of a Natura2000 network, some of these external influences are meant to be curbed.

Climate change may exacerbate these pressures (Fischlin et al., 2007). But despite many detailed studies it is practically unknown what climate change may mean for European forests and how forest owners should respond or anticipate. Some studies are available where Europe's forests are part of a global dynamic vegetation model (Gitay et al., 2001), or where an assessment of the extreme year 2003 were quantified (Ciais et al., 2005). Other studies are confined to very local modelling exercises, and there has been one study that used a combination of plant physiological models and a forest resource model. (Karjalainen et al., 2003; Nabuurs et al., 2003). The latter two publications were based on a set of seven plant physiological models that were applied to only 15 sites across Europe. At that time far less information was available on plant physiological responses to climate change, the climate scenarios are seen as outdated now, and the underlying database of the forest resource model was outdated for several countries. Furthermore, the views on forest management have changed. Since the oil prices have risen, and the EU has launched its bio energy policy plan, the forest resource is facing higher harvesting levels again. Thus future harvesting levels are foreseen to rise much higher and options for adaptive management are now much more under discussion.

The aim of this study is to quantify possible effects of environmental change, including changes in CO_2 concentration, climate (temperature and precipitation) and nitrogen deposition, and management intensity on forest growth, supply of timber and carbon stocks at European level.

8.2 Modelling approach

8.2.1 The EFISCEN model

We applied EFISCEN (European Forest Information SCENario) model version 3.1.3 in this study. The model is described by Schelhaas et al. (2007a) and it has been used to analyse possible future forest resources (Schelhaas et al., 2006a; Nabuurs et al., 2007) and to estimate forests carbon stocks and flows at regional scale (Karjalainen et al., 2003).

The state of a forest is described as an area distribution over age and volume classes in matrixes. A separate matrix is set up for each forest type provided in the inventory data. Forest types are distinguished by region, by owner class, by site class and by tree species, depending of the aggregation level of the provided data. In this way some 5000 forest types are distinguished. The projection of the growth in the model is based on growth functions that are calibrated based on the inventory data.

The input data for countries have been derived from their national forest inventories and the data has been gathered to the EFISCEN inventory database (Schelhaas et al., 2006b). The description of countries is in Table 8.1. The total area in the 23 countries under simulation was 109.5 million hectares and the average growing stock 176 $m^3.ha^{-1}$ in 2000.

Table 8.1 Metadata of the forest inventory initialisation data (Nabuurs et al., 2007). FAWS: Forest Available for Wood Supply.

Country	FAWS (UN-ECE/FAO, 2000) (1000 ha)	Area covered in EFISCEN (1000 ha)	Year of forest inventory
Austria	3,352	3354	1992-96
Belgium	639	581	1997-199
Bulgaria	3123	3328	2000
Czech Republic	2559	2493	2000
Denmark	440	442	1990
Estonia	1932	2048	1999-2001
Finland	20675	19628	1986-1994
France	14470	13873	1988-2000
Germany	10142	9905	1986-1990/1993
Hungary	1702	1861	2000
Ireland	580	329	1992-1993
Latvia	2413	2807	2000
Lithuania	1686	1939	2000
Luxembourg	85	71	1989
Netherlands	314	307	1995-1999
Norway	6609	6644	1996-2000
Poland	8300	6309	1993
Romania	5617	6211	80s
The Slovak Republic	1706	1909	1994
Slovenia	1035	1159	2000
Sweden	21236	20967	1996-2000
Switzerland	1060	1140	1994
United Kingdom	2108	2202	1995-2000
TOTAL	108434,352	109507	

EFISCEN is calculating carbon stocks and flows on site. The volume of growing stock is converted to biomass compartments using dry wood density, carbon content and Biomass Expansion Factors (BEF). Furthermore, litter production is calculated using species specific turnover rates for each biomass compartment (stem, branches, leaves, coarse roots and fine roots). Tree species and regional specific parameters have been estimated in the CarboInvent project (Schlamadinger, 2005). Litter production also includes felling residues left to the forest. Net Primary Production (NPP), i.e. biomass produced, is calculated as sum of tree carbon stock change, removed biomass and litter production. Net Ecosystem Exchange (NEE), i.e. the yearly flow observed above forest, is sum of tree carbon stock change, soil carbon stock change and removed forest biomass. Net Biome Production (NBP), i.e. change in forest carbon stock, is sum of tree carbon stock change and soil carbon stock change.

The predicted litterfall, is input to the Yasso soil module of EFISCEN, as described by Liski et al. (2005), to simulate annual soil carbon stocks and flows. The model uses the effective temperature sum in the growing season (0 °C threshold) and the drought index during the growing season (precipitation minus potential evapotranspiration during the growing season) to modify mineralization rate. Climate data of a climate scenario, including temperature change and precipitation change for the period 2000 – 2100 according to the IPCC A2 scenario evaluated with the

HADCM3 model were used to calculate country level estimates of climate variables for the soil module. The initial soil carbon stock in Yasso is set to steady state, i.e. during first simulation step there are no changes in the soil carbon stock if there is no climate change.

In this study, the projected growth rates in EFISCEN, as derived from calibrated growth functions on inventory data, are adapted in 20 year time steps as transient changes to account for the consequences of environmental change of forest growth. These transient changes are derived from the process based model SMART-SUMO-WATBAL (Wamelink et al., 2007c), as described below.

8.2.2 Assessment of impacts of environmental changes on forest growth in EFISCEN

The process based model chain SMART2-SUMO-WATBAL was applied on 166 forest plots all over Europe to assess the separate effects of an increase of (i) carbon dioxide, (ii) climate change (precipitation and temperature), (iii) nitrogen deposition change and (iv) the combined effect of all three factors on biomass accumulation in European forest (Wamelink et al. (2007c). The model chain was applied for the period 1990-2070 by comparing these four various scenarios with a reference run, consisting of the carbon dioxide concentration and nitrogen deposition of 1990 and repetitions of the data for temperature and precipitation from the period 1960-1990. Detailed description of the modelling and results can be found from Wamelink et al. (2007c).

In this study we only included the results of the combined environmental scenario as compared to the reference run. The change in CO_2 concentration is identical for all the simulated plots and is based on an extrapolation of the times series of observed CO_2 concentrations from Mauna Loa Observatory. The temperature change and precipitation change for the period 2000 – 2100 is plot specific and is derived from the IPCC A2 scenario evaluated with the HADCM3 model. The change in N deposition is also plot specific and is derived From the results of the Gothenburg protocol. More details about the scenarios are given in Wamelink et al. (2007c). In comparison to the refernce run, the temperature and CO_2 concentration are expected to rise, whereas the N deposition scenario decreases all over Europe. With respect to precipitation, the change differs per plot, in some plots there is a decreasing trend, in some plots an increasing trend.

Results of SMART2-SUMO-WATBAL, in terms of net primary production, varied depending of local climate, e.g. due to elevation, soil, tree species. Therefore, average results per region and tree species groups were used in EFISCEN. On three plots, which were removed from upscaling, the relative change was very high due to very low increment of the model under current climate. The country groups and tree species groups used are given in Table 8.2. In brackets, the numbers of plots available from the SMART2-SUMO-WATBAL model simulations are given.

Table 8.2 Number of plots available from the SMART2-SUMO-WATBAL model simulations for use in EFISCEN

Tree species	Numbers of simulated plots		
	Nordic[1]	Continental[2]	Atlantic[3]
Scots pine	24	13	4
Norway spruce	47	23	6
Other coniferous species[4]	71	38	22
Beech	24[5]	19	7
Oak	24[5]	8	11
Other deciduous species[5]	24[5]	27[6]	19[6]

[1] Nordic (Finland, Norway, Sweden, 42.7 million hectare)

[2] Continental (Austria, Bulgaria, Czech Republic, Estonia, Germany, Hungary, Latvia, Lithuania., Poland, Romania, Slovak Republic, Slovenia, Switzerland, 44.5 million hectare)

[3] Atlantic (Belgium, Denmark, France, Ireland, Luxemburg, The Netherlands, United Kingdom, 17.8 million hectare)

[4] For other coniferous species, we used the average of all coniferous species plots (Scots pine, Norway spruce and other coniferous species when available; see numbers in table).

[5] For the Nordic region, we used the average of Scots pine response since there was only 1 result for beech and oak plots in Nordic countries. These tree species are present only in the southern part of Nordic countries and have negligible importance in forestry

[6] For other deciduous species, we used the average of all beech and oak species plots for the Continental and Atlantic region.

8.2.3 Assessment of forest management in EFISCEN

Management activities in EFISCEN, i.e. thinning and final felling, are described by current practices for each kind of forest. These underlying management rules are based on forest age. In this study, final felling age limits were lowered to enable intensive management under higher increment. Lowest possible age of final felling was set 20 years lower if rotation length was more than 105 years, 10 years lower if rotation length was between 50 and 100 years and 5 years lower if rotation length was below 50 years.

Total wood demand is an important factor in the development of forest resources since average rotation length increases automatically if there is no demand for wood. In this study the basis of demand is FAOSTAT roundwood production per countries (FAOSTAT, 2007) which was available until 2005. Therefore, two rather extreme management scenarios were applied. First, current felling levels were applied at the present level as a present for the future 100 years. This level is rather low when we take into account current low utilization of increment and possible high demand in the future.

Second, an adaptive forest management was defined. This management takes into account that under climate change increment will further increase, and thus the risk for storm and insect damage as well. In order to avoid these risks, and to harvest additional stemwood for biomass for bio energy, we drastically increase the fellings. In this way (with a rather fast regeneration of the forest estate), we assume that the new tree population will be more suited to the new climate circumstances. Thus we increase fellings with 10% per 5 years and the felling was levelled off before the growing stock went below initial value.

8.3 Results

8.3.1 SMART2-SUMO-WATBAL (SSW) results

Table 8.3 presents the average growth response predicted by SMART2-SUMO-WATBAL (SSW) for various age classes of all 166 plots for the years 2010, 2030, 2050 and 2070. The responses are 10 years averages since we wanted to ignore annual variability. With increasing time, the SSW model predicts increasing growth change, but also with increasing age of the stand, the model predicts increasing growth changes. In 2050 the response is only slightly larger than in 2030 and this is due to less favourable climate change development during those years. Inversely, between 2050 and 2070, the SSW model predicts a rather sudden extra increase in growth. This effect is caused by the precipitation scenario; around 2050 the scenario contains some particular dry years giving a relative large growth reduction, whereas around 2070 relative wet years occur more often. As an average over the age classes for Europe, the growth changes with 19%, 28%, 29%, and 59% respectively in 2010, 2030, 2050, and 2070. More detailed analyses of process based modeling, including more details per tree species and region of Europe, can be found in Wamelink et al. (2007c).

Table 8.3 Average and standard deviation in growth change percentage of 166 simulated plots. by age classes in 2010, 2030, 2050 and 2070 compared to a baseline with no environmental change For more details see Wamelink et al. (2007c).

	Growth change, All, %				Standard deviation of growth change			
Age	2010	2030	2050	2070	2010	2030	2050	2070
0-19	11.9	20.7	25.7	44.5	12.7	16.9	18.3	27.3
20-39	18.8	26.0	29.1	58.3	17.4	16.6	26.8	41.4
40-59	19.9	27.9	29.4	61.1	17.7	16.9	25.8	43.4
60-79	20.5	28.9	29.9	62.1	17.9	17.3	25.9	43.9
80-99	20.9	29.6	30.1	62.6	18.0	18.0	26.2	44.0
100-160	21.3	30.5	30.4	63.1	18.1	18.4	27.0	44.5
>160	21.6	31.1	30.5	63.4	18.3	19.3	27.6	44.7

8.3.2 EFISCEN results

Average required fellings (both from thinnings and final fellings) per hectare of the 109 million ha of forest are depicted in Figure 8.1. These are scenario inputs, but also depict whether the required fellings were found in the forest (under the prescribed management regimes) and to what degree the fellings can increase under the climate change scenario. Under a no climate change scenario, the fellings can increase to from approximately 3.8 in 2000 to 5.3 $m^3.ha^{-1}.yr^{-1}$ in 2100 (or 407 million $m^3.yr^{-1}$ in total) to reach a stable growing stock volume between 170 and 180 $m^3.ha^{-1}$. In 2100 it was thus possible to cut 50% more under intensive management than current felling level. Climate change increased this possibility to 90% (from 3.8 to 7.2 $m^3.ha^{-1}.yr^{-1}$).

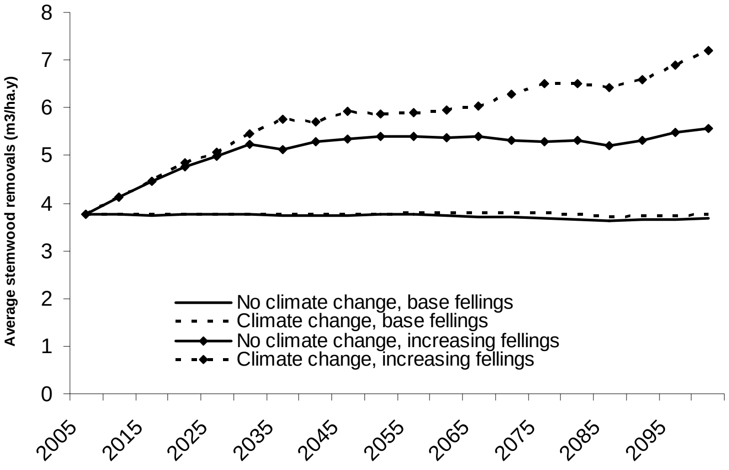

Figure 8.1 Average removals per hectare under the 4 different scenarios.

Enviromental change impacts as given in Table 8.3, result in temporal changes in Europe's average increment as depicted in Figure 8.2. Under no climate change, and base fellings, the increment declines (because of ageing) from 5.8 in 2005 to 4.8 $m^3.ha^{-1}.yr^{-1}$ in 2100.

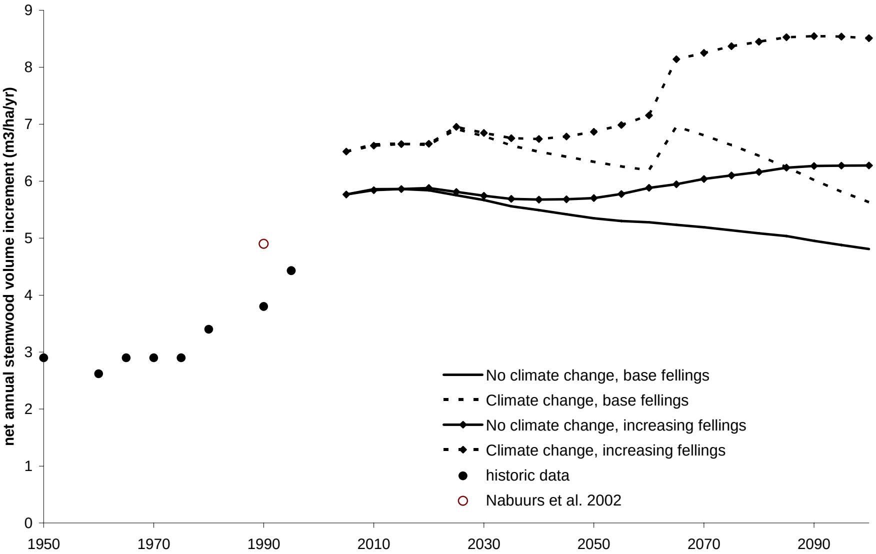

Figure 8.2 Net annual stem wood volume increment (average for 109 million ha), historically from statistics for 1950 to 1995 (UN ECE), the initial increment value of a former projection (Nabuurs et al., 2002), and projected increments (this study) until 2100 under 4 different scenarios. The increment for the start year of the current projections (2005) deviates between environmental change and no environmental change runs, because for some countries the runs start already in 1995.

Increasing fellings has a positive impact and keeps the increment at 6.3 $m^3.ha^{-1}.yr^{-1}$ in 2100. Merely environmental change, and no increase in fellings does not have such a large impact on increment. Eventually under environmental change and base fellings, the overall average increment declines to 5.6 $m^3.ha^{-1}.yr^{-1}$. The largest impact on increment has a combination of environmental change and increase in fellings that together result in an increment of 8.5 $m^3.ha^{-1}.yr^{-1}$ in 2100.

The growing stock in 2100 increased to 279 $m^3.ha^{-1}$ under felling level and no environmental change (Figure 8.3), compared to 185 $m^3.ha^{-1}$ in 2000. Under base fellings and environmental change, the rise was much sharper to 381 $m^3.ha^{-1}$ in 2100. These latter average volumes currently do occur in some parts of Switzerland and Southern Germany. However it is unrealistic to assume that these will be reached as averages for whole of Europe. But in these runs no mortality was assumed, nor any natural disturbances, allowing a gradual build up of growing stocks. Under increased fellings and environmental change, still some increase in growing stock occurs. This is caused by the way the management constraints have been set.

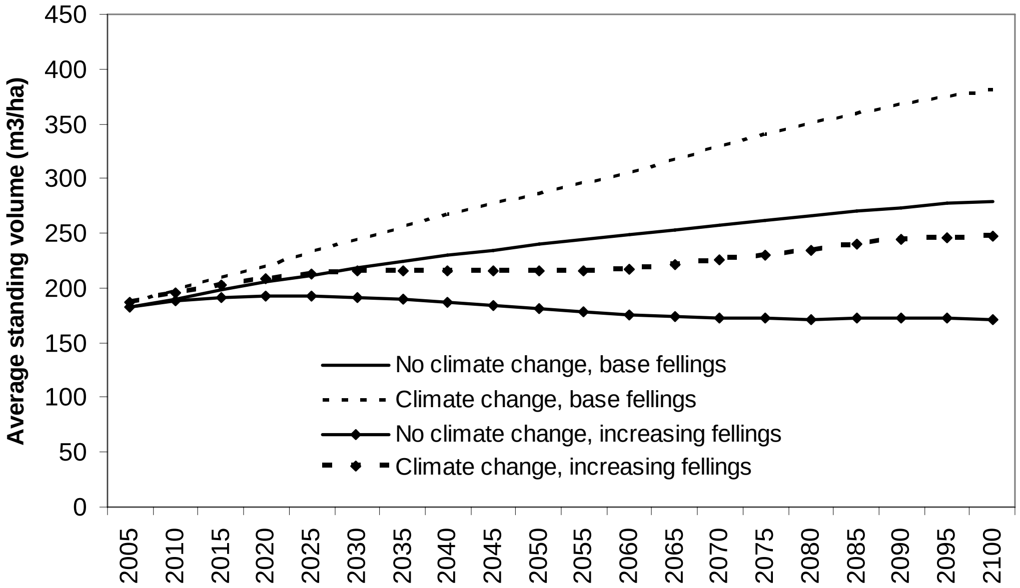

Figure 8.3 Average growing stock volume per hectare under 4 different scenarios

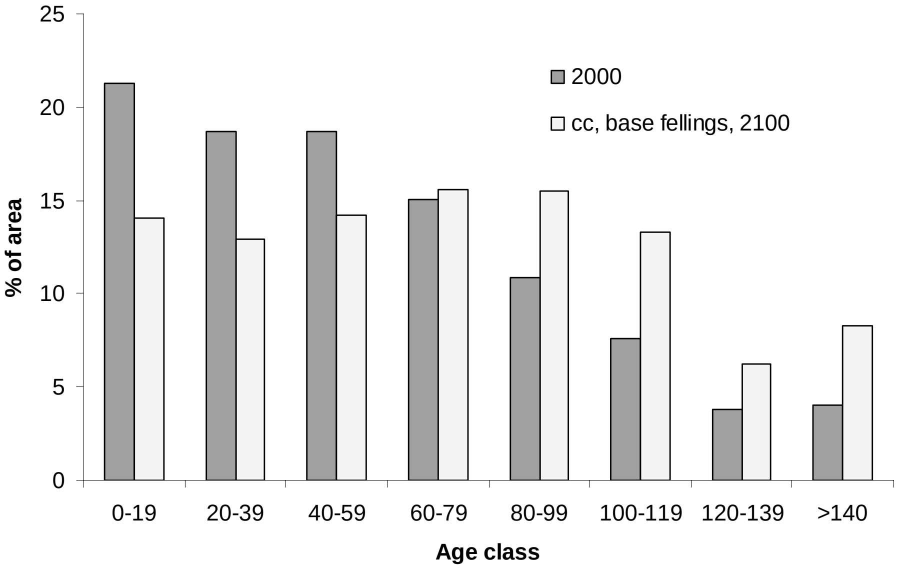

Figure 8.4 Age class distribution of 109 million ha of European forests in 2000 and in 2100 under environmental change and base fellings.

Environmental change as such would not lead to a difference in age class. However Figure 8.4 shows the scenario for 2100 with environmental change and base fellings. In this scenario the fastest ageing occurs, because the increased growing stocks (in combination with low fellings) lead to the smallest area of regeneration. The average age thus increases from 56 years in 2000 to 72 years in 2100.

8.3.3 Implications for carbon

The dynamics of carbon in whole tree biomass follows the same trends as given for stemwood volume growing stock in Figure 8.3, because we do not simulate allocation changes due to environmental change. However the model takes into account allocation changes due to ageing, specified by tree species. Consequently, small deviations compared to Figure 8.3 do occur because of scenario differences. The average carbon stock of whole tree biomass was 72 Mg.ha^{-1} carbon in 2005 and it increased to a predicted 104 Mg.ha^{-1} carbon in 2100 under no environmental change and base fellings. Environmental change enhanced the build up of carbon stocks to up to 143 Mg.ha^{-1} carbon in 2100.

The trends are different for soil carbon, and much smaller. Environmental change decreased the soil carbon stock in the beginning of the simulations due to higher decomposition rates. However, later on, the increased increment result in higher growing stocks, and thus higher litterfall rates, and this leads to higher carbon stocks in soil. Apparently the increased decomposition under environmental change is more than compensated by the increased literfall rates. More intensive management results in lower carbon stocks since part of produced biomass is removed from the forest. In the no environmental change, base fellings scenario, the average soil carbon stock increases from 94 to 107 Mg C.ha^{-1} in just 100 years time. Largest increase is found in the environmental change, base fellings scenario. Here the build up of carbon continues to 115 Mg C.ha^{-1} in 2100.

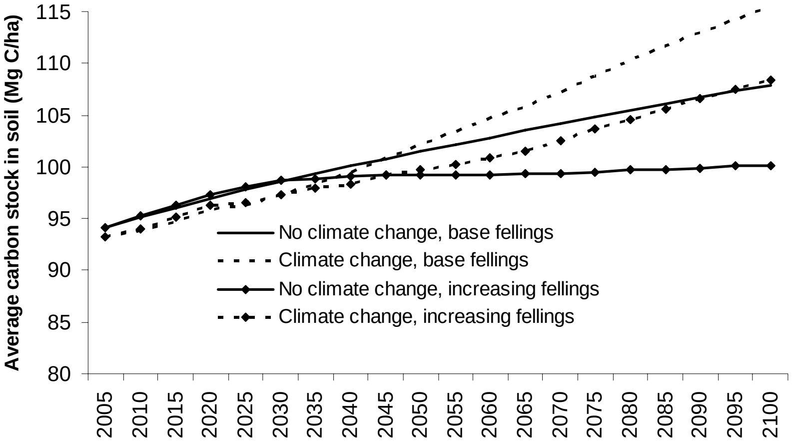

Figure 8.5 Predicted average carbon stock in the soil for four scenarios. (note the difference in y axis scale with Figure 8.3).

Net Primary Production (NPP), i.e. produced biomass, was relatively constant under current climate, about 6 Mg carbon per hectare per year. Environmental change increased NPP to 8 Mg carbon per hectare. Under intensive management NPP was always lower than current felling level since more trees produce more litter. Net Biome Production (NBP), i.e. NEE minus removals, showed clearly the importance of management level (Figure 8.6).

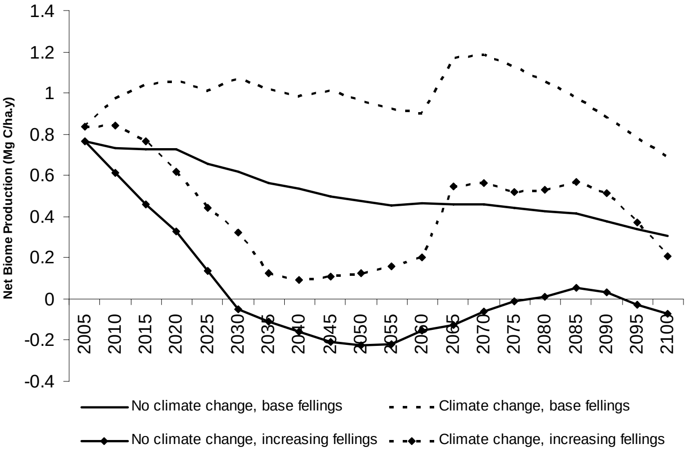

Figure 8.6 Average Net Biome Production (NBP) for 109 million ha of European forests under 4 scenarios.

In this study fire and other natural disturbances were not taken into account. Management is able to turn the sink of the forest biomass and soil compartment which is there until 2100 in the base scenario without environmental change, into a source by 2030. The increase of NBP under environmental change after 2060 is caused by the rather sudden increment change that the SSW model predicted for the 2000-2070 period. Environmental change will keep the system in a sink function also under increased fellings.

Table 8.4 summarises the carbon stock changes in trees and the carbon removals between 2010 and 2100 and the predicted carbon stock in trees in 2100 on a European wide scale for the four considered scenarios. It shows that the impact of environmental change on C stock change in trees is as significant as the impact of forest management. The impact of environmental change on C removals is however minimal, compared to forest management.

Table 8.4 Carbon stock change in trees between 2010 and 2100, removals between 2010 and 2100 and Carbon stock in trees in 2100

ALL 23 countries, 109,5 Mha	Carbon stock change in trees 2010-2100		Removals 2010-2100		Carbon stock in trees in 2100	
	Pg C	% of stock in 2010	Pg C	Difference compared to the first scenario, %	Pg C	Difference compared to the first scenario, %
No environmental change, base fellings	4.9	127	8.6		23.3	
No environmental change, increased fellings	-0.3	98	12.1	41	18.1	-22
Environmental change, base fellings	10.0	154	8.7	1	28.4	22
Environmental change, increased fellings	3.8	121	13.7	59	22.2	-5

Regionally, the impacts are quite different (Table 8.5) as the state of the forest is different; in Nordic countries productivity is low, in the Continental region the growing stock is high, and in Atlantic countries productivity is high. In 2000 the NPP of forests is low in Nordic countries, on average 3.97 Mg $C.ha^{-1}$, compared to Atlantic and Continental Europe where NPP is above 7 Mg $C.ha^{-1}$ (Table 8.5). Under environmental change and current management, the NPP of the Nordic region rises the most, to reach values close to current NPP in the Continental region. In the Continental region, environmental change is foreseen to have the smallest impact on NPP, only some 30% by 2100. Current average stock of carbon in trees in the Continental region (96.3 Mg $C.ha^{-1}$) is twice as much as in Nordic region (48.0 Mg $C.ha^{-1}$). Also for this variable, the largest changes are foreseen in the Nordic and Atlantic Region, with more than a doubling occurring. Current carbon stock in the soil reflects the amount of carbon in trees and productivity. In the Nordic countries the soil carbon stock is larger compared to growing stock than in other regions since environmental decreases the mineralization. Increased fellings only have a small impact in terms of decreasing the soil carbon stock, because they lower the growing stocks, but at the same time increase inputs to the soil due to felling residues.

Table 8.5 Tree carbon stock, soil carbon stock, removed carbon and NPP in three country groups in year 2010 and relative change between 2010 and 2100.(A = no environmental change and base fellings, B= no environmental change and increased fellings C= environmental change and base fellings D= environmental change and increased fellings)

	Scenario	Nordic, in 2010	in 2100, % of value in 2010	Atlantic in 2010	in 2100, % of value in 2010	Continental, in 2010	in 2100, % of value in 2010
Net Primary Production (NPP) Mg C.ha^{-1}.yr^{-1}	A	3.97	114	7.15	137	7.03	104
	B		95		98		100
	C		175		153		131
	D		160		115		132
Tree Carbon stock, Mg C.ha^{-1}	A	48.0	137	80.6	185	96.3	133
	B		88		87		92
	C		221		204		165
	D		149		102		121
Soil carbon stock Mg C.ha^{-1}	A	78.9	109	92.2	134	113.4	109
	B		102		109		105
	C		124		142		115
	D		117		116		113
Removed carbon from forest Mg C.ha^{-1}.yr^{-1}	A	0.68	100	0.79	100	1.03	95
	B		137		178		148
	C		100		101		99
	D		201		188		182

8.4 Discussion and conclusions

The results of this paper describe significant impacts of environmental change on mid and high latitude European forests. An average 30% higher increment is foreseen for 2100 compared to a no environmental change scenario (both under base fellings). The largest relative growth rate change is foreseen for the Nordic countries, with up to 75% growth increase. The question is now: How significant is this?

European internationally collected statistics (UN-ECE/FAO, 2000) give an increment of 2.9 m^3.ha^{-1}.yr^{-1} in 1950 and 4.4 m^3.ha^{-1}.yr^{-1} in 1995; a 52% increase in 45 years (Figure 8.2). From Figure 8.2, a trend break seems to occur between the statistics and the modelled projection. So, how significant is the projected growth change? There are large uncertainties in the statistics. The earliest assessments were based on European wide collection of data, but only four countries had a good forest inventory in place in 1950. For the other countries, the increment data were based on some permanent plots they might have in combination with expert judgement, which tended to be very conservative. Every time a country had completed its first inventory, increment appeared to be much higher than what they thought. A recent example is the second German national forest inventory that came out in 2006. It reported an increment of 12.1 m^3.ha^{-1}.yr^{-1}, while the first (compiled) inventory for 1986-1990 reported 9 m^3.ha^{-1}.yr^{-1}.

Thus the historical data do not give full insight in whether site productivity has changed. However, it is clear from several studies that site productivity has indeed increased (Spiecker et al., 1996). But at larger scales, age class distributions have changed as well, and growing stocks have changed, all contributing to forests reaching higher growth classes. Therefore we cannot relate all of the historic growth changes to real site changes. The contribution of each of these factors will probably never be understood, although recent analyses suggest a large role of nitrogen deposition, when data are corrected for age effects (Magnani et al., 2007). This result has however been criticized (see also De Vries et al., 2007a).

In historic perspective, the projected growth changes under environmental change do not seem very dramatic. In addition, we find that management (the level of fellings) has a large impact on the dynamics of forests as well. Namely by increasing fellings the general declining trend of increment over time is curbed. Thus we find that adaptive management (in this case harvesting more in case of higher increment and stocks) can influence the state of the forest and its carbon balance significantly.

European forests grow now more than utilised (UN-ECE/FAO, 2000). This means that forest owners, and industries have the flexibility to choose to what extend they prefer a (temporary) carbon sink in the forest, or a bigger source of renewable raw materials. Emissions of the simulated 23 countries were 3.35 Pg $CO_2.yr^{-1}$ in 2004 (UNFCC) or 0.91 Pg C. The carbon sink of trees under current climate and current management level between years 2005 and 2100 is on average 0.08 Pg $C.yr^{-1}$, i.e. 8.7% of emissions are sequestered into tree biomass and soil. Under environmental change and base fellings, 12% of emissions are sequestered. These are significant shares, and confirms that management does have a large impact on the net sink. This is also confirmed by Schelhaas et al. (2007a) who project that with a prolonged rotation and increased share of things, the net sink in 22 EU countries could be enhanced with 59 Tg $C.yr^{-1}$ compared to a baseline sink of 95 Tg $C.yr^{-1}$.

The results in increment changes as presented in the present study provide a stronger impact of climate change compared to Nabuurs et al. (2002) and Karjalainen et al. (2003) in which seven process based models were used on 14 sites across Europe. The same approach for upscaling was used by them as is used in the present study. They foresaw a 18% increase in increment across European forests (28 countries), compared to 30% in this study. However, one should be aware that this study includes not only climate change but also a change in CO_2 concentration and N deposition, the latter generally having a negative effect due to decreasing deposition. The reliability of the results depends on many factors:

- *Basic model and scenario assumptions:* For the SMART2-SUMO-WATBAL (SSW) model and the reliability of the environmental scenarios see Wamelink et al. (2007c). Concerning EFISCEN, several validations and sensitivity studies have been carried out (resp. Nabuurs et al., 2000; Schelhaas et al., 2007b). These conclude that EFISCEN is a reliable tool to make large scale projection of forest resources for up to 60 years. It is based on extensive collections of empirical data for European forests. Simulations are sensitive to three parameters, but for which extensive experience has been build up.
- *Coverage of forest:* we now only cover the mid and high latitude forest. The Mediterranean forest (the region where climate change is foreseen to have the most detrimental effects) was left out. This was because of the very small

number of ICP plots available for SSW runs, and the few sites available were located in mountainous regions and therefore did not represent the forests in the Mediterranean region very well, although in principle drought effects were represented very well for those regions where it occurred (southern France).

- *Knowledge on impacts of climate change:* This is related to the previous point. Let alone the uncertainty over the actual degree of climate change, and the change in extremes, our understanding of impacts of climate change on forest ecosystems is very limited. The present study only scales up some plant physiological processes that were modelled with a process based model. Understanding of these processes is already limited in terms of longer term impacts and saturation effects. Then in addition, the change in stand dynamics, competition, and mortality changes are not known at all, and not included here. These very site specific responses are difficult to be coped with at such large scales. In more detail one can think of overlays between forest inventory plot data with other GIS material, providing more detailed insights to forest managers (Loustau et al., 2007).
- *Risks of of high growing stocks:* High growing stocks, as developing in the present study, to averages of 381 $m^3.ha^{-1}.yr^{-1}$ in 2100 are unprecedented for Europe. Only in some regions, like Southern Germany, parts of Czech Republic and Austria these averages are known today. We also know that these regions are susceptible to storm damages and follow up insect attacks. In the present study these risks were not taken into account, but they can become substantial in the future. Management could adapt by bringing down the average growing stocks, through higher harvesting rates. Higher harvesting rates not only bring down the storm damage chance, but also lead to younger forest. Young forests are know to adapt better to changing climate and extreme weather events such as drought. These shorter rotations (providing biomass for bio energy at the same time) also enable tree species composition to adapt to more suitable tree species for the climatic envelope existing at that time.

Despite the many uncertainties the present study gives a very fair impression of what the impacts of climate change, in combination with a change in CO_2 concentration and N deposition, may be. With a robust empirical forest resource model, and the latest biomass expansion factors, we provide insight in the carbon sink behaviour of the forest and soil ecosystem. We have assumed that the soil is in steady state in the beginning which overestimates initial stocks and therefore may underestimate the carbon sink of the soil. Especially allocations and turnover rates of fine roots and leaves determine the soil balance to a large extent.

European forests are intensively managed, and it is thus likely that management will adapt, favouring the tree species that show positive responses to the environmental changes through alternative species choice, improved use of natural regeneration, altered mixtures of species, changed rotation length, and/or higher felling levels. These adaptations may be easier in European forests than in forest regions as e.g. Siberia that are hardly managed up until today.

Acknowledgements
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Evaluation

9 The impact of nitrogen deposition on carbon sequestration by terrestrial ecosystems

Abstract
In this study, we present estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in forests, heathlands and moorlands, based on: (i) empirical relationships between measured NEP and nitrogen deposition in the field, accounting for other influencing factors, (ii) results of ^{15}N experimental data on the fate of N, combined with C/N ratios in forest ecosystem compartments, (iii) results of long-term (15-30 year) low dose N fertilizer experiments on the C pool in biomass and soil and (iv) model simulations predicting carbon response to environmental change including N deposition. The results of the various studies are all well in agreement and show that the range in above ground accumulation of carbon in forests is generally within 15-30 kg C/kg N. For heathlands and moorlands, values are lower. A range of 5-15 kg C/kg N has been observed based on low dose N fertilizer experiments. The uncertainty in carbon sequestration per kg nitrogen addition in soils is larger than for above ground biomass and varies on average between 5-35 kg C/kg N. All data together indicate a total carbon sequestration that on average is below 50 kg C per kg N deposition.

9.1 Introduction

The productivity of many temperate ecosystems is nitrogen limited. Adding N via deposition thus has the potential to increase growth, and therefore to sequester CO2 from the atmosphere. The increase in N deposition on forests may increase C sequestration by increased growth and increased accumulation of soil organic matter through increased litter production and/or increased recalcitrance of N-enriched litter, leading to reduced long-term decomposition rates of organic matter. A range of studies have shown positive forest growth and C accumulation responses under low to moderate N additions (Vitousek & Howarth, 1991; Aber et al., 1995; Bergh et al., 1999; Franklin et al., 2003). Although fertilisation by atmospheric N deposition is thus thought to have increased C storage in biomass and soils of terrestrial ecosystems (specifically of forests), estimates of the magnitude of this sink vary widely (Peterson & Melillo, 1985; Schindler & Bayley, 1993; Townsend et al., 1996; Holland et al., 1997).

For example, some studies (e.g. Holland et al., 1997) have suggested very large (up to 2.0 Pg.yr-1) CO2 sequestration in forests due to N deposition. These studies assumed that most (~80%) of the deposited N would be stored in woody biomass with a high C/N ratio (250-500). This implies a carbon response to N deposition of approximately 200-400 kg C/kg N. By combining various tracer experiments, however, Nadelhoffer et al. (1999b) showed, however, that only a very small part of the added N (~5%) is stored in trees whereas most of the deposited N (~70%) is actually stored in soils with a much lower C/N ratio (10-30). Their data indicate a sequestration near 50 kg C/kg N. Currie et al. (2004), even suggest a net sequestration of approximately 5 kg C.ha^{-1}.yr^{-1} per kg N deposition only, based on model simulations for two forest types (red pine and mixed hardwoods) at Harvard Forest, USA, that best fitted decadal field data for pools and fluxes of C, N and ^{15}N. Inversely, in a recent letter to Nature, Magnani et al. (2007), reported a very strong correlation between mean lifetime net ecosystem production (NEP) and N deposition, with an extremely high response, being equal to approximately 725 kg C/ha/yr per kg N in wet deposition. Considering the ratio to wet and dry deposition mentioned by the authors, this would imply a net sequestration near 475 kg C per kg N of total deposition.

In general, there is thus no dispute about the beneficial effects of N fertilization on the terrestrial C sink, but the order of magnitude is clear an issue of debate. Literature data vary by two orders of magnitude (5-500 kg C/kg N). This largely affects the question whether N deposition affects the global warming potential in a positive or negative way. For example, extra nitrogen deposition increases nitrous oxide emissions, which offsets the carbon effect. If the lowest value would be representative, it would imply that the net impact of N deposition on the sequestration of carbon is on average in the same order of magnitude as the N_2O estimate in response to N deposition, in terms of global warming potential (GWP). Inversely, if the highest value would be representative, the effect of N_2O emission would be very small compared to the extra C sequestration induced by N deposition and the CO_2 sequestration by forests could be about 1/3-1/2 of the estimated 7.1 Pg yr^{-1} that is annually released by man, as earlier estimated by Holland et al. (1997).

The net impact of N deposition on the sequestration of carbon is not only a mere scientific issue but also one that may have political consequences by having an impact on the next generation of international control protocols which must address the negative effects of nitrogen. If forest carbon storage does respond very strongly to nitrogen deposition, one may consider less N emission reduction by counterbalancing the positive effects, in view of greenhouse gas emissions and climate change, to the negative effects, such as eutrophication and acidification affecting biodiversity in terrestrial and aquatic ecosystems and the effects on air and water quality (Galloway et al., 2003). Proper information on the carbon response to N deposition is thus an important point to evaluate the trade offs induced by excess nitrogen and the need for reducing N emissions and their effects induced by transboundary air pollution.

In this overview study, we present and compare estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in forests, heathlands and moorlands, based on: (i) empirical relationships between measured NEP and nitrogen deposition in the field, accounting for other influencing factors, (ii) results of ^{15}N experimental data on the fate of N, combined with C/N ratios in forest ecosystem compartments, (iii) results of long-term (15-30 year) low dose N fertilizer experiments on the C pool in biomass and soil and (iv) model simulations predicting carbon response to environmental change including N deposition. The results are evaluated in view of the above mentioned dispute on the beneficial role of N deposition on the terrestrial C sink.

9.2 Nitrogen stimulated carbon sequestration in forested ecosystems

9.2.1 Empirical relationships

Single factor analysis at five chronosequences

In their paper on "The human footprint in the carbon cycle of temperate and boreal forests" Magnani et al. (2007) demonstrate a strong positive relation between mean lifetime C sequestration (in terms of net ecosystem production; NEP) for five representative forest chronosequences and the wet deposition of nitrogen, which is based on interpolated measurements for the period 1978-1994. The slope of the response is approximately 725 kg C/ha/yr per kg N in wet deposition in the range between 4.9-9.8 kg N/ha/yr. According tot the authors, the maximum measured annual N wet deposition level of 9.8 kg N/ha/yr is equivalent to a total deposition of 15 kg N/ha/yr, implying an assumed total to wet deposition ratio near 1.5. Dividing the mentioned value of 725 with this ratio leads to a value near 475. This is slightly higher than an announced 400 kg of carbon sequestration per kg total N deposition in a press release, which states: "In an analysis that extends across the boreal and temperate forests of Eurasia and North America, the scientists find that for every kilogram of nitrogen raining down onto forests, some additional 400 kg of carbon is absorbed by the forest from the atmosphere."

As demonstrated by Sutton et al. (2007), the assumed total to wet to N deposition ratio is however not 1.5 but can vary from 2-7, depending on the area in Europe and is generally increasing with N deposition (Simpson et al., 2006). Sutton et al. (2007) plotted the measured NEP data of Magnani et al. (2007) against both modelled wet N deposition and total N deposition data, using the EMEP model, for these plots. The results show first that the modelled and interpolated wet N deposition data are quite comparable and secondly that the regression line with total N deposition is 177 kg C sequestration per kg total N deposition (R^2=0.88), being more than twice as low as the announced 400 kg C/kg N. Applying $N_{dep(tot)}$ for 1990 (being more consistent with the period used by Magnani et al. (2007) gave $\Delta C:\Delta N$=126:1 (R^2=0.87). When using dry deposition estimates for 2001-2005 according to the NEGTAP methodology (UK National Expert Group on Transboundary Air Pollution, 2001, Defra, London) $\Delta C:\Delta N$ reduced even further to 91:1. Using the re-interpreted results of Magnani et al. (2007) by Sutton et al. (2007) still imply a carbon response to N deposition in the range between 91-177 kg C/kg N.

Multi-factor analysis at hundreds of forest plots

Solberg et al. (2007) and Laubhann et al. (2007) investigated the influence of both site and environmental factors on forest growth, which in turn is related to carbon sequestration. They both carried out a multi-factor analysis of measured forest growth data at nearly 400 Intensively monitored forest plots in Europe, including Norway spruce, Scots pine, common beech, European oak and sessile oak.

In the study by Solberg et al. (2007), the influence of nitrogen and acid deposition was considered at stand level by using the deposition during the growth period (1993-2000), while the impacts of temperature, precipitation and drought were addressed by taking the deviation of these climatic parameters in the growth period (1993-2000) from the 30-year mean. They simultaneously accounted for site factors influencing measured tree growth, including site productivity, stand age and stand density, all at stand level. Relative tree growth, calculated as actual growth in % of expected growth, was then correlated to the deposition and climatic factors. The statistical models included both simple regressions, with a multivariate analysis-of-covariance, and a multivariate analysis where actual growth was regressed against both the site and stand factors, and the growth affecting factors simultaneously. The analysis of co-variance model was done in a backward stepwise way, where the model was reduced step-by-step by removing non-significant effects. The tests applied here were sequential (Type I) F-tests.

Results of multivariate analyses at stand level are shown in Table 9.1. The regression results indicate the relative change in stem volume growth per unit change in influencing factor. For example, a value of 0.010 for N deposition implies an increase of stem growth of 0.01 or 1.0% times its growth per kg N deposition The results indicated roughly a 1 % increase in site productivity in response to a fertilizing effect of N deposition of 1 kg of N/ha/yr for Scots pine and 2% for Norway spruce (actually, the latter value was not significant in a multivariate analysis, but it resulted as significant from a simple regression: Solberg et al. (2007). Similar results were obtained for a study with nationwide data-sets for Norway (Solberg et al., 2004), although higher growth responses to N deposition (up to 4%) have also been observed in selected Swiss observation plots (Braun et al., 1999). For beech and oak, the response was not significant.

These responses for pine and spruce were recalculated in terms of C sequestration, by taking the product of the measured mean annual volume increment times the mean wood density times the estimated growth increase (the modelled regression slope of the relative growth residuals against N deposition, being around 1% for pine and 2% for spruce), assuming a C content of 50%. The mean of the models gave around 38-76 kg of additionally produced wood for pine and spruce, respectively, converting to around 19 -38 kg C/ha/yr/kg N. The approach at stand level indicated a stronger response in N sensitive sites (high soil C/N ratio), having roughly a 1.3-2.2 % increase in growth for pine and spruce, respectively, in response to a fertilizing effect of 1 kg of N/ha/yr.

Table 9.1 Multivariate regression results at stand level indicating the relative change in stem volume growth per unit change in influencing factor. Note: - implies that the effect was insignificant (p>0.05).

Tree species	*Site prod*[1]	*Age*[2]	*SDI*[3]	*N dep*[4]	*Drought*[5]	*Temp change*[6]
All plots						
Norway spruce	0.054	-0.005	-	0.020 [7]	-	0.524
Scots pine	-	-0.017	-	**0.010**	-0.0032	-
Sensitive plots						
Norway spruce	0.039	-0.004	-	**0.022**	-	0.32
Scots pine	-	-0.017	0.001	**0.013**	-0.002	-

[1] *Site prod* is a variable for site productivity (m^3/ha/year) derived from selected European site index curves, with input variables being age and top height, [2] *Age* is stand age (yr), [3] *SDI* = stand density index (indexed number of trees/ha), [4] *Ndep* is total N deposition (kg/ha/yr), [5] *Drought* is a variable describing drought given as a relative value (in %) to the normal (30 years mean) drought stress at each site, [6] *Temp change* is the temperature difference during the growing period compared with the 30-year average temperature (^{0}C), [7] results from a simple linear regression gave a value of 0.020, but in the multivariate analysis, the coefficient was not significant at p <0.05.

Laubhann et al. (2007) applied a multi-factor analysis at tree level, with measured basal-area-increment of each individual tree as responding factor and tree size (tree diameter at breast height, dbh), tree competition (basal area of larger trees, BAL, and stand density index, SDI), site factors (soil C/N ratio, 30-year average temperature) and environmental factors (temperature change compared to long-term average, nitrogen and sulphur deposition) as influencing parameters. The multivariate regression analysis at tree level was carried out by using tree size and tree competition variables on tree level and site factors and environmental factors on plot level, including plot as a random effect and applying the restricted maximum likelihood (REML) method for parameter estimation. The procedure accounted for correlations, such as those between temperature and N deposition.

Results of multivariate analyses at individual tree level, shown in Table 9.2, indicated a 1.2-1.5 % increase in basal area increment (coefficients varying between 0.012 and 0.015 relative increase), depending on tree species in response to a fertilizing effect of N deposition of 1 kg of N/ha/yr. In this case, the response was significant for all included tree species (for beech it was nearly significant). Relating an increase in basal area increment to an increase in carbon fixation in stem wood is not trivial.

Laubhann et al. (2007) first plotted volume increment against basal area increment, limited to of those trees where both dbh and height measurements were available, to confirm that volume increment was linearly related to basal area increment. Referring to a total carbon uptake for European forests of 1729 kg carbon per hectare and year by De Vries et al. (2006b), they then estimated the response in terms of C sequestration between 20.7 and 25.8 kg carbon per hectare per kilogram nitrogen deposition, depending on tree species composition. In summary, the results of both studies indicate a response of trees between 20-38 kg C per kg N on the basis of this wide European growth dataset in the period 1993-2000.

Table 9.2 Multivariate regression results at tree level indicating the relative change in stem volume growth per unit change in influencing factor. Note: - implies that the effect was insignificant (p>0.05).

Tree species	*BAL1*	*SDI*	*C/Nsoil2*	*N dep*	*Temp3*	*Temp change6*
Norway spruce	-0.39	-0.00056	-0.023	**0.013**	-	-
Scots pine	-0.29	-0.00066	-	**0.015**	0.053	-
Common beech	-0.16	-	-	**0.012** ^{4}	-	0.064
Oak	-0.38	-0.00062	-	**0.013**	0.080	-

^{1}*BAL* is basal area of larger trees (m^2 ha^{-1}), ^{2} *C/N soil* is the C/N ratio of the mineral topsoil (0-30cm) and ^{3}*Temp* is 30-year average temperature (^{0}C). For common beech, the effect was almost significant at p = 0.05 (p=0.77).

9.2.2 Results of ^{15}N experimental data on the fate of N

The potential C fixation response to elevated N deposition is restricted by the C-N stoichiometry of the forest ecosystem compartments. Net ecosystem production (NEP) may be defined as the net rate of C accumulation in ecosystems was (Woodwell & Whittaker, 1968), which can either take place in the vegetation or the soil. Since C and N accumulate together in organic matter, the longer term average accumulation of C per unit N in a compartment can not exceed the C-N stoichiometry as described in Table 9.3. Because of the different C/N ratios, a lot more N is required to lock up C in soils, but also in foliage and roots, than in woody biomass. This aspect is the rationale behind using information on the fate of N in the soil to assess the related carbon sequestration.

Table 9.3 Data on C/N ratio in forest ecosystem compartments

C accumulation -NEP	Compartment	C/N ratio typical conifer §	Probable max C/N including also broadleaf species
NEP vegetation	Wood and bark	325	500
	Canopy	65	100
	Roots incl. stump	65	100
	Total vegetation	150	250
NEP soil	Organic layer	33	45
	Mineral soil	29	35
	Total soil	30	40

§ C/N ratios from a 80 yr Norway spruce plantation at Klosterhede, Denmark (Gundersen, 1998).

The above mentioned C/N ratios indicate the implausibility of the original results by Magnani et al. (2007). A nitrogen use efficiency (NUE), defined as NEP in response to N deposition, of 470 kg C/kg N would imply that all deposited nitrogen is ending up in stem wood. This is unreasonable since systems that are N-limited invest primarily in roots, not in wood. (Brouwer, 1983; Cannell & Dewar, 1994). The impossibility of near total N uptake by stem wood follows also from the expected N leaching rates for these sites. Below a total N deposition of 10 kg N/ha/yr, N leaching is not expected as illustrated by N budgets for hundreds of forest sites across Europe and North America (MacDonald et al., 2002; Gundersen et al., 2006b; De Vries et al., 2007b). However, in the range between 15-25 kg N/ha/yr, which is the likely range for total N deposition in most of the plots, the N leaching rate varies generally between 10-50 % of the N input (De Vries et al., 2007b).

Nadelhoffer et al. (1999b) presented results of the short-term fate (1-3 yr) of ^{15}N labelled tracer experiments in nine temperate forests, indicating average N retention fractions in stem wood of 0.05 only. Assuming an average C/N ratio in stem wood of 500, which stays constant with N deposition, these authors estimated a tree carbon response to N deposition (NUE) of 25 kg C/kg N. The largest part of the added N (70%) accumulated in the soil (Nadelhoffer et al., 1999b). Assuming an average soil C/N ratio of 30, they estimated a below ground accumulation of 21 kg C/kg N.

According to various authors (Jenkinson et al., 1999; Sievering, 1999), the above-ground carbon sequestration is likely to be underestimated by Nadelhoffer et al. (1999b), since the authors neglected the effect of direct foliar uptake. However, this effect is likely to be small, since above ground foliar N uptake is generally less than 5 kg N/ha/yr (Sievering et al., 2000), whereas below ground uptake is comparable to the N flux that is reaching the soil by litter fall, being mostly more than 50 kg N/ha/yr (in an equilibrium situation, litter fall, net mineralization and below ground N uptake are equal). De Vries et al. (2006b) assumed that the N retention fractions in stem wood could increase up to 0.1, depending upon N deposition, and even then, they found an NUE of 33 kg C/kg N.

9.2.3 Experimental N fertilization results

In an editorial comment, Högberg (2007) already cautions that the response presented by Magnani et al. (2007) is generally expected to be an order of magnitude smaller in view of long-term (15-30 year) nitrogen-fertilizer trials. Experimental N fertilization results in Sweden and Finland have indeed shown growth increases of nitrogen-limited forest. However, on average these forest sequestered 25 kg carbon in the trees per kilogram of nitrogen added to the ecosystem at rates of nitrogen addition comparable to (high) N deposition levels (below 50 kg nitrogen per hectare per year) (Högberg et al., 2006; Hyvönen et al., 2007b). In these experiments the additional carbon sequestration in the soil was approximately three times as low in the soil (Hyvönen et al., 2007b).

Experimental N fertilization results in Sweden and Finland (Högberg et al., 2006; Hyvönen et al., 2007b) showed an average response near 25 kg C/kg N depending on the site. Hyvönen et al. (2007b) investigated the impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe (Sweden and Finland). They quantified the effects of fertiliser N on C stocks in trees (stems, stumps, branches, needles, and coarse roots) and soils (organic layer +0–10 cm mineral soil) by analysing data from 15 long-term (14– 30 years) experiments in *Picea abies* and *Pinus sylvestris* stands in Sweden and Finland. Low application rates (30–50 kg N ha^{-1} yr^{-1}) were always more efficient per unit of N than high application rates (50–200 kg N ha^{-1} yr^{-1}). Addition of a cumulative amount of N of 600– 1800 kg N ha^{-1} resulted in a mean increase in 25 kg C/kg N in tree and 11 kg C/kg N in soil, respectively. The “N-use efficiency” for C sequestration in trees strongly depended on soil N status and increased from close to zero at C/N 25 in the humus layer up to

40 kg C/kg N at C/N 35 and decreased again to about 20 kg C/kg N at C/N 50 when N only was added. In contrast, addition of NPK resulted in higher N-use efficiencies, also at N rich (C/N 25) sites, reflecting a limitation of P and K for tree growth at these sites. N-use efficiency for soil organic carbon (SOC) sequestration was, on average, 3–4 times lower than for tree C sequestration.

Högberg et al. (2006) reported effects of a long-term (30 years) N fertilization experiment, with annual N loading, on tree growth and soil chemistry in an unpolluted boreal forest. Ammonium nitrate was added to replicated 0.09 ha plots at two doses, of 34 and 68 kg N ha^{-1} yr^{-1}, respectively. A third treatment of 108 kg N ha^{-1} yr^{-1} was terminated after 20 years, allowing assessment of recovery during 10 years. Tree growth initially responded positively to all N treatments, but the longer term response was highly rate dependent with no gain for the highest treatment and a gain of 100 m^3 ha^{-1} stem wood in excess of the control for the lowest treatment. Assuming a tree wood density of 500 kg m^{-3} and a C content of 50%, this implies a net C gain of 25.000 kg C at an accumulated N input of 1020 kg (30 years x 34 kg N ha^{-1} yr^{-1}) implying an "N-use efficiency" =of 25 kg C/kg N. This result seems most appropriate in view of the level of N deposition Adding higher doses of N up to 108 kg N ha^{-1} yr^{-1} do not mimic the long-term effects of N deposition at lower rates.

9.2.4 Model simulations

Simulations with process based models also indicate comparable results. For example, Rehfuess et al. (1999) presented simulation results of five process-based models on two forest sites showing a variation 15 - 25 kg C/kg N depending on the model used. Levy et al. (2004) presented a Monte Carlo approach to uncertainty and sensitivity analysis of three ecosystem models, Century, BGC and Hybrid. These models were applied to a coniferous forest ecosystem in Sweden. The best estimate of the change in total carbon content of the ecosystem with the cumulative change in nitrogen deposition over 100 years, was 20.1 kg C/kg N using with a standard deviation of 13.8 kg C/kg N. Variability in parameters accounted for 92% of the total uncertainty in this ratio. Only 8% was attributable to differences between models even though the models differed greatly in structure and parameterization. The most sensitive parameters were those, which controlled the allocation of assimilate between leaves, roots and stem.

In an analysis with a complex forest growth model (EFM), parameterized for Norway spruce and Scots pine, and tested against measurements from 22 forest locations across Europe, Milne and van Oijen (2005) showed that the main driver of increased forest growth in the 20th century has been increased nitrogen deposition, rather than increased CO_2 concentration or climate change. The EFM model was also used to predict the effects of future environmental change, and suggested that climate change and CO_2 concentration may become the dominant environmental drivers for forest carbon exchange. The impact of N-deposition was studied by repeating simulations with different values of N-deposition, which gave on average a change in NEP of 41 kg C per kg N deposition [Numbers derived from Milne & van Oijen (2005)].

More recently, four different models including EFM, EFIMOD, FinnFor and Q, were used to examine to what extent changes from 1920 to 2080 in nitrogen deposition, atmospheric CO_2 concentration and six different weather variables have affected and will affect forest growth of pine and spruce forests across Europe between (Van Oijen et al., 2007). As with the EFM model analysis by Milne and van Oijen (2005), all models identified increasing nitrogen deposition as the major cause of observed changes in European forest growth during the twentieth century, while future changes in forest growth are more likely to be caused by increasing atmospheric CO2 concentration and, especially in northern latitudes, by increasing temperature (Van Oijen et al., 2007). Using all four models together, the nitrogen use efficiency, defined as NPP divided by total N-uptake, was 131 kgC/kgN with a standard deviation of 29 kgC/kgN. Unfortunately, the paper does not allow to calculate nitrogen use efficiency in terms of NEP divided by N deposition.

Wamelink et al. (2007b) evaluated the impact of N deposition on forest growth by applying the succession model SUMO to Dutch forests, using a spatial resolution of 250m*250m grid cells (109374 and 38707 cells for coniferous and deciduous forests, respectively). They simulated an increase in average net carbon sequestration in living biomass, litter and dead wood from 0 to 1.1 ton.ha^{-1}.yr^{-1} for coniferous forest and from 0.4- 2.2 ton.ha^{-1}yr^{-1} for deciduous forest between the lowest (5 kg.ha^{-1}.yr^{-1}) and the highest nitrogen deposition level (70 kg.ha^{-1}yr^{-1}). The average simulated increase was 20-30 kg carbon per kg nitrogen deposition.

In a recent study, Wamelink et al. (2007c) used the SUMO model, combined with the soil model SMART2 and the hydrological model WATBAL to predict the effects of a change in CO_2 concentration, climatic parameters (temperature and precipitation) and nitrogen deposition on carbon sequestration in 166 intensively monitored forest plots in Europe. The predicted effects of a change in the investigated environmental variables on soil carbon sequestration was generally lower than on carbon sequestration by the trees (especially the response to changes in climate and CO_2) but the magnitude was similar. In the study, future nitrogen deposition was assumed to decrease, causing a decrease in carbon accumulation in both trees and soil all over Europe compared to a reference run in which N deposition was assumed constant. The change in carbon sequestration was largest in the Southern countries is largest and smallest Nordic countries, in accordance with the change in N deposition. However, when expressed per kg N change the effect was largest in the Nordic countries, as shown in Table 9.4.

Table 9.4 Carbon sequestration of European forest in 2070 compared to a reference run for the N-deposition per latitude class (after Wamelink et al., 2007c).

Latitude	ΔCseq (kg C.ha^{-1}.yr^{-1})			ΔCseq/ΔN (kg C.kg N^{-1})		
	tree	soil	total	tree	soil	total
40-50	-32	-35	-67	3.6	5.0	8.6
50-60	-25	-31	-56	3.1	4.2	7.3
60-70	-13	-13	-26	12	11	24

On average, the ratio in C sequestration per kg N deposition was comparable for trees and soil and decreased from an average value near 25 kg C/kg N in the Northern counties to a value near 8 kg C/kg N in Central and Southern Europe. These low results are in line with model simulation by Currie et al. (2004), who found a carbon sequestration of 5 kg C/kg N. In these areas, values ranged mostly between 1-20 kg C per kg N for both above and below ground biomass with some values going up to 30 kg C per kg N. The comparatively low C response to N deposition calculated by Wamelink et al. (2007c), also compared to earlier results by Wamelink et al. (2007b), indicate that a decrease in nitrogen deposition will not result in a similar decrease in carbon sequestration as the increase in carbon sequestration by increasing nitrogen deposition. Apparently, the build up N-pool is not decreasing as rapidly as it was built up due to the nitrogen deposition, implying a slow decrease in nitrogen availability for the vegetation and thus a limited effect on NPP and carbon sequestration. Despite the variation, the various model results are generally quite consistent and most of them show an average variation between 15 - 40 kg C/kg N depending on the model used and the forest compartment considered (only trees or trees and soil), with some exceptions, being as low as 5 kg C/kg N.

9.3 Nitrogen stimulated carbon sequestration in non-forested ecosystems

Studies of unforested systems show a range of responses to N additions, for example enhanced C sequestration in an Arctic wet sedge system (Johnson et al., 2000); no overall change in C storage in an alpine meadow system (Neff et al., 2002) and decreased C sequestration in European peat bogs associated with the out competing of Sphagnum by vascular plants and Polytrichum moss (Berendse et al., 2001). Available recent studies, based on both experimental data and modelling for heathland site in the UK show similar results for below ground soil C accumulation in response to N input as obtained by Nadelhoffer et al. (1999b) and De Vries et al. (2006b) for forests, as illustrated in Table 9.5. The above ground accumulation is, as expected, however less.

Table 9.5 Estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in heathlands at sites in the UK.

Heathland site	Carbon sequestration (kg C/kg N)		Approach	Author
	Above ground	Below ground		
Ruabon	9	20	Observed at high N addition	Evans et al. (2006)
(Moorland)	5	23	Observed at intermediate N addition	
	15	34	Observed at low N addition	
	-	28	Simulated	Evans et al. (2006)
Budworth (Sandy soil)	-	21	Simulated	Evans et al. (2006)
Thursley	-	32	Simulated	Evans (pers comm) based on Power et al. (2006)

Evidence of carbon accumulation in response to N addition has been presented by Evans et al. (2006) for two heathland N manipulation sites. The first site, Ruabon, is an upland (470 m) heath in North Wales dominated by heather (*Calluna vulgaris*). The manipulation experiment, established in 1989, includes a control treatment plus three N addition treatments of 40, 80 and 120 kg $N.ha^{-1}.yr^{-1}$, added monthly as finely sprinkled NH_4NO_3 solution. Research at the site included amongst others the N dynamics of the system (Pilkington et al., 2005a; 2005b).

Measurements of soil C pools allowed to calculate changes in the C pools at given N inputs during the 11 year experiment, thus allowing to calculate the C/N sequestration ratio, as presented in Table 9.6. Similarly the ratio between measured increases in vegetation C relative to control plots, and net N inputs under each treatment could be derived as presented earlier in Table 9.5. The system has shown remarkably clear responses to N addition, including increased biomass accumulation rates, and increased N storage in both vegetation and soil.

Table 9.6 Estimated soil carbon sequestration per kg nitrogen addition and soil C/N ratios at the Ruabon heathland N manipulation site (after Evans et al., 2006).

N input in 11 year	Soil C pool	Change in soil C pool compared to ambient	dC/dN	C/Nsoil
kg/ha	kg/ha	kg/ha	kg C/kg N	kg C/kg N
0	105360	-	-	33.4
440	120360	15000	34.1	31.9
880	125640	20280	23.0	31.2
1320	131880	26520	20.1	30.7

The second site, Budworth, is a lowland heath located in Northwest England dominated by heather (*Calluna vulgaris*, with small amounts of *Deschampsia flexuosa*) on humo-ferric podzol soils. Treatments at the Budworth began in 1996, with an experimental design similar to that at Ruabon, and NH_4NO_3 additions of 20, 60 and 120 kg $N.ha^{-1}.yr^{-1}$. At Budworth, there were no measurements of soil C pools, allowing to calculate a C/N sequestration ratio. Instead Evans et al. (2006) applied the model MAGIC at the Budworth and this model best reproduced observed C/N changes at Ruabon at a calibrated value of C/N sequestration of 21 kg C/kg N. Similarly Evans et al. (2006) also applied MAGIC at the Ruabon site, which best reproduced observed treatment C pool and C/N changes at a C/N sequestration near 28 kg C/kg N (see Table 9.5). Finally, data for two levels of N addition in a lowland heathland in southern England (Thursley Common), as presented in Power et al. (2006) were used by the MAGIC model to estimate a C/N sequestration of 32 kg C/kg N (see Table 9.5; Evans, pers. comm.).

Compared to forests, the above ground sequestration is much less varying between 5-15 kg C/kg N. Furthermore, unlike managed forests, where tree removal causes a continuous C sink, in non forest ecosystems the net C sequestration is ultimately negligible with the exception of from managed ecosystems, such as mown grasslands or heath lands with sod cutting.

9.4 Discussion and conclusions

A summary of the derived estimates is shown in Table 9.7. In general, all the figures are all well in agreement and show that the range in above ground accumulation of carbon in forests is within 15-40 kg C/kg N. For heathlands and moorlands, values are lower. A range of 5-15 kg C/kg N has been observed based on low dose N fertilizer experiments. The uncertainty in carbon sequestration per kg nitrogen addition in soils is larger than for above ground biomass although the results are also quite consistent and varies on average between 10-35 kg C/kg N for both forests and heathlands, being in the same order of magnitude as above round accumulation. These figures indicate a total carbon sequestration that is generally less than 50 kg C per kg N deposition.

The only response that is clearly higher is the result by Magnani et al. (2007) on NEP versus wet N deposition, re-interpreted by Sutton et al. (2007), such that it includes a proper total N deposition estimate. Even though accounting for the impact of dry deposition largely reduces the impact of N deposition on C sequestration, this result is still likely to be too high, owing to the fact that other factors that co varied with wet N deposition may have contributed to the increasing NEP. The impact of N deposition is based on a single relationship with NEP, only partly accounting for other factors that have an impact on growth, such as site fertility, tree species, stand age, tree density, moisture availability and temperature. Magnani et al. (2007) only filtered out the effects of age by taking the average of C fluxes over the entire rotation, removed a dry site and investigated the separate effect of temperature. However, they did not investigate the combined effects of N deposition and temperature to account for possible correlations, as done by Sutton et al. (2007). Furthermore, the authors lumped all tree species and their related site characteristics, such as tree species, site fertility and stand density into one relationship. Site fertility may well correlate to N emission and deposition, as human activities and N emissions are expected to be most intense in regions having fertile soils (see also De Vries et al., 2007a).

In general, terrestrial ecosystems will only respond to elevated N inputs if they are N limited. Since nitrogen often is the limiting nutrient in forests, nitrogen deposition does generally increase wood production and accumulation of soil organic matter, thus increasing C sequestration into the forest. An estimated range of 30-70 kg C/kg N seems most reasonable for this effect. In non forested ecosystems the net impact of N deposition on carbon sequestration is more limited to the soil, since the productivity of forests is generally higher, and consequently the impact is less. Furthermore, with increasing N-enrichment, soil and vegetation, N immobilization will reduce (N leaching will increase) and C/N will decline, and consequently less C will be sequestered per unit N deposition. This effect is likely to occur in high N deposition areas

Table 9.7 Estimated ranges in carbon sequestration per kg nitrogen addition in above and below ground biomass in forest at various scales.

Approach	Carbon sequestration (kg C/kg N)			Scale of application	Author
	Above ground	Below ground	Total		
Forests					
Empirical field data					
Correlation between NEP and total N deposition	-	-	91-177	Chronosequences (5) in boreal and temperate forests of Eurasia and North America	Magnani et al. (2007) as re-evaluated by Sutton et al. (2007)
Correlation between the average growth increase of nearly 400 Intensive Monitoring plots and N deposition in a multivariate analysis	15-38	-	-	Nearly 400 Intensive Monitoring plots	Solberg et al. (2007) Laubhann et al. (2007)
15N experimental data					
Extrapolation of ^{15}N experimental data with average C/N ratios of forest ecosystem compartments.	25	21	46	Generic average	Nadelhoffer et al. (1999b)
Extrapolation of ^{15}N experimental data with site specific data at 6000 plots in Europe	33	15	48	European average	De Vries et al. (2006b)
Results of fertilizer experiments					
Average results from 30 year low dose (34 kg N/ha/yr) fertilizer experiments	25	-	-	Forest in Sweden	Högberg et al. (2006)
Average results from 14-30 fertilizer experiments	25	11	36	Forest in Sweden and Finland	Hyvonen et al. (2007b)
Results of model simulations					
Range in results of five process based models	15-25	-	-	Two forest sites	Rehfuess et al. (1999)
Range in results of three process based models	-	-	10-30	One forest sites	Levy et al. (2004)
Average result of the process based model EFM	-	-	41	22 forest sites	Milne and van Oijen (2005)
Range in results of the process based model SUMO	20-30	-	-	Dutch forests	Wamelink et al. (2007b)
Range in average results per latitude of the process based model chain SMART2-SUMO-WATBAL	3-12	5 -11	7-24	166 forested plots in Europe	Wamelink et al. (2007c)
Heathlands					
Results from 5-11 year N fertilizer experiments at 20-120 kg N/ha/yr	5-15	20-34	25-49	2 heathland sites	Evans et al. (2006)
Model simulations for the N fertilizer experiment sites	-	21-32	-	3 heathland sites	Evans et al. (2006) Evans, pers. com.

Literature

Aber, J.D., A. Magill, S.G. McNulty, R.D. Boone, K.J. Nadelhoffer, M. Downs & R. Hallett, 1995. *Forest biogeochemistry and primary production altered by nitrogen saturation.* Water Air Soil Pollut. 85 (3), 1665-1670.

Aber, J.D., S.V. Ollinger, C.T. Driscoll, G.E. Likens, R.T. Holmes, R.J. Freuder & C.L. Goodale, 2002. *Inorganic nitrogen losses from a forested ecosystem in response to physical, chemical, biotic, and climatic perturbations.* Ecosystems 5 (7), 648-658.

Aerts, R. & F. Berendse, 1988. *The effect of increased nutrient availability on vegetation dynamics in wet heathlands.* Vegetatio 76, 63-69.

Aerts, R., F. Berendse, H. de Caluwe & M. Schmitz, 1990. *Competition in heathland along an experimental gradient of nutrient availability.* Oikos 57, 310-318.

Aerts, R. & G.W. Heil, 1993. *Heathlands: patterns and processes in a changing environment.* Geobotany 20, Dordrecht, Kluwer.

Aerts, R., H. Caluwe & B. Beltman, 2003. *Is the relation between nutrient supply and biodiversity co-determined by the type of nutrient limitation?* Oikos 101, 489-498.

Ainsworth, E.A. & S.P. Long, 2005. *What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy.* New Phytol. 165 (2), 351-371.

Al-Mufti, M.M., C.L. Sydes, S.B. Furness, J.P. Grime & S.R. Band, 1977. *A quantitative analysis of shoot phenology and dominance in herbeceous vegetation.* J. Ecol. 65 (3), 759-791.

André, F. & Q. Ponette, 2003. *Comparison of biomass and nutrient content between oak (Quercus petraea) and hornbeam (Carpinus betulus) trees in a coppice-with-standards stand in Chimay (Belgium).* Ann. For. Sci. 60 (6), 489-502.

Andreassen, K. & S.M. Tomter, 2003. *Basal area growth models for individual trees of Norway spruce, Scots pine, birch and other broadleaves in Norway.* Forest Ecol. Manage. 180 (1-3), 11-24.

Andreassen, K., S. Solberg, O.E. Tveito & S.L. Lystad, 2006. *Regional differences in climatic responses of Norway spruce (Picea abies L. Karst) growth in Norway.* Forest Ecol. Manage. 222 (1-3), 211-221.

Anonymous, 1989. *Biologic markers of air pollution stress and damage in forests.* Washington DC, Committee on Biologic Markers of Air Pollution Damage in Trees. National Academy Press.

Ashby, J.A., W.B. Bowden & P.S. Murdoch, 1998. *Controls on denitrification in riparian soils in headwater catchments of a hardwood forest in the Catskill Mountains, U.S.A.* Soil Biol. Biochem. 30 (7), 853-864.

Assmann, E. & F. Franz, 1963. *Vorläufige Fichten-Ertragstafel für Bayern.* München, Institut für Ertragskunde der Forstl. Forschungsanstalt.

Assmann, E., 1970. *The principles of forest yield study.* Oxford, Pergamon Press.

Augusto, L., J. Ranger, D. Binkley & A. Rothe, 2002. *Impact of several common tree species of European temperate forests on soil fertility.* Ann. For. Sci. 59 (3), 233-253.

Bakker, J.P., 1989. *Nature management by grazing and cutting. On the ecological significance of grazing and cutting regimes applied to restore former species-rich grassland communities in the Netherlands.* Dordrecht, the Netherlands, Kluwer Academic Publishers.

Barber, V.A., G.P. Juday & B.P. Finney, 2000. *Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress.* Nature 405, 668-673.

Barrio, M., 2003. *Crecimiento y producción de masas naturales de Quercus robur L. en Galicia.* Universidad de Santiago de Compostela.

Bartelink, H.H., K. Kramer & G.M.J. Mohren, 1997. *Applicability of the radiation-use efficiency concept for simulating growth of forest stands.* Agric. for. meteorol. 88 (1-4), 169-179.

Bartnicki, J., K. Olendrzynski, J.E. Jonson, E. Berge & S. Unger, 2002. *Description of the Eulerian acid deposition model.* In: EMEP/MSC-W Report 1/98. EMEP/MSC-W.

Batjes, N.H., 1996. *Development of a world data set of soil water retention properties using pedotransfer rules.* Geoderma 71 (1-2), 31-52.

Bauer, H., K. Plattner & W. Volgger, 2000. *Photosynthesis in norway spruce seedlings infected by the needle rust Chrysomyxa rhododendri.* Tree Physiol. 20 (3), 211-216.

Bazzaz, F.A., S.L. Miao & P.M. Wayne, 1993. *CO_2-induced growth enhancements of co-occurring tree species decline at different rates.* Oecologia 96 (4), 478-482.

Berendse, F., 1979. *Competition between plant-populations with different rooting depths. 1. Theoretical considerations.* Oecologia 43 (1), 19-26.

Berendse, F. & R. Aerts, 1984. *Competition between Erica tetralix (L.) and Molinia caerulea (L.) Moench as affected by the availability of nutrients.* Acta Oecol.-Oec. Plant. 5 (19), 3-14.

Berendse, F., H. Oudhof & J. Bol, 1987. *A comparative-study on nutrient cycling in wet heathland ecosystems. 1. Litter production and nutrient losses from the plant.* Oecologia 74 (2), 174-184.

Berendse, F., 1990. *Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems.* J. Ecol. 78, 413-427.

Berendse, F., M.J.M. Oomes, H.J. Altena & W.T. Elberse, 1992. *Experiments on the restoration of species-rich meadows in The Netherlands.* Biol. Conserv. 62 (1), 59-65.

Berendse, F., 1994a. *Litter decomposability - a neglected component of plant fitness.* J. Ecol. 82 (1), 187-190.

Berendse, F., 1994b. *Competition between plant populations at low and high nutrient supplies.* Oikos 71 (2), 253-260.

Berendse, F., M. Schmitz & W. de Visser, 1994. *Experimental manipulation of succession in heathland ecosystems.* Oecologia 100, 38-44.

Berendse, F., N. van Breemen, H. Rydin, A. Buttler, M. Heijmans, M.R. Hoosbeek, J.A. Lee, E. Mitchell, T. Saarinen, H. Vasander & B. Wallen, 2001. *Raised atmospheric* CO_2 *levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs.* Glob. Change Biol. 7 (5), 591-598.

Berg, B. & G. Eckbohm, 1991. *Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Longterm decomposition in a Scots pine forest VII.* Can. j. bot. 69, 1449–1456.

Berg, B., G. Ekbohm, M.-B. Johansson, C. McClaugherty, F. Rutigliano & A. Virzo De Santo, 1996. *Maximum decomposition limits of forest litter types: a synthesis.* Can. j. bot. 74 (5), 659-672.

Berg, B. & E. Matzner, 1997. *Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems.* Environ. rev. 5 (1), 1-25.

Berg, B., R. Laskowski & A. Virzo De Santo, 1999. *Estimated nitrogen concentrations in humus based on initial nitrogen concentrations in foliar litter: a synthesis. XII. Long-term decomposition in a Scots pine forest.* Can. j. bot. 77, 1712–1722.

Berg, B., C. McClaugherty, A. Virzo De Santo & D. Johnson, 2001. *Humus buildup in boreal forests: effects of litter fall and its N concentration.* Can. j. for. res. 31 (6), 988-998.

Berg, B. & V. Meentemeyer, 2001. *Litter fall in some European coniferous forests as dependent on climate: a synthesis.* Can. j. for. res. 31 (2), 292–301.

Berg, B. & V. Meentemeyer, 2002. *Litter quality in a north European transect versus carbon storage potential.* Plant soil 242 (1), 83-92.

Berg, B. & C. McClaugherty, 2003. *Plant litter: decomposition, humus formation, carbon sequestration*. Berlin, Springer Verlag Heidelberg.

Berg, B. & N. Dise, 2004. *Validating a New Model for N Sequestration in Forest Soil Organic Matter.* Water Air Soil Poll. Focus 4 (2-3), 343-358.

Bergh, J., S. Linder, T. Lundmark & B. Elfving, 1999. *The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden.* Forest Ecol. Manage. 119 (1-3), 51-62.

Bhagsari, A.S. & R.H. Brown, 1986. *Leaf photosynthesis and its correlation with leaf area.* Crop sci. 26, 127-132.

Bobbink, R. & J.G.M. Roelofs, 1995. *Nitrogen critical loads for natural and semi-natural ecosystems: The empirical approach.* Water Air Soil Pollut. 85 (4), 2413-2418.

Bobbink, R., M. Hornung & J.G.M. Roelofs, 1998. *The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation.* J. Ecol. 86 (5), 717-738.

Boisvenue, C. & S.W. Running, 2006. *Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century.* Glob. Change Biol. 12 (5), 862-882.

Bokdam, J., 2001. *Effects of browsing and grazing on cyclic succession in nutrient-limited ecosystems.* J. Veg. Sci. 12 (6), 875-886.

Bonten, L.T.C. & D.J. Brus, 2006. *Belasting van het oppervlaktewater in het landelijk gebied door uitspoeling van zware metalen; Modelberekeningen t.b.v. emissieregistratie 2006 en invloed van redoxcondities.* Wageningen, Alterra. Report 1340.

Bousquet, P., P. Ciais, P. Peylin, M. Ramonet & P. Monfray, 1999. *Inverse modeling of annual atmospheric CO2 sources and sinks, 1, Method and control inversion.* J. Geophys. Res. 104 (D21), 26161-26178.

Bowden, R.D., E. Davidson, K. Savage, C. Arabia & P. Steudler, 2004. *Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest.* Forest Ecol. Manage. 196 (1), 43-56.

Bradley, R.T., J.M. Christie & D.R. Johnston, 1971. *Forest management tables (metric).* Bookl. For. Comm. 34, 1-201.

Bradu, D. & Y. Mundlak, 1970. *Estimation in Lognormal Linear Models.* J. Amer. Statistical Assoc. 65, 198-211.

Braun, S., B. Rihm, C. Schindler & W. Flückiger, 1999. *Growth of mature beech in relation to ozone and nitrogen deposition: an epidemiological approach.* Water Air Soil Pollut. 116 (1-2), 357-364.

Broadmeadow, M.S.J. & S.B. Jackson, 2000. *Growth responses of Quercus petraea, Fraxinus excelsior and Pinus sylvestris to elevated carbon dioxide, ozone and water supply.* New Phytol. 146 (3), 437-451.

Brouwer, R., 1983. *Functional equilibrium: sense or nonsense.* Neth. J. Agric. Sci. 31, 335-348.

Buckley, G.P., R. Howell, T.A. Watt, R. Ferris-Kaan & M.A. Anderson, 1997. *Vegetation succession following ride edge management in lowland plantations and woods. 1. The influence of site factors and management practices.* Biol. Conserv. 82 (3), 289-304.

Bugmann, H.K.M., X. Yan, M.T. Sykes, P. Martin, M. Lindner, P.V. Desanker & S.G. Cumming, 1996. *A comparison of forest gap models: Model structure and behaviour.* Clim. Chang. 34 (2), 289-313.

Burns, D.A., 2003. *Atmospheric nitrogen deposition in the Rocky Mountains of Colorado and southern Wyoming - a review and new analysis of past study results.* Atmos. Environ. 37 (7), 921-932.

Calfapietra, C., B. Gielen, M. Sabatti, P. De Angelis, F. Miglietta, G. Scarascia-Mugnozza & R. Ceulemans, 2003. *Do above-ground growth dynamics of poplar change with time under CO 2 enrichment?* New Phytol. 160 (2), 305-318.

Cannell, M.G.R. & R.C. Dewar, 1994. *Carbon allocation in trees: a review of concepts for modelling.* Adv. Ecol. Res., 59-104.

Cashen, R.O., 1947. *The influence of rainfall on the yield and botanical composition of permanent grass at Rothamstead.* J. Agric. Sci. 37, 1-9.

Ceulemans, R. & M. Mousseau, 1994. *Tansley review no. 71 - Effects of elevated atmospheric* CO_2 *on woody plants.* New Phytol. 127, 425-446.

Chapin, F.S., III, O.E. Sala, I.C. Burke, J.P. Grime, D.U. Hooper, W.K. Lauenroth, A. Lombard, H.A. Mooney, A.R. Mosier, S. Naeem, S.W. Pacala, J. Roy, W.L. Steffen & D. Tilman, 1998. *Ecosystem consequences of changing biodiversity - Experimental evidence and a research agenda for the future.* Bioscience 48, 45-52.

Chapin, F.S., III, E.S. Zavaleta, V.T. Eviner, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper, S. Lavorel, O.E. Sala, S.E. Hobbie, M.C. Mack & S. Díaz, 2000. *Consequences of changing biodiversity.* Nature 405, 234-242.

Chen, D.X. & J.H. Lieth, 1993. *A 2-Dimensional, Dynamic Model for Root Growth Distribution of Potted Plants.* J. Amer. Soc. Hort. Sci. 118 (2), 181-187.

Chertov, O.G. & A.S. Komarov, 1997. *SOMM: A model of soil organic matter dynamics.* Ecol. Model. 94 (2-3), 177-189.

Ciais, P., P.P. Tans, J.W.C. White, M. Trolier, R.J. Francey, J.A. Berry, D.R. Randall, P.J. Sellers, J.G. Collatz & D.S. Schimel, 1995. *Partitioning of ocean and land uptake of CO2 as inferred by 13C measurements from the NOAA Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network.* J. Geophys. Res. 100 (D3), 5051-5070.

Ciais, P., M. Reichstein, N. Viovy, A. Granier, J. Ogee, V. Allard, M. Aubinet, N. Buchmann, C. Bernhofer, A. Carrara, F. Chevallier, N. de Noblet, A.D. Friend, P. Friedlingstein, T. Grunwald, B. Heinesch, P. Keronen, A. Knohl, G. Krinner, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J.M. Ourcival, D. Papale, K. Pilegaard, S. Rambal, G. Seufert, J.F. Soussana, M.J. Sanz, E.D. Schulze, T. Vesala & R. Valentini, 2005. *Europe-wide reduction in primary productivity caused by the heat and drought in 2003.* Nature 437, 529-533.

Cofala, J. & S. Syri, 1998a. *Nitrogen oxides emissions, abatement technologies and related costs for Europe in the RAINS model database.* Laxenburg, Austria, International Institute for Applied Systems Analysis. IIASA Interim Report IR-98-88.

Cofala, J. & S. Syri, 1998b. *Sulfur emissions, abatement technologies and related costs for Europe in the RAINS model database.* Laxenburg, Austria, International Institute for Applied Systems Analysis. IIASA Interim Report IR-98-035 (update 19.10.1998).

Coleman, K. & D.S. Jenkinson, 1996. *RothC-26.3 - A Model for the turnover of carbon in soil.* In: Powlson, D.S., P. Smith & J.U. Smith (Eds). Evaluation of Soil organic matter models, Using Existing Long-Term Datasets. Heidelberg, Springer-Verlag, pp. 237-246.

Compaq Computer Corporation, 1999. *Compaq Fortran: language reference manual.* Houston, Compaq Computer Corporation.

Condes, S. & H. Sterba, 2005. *Derivation of compatible crown width equations for some important tree species of Spain.* Forest Ecol. Manage. 217 (2-3), 203-218.

Conijn, J.G., 1991. *De simulatie van de concurentie tussen Calluna vulgaris en Molinia caerulea in droge heidevelden.* Arnhem, RIN. RIN rapport 91/6.

Cooksley, D.G., J.H. Prinsen, C.J. Paton & A.T. Lisle, 1993. *Rate of decomposition and release of nutriens for litter in a Heteropogon contours-Biothriochloa bladhii dominant native pasture.* Proceedings of the XVII International Grasslands Congress,

Coûteaux, M.M., K.B. McTiernan, B. Berg, D. Szuberla, P. Dardenne & P. Bottner, 1998. *Chemical composition and carbon mineralisation potential of scots pine needles at different stages of decomposition.* Soil Biol. Biochem. 30 (5), 583-595.

Currie, W.S., K.J. Nadelhoffer & J.D. Aber, 2004. *Redistributions of* 15^N *highlight turnover and replenishment of mineral soil organic N as a long-term control on forest C balance.* Forest Ecol. Manage. 196 (1), 109-127.

Curtis, P.S., 1996. *A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide.* Plant Cell. Environ. 19 (2), 127-137.

Curtis, P.S. & X.Z. Wang, 1998. *A meta-analysis of elevated* CO_2 *effects on woody plant mass, form, and physiology.* Oecologia 113 (3), 299-313.

Cutini, A., 2002. *Litterfall and Leaf Area Index in the CONECOFOR Permanent Monitoring Plots.* J. of Limnol. 61 (S1), 62-68.

Davidson, E.A., J. Chorover & D.B. Dail, 2003. *A mechanism of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis.* Glob. Change Biol. 9 (2), 228-236.

De Vries, W., A. Hol, S. Tjalma & J.C. Voogd, 1990. *Literatuurstudie naar voorraden en verblijftijden van elementen in een bosecosysteem.* Wageningen, Staring Centrum. Rapport 94.

De Vries, W., 1994. *Soil response to acid deposition at different regional scales; Field and laboratory data, critical loads and model predictions.* PhD Thesis, Wageningen, The Netherlands, Wageningen University.

De Vries, W., G.J. Reinds & M. Posch, 1994. *Assessment of critical loads and their exceedance on European forests using a one-layer steady-state model.* Water Air Soil Pollut. 72 (1/4), 357-394.

De Vries, W., G.J. Reinds, M.A. van Kerkvoorde, C.M.A. Hendriks, E.E.J.M. Leeters, C.P. Gross, J.C.H. Voogd & E.M. Vel, 2000. *Intensive Monitoring of Forest Ecosystems in Europe. Technical Report 2000.* UN/ECE, EC, Forest Intensive Monitoring Coordinating Institute.

De Vries, W., G.J. Reinds, C. van der Salm, G.P.J. Draaijers, A. Bleeker, J.W. Erisman, J. Auee, P. Gundersen, H.L. Kristensen, H. van Dobben, D. de Zwart, J. Derome, J.C.H. Voogd & E.M. Vel, 2001. *Intensive Monitoring of Forest Ecosystems in Europe. Technical Report 2001.* Geneva and Brussels, UN/ECE, EC, Forest Intensive Monitoring Coordinating Institute.

De Vries, W., G.J. Reinds, M. Posch, M.J. Sanz, G.H.M. Krause, V. Calatayud, J.P. Renaud, J.L. Dupouey, H. Sterba, P. Gundersen, J.C.H. Voogd & E.M. Vel, 2003a. *Intensive Monitoring of Forest Ecosystems in Europe. Technical Report 2003.* Geneva and Brussels, UN/ECE and EC, Forest Intensive Monitoring Coordinating Institute.

De Vries, W., G.J. Reinds & E. Vel, 2003b. *Intensive monitoring of forest ecosystems in Europe: 2. Atmospheric deposition and its impacts on soil solution chemistry.* Forest Ecology and Management 174 (1-3), 97-115.

De Vries, W., E. Vel, G.J. Reinds, H. Deelstra, J.M. Klap, E.E.J.M. Leeters, C.M.A. Hendriks, M. Kerkvoorden, G. Landmann, J. Herkendell, T. Haussmann & J.W. Erisman, 2003c. *Intensive monitoring of forest ecosystems in Europe: 1. Objectives, set-up and evaluation strategy.* Forest Ecology and Management 174 (1-3), 77-95.

De Vries, W., G.J. Reinds & P. Gundersen, 2005. *Impacts of nitrogen depositon on carbon sequestration by forests in Europe.* Global Change Biology (Submitted).

De Vries, W., K.B. Bahl, H. Denier van der Gon & O. Oenema, 2006a. *Quantification of the impact of nitrogen deposition on the exchange of green house gases from European forests.* Glob. Change Biol., (Submitted).

De Vries, W., G.J. Reinds, P. Gundersen & H. Sterba, 2006b. *The impact of nitrogen deposition on carbon sequestration in European forests and forest soils.* Glob. Change Biol. 12 (7), 1151-1173.

De Vries, W., S. Solberg, M. Dobbertin, H. Sterba, D. Laubhann, G.J. Reinds, G.J. Nabuurs & P. Gundersen, 2007a. *Ecologically implausible carbon response.* Nature submitted.

De Vries, W., C. van der Salm, G.J. Reinds & J.W. Erisman, 2007b. *Element fluxes through European forest ecosystems and their relationships with stand and site characteristics.* Environ. pollut. 148 (2), 501-513.

Demidenko, E., 2004. *Mixed Models: Theory and Application.* Hoboken, New Jersey, Wiley.

Denier van der Gon, H.A.C. & A. Bleeker, 2005. *Indirect N_2O emission due to atmospheric N deposition for the Netherlands.* Atmos. Environ. 39 (32), 5827-5838.

Di Stefano, J.F., L.A. Fournier & T. Mejía, 1997. *Formación de nódulos en estacas recién establecidas de Gliricidia sepium (Fabaceae) en tres suelos de Ciudad Colón, Costa Rica.* Rev Biol Trop. 45 (2), 919-922.

Diemont, W.H., 1994. *Effects of removal of organic matter on the productivity of heathlands.* J. Veg. Sci. 5 (3), 409-414.

Diemont, W.H. & J.H. Oude Voshaar, 1994. *Effects of climate and management on the productivity of Dutch heathlands.* J. appl. ecol. 31 (4), 709-716.

Dijkstra, P., 1990. *Physiological aspects of a genotypic difference in relative growth rate within Plantago major.* Dissertatie,

Dise, N.B., E. Matzner & M. Forsius, 1998a. *Evaluation of organic horizon C:N ratio as an indicator of nitrate leaching in conifer forests across Europe.* Environ. Pollut. 102 (Supp 1), 453-456.

Dise, N.B., E. Matzner & P. Gundersen, 1998b. *Synthesis of Nitrogen Pools and Fluxes from European Forest Ecosystems.* Water Air Soil Pollut. 105 (1-2), 143-154.

Dobbertin, M., 2000. *Forest Growth.* In: Haussmann, T., M. Lorenz & R. Fischer (Eds). International Review of ICP Forests. UN/ECE, Federal Research Centre for Forestry and Forest Products, pp. 84-102.

Dobbertin, M., 2004. *Estimation of growth and Yield.* In: Programme Coordinating Centre (Ed). Manual on Methods and Criteria for Harmonized Sampling, Assessment, Monitoring and Analysis of the Effects of Air Pollution on Forests. Hamburg, Federal Research Centre for Forestry and Forest Products.

Dobbertin, M., 2005. *Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review.* European Journal of Forest Research 124 (4), 319-333.

Dobson, A., 2005. *Monitoring global rates of biodiversity change: challenges that arise in meeting the Convention on Biological Diversity (CBD) 2010 goals.* Phil. Trans. R. Soc. Lond. B 360, 229-241.

Dodd, M.E., J. Silvertown, K. McConway, J. Potts & M. Crawley, 1994. *Stability in the plant communities of the Park Grass experiment: the relationships between species richness, soil pH and biomass variability.* Philosophical Transactions: Biological Sciences 346 (1316), 185-193.

Duvigneaud, P. & S. Denaeyer-De Smet, 1970. *Biological cycling of minerals in temperate deciduous forests.* In: Reichel, D.E. (Ed). Ecological studies I; temperate forest ecosystems. New York, Springer, pp. 199-205.

Dyck, G.W. & R.E. Bement, 1972. *Herbage growth rate, forage intake, and forage quality in 1971 on heavely- and lightly-grazed blue grame pastures.* Fort Collins, USA, USDA-ARS, Crop Research Division Forage and Range Research Branch, Colorado State University.

EAFV, Eidgenössische Anstalt für das forstliche Versuchswesen, 1983. *Ertragstafeln Buche. 3. Ed.* Birmensdorf, Switzerland.

EFI, 2002. *Forest management guidelines and practices in Finland, Sweden and Norway.* EFI internal report 11.

Elberse, W.T., J.P. van den Bergh & J.P.G. Dirven, 1983. *Effects of use and mineral supply on the botanical composition and yield of old grassland on heavy-clay soil.* Neth. J. Agric. Sci. 31, 63-88.

Elberse, W.T. & F. Berendse, 1993. *A comparative study of growth and morphology of eight grass species from habitats with different nutrient availabilities.* Function. Ecol. 7 (2), 223-229.

Ellenberg, H., H.E. Weber, R. Düll, V. Wirth, W. Werner & D. Paulißen, 1992. *Zeigerwerte von Pflanzen in Mitteleuropa.* Scr. Geobot. 18, 1-248.

Emmett, B.A., D. Boxman, M. Bredemeier, P. Gundersen, O.J. Kjønaas, F. Moldan, P. Schleppi, A. Tietema & R.F. Wright, 1998. *Predicting the effects of atmospheric nitrogen deposition on conifer stand: evidence from the NITREX ecosystem-scale experiments.* Ecosystems 1 (4), 352-360.

Ericsson, T.S., H. Berglund & L. Ostlund, 2005. *History and forest biodiversity of woodland key habitats in south boreal Sweden.* Biol. Conserv. 122 (2), 289-303.

Eriksson, K.-E.L., R.A. Blanchette & P. Ander, 1990. *Microbial and enzymatic degradation of wood and wood components.* Berlin, Germany, Springer Verlag.

Esser, G., 1998. *NPP Multi-Biome: Global Osnabruck Data, 1937-1981. Data set.* Available on-line [http://www.daac.ornl.gov; http://www-eosdis.ornl.gov/NPP/html_docs/ods_des.html] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

Evans, C.D., S.J.M. Caporn, J.A. Carroll, M.G. Pilkington, D.B. Wilson, N. Ray & N. Cresswell, 2006. *Modelling nitrogen saturation and carbon accumulation in heathland soils under elevated nitrogen deposition.* Environ. Pollut. 143 (3), 468-478.

Falloon, P., P. Smith, J. Szabo & L. Pasztor, 2002. *Comparison of approaches for estimating carbon sequestration at the regional scale.* Soil Use and Man. 18, 164-174.

Fan, S., M. Gloor, J. Mahlman, S. Pacala, J. Sarmiento, T. Takahashi & P. Tans, 1998. *A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models.* Science 282 (5388), 442-446.

FAOSTAT, 2007. *http://faostat.fao.org/.*

Farrell, E.P., E. Fuhrer, D. Ryan, F. Andersson, R. Hüttl & P. Piussi, 2000. *European forest ecosystems: building the future on the legacy of the past.* Forest Ecol. Manage. 132, 5-20.

Fenn, M.E., R. Haeuber, G.S. Tonnesen, J.S. Baron, S. Grossman-Clarke, D. Hope, D.A. Jaffe, S. Copeland, L. Geiser, H.M. Rueth & J.O. Sickman, 2003. *Nitrogen emissions, deposition, and monitoring in the western United States.* Bioscience 53 (4), 391-403.

Finér, L., 1989. *Biomass and nutrient cycle in fertilized and unfertilized pine, mixed birch and pine and spruce stands on a drained mire.* Acta forestalia fennica 208, 3-19.

Fischlin, A., G.F. Midgley & et al., 2007. *Chapter 4: Ecosystems, their Properties, Goods, and Services.* In: WG III (Ed). IPCC 4AR. Cambridge University Press, in press.

Flückiger, W. & S. Braun, 1995. *Revitalization of an alpine protective forest by fertilization.* Plant soil 168-169 (1), 481-488.

Fog, K., 1988. *The effect of added nitrogen on the rate of decomposition of organic matter.* Biol. Rev. 63, 433-462.

Fourqurean, J.W. & J.E. Schrlau, 2003. *Changes in nutrient content and stable isotope ratios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA.* Chemistry and Ecology 19 (5), 373-390.

Franklin, O., P. Högberg, A. Ekblad & G.I. Ågren, 2003. *Pine forest floor carbon accumulation in response to N and PK additions - bomb ^{14}C modelling and respiration studies.* Ecosystems 6 (7), 644-658.

Friedlingstein, P., I. Fung, E. Holland, J. John, G. Brasseur, D. Erickson & D. Schimel, 1995. *On the contribution of CO_2 fertilization to the missing biospheric sink.* Glob. Biogeochem. Cycles 9 (4), 541-556.

Galloway, J.N., G.E. Likens, W.C. Keene & J.M. Miller, 1982. *The composition of precipitation in remote areas of the world.* J. Geophys. Res. 87, 8771-8776.

Galloway, J.N., G.E. Likens & M.E. Hawley, 1984. *Acid precipitation: Natural versus anthropogenic components.* Science 226, 829-831.

Galloway, J.N., J.D. Aber, J.W. Erisman, S.P. Seitzinger, R.W. Howarth, E.B. Cowling & B.J. Cosby, 2003. *The Nitrogen Cascade.* Bioscience 53 (4), 341-356.

Gielen, B. & R. Ceulemans, 2001. *The likely impact of rising atmospheric CO_2 on natural and managed Populus: a literature review.* Environ. Pollut. 115 (3), 335-358.

Gifford, R.M., 1980. *Carbon storage by the biosphere.* In: Pearman, G.I. (Ed). Carbon dioxide and climate: Australian research. Canberra, Australian Academy of Science, pp. 167-181.

Gimingham, C.H., 1972. *Ecology of heathlands.* New York, John Wiley and Sons, Inc.

Gitay, H., S. Brown, W. Easterling & B. Jallow, 2001. *Forest ecosystems and their goods and services.* In: McCarthy, J.J., O.F. Canziani, N.A. Leary, D.J. Dokken & K.S. White (Eds). Climate Change 2001: Impacts, Adaptation and Vulnerability. IPCC, pp. 237-342.

Gond, V., D.G.G. de Pury, F. Veroustraete & R. Ceulemans, 1999. *Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest.* Tree Physiol. 19 (19), 673-679.

Gough, L. & S.E. Hobbie, 2003. *Responses of moist non-acidic arctic tundra to altered environment: productivity, biomass, and species richness.* Oikos 103 (1), 204-216.

Grime, J.P., 1979. *Plant strategies and vegetation processes.* Chichester, Wiley & Sons.

Groenendijk, P. & J.G. Kroes, 1999. *Modelling the nitrogen and phosphorus leaching to groundwater and surface water with ANIMO 3.5.* Wageningen, Winand Staring Centre. Report 144.

Gundersen, P. & L. Rasmussen, 1995. *Nitrogen mobility in a nitrogen limited forest at Klosterhede, Denmark, examined by NH4NO3 addition.* Forest Ecol. Manage. 71 (1-2), 75-88.

Gundersen, P., 1998. *Effects of enhanced nitrogen deposition in a spruce forest at Klosterhede, Denmark, examined by moderate* NH_4NO_3 *addition.* Forest Ecol. Manage. 101 (1-3), 251-268.

Gundersen, P., I. Callesen & W. de Vries, 1998. *Nitrate leaching in forest ecosystems is related to forest floor C/N ratios.* Environ. Pollut. 102 (1), 403-407.

Gundersen, P., B. Berg, W.S. Currie, N.B. Dise, B.A. Emmett, V. Gauci, M. Holmberg, O.J. Kjønaas, J. Mol-Dijkstra, C. van der Salm, I.K. Schmidt, A. Tietema, W.W. Wessel, L.S. Vestgarden, C. Akselsson, W. de Vries, M. Forsius, H. Kros, E. Matzner, F. Moldan, K.J. Nadelhoffer, L.-O. Nilsson, G.J. Reinds, U. Rosengren, A.O. Stuanes & R.F. Wright, 2006a. *Carbon-nitrogen interactions in forest ecosystems - Final report.* Danish Centre for Forest, Landscape and Planning, KVL. Forest & Landscape Working Papers 17.

Gundersen, P., I.K. Schmidt & K. Raulund-Rasmussen, 2006b. *Leaching of nitrate from temperate forests – effects of air pollution and forest management.* Environ. rev. 14 (1), 1-57.

Gustafsson, L., L. Appelgren & A. Nordin, 2005. *Biodiversity value of potential forest fertilisation stands, as assessed by red-listed and 'signal' bryophytes and lichens.* Silva Fenn. 39 (2), 191-200.

Hagberg, E. & B. Matérn, 1975. *Tabeller för kubering av ek och bok. Skogshögskolan.* Inst. f. skoglig matematisk statistik. Rapporter och Uppsatser 14.

Hagedoorn, F., D. Spinnler & R. Siegwolf, 2003. *Increased N deposition retards mineralisation of old soil organic matter.* Soil Biol. Biochem. 35 (12), 1683-1692.

Hagen-Thorn, A., I. Callesen, K. Armolaitis & B. Nihlgård, 2004. *The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land.* Forest Ecol. Manage. 195 (3), 373-384.

Harrison, A.F., D.D. Harkness, A.P. Rowland, J.S. Garnett & P.J. Bacon, 2000. *Annual carbon and nitrogen fluxes in soils along the European forest transect determined using* ^{14}*C-bomb.* In: Schulze, E.D. (Ed). Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies 142. Berlin Heidelberg New York, Springer, pp. 237-256.

Hasenauer, H. & R.A. Monserud, 1997. *Biased predictions for tree height increment models developed from smoothed "data".* Ecol. Model. 98 (1), 13-22.

Hasenauer, H., R.R. Nemani, K. Schadauer & S.W. Running, 1999. *Forest growth response to changing climate between 1961 and 1990 in Austria.* Forest Ecol. Manage. 122 (3), 209-219.

Hatakka, A., 2001. *Biodegradation of lignin.* In: Hofrichter, M. & A. Steinbüchel (Eds). Lignin, humic substances and coal, vol. 1. Weinheim, Germany, Wiley-VCH, pp. 129-180.

Hättenschwiler, S. & C. Körner, 1996. *Effects of elevated CO_2 and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems.* Oecologia 106 (2), 172-180.

Hättenschwiler, S., 2001. *Tree seedling growth in natural deep shade: Functional traits related to interspecific variation in response to elevated CO_2.* Oecologia 129 (1), 31-42.

Haußmann, T. & M. Lorenz, 2004. *Manual on the methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. Part I. Mandate of ICP Forests and Programme Implementation.*

Heil, G.W. & R. Bobbink, 1993. *"Calluna", a simulation model for evaluation of impacts of atmospheric nitrogen deposition on dry heathlands.* Ecol. Model. 68 (3-4), 161-182.

Hickler, T., B. Smith, M.T. Sykes, M.B. Davis, S. Sugita & K. Walker, 2003. *Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA.* Ecology 85 (2), 519–530.

Hobbie, S.E., 2000. *Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest.* Ecosystems 3 (5), 484-494.

Högberg, P., H. Fan, M. Quist, D. Binkley & C.O. Tamm, 2006. *Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest.* Glob. Change Biol. 12 (3), 489-499.

Högberg, P., 2007. *Nitrogen impacts on forest carbon.* Nature 447, 781-782.

Hogg, P., P. Squires & A.H. Fitter, 1995. *Acidification, nitrogen deposition and rapid vegetational change in a small valley mire in Yorkshire.* Biol. Conserv. 71 (2), 143-153.

Hökkä, H., V. Alenius & T. Penttilä, 1997. *Individual-tree basal area growth models for Scots pine, Pubescent Birch and Norway spruce in drained peatlands in Finland.* Silva Fenn. 31 (2), 161-178.

Holland, E.A., B.H. Braswell, J.F. Lamarque, A.R. Townsend, J. Sulzman, J.F. Müller, F. Dentener, G. Brasseur, H. Levy, II, J.E. Penner & G.J. Roelofs, 1997. *Variations in* *the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestial ecosystems.* J. Geophys. Res. 102 (13), 15849-15866.

Hollinger, D.Y., 1987. *Gas exchange and dry matter allocation responses to elevation of atmospheric* CO_2 *concentration in seedlings of three tree species.* Tree Physiol. 3 (3), 193-202.

Holst, N., I.A. Rasmussen & L. Bastiaans, 2007. *Field weed population dynamics: a review of model approaches and applications.* Weed Res. 47 (1), 1-14.

Houghton, R.A., E.A. Davidson & G.M. Woodwell, 1998. *Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global carbon balance.* Glob. Biogeochem. Cycles 12 (1), 25-34.

Huisman, J. & F.J. Weissing, 1994. *Light-limited growth and competition for light in well-mixed aquatic environments - an elementary model.* Ecology 75, 507-520.

Hungate, B.A., J.S. Dukes, M.R. Shaw, Y. Luo & C.B. Field, 2003. *Nitrogen and Climate Change.* Science 302 (5650), 1512-1513.

Hunter, I.R. & A. Schuck, 2002. *increasing forest growth in Europe - possible causes and implications for sustainable forest management.* Plant Biosystems 136 (2), 133-141.

Huston, M.A. & G. Marland, 2003. *Carbon management and biodiversity.* J. Environ. Manag. 67 (1), 77-86.

Hüttl, R.F., B.U. Schneider & E.P. Farrell, 2000. *Forests of the temperate region: gaps in knowledge and research needs.* Forest Ecol. Manage. 132, 83-96.

Hymus, G. & R. Valentini, 2006. *Terrestrial vegetation as a carbon dioxide sink.* In: Reay, D., N. Hewitt, J. Grace & K. Smith (Eds). Greenhouse gas sinks: The expert view on sinks for the 'big three' anthropogenic greenhouse gases. This issue.

Hyvönen, R., G.I. Ågren, S. Linder, T. Persson, F. Cotrufo, A. Ekblad, M. Freeman, A. Grelle, I.A. Janssens, P.G. Jarvis, S. Kellomäki, A. Lindroth, D. Loustau, T. Lundmark, R.J. Norby, R. Oren, K. Pilegaard, M.G. Ryan, B.D. Sigurdsson, M. Strömgren, M. van Oijen & G. Wallin, 2007a. *The likely impact of elevated* [CO_2], *nitrogen deposition, increased temperature, and management on carbon sequestration in temperate and boreal forest ecosystems. A literature review.* New Phytol. in press.

Hyvönen, R., T. Persson, S. Andersson, B. Olsson, G.I. Ågren & S. Linder, 2007b. *Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe.* Biogeochem. in print.

Ilic, J., D. Boland, M. McDonald, G. Downes & P. Blakemore, 2000. *Woody density Phase 1 - State of knowledge.* Australian Greenhouse Office. National carbon accounting system. Technical Report 18.

Ivens, W.P.M.F., 1990. *Atmospheric deposition onto forests: an analysis of the deposition variability by means of throughfall measurements.* PhD thesis, Utrecht, The Netherlands, University of Utrecht.

Jacobsen, C., P. Rademacher, H. Meesenburg & K.J. Meiwes, 2002. *Gehalte chemischer Elemente in Baumkompartimenten.* Göttingen, Niedersächsische Forstliche Versuchsanstalt.

Jans, W.W.P., G.M. van Roekel, W.H. van Orden & E.G. Steingröver, 1994. *Above ground biomass of adult Douglas fir. A data set collected in Garderen and Kootwijk from 1986 onwards.* Wageningen, Institute for Forestry and Nature Research. IBN Research Report 94/1.

Jansen, J.J., J. Sevenster & P.J. Faber, 1996. *Opbrengsttabellen voor belangrijke boomsoorten in Nederland.* Wageningen, IBN-DLO / LUW vakgroep Bosbouw. IBN-rapport 221 Hinkeloord Report 17.

Janssen, B.H., 1984. *A simple method for calculating decomposition and accumulation of 'young' soil organic matter.* Plant soil 76, 297-304.

Jenkinson, D.S., J.M. Potts, J.N. Perry, V. Barnett, K. Coleman & A.E. Johnston, 1994. *Trends in herbage yields over the last century on the Rothamsted long-term continuous hay experiment.* J. Agric. Sci. 122, 365-374.

Jenkinson, D.S., K. Goulding & D.S. Powlson, 1999. *Reply to Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests.* Nature 400, 629.

Jensen, M.E. & H.R. Haise, 1963. *Estimating evapotranspiration from solar radiation.* J. Irrig. Drain. Div. 89, 15-41.

Johnson, D.W. & S.E. Lindberg, 1992. *Atmospheric deposition and forest nutrient cycling.* Ecological Studies 91, New York, Springer.

Johnson, L.C., G.R. Shaver, D.B. Cades, E. Rastetter, K. Nadelhoffer, A. Giblin, J. Laundre & A. Stanley, 2000. *Plant carbon-nutrient interactions control CO_2 exchange in Alaskan wet sedge tundra ecosystems.* Ecology 81 (2), 453-469.

Jolly, W.M., M. Dobbertin, N.E. Zimmermann & M. Reichstein, 2005. *Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps.* Geophys. Res. Lett. 32 (22), L18409.

Joos, K., 1997. *Untersuchung der Zusammenhänge zwischen Nadeldichte, Zuwachsleistung und Nährstoffversorgung bei der Fichte unter besonderer Berücksichtigung des Ionentransportes im Splintsaft.* Diss. ETH, No. 12117, ETH Zürich.

Jorritsma, I.T.M., A.F.M. van Hees & G.M.J. Mohren, 1999. *Forest development in relation to ungulate grazing: a modelling approach.* Forest Ecol. Manage. 120 (1-3), 23-34.

Kahle, H.-P., H. Spiecker, P.-J. Perez-Martinez & R. Unseld, 2005. *Causes of changes in growth of European Forests: Analysis of the role of climatic factors and nitrogen nutrition.* The International Forestry Review 7 (5), 99.

Karjalainen, G., A. Schuck, J. Prietzel, K.-H. Mellert, H.-P. Kahle, H. Spiecker, G. Agren, M. Oijen & S. Kellomäki, in press. *Causes and Consequences of Forest Growth Trends in Europe - Results of the RECOGNITION Project.* European Forest Institute. Research Report.

Karjalainen, T., A. Pussinen, J. Liski, G.-J. Nabuurs, M. Erhard, T. Eggers, M. Sonntag & G.M.J. Mohren, 2002. *An approach towards an estimate of the impact of forest management and climate change on the European forest sector carbon budget: Germany as a case study.* Forest Ecol. Manage. 162, 87-103.

Karjalainen, T., A. Pussinen, J. Liski, G.J. Nabuurs, T. Eggers, T. Lapvetelainen & T. Kaipainen, 2003. *Scenario analysis of the impacts of forest management and climate change on the European forest sector carbon budget.* Forest policy and economics 5 (2), 141-155.

Kaufmann, E., 2000. *Estimation of standing timber, growth and cut.* In: Brassel, P. & H. Lischke (Eds). Swiss National Forest Inventory: Methods and models of the second assessments. Birmensdorf, Swiss Federal Research Institute WSL, pp. 162-196.

Kaufmann, R.K., R.D. D'Arrigo, C. Laskowski, R.B. Myneni, L. Zhou & N.K. Davi, 2004. *The effect of growing season and summer greenness on northern forests.* Geophys. Res. Lett. 31 (9), L09205.

Kauppi, P.E., K. Mielikäinen & K. Kuusela, 1992. *Biomass and carbon budget of European forests, 1971 to 1990.* Science 256, 70-74.

Keeling, C.D., T.P. Whorf & Carbon Dioxide Research Group, 2005. *Atmospheric CO_2 concentrations (ppmv) derived from in situ air samples collected at Mauna Loa Observatory, Hawaii.* http://cdiac.ornl.gov/ftp/trends/co2/maunaloa.co2, Scripps Institution of Oceanography (SIO), University of California.

Kelly, V.R., G.M. Lovett, K.C. Weathers & G.C. Likens, 2002. *Trends in atmospheric concentration and deposition compared to regional and local pollutant emissions at a rural site in southeastern New York, USA.* Atmos. Environ. 36 (10), 1569-1575.

Kesik, M., P. Ambus, R. Baritz, N. Brüggemann, K. Butterbach-Bahl, M. Damm, J. Duyzer, L. Horváth, R. Kiese, B. Kitzler, A. Leip, C. Li, M. Pihlatie, K. Pilegaard, G. Seufert, D. Simpson, U. Skiba, G. Smiatek, T. Vesala & S. Zechmeister-Boltenstern, 2005. *Inventories of N_2O and NO emissions from European forest soils.* Biogeosciences 2 (4), 353-375.

Kettunen, R., S. Saarnio, P.J. Martikainen & J. Silvola, 2006. *Increase of N_2O fluxes in agricultural peat and sandy soil under elevated CO_2 concentration: concomitant changes in soil* *moisture, groundwater table and biomass production of Phleum pratense.* Nutr. Cycl. Agroecosyst. 74, 175-189.

Kirschbaum, M.U.F., D.A. King, H.N. Comins, R.E. Mcmurtrie, B.E. Medlyn, S. Pongracic, D. Murty, H. Keith, R.J. Raison, P.K. Khanna & D.W. Sheriff, 1994. *Modelling forest response to increasing* CO_2 *concentration under nutrient-limited conditions.* Plant Cell. Environ. 17 (10), 1081-1099.

Kirschbaum, M.U.F., 2000a. *Will changes in soil organic carbon act as a positive or negative feedback on global warming?* Biogeochem. 48 (1), 21-51.

Kirschbaum, M.U.F., 2000b. *Forest growth and species distribution in a changing climate.* Tree Physiol. 20 (5-6), 309-322.

Kirschbaum, M.U.F. & K.I. Paul, 2002. *Modelling C and N dynamics in forest soils with a modified version of the CENTURY model.* Soil Biol. Biochem. 34 (3), 341-354.

Kittel, T.G.F., N.A. Rosenbloom, T.H. Painter & D.S. Schimel, 1995. *The VEMAP Integrated Database for Modelling United States Ecosystem/Vegetation Sensitivity to Climate Change.* J. Biogeogr. 22 (4-5), 857-8622.

Klap, J.M., W. de Vries, J.W. Erisman & E.P. van Leeuwen, 1997. *Relationships between forest condition and natural and anthropogenic stress factors on the European scale; pilot study.* Wageningen, the Netherlands, DLO Winand Staring Centre for Integrated Land, Soil and Water Research. Report 150.

Knops, J.M.H., K.L. Bradley & D.A. Wedin, 2002. *Mechanisms of plant species impacts on ecosystem nitrogen cycling.* Ecology Letters 5 (3), 454-466.

Koerselman, W., M.W.A. de Haan & A.F.M. Meuleman, 1999. *Ecohydrologische effectvoorspelling duinen: standplaatsmodellering in NICHE duinen.* Nieuwegein, KIWA.

Komarov, A., O. Chertov, S. Zudin, M. Nadporozhskaya, A. Mikhailov, S. Bykhovets, E. Zudina & E. Zoubkova, 2003. *EFIMOD2 - a model of growth and cycling of elements in boreal forest ecosystems.* Ecol. Model. 170 (2-3), 373-392.

Konohira, E., M. Yoh, J. Kubota, K. Yagi & H. Akiyama, 2001. *Effects of riparian denitrification on stream nitrate.* Water Air Soil Pollut. 130 (1-4), 667-672.

Kooijman, A.M. & M. Besse, 2002. *The higher availability of N and P in lime-poor than in lime-rich coastal dunes in the Netherlands.* J. Ecol. 90 (2), 394-403.

Koop, H.G.J.M. & A.P.P.M. Clerkx, 1995. *Bosreservaat Zeesserveld, Ommen.* Wageningen, IBN-DLO.

Korner, C., R. Asshoff, O. Bignucolo, S. Hattenschwiler, S.G. Keel, S. Pelaez-Riedl, S. Pepin, R.T.W. Siegwolf & G. Zotz, 2005. *Carbon flux and growth in mature deciduous forest trees exposed to elevated* CO_2. Science 309, 1360-1362.

Korner, C., 2006. *Plant* CO_2 *responses: an issue of definition, time and resource supply.* New Phytol. 172, 393-411.

Kozlowski, T.T. & S.G. Pallardy, 1996. *Physiology of woody plants.* San Diego, Academic Press.

Kramer, T., T.A. Groen & S.E. van Wieren, 2003. *The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE.* Forest Ecol. Manage. 181 (1-2), 205-222.

Kros, H., J. Mol, B.J. Groenenberg, G.J. Reinds, G. Heil, W. van Deursen & W. de Vries, 2007. *Modelling the afforested system: the soil and water compartment.* In: Heil, G.W., B. Muys & K. Hansen (Eds). Environmental Effects of Afforestation in North-Western Europe. From Field Observations to Decision Support. Springer Series: Plant and Vegetation, Vol. 1. Dordrecht, the Netherlands, Kluwer Academic Publishers.

Kros, J., G.J. Reinds, W. de Vries, J.B. Latour & M.J.S. Bollen, 1995. *Modelling of soil acidity and nitrogen availability in natural ecosystems in response to changes in acid deposition and hydrology.* Wageningen, The Netherlands. SC-DLO Report 95.

Kros, J., 2002. *Evaluation of biogeochemical models at local and regional scale.* PhD thesis, Wageningen, The Netherlands, Wageningen University.

Kros, J., J.P. Mol Dijkstra & E.J. Pebesma, 2002. *Assessment of the prediction error in a large-scale application of a dynamic soil acidification model.* Stochastic Environmental Research and Risk Assessment 16 (4), 279-306.

Kytoviita, M.M., D. le Thiec & P. Dizengremel, 2001. *Elevated* CO_2 *and ozone reduce nitrogen acquisition by Pinus halepensis from its mycorrhizal symbiont.* Physiol. Plant. 111 (3), 305-312.

Laitat, E., B. Chermanne & B. Portier, 2000. *Biomass, carbon and nitrogen allocation in open top chambers under ambient and elevated* CO_2 *and in a mixed forest stand. A tentative approach for scaling up from the experiments of Vielsalm.* In: Ceulemans, R.J.M., V. Veroustraete, V. Gond & J.B.H.F. van Rensbergen (Eds). Forest Ecosystem Modelling, Upscaling and Remote Sensing. The Hague, The Netherlands, SPB, Academic Publishing bv, pp. 33–59.

Lameire, S., M. Hermy & O. Honnay, 2000. *Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape.* J. Veg. Sci. 11 (5), 695-704.

Lappi, J. & R.L. Bailey, 1988. *A height prediction model with random stand and tree parameters: an alternative to traditional site index methods.* For. sci. 34 (4), 907-927.

Laubhahn, D., H. Sterba, G.J. Reinds & W. de Vries, 2007. *The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical tree growth model.* Forest Ecol. Manage. this issue (in prep).

Laubhann, D., H. Sterba, G.J. Reinds & W. de Vries, 2007. *The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical tree growth model.* Forest Ecol. Manage. (submitted).

Lawes, J.B. & J.H. Gilbert, 1880. *Agricultural, Botanical, and Chemical Results of Experiments on the Mixed Herbage of Permanent Meadow, Conducted for More Than Twenty Years in Succession on the Same Land. Part I.* Philos. Trans. R. Soc. Lond. 171, 289-415.

Lee, H.S.J. & P.G. Jarvis, 1995. *Trees differ from crops and from each other in their responses to increases in* CO_2 *concentration.* J. Biogeogr. 22 (2-3), 323-330.

Leeters, E.E.J.M. & W. de Vries, 2001. *Chemical composition of the humus layer, mineral soil and soil solution of 200 forest stands in the Netherlands in 1995.* Wageningen (Netherlands), Alterra, Green World Research. Alterra rapport 424.2.

Lefèvre, F., E. Laitat, B. Medlyn, M. Aubinet & B. Longdoz, 2000. *Carbon pools and annual carbon fluxes in the beech forest sub-plot at the Vielsalm pilot station.* In: Ceulemans, R.J.M., F. Veroustraete, V. Gond & J.B.H.F. Van Rensbergen (Eds). Forest Ecosystem Modelling, Upscaling and Remote Sensing. The Hague, The Netherlands, Academic Publishing, pp. 137-153.

Leuzinger, S., G. Zotz, R. Asshof & C. Körner, 2005. *Responses of deciduous forest trees to severe drought in Central Europe.* Tree Physiol. 25, 641-650.

Levy, P.E., R. Wendler, M. Van Oijen, M.G.R. Cannell & P. Millard, 2004. *The Effect of Nitrogen Enrichment on the Carbon Sink in Coniferous Forests: Uncertainty and Sensitivity Analyses of Three Ecosystem Models.* Water Air Soil Poll. Focus 4 (6), 67-74.

Lincoln, D.E., N. Sionit & B.R. Strain, 1984. *Growth and feeding response of Pseudoplusia includens (Lepidoptera: Noctuidae) to host plants grown in controlled* CO_2 *atmospheres.* Env. Entomol. 13 (6), 1527-1530.

Linderholm, H.W., 2006. *Growing season changes in the last century.* Agric. for. meteorol. 137 (1-2), 1-14.

Liski, J., D. Perruchoud & T. Karjalainen, 2002. *Increasing carbon stocks in the forest soils of western Europe.* Forest Ecol. Manage. 169 (1-2), 159-175.

Liski, J., T. Palosuo, M. Peltoniemi & R. Sievänen, 2005. *Carbon and decomposition model Yasso for forest soils.* Ecol. Model. 189 (1-2), 168-182.

Liu, C., C.J. Westman, B. Berg, W. Kutsch, G.Z. Wang, R. Man & H. Ilvesniemi, 2004. *Variation in litterfall-climate relationships between coniferous and broadleaf forests in Eurasia.* Global Ecol. Biogeogr. 13 (2), 105-114.

Loiseau, P. & J.F. Soussana, 2000. *Effects of elevated* CO_2*, temperature and N fertilization on nitrogen fluxes in a temperate grassland ecosystem.* Glob. Change Biol. 6 (8), 953-965.

Long, S.P., E.A. Ainsworth, A. Rogers & D.R. Ort, 2004. *Rising atmospheric carbon dioxide: Plants face the future.* Annu. Rev. Plant Biol. 55, 591-628.

Loustau, D., J. Ogee, E. Dufrene, M. Dequey, J.-L. Dupouey, V. Badeau, N. Viovy & P. Ciais, et al., 2007. *Chapter 18, Impacts of Climate Change on Temperate Forests and Interaction with Management.* Freer Smith, P.H. (Ed). Proceedings of the Wilton Park Meeting, November 2006.

Lowrance, R., 1992. *Groundwater nitrate and denitrification in a coastal plain riparian forest.* J. Environ. Qual. 21, 401-405.

MacDonald, J.A., N.B. Dise, E. Matzner, M. Armbruster, P. Gundersen & M. Forsius, 2002. *Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests.* Glob. Change Biol. 8 (10), 1028-1033.

Mace, G.M. & S.N. Stuart, 1994. *Draft IUCN Red List Categories, Version 2.2.* Species 21-22, 13-24.

Madrigal, A., J.G. Álvarez, R. Rodriguez & A. Rojo, 1999. *Tablas de Producción para los Montes Españoles (In Spanish).* Madrid, Fundación Conde del Valle de Salazar.

Magill, A.H., J.D. Aber, J.J. Hendricks, R.D. Bowden, J.M. Melillo & P.A. Steudler, 1997. *Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition.* Ecol. appl. 7 (2), 402-415.

Magill, A.H., J.D. Aber, W. Currie, K. Nadelhoffer, M. Martin, W.H. McDowell, J.M. Melillo & P. Steudler, 2004. *Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA.* Forest Ecol. Manage. 196 (1), 7-28.

Magnani, F., S. Leonardi, R. Tognetti, J. Grace & M. Borghetti, 1998. *Modelling the surface conductance of a broad-leaf canopy: effects of partial decoupling from the atmosphere.* Plant Cell. Environ. 21 (8), 867-879.

Magnani, F., M. Mencuccini, M. Borghetti, P. Berbigier, F. Berninger, S. Delzon, A. Grelle, P. Hari, P.G. Jarvis, P. Kolari, A.S. Kowalski, H. Lankreijer, B.E. Law, A. Lindroth, D. Loustau, G. Manca, J.B. Moncrieff, M. Rayment, V. Tedeschi, R. Valentini & J. Grace, 2007. *The human footprint in the carbon cycle of temperate and boreal forests.* Nature 447, 848-850.

Malcom, J.R., A. Markham, R.P. Neilson & M. Garaci, 2002. *Estimated migration rates under scenarios of global climate change.* J. Biogeogr. 29 (7), 835-849.

Maliondo, S.M., M.K. Mehendrappa & G.D. van Raalte, 1990. *Distribution of biomass and nutrients in some New Brunswick forest stands: possible implications of whole-tree harvesting.* Forestry Canada, Maritimes Region.

Marriott, C.A., M. Fothergill, B. Jeangros, M. Scotton & F. Louault, 2004. *Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review.* Agronomie 24 (8), 447-462.

Marschall, J., 1975. *Hilfstafeln für die Forsteinrichtung.* Österreichischer Agrarverlag Vienna (compilation of Norway spruce, fir, larch, Scots pine, beech and oak).

Martin, P.H., R. Valentini, M. Jacques, K. Fabbri, D. Galati, R. Quaratino, J.B. Moncrieff, P. Jarvis, N.O. Jensen, A. Lindroth, A. Grelle, M. Aubinet, R. Ceulemans, A.S. Kowalski, T. Vesala, P. Keronen, G. Matteucci, A. Grainer, P. Berbingier, D. Loustau, E.D. Schulze, J. Tenhunen, C. Rebman, A.J. Dolman, J.E. Elbers, C. Bernhofer, T. Grunwald, H. Thorgeirsson, P. Kennedy & S. Folving, 1998. *New estimate of the carbon sink strength of EU forests integrating flux measurements, field surveys, and space observations : 0.17-0.35 Gt (C).* Ambio 27 (7), 582-584.

Masera, O.R., J.F. Garza-Caligaris, M. Kanninen, T. Karjalainen, J. Liski, G.J. Nabuurs, A. Pussinen, B.H.J. de Jong & G.M.J. Mohren, 2003. *Modeling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach.* Ecol. Model. 164 (2-3), 177-199.

McFadden, D., 1979. *Quantitative methods for analysing travel behaviour of individuals. Some recent developments.* In: Hensher, D.A. & P.R. Stopher (Eds). Behavioural travel modelling. London, Croom Helm.

McMurtrie, R.E., B.E. Medlyn & R.C. Dewar, 2001. *Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years.* Tree Physiol. 21, 831-839.

Medlyn, B.E. & P.G. Jarvis, 1999. *Design and use of a database of model parameters from elevated [CO_2] experiments.* Ecol. Model. 124 (1), 69-83.

Medlyn, B.E., R.E. McMurtrie, R.C. Dewar & M.P. Jeffreys, 2000. *Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration.* Can. j. for. res. 30, 873-888.

Meentemeyer, V., E.O. Box & R. Thompson, 1982. *World patterns and amounts of terrestrial plant litter production.* Bioscience 32 (2), 125-128.

Meeuwsen, T.W.M. & H. Rottier, 1984. *Geschiedenis, biomassa en structuur van enige elzenbossen, wilgen-, gagel-, en kruipwilgstruwelen in Drenthe.* Wageningen, LH. Rapport 1896.

Meining, S., H. Schröter & K. von Wilpert, 2004. *Waldzustandsbericht 2004.* Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg.

Melillo, J.M., J.D. Aber & J.F. Muratore, 1982. *Nitrogen and Ligning control of hardwood leaf litter decomposition.* Ecology 63 (3), 621-626.

Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore, III, C.J. Vorosmarty & A.L. Schloss, 1993. *Global climate change and terrestrial net primary production.* Nature 363, 234-240.

Mellert, K.H., J. Prietzel, R. Straussberger & K.E. Rehfuess, 2004. *Long-term nutritional trends of conifer stands in Europe: results from the RECOGNITION project.* European Journal of Forest Research 123 (4), 305-319.

Menzel, A. & P. Fabian, 1999. *Growing season extended in Europe.* Nature 397, 659.

Mery, G., S. Laaksonen-Craig & J. Uuisvuori, 1999. *Forests, societies and environments in North America and Europe.* In: Palo, M. & J. Uusivuori (Eds). World Forests, Society and Environment. Volume 1. Dordrecht, Kluwer Academic Publishers, pp. 266-275.

Miller, H.G., J.D. Miller & J.M. Cooper, 1980. *Tables of biomass and accumulated nutrients at different growth rates in thinned plantations of Corsican Pine.* The Maculate institute for soil research.

Milne, R. & M. Van Oijen, 2005. *A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe.* Ann. For. Sci. 62 (8), 911-923.

Mitchell, T.D. & P.D. Jones, 2005. *An improved method of constructing a database of monthly climate observations and associated high-resolution grids.* Int. J. Climatol. 25 (6), 693-712.

Mol-Dijkstra, J., G.J. Reinds, J. Kros, B. Berg & W. de Vries, 2007. *Modelling interaction between carbon and nitrogen sequestration in forest soils on intensively monitored plots.* Forest Ecol. Manage., in prep.

Moldan, F., R.F. Wright, K.W. van der Hoek, J.W. Erisman, S. Smeulders & J.R. Wisniewski, 1998. *Episodic behaviour of nitrate in runoff during six years of nitrogen addition to the NITREX catchment at Gardsjon, Sweden.* Environ. Pollut. 102 (Supp 1), 439-444.

Monserud, R.A. & H. Sterba, 1996. *A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria.* Forest Ecol. Manage. 80 (1-3), 57-80.

Monteith, D.T., C.D. Evans & B. Reynolds, 2000. *Are temporal variations in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation?* Hydrol. Proc. 14 (10), 1745-1749.

Montgomery, D.C. & E.A. Peck, 1992. *Introduction to Linear Regression Analysis. 2nd Ed.* New York, John Wiley and Sons.

Müller, M., 2000. *Waldbaurahmenrichtlinie der Landesforstverwaltung Brandenburg.* AFZ-Der Wald 5/2000, 239-243.

Münier, B., B. Nygaard, R. Ejrnaes & H.G. Bruun, 2001. *A biotope landscape model for prediction of semi-natural vegetation in Denmark.* Ecol. Model. 139 (2-3), 221-233.

Murphy, K.L., J.M. Klopatek & C. Coe Klapotek, 1998. *The effects of litter quality and climate on decomposition along an elevational gradient.* Ecol. appl. 8 (4), 1061-1071.

Mussche, S., R. Samson, L. Nachtergale, A. de Schrijver, R. Lemeur & N. Lust, 2001. *A comparison of optical and direct methods for monitoring the seasonal dynamics of leaf area index in deciduous forests.* Silva Fenn. 35 (4), 373–384.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar & R.R. Nemani, 1997. *Increased plant growth in the northern high latitudes from 1981 to 1991.* Nature 386, 698-702.

Nabuurs, G.J., R. Päivinen, R. Sikkema & G.M.J. Mohren, 1997. *The role of European forests in the global carbon cycle--a review.* Biomass and Bioenergy 13 (6), 345-358.

Nabuurs, G.J., M.J. Schelhaas & A. Pussinen, 2000. *Validation of the European Forest Information Scenario Model (EFISCEN) and a projection of Finnish forests.* Silva Fenn. 34 (2), 167-179.

Nabuurs, G.J., R. Päivinen & H. Schanz, 2001. *Sustainable management regimes for Europe's forests - A projection with EFISCEN until 2050.* Forest policy and economics 3 (3-4), 55-173.

Nabuurs, G.J., R. Päivinen, A. Pussinen & M.J. Schelhaas, 2002. *Development of European forests until 2050.* Leiden, Brill. EFI Research Report 15.

Nabuurs, G.J. & M.J. Schelhaas, 2002. *Carbon profiles of typical forest types across Europe assessed with CO2FIX.* Ecological Indicators 1 (3), 213-223.

Nabuurs, G.J. & M.J. Schelhaas, 2003. *Spatial distribution of whole-tree carbon stocks and fluxes across the forests of Europe: where are the options for bio-energy?* Biomass and Bioenergy 24 (4-5), 311-320.

Nabuurs, G.J., M.J. Schelhaas, A. Ouwehand, A. Pussinen, J. van Brusselen, E. Pesonen, A. Schuck, M.F.F.W. Jans & L. Kuiper, 2003. *Future wood supply from*

European forests. Implications to the pulp and paper industry. Wageningen, Alterra, Green World Research. Alterra-rapport 927.

Nabuurs, G.J., A. Pussinen, J. van Brusselen & M.J. Schelhaas, 2007. *Future harvesting pressure on European forests.* European Journal of Forest Research 126 (3), 391-400.

Nadelhoffer, K.J., M.R. Downs, B. Fry, J.D. Aber, A.H. Magill & J.M. Melillo, 1995. *The fate of* ^{15}*N labelled nitrate additions to a northern hardwood forest in eastern Maine, USA.* Oecologia 103 (3), 292-301.

Nadelhoffer, K.J., M.R. Downs & B. Fry, 1999a. *Sinks for* ^{15}*N-enriched additions to an oak forest and a red pine plantation.* Ecol. appl. 9 (1), 72–86.

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

Nagel, J., 1999. *Konzeptionelle Überlegungen zum schrittweisen Aufbau eines waldwachstumkundlichen Simulationsssytems für Nordwestdeutschland.* Schriften aus der Fortslichen Fakultät der Universität Göttingen un der Niedersächsischen Forstlichen Versuchsanstalt. Band 128.

Nash, J.E. & V. Sutcliffe, 1970. *River flow forecasting through conceptual models. I. A discussion of principles.* J. Hydrol. 10 (3), 282-290.

Näslund, M., 1947. *Funktioner och tabeller för kubering av stående träd. Tall, gran och björk i södra Sverige samt hela landet (In Swedish with English summary).* Meddelande från Statens Skogsforskningsinstitut 36.

Neff, J.C., A.R. Townsend, G. Gleixner, S.J. Lehman, J. Turnbull & W.D. Bowman, 2002. *Variable effects of nitrogen additions on the stability and turnover of soil carbon.* Nature 419, 915-917.

Nellemann, C. & M.G. Thomsen, 2001. *Long-term changes in forest growth: Potential effects of nitrogen deposition and acidification.* Water Air Soil Pollut. 128 (3-4), 197-205.

Ni, J., X.-S. Zhang & J.M.O. Scurlock, 2001. *Synthesis and analysis of biomass and net primary productivity in Chinese forests.* Ann. For. Sci. 58 (4), 351-384.

Nierop, K.G.J., B. van Lagen & P. Buurman, 2001. *Composition of plant tissues and soil organic matter in the first stages of a vegetation succession.* Geoderma 100 (1-2), 1-24.

Nilsen, P. & J. Larsson, 1992. *Bonitering av skog ved hjelp av vegetasjontype og egenskaper ved voksestedet [Site index estimation from vegetation type and site properties].* Cs, Norsk Institutt for Skogsforskning. Rapport Skogsforskning 22/92.

Nilsen, P., 2001. *Fertilization Experiments on Forest Mineral Soils: A Review of the Norwegian Results.* Scand. J. For. Res. 16, 541-554.

Nilsen, P. & G. Abrahamsen, 2003. *Scots pine and Norway spruce stands responses to annual N, P and Mg fertilization.* Forest Ecol. Manage. 174 (1-3), 221-232.

Nilsson, S.G., J. Hedin & M. Niklasson, 2001. *Biodiversity and its assessment in boreal and nemoral forests.* Scand. J. For. Res. 16 (S3), 10-26.

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson & R. Ceulemans, 1999. *Tree responses to rising* CO_2 *in field experiments: Implications for the future forest.* Plant Cell. Environ. 22 (6), 683-714.

Norby, R.J., E.H. DeLucia, B. Gielen, C. Calfapietra, C.P. Giardina, J.S. King, J. Ledford, H.R. McCarthy, D.J.P. Moore, R. Ceulemans, P. De Angelis, A.C. Finzi, D.F. Karnosky, M.E. Kubiske, M. Lukac, K.S. Pregitzer, G.E. Scarascia-Mugnozza, W.H. Schlesinger & R. Oren, 2005. *Forest response to elevated* CO_2 *is conserved across a broad range of productivity.* Proc. Natl. Acad. Sci. USA 102 (50), 18052-18056.

Nowak, R.S., D.S. Ellsworth & S.D. Smith, 2004. *Functional responses of plants to elevated atmospheric* CO_2 *- do photosynthetic and productivity data from FACE experiments support early predictions?* New Phytol. 162 (2), 253-280.

O'Connell, A.M., 1994. *Decomposition and nutrient content of litter in a fertilized eucalypt forest.* Biol. fertil. soils 17, 169-166.

Ogaya, R., J. Peñuelas, J. Martínez-Vilalta & M. Mangirón, 2003. *Effect of drought on diameter increment of Quercus ilex, Phillyrea latifolia, and Arbutus unedo in a holm oak forest of NE Spain.* Forest Ecol. Manage. 180 (1-3), 175-184.

Ogink-Hendriks, M.J., 1995. *Modelling surface conductance and transpiration of an oak forest in The Netherlands.* Agric. for. meteorol. 74 (1-2), 99-119.

Ohlson, M., L. Soderstrom, G. Hornberg, O. Zackrisson & J. Hermansson, 1997. *Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests.* Biol. Conserv. 81 (3), 221-231.

Olff, H., J. de Leeuw, J.P. Bakker, R.J. Platerink, H.J. van Wijnen & W. de Munck, 1997. *Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient.* J. Ecol. 85 (6), 799-814.

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

Oura, N., J. Shindo, T. Fumoto, H. Toda & H. Kawashima, 2001. *Effects of nitrogen deposition on nitrous oxide emissions from the forest floor.* Water Air Soil Pollut. 130, 673-678.

Pacala, S.W., G.C. Hurtt, D. Baker, P. Peylin, R.A. Houghton, R.A. Birdsey, L. Heath, E.T. Sundquist, R.F. Stallard, P. Ciais, P. Moorcroft, J.P. Caspersen, E. Shevliakova, B. Moore, G. Kohlmaier, E. Holland, M. Gloor, M.E. Harmon, S.-M. Fan, J.L. Sarmiento, C.L. Goodale, D. Schimel & C.B. Field, 2001. *Consistent Land- and Atmosphere-Based U.S. Carbon Sink Estimates.* Science 292 (5525), 2316-2320.

Pajuoja, H., 1995. *The outlook for the European Forest Resources and roundwood supply.* Geneva, United Nations Economic Commission for Europe. Geneva Timber and Forest Discussion Papers ECE/TIM/DP/4.

Papale, D. & R. Valentini, 2003. *A new assessment of European forests carbon exchanges by eddy fluxes and artificial neural network spatialization.* Glob. Change Biol. 9 (4), 525-535.

Parton, W.J., D.S. Schimel, C.V. Cole & D.S. Ojima, 1987. *Analysis of factors controlling soil oranic matter levels in Great Plains Grasslands.* Soil Sci. Soc. Am. J. 51, 1173-1179.

Parton, W.J., J.M.O. Scurlock, D.S. Ojima, T.G. Gilmanov, R.J. Scholes, D.S. Schimel, T. Kirchner, J.C. Menaut, T. Seastedt, E.G. Moya, A. Kamnalrut & J.I. Kinyamario, 1993. *Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide.* Glob. Biogeochem. Cycles 7 (4), 785-809.

Paul, K., 2001. *Temperature and moisture effects on decomposition.* Procedings of the NEE workshop, 18-20 april 2001.

Paul, K.I., P.J. Polglase, A.M. O'Connell, J.C. Carlyle, P.J. Smethurst & P.K. Khanna, 2002. *Soil nitrogen availability predictor (SNAP): a simple model for predicting mineralisation of nitrogen in forest soils.* Aust. J. Soil Res. 40 (6), 1011-1026.

Peck, T., 1998. *General introduction to the main forest challenges worldwide: a European perspective.* Proceedings of the 2nd International Forest Policy Forum (CTFC). Vol 4. Solsona,

Peng, C., J.M. Apps, D.T. Price, I.A. Nalder & D.H. Halliwell, 1998. *Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada, 1, Model testing.* Glob. Biogeochem. Cycles 12, 381-392.

Perruchoud, D., L. Walthert, S. Zimmermann & P. Lüscher, 1999. *Contemporary carbon stocks of mineral forest soils in the Swiss Alps.* Biogeochem. 50 (2), 111–136.

Persson, O.A., H. Eriksson & U. Johansson, 1995. *An attempt to predict long-term effects of atmospheric nitrogen deposition on the yield of Norway spruce stands (Picea abies (L.) Karst.) in southwestern Sweden.* Plant soil 168-169 (1), 249-254.

Persson, T., A. Rudebeck, J.H. Jussy, M. Colin-Belgrand, A. Primé, E. Dambrine, P.S. Karlsson & R.M. Sjöberg, 2000. *Soil Nitrogen Turnover-Mineralisation, Nitrifacation and Denitrification in European Forest Soils.* In: Schulze, E.-D. (Ed). Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies 142. Berlin Heidelberg New York, Springer, pp. 297-331.

Peterson, B.J. & J.M. Melillo, 1985. *The potential storage of carbon caused by eutrophication of the biosphere.* Tellus 37B, 117-127.

Pettersson, F., 1994. *Predictive Functions for Impact of Nitrogen Fertilization on Growth over Five Years.* Forestry Research Institute of Sweden. Report 3.

Pilkington, M.G., S.J.M. Caporn, J.A. Carroll, N. Cresswell, J.A. Lee, T.W. Ashenden, S.A. Brittain, B. Reynolds & B.A. Emmett, 2005a. *Effects of increased deposition of atmospheric nitrogen on an upland moor: leaching of N species and soil solution chemistry.* Environ. Pollut. 135 (1), 29-40.

Pilkington, M.G., S.J.M. Caporn, J.A. Carroll, N. Cresswell, J.A. Lee, B.A. Emmett & D. Johnson, 2005b. *Effects of increased deposition of atmospheric nitrogen on an upland Calluna moor: N and P transformations.* Environ. Pollut. 135 (3), 469-480.

Pollanschütz, J., 1974. *Formzahlfunktionen der Hauptbaumarten Österreichs.* Allg. Forstzeitung 85 (12), 341-343.

Poorter, H., 1993. *Interspecific variation in the growth response of plants to an elevated ambient* CO_2 *concentration.* Vegetatio 104-105 (1), 77-97.

Porté, A. & H.H. Bartelink, 2002. *Modelling mixed forest growth: a review of models for forest management.* Ecol. Model. 150 (1-2), 141-188.

Power, S.A., E.R. Green, C.G. Barker, J.N.B. Bell & M.R. Ahmore, 2006. *Ecosystem recovery: heathland response to a reduction in nitrogen deposition.* Glob. Change Biol. 12 (7), 1241-1252.

Powlson, D.S., P. Smith & J.U. Smith, 1996. *Evaluation of Soil Organic Matter Models.* Berlin, Springer.

Prach, K., S. Bartha, C.B. Joyce, P. Pysek, R. van Diggelen & G. Wiegleb, 2001. *The role of spontaneous vegetation succession in ecosystem restoration: A perspective.* Appl. Veg. Sci. 4 (1), 111-114.

Pretzsch, H., 1992. *Zunehmende Unstimmigkeit zwischen erwartetem und wirklichem Wachstum unserer Waldbestände.* Forstw. Cbl. 111, 366-382.

Pretzsch, H. & P. Biber, 2005. *A Re-Evaluation of Reineke's Rule and Stand Density Index.* For. sci. 51 (4), 304-320.

Prins, H., J. Postmus, A.M. Reker & B. Ruiter, 1988. *Nitrogen use on grassland in spring in the Netherlands and elsewhere in Europe: temperature sum, stage of growth, rate and source of nitrogen.* Netherlands fertilizer technical bulletin 17.

Probert, M.E., J.P. Dimes, B.A. Keating, R.C. Dalal & W.M. Strong, 1998. *APSIM's water and nitrogen modules and simulation of the dynamics of water and nitrogen in fallow systems.* Agricultural Systems 56 (1), 1-28.

Prodan, M., 1965. *Holzmeßlehre.* Frankfurt/M., J. D. Sauerländer.

Puértolas, J., L. Gil & J.A. Pardos, 2005. *Effects of nitrogen fertilization and temperature on frost hardiness of Aleppo pine (Pinus halepensis Mill.) seedlings assessed by chlorophyll fluorescence.* Forestry 78 (5), 501-511.

Pussinen, A., G.J. Nabuurs, R. Wieggers, G.J. Reinds, J. Kros, W. Wamelink, J.P. Mol-Dijkstra & W. de Vries, 2007. *Upscaling impacts of changes in nitrogen deposition, climate and carbon dioxide concentration on growth and carbon sequestration of European forests.* Forest Ecol. Manage. (in prep).

Radoglou, K.M. & P.G. Jarvis, 1990. *Effects of* CO_2 *Enrichment on Four Poplar Clones. I. Growth and Leaf Anatomy.* Ann. Bot. 65 (6), 617-626.

Rastetter, E.B., G.I. Ågren & G.R. Shaver, 1997. *Responses of N-limited ecosystems to increased* CO_2*: A balanced- nutrition, coupled-element-cycles model.* Ecol. appl. 7 (2), 444-460.

Reddy, K.R., M.L. Boone, A.R. Reddy, H.F. Hodges, S.B. Turner & J.M. Mckinion, 1995. *Developing and validating a model for a plant growth regulator.* Agronomy 87 (6), 1100-1105.

Rehfuess, K.-E., G.I. Ågren, F. Andersson, M.G.R. Cannell, A. Friend, I. Hunter, H.-P. Kahle, J. Prietzel & H. Spiecker, 1999. *Relationships between recent changes of growth and nutrition of Norway spruce, Scots pine and European beech forests in Europe-RECOGNITION.* Working Paper 19, Joensuu, Finland, European Forest Institute.

Reich, P.B., J. Knops, D. Tilman, J. Craine, D. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S. Naeem, D. Bahauddin, G. Hendrey, S. Jose, K. Wrage, J. Goth & W. Bengston, 2001. *Plant diversity enhances ecosystem responses to elevated* CO_2 *and nitrogen deposition.* Nature 410, 809-810.

Reichle, D.E. (Ed.) 1981. *Dynamic Properties of Forest Ecosystems.* Cambridge, UK, Cambridge University Press.

Reineke, L.H., 1933. *Perfecting a stand-density index for even-aged forests.* J. Agric. Res. 46 (7), 627-638.

Roem, W.J. & F. Berendse, 2000. *Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities.* Biol. Conserv. 92 (2), 151-161.

Rosenqvist, L., K. Hansen, L. Vesterdal, H. Denier van der Gon, C. van der Salm, A. Bleeker & M.-B. Johansson, 2007. *Nitrogen deposition and nitrate leaching following afforestation: Experiences from oak and Norway spruce chronosequences in Denmark, Sweden and the Netherlands.* In: Heil, G.W., B. Muys & K. Hansen (Eds). Environmental Effects of Afforestation in North-Western Europe. From Field Observations to Decision Support. Springer Series: Plant and Vegetation, Vol. 1, pp. 79-108.

Ruess, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Sveinbjornssön, M.F. Allen & G.E. Maurer, 2003. *Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska.* Ecol. monogr. 73 (4), 643-662.

Runhaar, J., P.E.V. van Walsum & F.J.E. van der Bolt, 1999. *Natuurgericht Landevaluatiesysteem (NATLES).* Wageningen, Staring Centrum.

Sariyildiz, T., 2003. *Litter decomposition of Picea orientalis, Pinus sylvestris and Castanea sativa trees grown in Artvin in relation to their initial litter quality variables.* Turk. J. Agric. For. 27 (4), 237-243.

Saxe, H., D.S. Ellsworth & J. Heath, 1998. *Tree and forest functioning in an enriched* CO_2 *atmosphere.* New Phytol. 139, 395-436.

Schaffers, A.P., 2002. *Soil, biomass, and management of semi-natural vegetation. Part II. Factors controlling species diversity.* Plant Ecol. 158 (2), 247-268.

Schär, C., P. Vidale, D. Lüthi, C. Frei, C. Häberli, M. Liniger & C. Appenzeller, 2004. *The role of increasing temperature variability in European summer heatwaves.* Nature 427, 332-336.

Schelhaas, M.J., J. van Brusselen, A. Pussinen, E. Pesonen, A. Schuck, G.J. Nabuurs & V. Sasse, 2006a. *Outlook for the development of European forest resources. A study prepared for the European Forest Sector Outlook Study (EFSOS).* Geneva, UN-ECE. Geneva Timber and Forest Discussion Paper, ECE/TIM/DP/41.

Schelhaas, M.J., S. Varis, A. Schuck & G.J. Nabuurs, 2006b. *EFISCEN Inventory Database.* Joensuu, Finland, European Forest Institute. http://www.efi.int/databases/efiscen/

Schelhaas, M.J., E. Cienciala, M. Lindner, G.J. Nabuurs & G. Zianchi, 2007a. *Selection and quantification of forestry measures targeted at the Kyoto Protocol and the Convention on Biodiversity. MEACAP project.* Alterra Report in press.

Schelhaas, M.J., J. Eggers, M. Lindner, G.J. Nabuurs, A. Pussinen, R. Paivinen, A. Schuck, P.J. Verkerk, D.C. van der Werf & S. Zudin, 2007b. *Model documentation for the European Forest Information Scenario Model (EFISCEN 3.1.3).* Alterra Report in press.

Schenk, U., R. Manderscheid, J. Hugen & H.J. Weigel, 1995. *Effects of CO_2 enrichment and intraspecific competition on biomass partitioning, nitrogen content and microbial biomass carbon in soil of perennial ryegrass and white clover.* J. Exp. Bot. 46 (8), 987-993.

Schieler, K., 1988. *Methodische Fragen in Zusammenhang mit der Österreichischen Forstinventur.* Dissertation, Wien, Universität für Bodenkultur Wien.

Schindler, D.W. & S.E. Bayley, 1993. *The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition.* Glob. Biogeochem. Cycles 7, 717-733.

Schindler, D.W., 1999. *Carbon cycling: The mysterious missing sink.* Nature 398, 105-107.

Schlamadinger, B., 2005. *Multi-source inventory methods for quantifying carbon stocks and stock changes in European forests.* Graz, Austria, Joanneum Research. CarboInvent Final Report to the EC. Executive Summary.

Schmid, S., E. Thürig, E. Kaufmann, H. Lischke & H. Bugmann, 2006. *Effect of forest management on future carbon pools and fluxes: A model comparison.* Forest Ecol. Manage. 237 (1-3), 65-82.

Schmidt, A., 1969. *Der Verlauf des Höhenwachstums von Kiefern auf einigen Standorten der Oberpfalz.* Forstw. Cbl. 88, 33-40.

Scholze, M., W. Knorr, N.W. Arnell & I.C. Prentice, 2006. *A climate-change risk analysis for world ecosystems.* Proc. Natl. Acad. Sci. USA 103, 13116-13120.

Schöpp, W., M. Posch, S. Mylona & M. Johansson, 2003a. *Long-term development of acid deposition (1880-2030) in sensitive freshwater regions in Europe.* Hydrol. Earth Syst. Sci. 7 (4), 436-446.

Schöpp, W., M. Posch, S. Mylona & M. Johansson, 2003b. *Long-term development of acid deposition (1880–2030) in sensitive freshwater regions in Europe.* Hydrology and Earth System Sciences 7 (4), 436-446.

Schulze, E.D. (Ed.) 2000. *Carbon and Nitrogen Cycling in European Forest Ecosystems.* Ecological Studies 142, Berlin Heidelberg New York, Springer.

Schulze, E.D., L. Högberg, H. van Oene, T. Persson, A.F. Harrison, D. Read, A. Kjøller & G. Matteucci, 2000. *Interactions between the carbon and nitrogen cycle and the role of biodiversity: A synopsis of a study along a North-south transect through Europe.* In: Schulze, E.D. (Ed). Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies 142. Berlin Heidelberg New York, Springer, pp. 468-492.

Schweingruber, F.H., 1996. *Tree rings and environment.* Bern, Paul Haupt.

Shaver, G.R., M.S. Bret-Harte, M.H. Jones, J. Johnstone, L. Gough, J. Laundre & F.S. Chapin, III, 2001. *Species composition interacts with fertilizer to control long-term change in tundra productivity.* Ecology 82 (11), 3163-3181.

Sievering, H., 1999. *Reply to Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests.* Nature 400, 629-630.

Sievering, H., I. Fernandez, J. Lee, J. Hom & L. Rustad, 2000. *Forest canopy uptake of atmospheric nitrogen deposition at eastern US conifer sites: Carbon storage implications?* Glob. Biogeochem. Cycles 14, 1153-1159.

Silva, F.C.E., A. Shvaleva, J.P. Maroco, M.H. Almeida, M.M. Chaves & J.S. Pereira, 2004. *Responses to water stress in two Eucalyptus globulus clones differing in drought tolerance.* Tree Physiol. 24, 1165-1172.

Silver, W.L. & R.K. Miya, 2001. *Global patterns in root decomposition: comparisons of climate and litter quality effects.* Oecologia 129 (3), 407-419.

Simpson, D., H. Fagerli, J.E. Jonson, S. Tsyro, P. Wind & J.-P. Tuovinen, 2003. *Transboundary Acidification, Eutrophication and Ground Level Ozone in Europe PART I. Unified EMEP Model Description.* Norwegian Meteorological Institute. EMEP Status Report 2003.

Simpson, D., K. Butterbach-Bahl, H. Fagerli, M. Kesik, U. Skiba & S. Tang, 2006. *Deposition and emissions of reactive nitrogen over European forests: A modelling study.* Atmos. Environ. 40, 5712-5726.

Sitch, S., B. Smith, I.C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J.O. Kaplan, S. Levis, W. Lucht, M.T. Sykes, K. Thonicke & S. Venevsky, 2003. *Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model.* Glob. Change Biol. 9 (2), 161-185.

Smith, B., I.C. Prentice & M.T. Sykes, 2001. *Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space.* Global Ecol. Biogeogr. 10 (6), 621-637.

Smith, P., J.U. Smith, D.S. Powlson, W.B. McGill, J.R.M. Arah, O.G. Chertov, K. Coleman, U. Franko, S. Frolking, D.S. Jenkinson, L.S. Jensen, R.H. Kelly, H. Klein-Gunnewiek, A.S. Komarov, C. Li, J.A.E. Molina, T. Mueller, W.J. Parton, J.H.M. Thornley & A.P. Whitmore, 1997. *A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments.* Geoderma 81 (1-2), 153-225.

Smith, S.D., T.E. Huxman, S.F. Zitzer, T.N. Charlet, D.C. Housman, J.S. Coleman, L.K. Fenstermaker, J.R. Seemann & R.S. Nowak, 2000. *Elevated CO_2 increases productivity and invasive species success in an arid ecosystem.* Nature 408, 79-82.

Solberg, S., K. Andreassen, N. Clarke, K. Torseth, O.E. Tveito, G.H. Strand & S. Tomter, 2004. *The possible influence of nitrogen and acid deposition on forest growth in Norway.* Forest Ecol. Manage. 192 (2-3), 241-249.

Solberg, S., M. Dobbertin, G.J. Reinds, K. Andreassen, H. Lange, P.G. Fernandez, A. Hildingsson & W. de Vries, 2007. *The impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: An empirical stand growth model.* Forest Ecol. Manage. (submitted).

Spiecker, H., 1990. *Growth variation and environmental stresses: long-term observations on permanent research plots in Southwestern Germany.* Water Air Soil Pollut. 54 (1), 247-256.

Spiecker, H., 1995. *Growth dynamics in a changing environment - Long-term observations.* Plant soil 168-169 (1), 555-561.

Spiecker, H., K. Mielikäinen, M. Kölh & J.P. Skovsgaard (Eds.), 1996. *Growth trends in European forests. Studies from 12 Countries.* Research Report 5, Berlin, Heidelberg, Springer-Verlag.

Starr, M., 1999. *WATBAL: a model for estimating monthly water balance components, including soil water fluxes.* In: Kleemola, S. & M. Forsius (Eds). 8th Annual report 1999. UN ECE ICP Intergrated Monitoring. Helsinki, Finland, The Finnish Environment 325. Finnish Environment Institute, pp. 31-35.

Stefan, K., A. Fürst, R. Hacker & U. Bartels, 1997. *Forest Foliar Condition in Europe. Results of large-scale foliar chemistry surveys (survey 1995 and data from previous years).* Brussels, Geneva, EC-UN/ECE.

Steffen, W., I. Noble, J. Canadel, M. Apps, E.-D. Schultze, P. Jarbis, D. Baldocchi, P. Ciais, W. Cramer, J. Ehleringer, G. Farquhar, C.B. Field, R. Gifford & M. Heimann, 1998. *The terrestrial carbon cycle: implications for the Kyoto protocol.* Science 280, 1393-1394.

Stevens, C.J., N.B. Dise, J.O. Mountford & D.J. Gowing, 2004. *Impact of nitrogen deposition on the species richness of grasslands.* Science 303, 1876-1879.

Streck, N.A., F.L.M. de Paula, D.A. Bisognin, A.B. Heldwein & J. Dellai, 2007. *Simulating the development of field grown potato (Solanum tuberosum L.).* Agric. for. meteorol. 142 (1), 1-11.

Sutton, M.A., D. Simpson, P.E. Levy, R.I. Smith, S. Reis & M. van Oijen, 2007. *Exceptional effect of N on forest carbon?* Nature submitted.

Swift, M.J., O. Andren, L. Brussaard, M. Briones, M.-M. Couteaux, K. Ekschmitt, A. Kjoller, P. Loiseau & P. Smith, 1998. *Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies.* Glob. Change Biol. 4 (7), 729-743.

Tamm, C.O., A. Aronsson, B. Popovic & J. Flower-Ellis, 1999. *Optimum nutrition and nitrogen saturation in Scots pine stands.* Stud. for. suec. 209, 1-126.

Tarasón, L. & J. Schaug, 2000. *Transboundery acidification and eutrophication in Europe.* Oslo, Norway, Norwegian meteorological institute. EMEP Summary Report.

Tarasón, L., J.E. Jonson, H. Fagerli, A. Benedictow, P. Wind, D. Simpson & H. Klein, 2003. *Transboundary Acidification, Eutrophication and Ground Level Ozone in Europe PART III. Source-receptor relationships.* Oslo, Norway, Norwegian meteorological institute. EMEP Status Report.

Tausz, M., W. Trummer, A. Wonisch, W. Goessler, D. Grill, M.S. Jimenez & D. Morales, 2004. *A survey of foliar mineral nutrient concentrations of Pinus canariensis at field plots in Tenerife.* Forest Ecol. Manage. 189 (1-3), 49-55.

Terry, A.C., M.R. Ashmore, S.A. Power, E.A. Allchin & G.W. Heil, 2004. *Modelling the impacts of atmospheric nitrogen deposition on Calluna-dominated ecosystems in the UK.* J. appl. ecol. 41 (5), 897-909.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-huerta, A. Townsend peterson, O.L. Phillips & S.E. Williams, 2004. *Extinction risk from climate change.* Nature 427, 145-148.

Thomas, S.C., C.B. Halpern, D.A. Falk, D.A. Liguori & K.A. Austin, 1999. *Plant diversity in managed forests: Understory responses to thinning and fertilization.* Ecol. appl. 9 (3), 864-879.

Thornthwaite, C.W. & J.R. Mather, 1957. *Instructions and tables for computing potential evapotranspiration and the water balance.* Publications in Climatology 10, 185-311.

Thornton, P.E., B.E. Law, H.L. Gholz, K.L. Clark, E. Falge, D.S. Ellsworth, A.H. Goldstein, R.K. Monson, D. Hollinger, M. Falk, J. Chen & J.P. Sparks, 2002. *Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests.* Agric. for. meteorol. 113 (1-4), 185-222.

Thurston, J.M., E.D. Williams & A.E. Johnston, 1976. *Modern developments in an experiment on permanent grassland started in 1856: effects of fertilizers and lime on botanical composition and crop and soil analyses.* Ann. agron. 27, 1043-1082.

Tietema, A., B.A. Emmett, P. Gundersen, O.J. Kjønaas & C. Koopmans, 1998. *The fate of ^{15}N-labelled nitrogen deposition in coniferous forest ecosystems.* Forest Ecol. Manage. 101 (1-3), 19-27.

Tietema, A., J.P. Mol Dijkstra, J. Kros & W. de Vries, 2002. *Dynamic nitrogen deposition thresholds during forest stand developments in a Douglas fir forest analysed with two nitrogen models SMART2 and MERLIN.* Hydrol. Earth Syst. Sci. 6 (3), 375-382.

Tognetti, R., P. Cherubini & J.L. Innes, 2000. *Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO2 concentrations.* New Phytol. 146 (1), 59-74.

Townsend, A.R., B.H. Braswell, E.A. Holland & J.E. Penner, 1996. *Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen.* Ecol. appl. 6 (3), 806-814.

Tveite, B. & H. Braastad, 1981. *Bonitering av gran, furu og bjørk (In Norwegian).* In: Norsk Skogbruk 1981. pp. 17-22.

Tveite, B., G. Abrahamsen & A.O. Stuanes, 1990. *Liming and wet acid deposition effects on tree growth and nutrition - experiemental results.* Water Air Soil Pollut. 54, 409-422.

Ulrich, B., R. Mayer & P.K. Khanna, 1979. *Die Deposition von Luftverunreinigungen und ihre Auswirkungen in Waldokosystemen im Solling.* Schriften aus der Forstl. Fak. D. Univ. Göttingen und der Nierders. Vers. Anst. Bd. 58.

UN-ECE/FAO, 2000. *Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand.* Geneva Timber and Forest Study Papers, No 17.

UN/ECE & EC, 2001. *Forest condition in Europe. Report on the 2000 survey.* Brussels, Geneva, UN/ECE CEC.

Uuttera, J., M. Maltamo & K. Kuusela, 1996. *Impact of forest management history on the state of forests in relation to natural forest succession - Comparative study, north Karelia, Finland vs Republic of Karelia, Russian Federation.* Forest Ecol. Manage. 83 (1-2), 71-85.

Uzoh, F. & W.W. Oliver, 2006. *Individual tree height increment model for managed even-aged stands of ponderosa pine throughout the western United States using linear mixed effects models.* Forest Ecol. Manage. 221 (1-3), 147-154.

Valentini, R., G. Matteucci, A.J. Dolman, E.D. Schulze, C. Rebmann, E.J. Moors, A. Granier, P. Gross, N.O. Jensen, K. Pilgaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grünwald, M. Aubinet, R. Ceulemans, A.S. Kowalski, T. Vesala, Ü. Rannik, P. Berbigier, D. Loustau, J. Gudmundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Montagnani, S. Minerbi & P.G. Jarvis, 2000. *Respiration as the main determinant of carbon balance in European forests.* Nature 404 (20 April), 861-865.

Van Andel, J., J.P. Bakker & A.P. Grootjans, 1993. *Mechanisms of vegetation succession - a review of concepts and perspectives.* Acta Bot. Neerl. 42 (4), 413-433.

Van den Burg, J., 1985. *Foliar analysis for determination of tree nutrient status - a compilation of literature data.* Wageningen, Rijksinstituut voor onderzoek in de bos- en landschapsbouw "De Dorschkamp". Rapport nr. 414.

Van den Burg, J., 1987. *Relaties tussen het vochtleverend vermogen van de grond, het waterverbruik en de groei van een aantal boomsoorten : een literatuurstudie.* Utrecht, Studiecommissie Waterbeheer Natuur, Bos en Landschap. SNWBL rapport 7.

Van den Burg, J., 1989. *Verloop van de ammonium- en nitraatgehalten van de minerale bovengrond en van de naaldsamenstelling van vijf naaldboomcultures in de boswachterij Oostereng 1987 - 1988.* Wageningen, "De Dorschkamp"; Instituut voor Bosbouw en Groenbeheer.

Van der Putten, W.H., S.R. Mortimer, K. Hedlund, C. van Dijk, V.K. Brown, J. Lepš, C. Rodriguez-Barrueco, J. Roy, T.A.D. Len, D. Gormsen, G.W. Korthals, S. Lavorel, I. Santa Regina & P. Smilauer, 2000. *Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach.* Oecologia 124 (1), 91-99.

Van der Salm, C., G.J. Reinds & W. de Vries, 2007a. *Water balances in intensively monitored forest ecosystems in Europe.* Environ. Pollut. 148 (1), 201-212.

Van der Salm, C., L. Rosenqvist, L. Vesterdal, K. Hansen, H. Denier van der Gon, A. Bleeker, R. Wieggers & A. Van den Toorn, 2007b. *Interception and water recharge following afforestation: Experiences from oak and Norway spruce chronosequences in Denmark, Sweden and the Netherlands.* In: Heil, G.W., B. Muys & K. Hansen (Eds). Environmental Effects of Afforestation in North-Western Europe. From Field Observations to Decision Support. Vol. Springer Series: Plant and Vegetation, Vol. 1, pp. 53-77.

Van der Wal, R., S. van Lieshout, D. Bos & R.H. Drent, 2000. *Are spring staging brent geese evicted by vegetation succession?* Ecography 23 (1), 60-69.

Van Diggelen, R., W.J. Molenaar & A.M. Kooijman, 1996. *Vegetation succession in a floating mire in relation to management and hydrology.* J. Veg. Sci. 7 (6), 809-820.

Van Dobben, H.F., C.J.F. ter Braak & G.M. Dirkse, 1999. *Undergrowth as a biomonitor for deposition of nitrogen and acidity in pine forest.* Forest Ecol. Manage. 114 (1), 83-95.

Van Dobben, H.F., M. van Elswijk, M.S. Grobben, P. Groenendijk, H. Houweling, M.J.W. Jansen, J.P. Mol-Dijkstra, A.J. Otjens, J.A. te Roller, E.P.A.G. Schouwenberg & G.W.W. Wamelink, 2002a. *Technische Documentatie Modellen Raamwerk Ecologie: Herstructurering van het modelinstrumentarium voor integrale analyse van de ecologische effecten van milieumaatregelen, veranderend landgebruik en waterbeheer.* Wageningen, Alterra. Report 549.

Van Dobben, H.F., G.W.W. Wamelink, E.P.A.G. Schouwenberg & J.P. Mol, 2002b. *Use of coupled models to predict biodiversity in managed ecosystems.* Reports in ecology and environmental engineering 1, 76 - 86.

Van Dobben, H.F., A. van Hinsberg, E.P.A.G. Schouwenberg, M.J.W. Jansen, J.P. Mol-Dijkstra, H.J.J. Wieggers, J. Kros & W. de Vries, 2006. *Simulation of critical loads for nitrogen for terrestrial plant communities in the Netherlands.* Ecosystems 9 (1), 32-45.

Van Oene, H., F. Berendse & C.G.F. de Kovel, 1999a. *Model analysis of the effects of historic CO_2 levels and nitrogen inputs on vegetation succession.* Ecol. appl. 9 (3), 920-935.

Van Oene, H., M. van Deursen & F. Berendse, 1999b. *Plant-herbivore interaction and its consequences for succession in wetland ecosystems: a modelling approach.* Ecosystems 2 (2), 122-138.

Van Oijen, M., M.G.R. Cannell & P.E. Levy, 2004. *Modelling biogeochemical cycles in forests: state of the art and perspectives.* In: Andersson, F., Y. Birot & R. Päivinen (Eds). Towards the Sustainable Use of Europe's Forests - Forest Ecosystem and Landscape Research: Scientific Challenges and Opportunities. European Forest Institute, pp. 157-169.

Van Oijen, M. & R. Jandl, 2004. *Nitrogen fluxes in two Norway spruce stands in Austria: An analysis by means of process-based modelling.* Austrian Journal of Forest Science 121 (3), 167-182.

Van Oijen, M., G.I. Ågren, O. Chertov, S. Kellomäki, A. Komarov, D.C. Mobbs & M.B. Murray, 2007. *Evaluation of past and future changes in European forest growth by means of four process-based models.* In: Karjalainen, T. & A. Schuck (Eds). Causes and Consequences of Forest Growth Trends in Europe - Results of the RECOGNITION Project. (in press), pp. Chapter 4.4.

Van Veen, J.A., 1977. *The behaviour of nitrogen in soil: a computer simulation model.* PhD Thesis, Amsterdam, Free University Amsterdam.

Van Wijnen, H.J. & J.P. Bakker, 1999. *Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession.* J. Ecol. 87 (2), 265-272.

Verboom, J. & G.W.W. Wamelink, 1999. *Spatial modelling in landscape ecology.* In: Wiens, M.R. & J.A. Moss (Eds). Issues and perspectives in landscape ecology. Cambridge, Cambridge University Press, pp. 79-89.

Vesterdal, L., 1999. *Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce.* Can. j. for. res. 29 (1), 95-105.

Vesterdal, L., E. Ritter & P. Gundersen, 2002. *Change in soil organic carbon following afforestation of former arable land.* Forest Ecol. Manage. 169 (1-2), 137-147.

Vesterdal, L., L. Rosenqvist, C. van der Salm, K. Hansen, B.J. Groenenberg & M.-B. Johansson, 2007. *Carbon sequestration in soil and biomass following afforestation: Experiences from oak and Norway spruce chronosequences in Denmark, Sweden and the Netherlands.* In: Heil, G.W., B. Muys & K. Hansen (Eds). Environmental Effects of Afforestation in

North-Western Europe. From Field Observations to Decision Support. Vol. Springer Series: Plant and Vegetation, Vol. 1., pp. 19-51.

Vitousek, P.M. & R.W. Howarth, 1991. *Nitrogen limitation on land and in the sea: How can it occur?* Biogeochem. 13 (2), 87-115.

Vitousek, P.M., H.A. Mooney, J. Lubchenco & J.M. Melillo, 1997. *Human domination of Earth's ecosystems.* Science 277, 494-499.

Vleeshouwers, L.M. & A. Verhagen, 2002. *Carbon emission and sequestration by agricultural land use: a model study for Europe.* Glob. Change Biol. 8 (6), 519-530.

Wagenfuhr, R. & C. Schreiber, 1989. *Holzatlas.* 3 Auflage, Leipzig, Germany, Fachbuchverlag.

Wallman, P., M. Svenssson, H. Sverdrup & S. Belyazid, 2005. *ForSAFE - an integrated process-oriented forest model for long-term sustainability assessments.* Forest Ecol. Manage. 207 (1-2), 19-36.

Wamelink, G.W.W., J.P. Mol-Dijkstra, H.F. van Dobben, J. Kros & F. Berendse, 2000a. *Eerste fase van de ontwikkeling van het Successie Model SUMO 1; Verbetering van de vegetatiemodellering in de Natuurplanner.* Wageningen, Alterra, Research Instituut voor de Groene Ruimte. Alterra rapport 45.

Wamelink, G.W.W., R. Wegman & H.F. van Dobben, 2000b. *Modellering van bosbeheer in SUMO.* Wageningen, Alterra. Report nr 066.

Wamelink, G.W.W., H. van Oene, J.P. Mol-Dijkstra, J. Kros, H.F. van Dobben & F. Berendse, 2001. *Validatie van de modellen SMART2, SUMO1, NUCOM en MOVE op site-, regionaal en national niveau.* Wageningen, Alterra, Research Instituut voor de Groene Ruimte. Alterra rapport 65.

Wamelink, G.W.W., C.F.J. ter Braak & H.F. van Dobben, 2003. *Changes in large-scale patterns of plant biodiversity predicted from environmental economic scenarios.* Landscape Ecol. 18 (5), 513-527.

Wamelink, G.W.W., R. Wegman & H.F. van Dobben, 2004. *Verbetering van de modellering van de effecten van vochttekort op de vegetatieontwikkeling in SUMO en de Natuurplanner.* Wageningen, Alterra. Alterra rapport 910.

Wamelink, G.W.W., J.J. de Jong, H.F. van Dobben & M.N. van Wijk, 2005. *Additional costs of nature management caused by deposition.* Ecol. Econ. 52 (4), 437-451.

Wamelink, G.W.W., H.F. van Dobben & F. Berendse, 2007a. *Vegetation succession as affected by decreasing nitrogen deposition, soil characteristics and site management: a modelling approach.* Forest Ecol. Manage. (In prep.).

Wamelink, G.W.W., H.F. van Dobben, J.P. Mol-Dijkstra, E.P.A.G. Schouwenberg, J. Kros, W. de Vries & F. Berendse., 2007b. *Effect of nitrogen deposition reduction on biodiversity and carbon sequestration.* Forest Ecol. Manage. (submitted).

Wamelink, G.W.W., H.J.J. Wieggers, G.J. Reinds, J. Kros, J.P. Mol-Dijkstra, M. van Oijen & W. de Vries, 2007c. *Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on NPP and carbon sequestration of Intensive Forest Monitoring plots in Europe.* Forest Ecol. Manage. (submitted).

Wamelink, W.W.G., 2006. *Adaptations of SUMO for Forest Focus.* Wageningen, Alterra. Internal memo.

Wargo, P.M., R. Minocha, B.L. Wong, R.P. Long, S.B. Horsley & T.J. Hall, 2002. *Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania.* Can. j. for. res. 32 (4), 629-641.

Waring, R.H., 1987. *Characteristics of trees predisposed to die.* Bioscience 37 (8), 569-574.

Wassen, M.J., H. Olde Venterink, E.D. Lapshina & F. Tanneberger, 2005. *Endangered plants persist under phosphorus limitation.* Nature 437, 547-550.

White, M.A. & R.R. Nemani, 2003. *Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest.* Glob. Change Biol. 9 (7), 967-972.

Wiselius, S.I., 1994. *Houtvademecum.* Almere, The Netherlands, Stichting Centrum Hout.

Woodwell, G.M. & R.H. Whittaker, 1968. *Primary Production in Terrestrial Ecosystems.* Amer. Zool. 8 (1), 19-30.

Wright, R.F., C. Alewell, J.M. Cullen, C.D. Evans, A. Marchetto, F. Moldan, A. Prechtel & M. Rogora, 2001. *Trends in nitrogen deposition and leaching in acid-sensitive streams in Europe.* Hydrol. Earth Syst. Sci. 5 (3), 299-310.

Wykoff, W.R., 1990. *A basal area increment model for individual conifers in the Northern Rocky Mountains.* For. sci. 36 (4), 1077-1104.

Xu, X. & E. Hirata, 2005. *Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: N and P dynamics.* Plant soil 273 (1-2), 279-289.

Zebisch, M., F. Wechsung & H. Kenneweg, 2004. *Landscape response functions for biodiversity - assessing the impact of land-use changes at the county level.* Landsc. Urban Plan. 67 (1-4), 157-172.

Description of the SUMO model

The model SMART2 considers linked biotic and abiotic processes in the soil solution as well as in the solid phase. It includes the inorganic soil and two organic soil compartments and simulates the full soil nitrogen cycle. The model consists of a set of mass balance equations, describing the soil input-output relationships and rate-limited and equilibrium soil processes. The soil solution chemistry depends on the net element input from the atmosphere and groundwater, canopy interactions, geochemical interactions in the soil (CO_2 equilibria, weathering of carbonates, silicates and/or Al hydroxides, SO_4 sorption and cation exchange), and nutrient cycling (litterfall, mineralisation, root uptake, nitrification and denitrification). Nutrient uptake by the vegetation and litterfall (including the amount of dead roots and dead wood) are provided by SUMO. SMART2 delivers the nitrogen availability to SUMO as the sum of external N input and mineralisation. Solute transport is described by assuming complete mixing of the element input within one homogeneous soil compartment with a constant density and fixed depth. The time step of the model is one year.

Competition for light

The interception of light is simulated by assuming an exponential decrease of light intensity with decreasing height within the canopy, using the Lambert-Beer equation (Equation A1.3, cf. Huisman & Weissing, 1994). The light interception per functional type is based on the biomass and position of the leaves. For each functional type the leaves are considered to be equally distributed over the height of the functional type, except for trees higher than 7 m, where the canopy does not start at the ground level but at a height of 1.5 m. In total five canopy layers are distinguished in which at least one and at most five functional types are present. The highest layer starts at the top of the highest functional type and ends at the height of the second highest functional type. It contains a fraction of the leaf biomass of the highest functional type equal to the thickness of the layer relative to the height of the functional type. The light that is not intercepted passes to the next layer. The second layer consists of two functional types, the highest and the second highest, and this layer ends at the height of the third highest functional type. The leaf biomass of the two functional types in this layer is again computed, and added to give the total leaf biomass for the layer. The light interception computed on the basis of this total biomass is subsequently divided over the two functional types according to their proportion in the total leaf biomass in that layer (Equation A1.3). The light interception of the functional types in the other three layers is calculated in a similar way. Per functional type the interception of the layers is summed to give the total light interception. The maximum growth of the functional type is reduced by light interception according to Equation A1.2.

Competition for nitrogen

In SUMO, nitrogen comes from three sources: (1) uptake from the soil, (2) foliar uptake of atmospheric deposition, and (3) internal reallocation from one organ to another.

(1) The nitrogen release from the soil and litter is simulated by SMART2. The fraction of soil nitrogen absorbed by each functional type is assumed to be equal to the proportion of its root biomass in the total root biomass.
(2) Atmospheric nitrogen is assumed to be taken up by the canopy, with a rate that declines exponentially with height. For the sake of simplicity the deposition is distributed over the functional types proportional to their light interception and thus dependent on their fraction of total leaf biomass (Equation A1.4). Data on atmospheric deposition comes from external sources (i.e. deposition models or maps). The actual available atmospheric nitrogen for the vegetation is calculated by SMART2 and depends on the structure of the vegetation (forests catch more deposition than grasslands).
(3) Before litterfall part of the nitrogen in the litter is reallocated, stored and used for growth in the next year (see below). This reallocated nitrogen remains within the plant and is therefore not available to the other functional types.
The total nitrogen availability for each functional type is calculated by summing (1), (2) and (3) (Equation A1.5).
The influence of the nitrogen availability on the growth of each functional type is described by a saturation equation based on potential growth, total nitrogen availability, and the minimum nitrogen content per functional type (Equation A1.6). In principle, all available nitrogen is taken up, but the nitrogen uptake of each functional type is limited by its maximum growth and maximum nitrogen content. The nitrogen that is not taken up by the roots remains in the soil.

The newly taken up nitrogen is divided over the organs (Equation A1.7). The nitrogen content in the organs is calculated after adding the new biomass and new nitrogen, and subtracting litterfall and the nitrogen left in it (Equation A1.8 and A1.9). The amount of reallocated nitrogen depends on the organ and the nitrogen content of the organ. When the nitrogen content is lower than a threshold value no nitrogen is reallocated (Equation A1.10).

In the present version of SUMO the effect of moisture availability on the vegetation is neglected. It is assumed that no water shortage occurs that limits the growth and that the growth is not reduced due to high groundwater levels.

Biomass

The biomass of each functional type is computed as the result of the biomass in the previous year, the newly formed biomass, the production of dead biomass and the amount of biomass removed by management (Equation A1.1). The newly formed biomass is the result of the reduction of the maximum growth of each functional type by the reduction factors for light interception (Equation A1.3) and nitrogen availability (Equation A1.6). Each year, a small amount of a small amount of biomass is added to each organ of each functional type to simulate seed input (0.0001 ton.ha^{-1}.yr^{-1}). For several processes in SUMO the amount of biomass per organ is required. To this end the newly formed biomass is divided over the organs according Equation A1.11, where the division over the three organs differs per functional type. The total biomass the biomass per organ is corrected for death and biomass removal, like the total biomass.

Litter

Each year part of the biomass dies. The fraction that dies depends on the organ and the functional type, and varies from 1.0 yr^{-1} for leaves of herbs, shrubs and deciduous trees to 0.01 yr^{-1} for stems of climax trees (Equation A1.12). The nitrogen content of the dead organs is calculated by Equation 10. The nitrogen content in litter and dead wood is lower than in living material due to reallocation. However, when the nitrogen content drops below a given threshold value no reallocation takes place. The biomass of dead roots and leaves is transferred to the litter pool and nitrogen release from the dead plant parts is simulated by SMART2. SMART2 assumes that dead stems do not release nitrogen.

Height

The height of the five functional types is calculated yearly. As height growth is assumed to decline with age, SUMO also keeps track of the 'age' (i.e., the number of years since colonisation or plantation occurred) per functional type. For the functional types herbs/grasses and dwarf shrubs the height is based on the biomass present in the functional type (Equation A1.13).

The height of shrubs is calculated with Equation A1.14. It depends on the age of the stand. Over the years the height growth is decreasing until the maximum height has been reached.

The computation of the height of the trees is more complicated. It is based on the height in the previous year, the biomass growth in the current year, a minimum and maximum height growth, and the 'age' of the functional type (Equations A1.15 and A1.16). The maximum and minimum height growth of the trees is based on growth curves for the Netherlands on rich and poor soil, respectively (Jansen et al., 1996). The realised height growth per tree species per year lies between values determined by the growth curves at the tree's 'age' and the biomass increment in that year, according to Equation A1.17. The height growth of shrubs and trees is assumed to start at a given threshold biomass (0.15 $ton.ha^{-1}$ for the sum of stem biomass of shrubs and trees. These threshold values are equal to the threshold values for succession (Table 3.1). If the biomass is below this threshold the height is set to the minimum height given above, and the ‘age’ is kept at 1 year. A maximum height is explicitly imposed only for dwarf shrubs (1 m). For shrubs and trees the maximum height is determined by parameters k_1 and k_4 in Equations A1.15 and A1.16.

Management

Management implies the removal of biomass and therefore nitrogen from the system. In some cases management also influences the height of the functional types. SUMO can simulate four types of management: mowing (grassland), turf stripping (heathland), cutting (forests) and grazing. Grazing may be combined with any other management form.

1. Mowing. In mown grassland the leaf biomass of the functional type grasses/herbs is reduced to 1 $ton.ha^{-1}$. The aboveground biomass of the other functional types is reduced to 0.002 $ton.ha^{-1}$. The biomass of the roots is not reduced. The height of all

functional types except for herbs/grasses is reduced to the height of their seedlings. For herbs/grasses the height depends on the remaining biomass according to Equation A1.13. The age of the shrubs and trees is set back to 1 year.

2. Turf stripping. After turf stripping the total biomass of the functional types is minimised to 0.002 $ton.ha^{-1}$ for dwarf shrubs and to 0.0002 $ton.ha^{-1}$ for the other functional types. It is assumed that there remains more biomass, especially seeds, of dwarf shrubs in the soil than for the other functional types. Since after turf stripping the humus layer is also removed, SUMO signals SMART2 to remove the humus layer from the system.

3. Cutting. Cutting can influence all functional types. Three different types of forest management are modelled in SUMO. The first is extensive management. In this type of management, every 10 years 10% of the trees are harvested; this is implemented by reducing the biomass of all organs by 10%. The dead roots are transported to the dead roots-pool in SMART2. The rest of the cut biomass is removed from the system. The pool of reallocatable nitrogen is also reduced by 10%. The height of the trees is not influenced by cutting. The second management form is traditional (intensive) forest management with thinning every 5 years and clear-cutting at the end of the management cycle (Equation A1.18). The amount of thinning depends on the tree species and the age of the stand (after Jansen et al., 1996). The cut biomass and its nitrogen content are removed from the system. In the case of a clear-cut this is the total aboveground biomass and the nitrogen it contains. The biomass of the non-tree functional types is assumed to be destroyed for 90% due to the cutting activities and added to the litter. The forest is replanted after clear-cutting. The height and age are set back to the height of planted young trees. The third management type is coppicing, which is simulated for a few tree species only: willow, ash, alder and oak. For willow, ash and alder the shoots are harvested every seven years, for oak every 30 years. For all tree species 80% of the above ground biomass is harvested. A large part of the herbs and grasses is assumed to be destroyed (90%) and is added to the dead roots and litter pools, shrubs are assumed to be actively removed from the system. The height of the remaining stub after management is set to 0.3 m.

4. Grazing. Grazers are modelled as biomass removing objects, similar to the other forms of management. The model does not contain a population dynamic module for the grazers. In SUMO the effect of grazing can be simulated for 15 different grazers (young cattle, domestic cow, 'wild' cow, horse, pony, sheep, wild boar, roe deer, red deer, fallow deer, European bison, moose, moufflon, goose and rabbit). Their effect is that they eat from the three organs, of which a part is returned to the system as manure. The nitrogen in the manure is available for the vegetation in the next year and is handled by SMART2. The model was adjusted for this purpose. The amount of nitrogen in the manure is simply added to the available nitrogen pool which is returned to SUMO. It is assumed that all nitrogen is available in the next year. The grazers differ from each other in the amount of biomass they have to eat and the preference for different organs and functional types. For instance, only wild boar eats roots. The amount of grazers depends on the amount of food that is

available. When there is a surplus of food then the amount of grazers will increase gradually, till a maximum of five times the original amount. When the amount of food is not sufficient the number of grazers is adjusted to the amount of available food where the maximum possible increase is halved to correct for generation time. For domesticated grazers it is also possible to fix the amount of grazers. Not all the in principle eatable biomass is available for the grazers. For all functional types there is an organ specific threshold value and of shrubs and trees higher than 1.5 m only a limited part of the leaves are available. When the trees are higher than 10 m only 10% of this reduced amount is available. All the values are based on expert judgement. To calculate the available amount the leaves are equally divided over the length of the trees and only the biomass that is below the threshold amount is available. Although a preference per grazer is given beforehand it is not fixed, the actually eaten amount of biomass per organ and functional type also depends on the amount of available biomass per organ.

For all Equations: t: time step, j: vegetation type, i: functional type, o: organ, g: tree species

Overall description of biomass

$$B_{i,j,t} = B_{i,j,t-1} + \left(Aact_{i,j,t} - D_{i,j,t} - M_t + Bs_{i,j,t}\right) \cdot \Delta t \qquad \text{(A1.1)}$$

$B_{i,j,t}$ = biomass (ton.ha^{-1}.yr^{-1})
$Aact_{s,i,j,t}$ = actual growth (ton.ha^{-1}.yr^{-1})
$D_{i,j,t}$ = actual mortality (ton.ha^{-1}.yr^{-1})
M_t = actual removal by management (ton.ha^{-1}.yr^{-1})
$Bs_{i,j,t}$ = actual seed biomass (ton.ha^{-1}.yr^{-1})
Δt = time step (yr^{-1})

Overall description of growth

$$Aact_{i,j,t} = Amax_{i,j} \cdot RI_{i,j,t} \cdot RNav_{i,j,t} \qquad \text{(A1.2)}$$

$Aact_{i,j,t}$ = actual growth (ton.ha^{-1}.yr^{-1})
$Amax_{i,j}$ = maximum growth (ton.ha^{-1}.yr^{-1})
$RI_{i,j,t}$ = reduction factor for light availability (-)
RNavi,j,t = reduction factor for nitrogen availability (-)

Light interception

$$RI_{i,j,t} = \sum_{n-1,5} \left(fI_{i,t,n-1} \cdot \left(1 - e^{\left(-k_{i,j} \cdot fBl_{i,t,n}\right)} \right) \right) \qquad \text{(A1.3)}$$

$RI_{i,j,t}$ = reduction factor for light interception (-)

$fI_{i,t,n-1}$ = fraction light remaining after interception in canopy layer n-1 (-)
$k_{i,j}$ = interception factor (-)
$fBl_{i,t,n}$ = fraction leaf biomass of functional type i in canopy layer n ($ton.ha^{-1}.yr^{-1}$)
n = number of functional types present in a canopy layer (-)

Nitrogen deposition interception

$$Nint_{i,j,t} = \left(\frac{RI_{i,j,t}}{\sum\limits_{i=1,5} RI_{i,j,t}} \right) \cdot Ndep_t \qquad \text{(A1.4)}$$

$Nint_{i,j,t}$ = actual intercepted nitrogen deposition ($ton.ha^{-1}.yr^{-1}$)
$RI_{i,j,t}$ = light interception (-)
$Ndep_t$ = actual nitrogen deposition ($ton.ha^{-1}.yr^{-1}$)

Nitrogen availability

$$Nav_{i,j,t} = Nint_{i,j,t} + \sum_{o=1,3} \left(Nrea_{o,i,j,t-1} \right) + \left\{ \left(\frac{B_{o=r,i,j,t}}{\sum\limits_{i=1,5} B_{o=r,i,j,t}} \right) \cdot Ns_t \right\} \qquad \text{(A1.5)}$$

$Nav_{i,j,t}$ = actual nitrogen availability ($ton.ha^{-1}.yr^{-1}$)
$Nint_{i,j,t}$ = actual intercepted nitrogen deposition ($ton.ha^{-1}.yr^{-1}$)
$Nrea_{o,i,j,t-1}$ = actual nitrogen reallocation ($ton.ha^{-1}.yr^{-1}$)
$B_{o,i,j,t}$ = actual biomass ($ton.ha^{-1}.yr^{-1}$)
r = root
Ns_t = actual nitrogen release from the soil ($ton.ha^{-1}.yr^{-1}$)

Reduction factor for nitrogen availability

$$RNav_{i,j,t} = \frac{Nav_{i,j,t}}{Nav_{i,j,t} + (Amax_{i,j} \cdot RI_{i,j,t} \cdot Nmin_{i,j})} \qquad \text{(A1.6)}$$

$RNav_{i,j,t}$ = reduction factor for nitrogen availability (-)
$Nav_{i,j,t}$ = actual nitrogen availability ($ton.ha^{-1}.yr^{-1}$)
$Amax_{i,j}$ = maximum growth ($ton.ha^{-1}.yr^{-1}$)
$RI_{i,j,t}$ = reduction factor for light availability (-)
$Nmin_{i,j}$ = minimum nitrogen content (-)

New nitrogen mass per functional type

$$Nnew_{o,i,j,t} = Nav_{i,j,t} \cdot fN_{o,i,j} \qquad \text{(A1.7)}$$

$Nnew_{o,i,j,t}$ = actual nitrogen mass change ($ton.ha^{-1}.yr^{-1}$)
$Nav_{i,j,t}$ = actual nitrogen availability ($ton.ha^{-1}.yr^{-1}$)
$fN_{o,i,j}$ = factor for the partitioning of nitrogen (-)

Nitrogen mass organs

$$N_{o,i,j,t} = N_{o,i,j,t\text{-}1} - \left(N_{o,i,j,t\text{-}1} \cdot fd_{o,i,j}\right) + Nnew_{o,\,i,\,j,\,t} \cdot \Delta t \qquad \text{(A1.8)}$$

$N_{o,i,j,t}$ = nitrogen mass (ton.ha^{-1})
$fd_{o,i,j}$ = biomass mortality factor (-)
$Nnew_{o,i,j,t}$ = new nitrogen mass (ton.ha^{-1}.yr^{-1})
Δt = time step (yr^{-1})

Nitrogen content organs

$$NC_{o,i,j,t} = \frac{N_{o,i,j,t}}{B_{o,i,j,t} \cdot fB_{o,i,j}} \qquad \text{(A1.9)}$$

$NC_{o,i,j,t}$ = nitrogen content (-)
$N_{o,i,j,t}$ = nitrogen mass (ton.ha^{-1})
$B_{o,i,j,t}$ = biomass (ton.ha^{-1})
$fB_{o,i,j}$ = factor for the partitioning of nitrogen (-)

Nitrogen content litter, dead wood and dead roots

$$NCd_t = \frac{\sum\limits_{i=1,5} \left\langle \sum\limits_{o=1,3} (1 - frea_o) \cdot N_{o,i,j,t} \right\rangle}{\sum\limits_{i=1,5} \left\langle \sum\limits_{o=1,3} (B_{o,i,j,t} \cdot fd_{o,i,j}) \right\rangle} \qquad \text{(A1.10)}$$

NCd_t = nitrogen content of litter/dead wood/dead roots (-)
$N_{o,i,j,t}$ = nitrogen mass (ton.ha^{-1})
$frea_o$ = nitrogen reallocation factor (-)
$N_{o,i,j,t}$ = nitrogen mass (ton.ha^{-1})
$B_{o,i,j,t}$ = biomass (ton.ha^{-1})
$fd_{o,i,j}$ = biomass mortality factor (-)

Biomass per organ

$$B_{o,i,j,t} = B_{i,j,t} \cdot fB_{o,i,j} \qquad \text{(A1.11)}$$

$B_{o,i,j,t}$ = biomass in a given organ (ton.ha^{-1})
$B_{i,j,t}$ = biomass (ton.ha^{-1})
$fB_{o,i,j}$ = factor for the distribution of biomass (-)

Dead biomass

$$D_{i,j,t} = \sum_{o=1,3} \left(B_{o,i,j,t\text{-}1} \cdot fd_{o,i,j}\right) \qquad \text{(A1.12)}$$

$D_{i,j,t}$ = dead biomass (ton.ha^{-1})
$B_{o,i,j,t}$ = Biomass (ton.ha^{-1})
$fd_{o,i,j}$ = biomass mortality factor (-)

Height of grasses and herbs and dwarfshrubs

$$H_{i=(gh,d),j,t} = k \cdot B_{i=(gh,d),j,t} \tag{A1.13}$$

$H_{i,j,t}$ = height (m)
gh = grasses/herbs
d = dwarf shrubs
k = regression coefficient; fixed at 1 (m^3.kg^{-1})
$B_{i,j,t}$ = biomass (ton.ha^{-1})

Height of shrubs

$$H_{i=s,j,t} = H_{max} + \left(- k_{s1} \cdot \left(k_{s2}\right)^{\left[age_{s,t}/\Delta t\right]}\right) \tag{A1.14}$$

$H_{i,j,t}$ = height (m)
H_{max} = maximum height; fixed at 3.104 (m)
s = shrubs
k_{s1} = regression coefficient 1; fixed at 3.395 (-)
k_{s2} = regression coefficient 2; fixed at 0.90526 (-)
$age_{s,t}$ = age shrubs (yr)
Δt = time step set at 1 (yr^{-1})

Minimum height trees

$$Hmin_{t,g} = k_{1,g} + \left(- k_{2,g} \cdot (k_{3,g})^{\left\lfloor age_{g,t} / \Delta t\right\rfloor}\right) \tag{A1.15}$$

$Hmin_{t,g}$ = minimum height (m)
$k_{1,g}$ = regression coefficient 1 (m)
$k_{2,g}$ = regression coefficient 2 (-)
$k_{3,g}$ = regression coefficient 3 (-)
$age_{g,t}$ = age trees (yr)
Δt = time step set at 1 (yr^{-1})

Maximum height trees

$$Hmax_{t,g} = k_{4,g} + \left(- k_{5,g} \cdot \left(k_{6,g}\right)^{\left[age_{g,t} / \Delta t\right]}\right) \tag{A1.16}$$

$Hmax_{t,g}$ = maximum height (m)
$k_{4,g}$ = regression coefficient 4 (m)
$k_{5,g}$ = regression coefficient 5 (-)
$k_{6,g}$ = regression coefficient 6 (-)

$age_{g,t}$ = age trees (yr)
Δt = time step set at 1 (yr^{-1})

Actual height trees

$$H_{g,t} = H_{g,t-1} + \left\langle Hgrmin_{g,t} + \left\{ (Hgrmax_{g,t} - Hgrmin_{g,t}) \cdot \left(\frac{Aact_{i=g,j,t} - B\min}{B\max - B\min} \right) \right\} \right\rangle \cdot \Delta t \qquad \text{(A1.17)}$$

$H_{g,t}$ = Actual height (m)
$Hgrmin_{g,t}$ = minimum height growth; difference between $Hmin_{t,g}$ and $Hmin_{t-1,g}$ ($m.yr^{-1}$)
$Hgrmax_{g,t}$ = maximum height growth; difference between $Hmax_{t,g}$ and $Hmax_{t-1,g}$ ($m.yr^{-1}$)
$Aact_{g,j,t}$ = biomass growth for tree species g ($ton.ha^{-1}.yr^{-1}$)
Bmin = minimum biomass growth ($ton.ha^{-1}.yr^{-1}$)
Bmax = maximum biomass growth ($ton.ha^{-1}.yr^{-1}$)

Tree thinning

$$\begin{aligned} &\text{If } rt = tt \\ &M_t = B_{i=g,j,t} \cdot kT_{g,t} \end{aligned} \qquad \text{(A1.18)}$$

rt = runtime (yr)
tt = thinning time (yr)
$B_{i=g,j,t}$ = biomass tree species g ($ton.ha^{-1}$)
$kT_{g,t}$ = thinning factor (-)

Parameter values for SUMO

Table A1.1 Initial biomass for different vegetation types and (successional) stadia. Note that for some of the validations site specific data were used. For tree species 1 birch is used except for alder where ash is used as tree species 1.

vegetation type		dune shrub	open dune	salt marsh	reed	rough land	grassland	extensive natural'	heath land <75%	heath land >75%	peat bog	bare sand	natural land
Root	Herbs	1	1	5	4	3	4	3	1	4	4	0.1	3
	Dwarf shrubs	4	2	2	0.1	0.1	0.1	0.1	3	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 1	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 2	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
Wood	Herbs	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	7	3	5	0.1	0.1	0.1	0.1	2	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1
Leaves	Herbs	1	1	5	4	3	4	3	1	4	3	0.1	3
	Dwarf shrubs	3	2	3	0.1	0.1	0.1	0.1	3	1	1	0.1	0.1
	Shrubs	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 1	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1
	tree 2	0.1	0.1	0.1	0.1	1	0.1	0.1	0.1	0.1	0.1	0.1	1

tree species		Northern red oak	Northern red oak	Northern red oak	Northern red oak	Beech	Beech	Beech	Beech	Douglas	Douglas	Douglas	Douglas
age class		<40y	40-80y	80-120y	>120y	<40y	40-80y	80-120y	>120y	<40y	40-80y	80-120y	>120y
Root	Herbs	1	1	1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
Wood	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.8	2	2	2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	Shrubs	2.5	2.5	3	5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 1	11	12	15	19	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	tree 2	11	40	80	90	20	50	80	100	20	50	80	100
Leaves	Herbs	1	1	1	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3

tree species age class		Oak <40y	Oak 40-80y	Oak 80-120y	Oak >120y	Alder <40y	Alder 40-80y	Alder 80-120y	Alder >120y	Pine <40y	Pine 40-80y	Pine 80-120y	Pine >120y
Root	Herbs	1	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.3	0.3	0.3	0.3
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3
Wood	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.2	1.4	1.8	1.2	0.1	0.1	0.1	0.1	0.2	1.4	1.8	1.2
	Shrubs	2.5	2.2	2.5	6	2.5	1.7	2.5	4.5	2.5	2.2	2.5	6
	tree 1	10	12	15	20	10	12	15	17	10	12	15	20
	tree 2	15	40	70	80	15	40	70	80	15	40	60	90
Leaves	Herbs	1	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.3	0.3	0.3	0.3
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 2	3	3	3	3	3	3	3	3	3	3	3	3

tree species age class		Larch <40y	Larch 40-80y	Larch 80-120y	Larch >120y	Poplar <40y	Poplar 40-80y	Poplar 80-120y	Willow <40y	Willow 40-80y	Willow 80-120y	Willow >120y
Root	Herbs	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 2	3	3	3	3	3	3	3	3	3	3	3
Wood	Herbs	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.2	1.4	1.8	1.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	2.5	2.2	2.5	6	2	0.7	0.7	2	0.7	0.7	0.7
	tree 1	10	12	15	20	7	7	4	7	7	4	3
	tree 2	20	40	70	90	20	40	70	20	40	60	80
Leaves	Herbs	1	1	1	1	1	1	1	1	1	1	1
	Dwarf shrubs	0.3	0.3	0.3	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Shrubs	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	tree 1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
	tree 2	3	3	3	3	3	3	3	3	3	3	3

tree species		New forest	clear cut	Alder coppice	Willow coppice	Oak coppice	Ash coppice
Root	Herbs	1	0.1	0.5	0.5	0.5	0.5
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.2	2	2	2	2
	tree 2	1	0.2	2	2	2	2
Wood	Herbs	0.1	0.1	0.1	0.1	0.1	0.1
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.1	12	12	12	12
	tree 2	1	0.1	12	12	12	12
Leaves	Herbs	1	0.1	0.5	0.5	0.5	0.5
	Dwarf shrubs	0.5	0.1	0.1	0.1	0.3	0.3
	Shrubs	1	0.1	0.1	0.1	0.1	0.1
	tree 1	1	0.2	2	2	2	2
	tree 2	1	0.2	2	2	2	2

Table A1.2Parameter values for herbs and grasses, dwarf shrubs and shrubs per vegetation type; k_{int} *light interception factor, Nmin minimal N content of the biomass, Nmax maximal N content of the biomass and Amax maximum growth rate.*

Vegetation type	Functional type	k_{int}	Nmin	Nmax	Amax (ton.ha^{-1}.yr^{-1})
Grassland	Herbs	0.7	0.0085	0.025	24
	Dwarf shrubs	0.7	0.0085	0.023	10
	Shrubs	0.6	0.0085	0.023	16
Salt marsh	Herbs	0.7	0.01	0.02	15
	Dwarf shrubs	0.8	0.01	0.018	20
	Shrubs	0.001	0.01	0.001	10
Reed	Herbs	0.7	0.01	0.02	30
	Dwarf shrubs	0.7	0.01	0.018	8
	Shrubs	0.7	0.01	0.018	18
Heathland	Herbs	0.6	0.01	0.02	18
	Dwarf shrubs	0.7	0.01	0.018	12
	shrubs	0.4	0.01	0.018	13
Shrub	herbs	0.7	0.01	0.025	15
	Dwarf shrubs	0.7	0.01	0.023	12
	Shrubs	0.6	0.01	0.023	13
Forest	Herbs	0.8	0.01	0.025	24
	Dwarf shrubs	0.7	0.01	0.023	10
	Shrubs	0.6	0.01	0.023	14

Table A1.3 Parameter values for herbs and grasses, dwarf shrubs and shrubs per vegetation type; fB new biomass distribution over the organs, fN new nitrogen distribution over the organs, fd mortality factor per organ and Bs yearly seed biomass input.

Vegetation type	Functional type	organ	fB	fN	fd	Bs (ton.ha^{-1}.yr^{-1})
Grassland	Herbs	Root	0.49	0.45	1	0.0001
		Wood	0.4	0.41	0.7	0.0001
		Leaves	0.4	0.41	0.3	0.01
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.2	0.02	0.3	0.0001
		Leaves	0.1	0.02	0.04	0.01
	Shrubs	Root	0.5	0.54	0.9	0.0001
		Wood	0.4	0.57	0.6	0.0001
		Leaves	0.5	0.57	1	0.01
Salt marsh	Herbs	Root	0.49	0.49	0.9	0.0001
		Wood	0.35	0.45	0.8	0.0001
		Leaves	0.4	0.4	1	0.0001
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.3	0.1	0.2	0.0001
		Leaves	0.1	0.1	1	0.0001
	Shrubs	Root	0.5	0.5	0.7	0.0001
		Wood	0.35	0.45	0.6	0.0001
		Leaves	0.5	0.5	1	0.0001
Reed	Herbs	Root	0.45	0.45	0.8	0.0001
		Wood	0.35	0.42	0.6	0.0001
		Leaves	0.35	0.42	0.6	0.0001
	Dwarf shrubs	Root	0.01	0.01	0.9	0.0001
		Wood	0.2	0.01	0.1	0.0001
		Leaves	0.2	0.01	0.03	0.0001
	Shrubs	Root	0.54	0.54	0.8	0.0001
		Wood	0.45	0.57	0.6	0.0001
		Leaves	0.45	0.57	1	0.0001
Heathland	Herbs	Root	0.49	0.49	1	0.0001
		Wood	0.45	0.45	0.6	0.0001
		Leaves	0.4	0.42	0.3	0.0001
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.1	0.05	0.3	0.0001
		Leaves	0.1	0.01	0.04	0.0001
	Shrubs	Root	0.5	0.5	1	0.0001
		Wood	0.45	0.5	0.5	0.0001
		Leaves	0.5	0.57	1	0.0001
Shrub	Herbs	Root	0.45	0.45	0.9	0.0001
		Wood	0.35	0.42	0.6	0.0001
		Leaves	0.4	0.42	0.7	0.01
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.15	0.01	0.3	0.0001
		Leaves	0.1	0.01	0.1	0.01
	Shrubs	Root	0.54	0.54	0.9	0.0001
		Wood	0.5	0.57	0.5	0.0001
		Leaves	0.5	0.57	0.8	0.01
Forest	Herbs	Root	0.45	0.45	0.8	0.0001
		Wood	0.35	0.42	0.6	0.0001
		Leaves	0.35	0.42	0.6	0.01
	Dwarf shrubs	Root	0.01	0.01	1	0.0001
		Wood	0.15	0.01	0.1	0.0001

Vegetation type	Functional type	organ	fB	fN	fd	Bs (ton.ha^{-1}.yr^{-1})
		Leaves	0.2	0.01	0.03	0.01
	Shrubs	Root	0.54	0.54	0.8	0.0001
		Wood	0.5	0.57	0.5	0.0001
		Leaves	0.45	0.57	1	0.01

Table A1.4 Parameter values for tree species; k_{int} light interception factor, Nmin minimal N content of the biomass, Nmax maximal N content of the biomass and Amax maximum growth rate.

Species	k_{int}	Nmin	Nmax	Amax (ton.ha^{-1}.yr^{-1})
Scots pine	0.4	0.0085	0.023	15
Larch	0.4	0.005	0.018	13
Douglas fir	0.4	0.01	0.018	17
Norway spruce	0.4	0.01	0.018	17
Birch	0.3	0.0085	0.023	15
Ash	0.8	0.01	0.023	15
Alder	0.3	0.01	0.023	15
Poplar	0.9	0.01	0.018	16
Oak	0.7	0.01	0.018	14
Northern red oak	0.7	0.01	0.018	15
Beech	0.7	0.01	0.023	14
Willow	0.8	0.01	0.018	15

Table A1.5 Parameter values for tree species; fB new biomass distribution over the organs, fN new nitrogen distribution over the organs, fd mortality factor per organ and Bs yearly seed biomass input.

species	organ	fB	fN	fd	Bs ($ton.ha^{-1}.yr^{-1}$)
Scots pine	Root	0.4	0.41	0.7	0.0001
	Wood	0.25	0.02	0.01	0.0001
	Leaves	0.35	0.57	0.7	0.0001
Larch	Root	0.35	0.41	0.7	0.001
	Wood	0.3	0.02	0.01	0.001
	Leaves	0.35	0.57	1	0.001
Douglas fir	Root	0.3	0.41	0.6	0.001
	Wood	0.25	0.02	0.03	0.001
	Leaves	0.45	0.57	0.6	0.001
Norway spruce	Root	0.35	0.41	0.3	0.001
	Wood	0.2	0.02	0.03	0.001
	Leaves	0.45	0.57	0.6	0.001
Birch	Root	0.4	0.41	0.3	0.01
	Wood	0.15	0.02	0.01	0.01
	Leaves	0.45	0.57	1	0.01
Ash	Root	0.28	0.42	0.7	0.001
	Wood	0.32	0.01	0.01	0.001
	Leaves	0.4	0.57	1	0.001
Alder	Root	0.35	0.41	0.3	0.001
	Wood	0.15	0.02	0.01	0.001
	Leaves	0.5	0.57	1	0.001
Poplar	Root	0.3	0.41	0.3	0.001
	Wood	0.25	0.02	0.03	0.001
	Leaves	0.45	0.57	1	0.001
Oak	Root	0.3	0.42	0.7	0.01
	Wood	0.3	0.01	0.01	0.01
	Leaves	0.4	0.57	1	0.01
Northern red oak	Root	0.3	0.42	0.7	0.01
	Wood	0.35	0.01	0.02	0.01
	Leaves	0.35	0.57	1	0.01
Beech	Root	0.3	0.41	0.7	0.001
	Wood	0.3	0.02	0.03	0.001
	Leaves	0.4	0.57	1	0.001
Willow	Root	0.28	0.42	0.7	0.001
	Wood	0.32	0.01	0.01	0.001
	Leaves	0.4	0.57	1	0.001

Table A1.6 Height growth regression coefficients for trees (Formula A1.15 and A1.16). All coefficients are derived from Jansen et al. (1996). It is assumed that willow has the same growth characteristics as ash.

Species	k_1	k_2	k_3	k_4	k_5	k_6
Scots pine	14.392	-14.63	0.96952	29.847	-30.5	0.97154
Larch	20.332	-20.992	0.96332	33.616	-34.759	0.96332
Douglas fir	24.49	-24.919	0.972	36	-37	0.965
Norway spruce	21.318	-21.7	0.97742	36.357	-37.18	0.97356
Birch	15.925	-16.2	0.97	31	-31.5	0.977
Ash	18.506	-18.9	0.97	34.13	-34.8	0.97318
Alder	16.414	-16.8	0.96557	29.105	-30.18	0.95754
Poplar	24.293	-25.51	0.9408	40.544	-43.7	0.92
Oak	17.85	-17.95	0.98546	42.47	-42.99	0.98396
Northern red oak	16.283	-16.5	0.97101	30.531	-31.2	0.97
Beech	39.09	-39.18	0.99345	41.7	-42.3	0.97524
Willow	16.414	-16.8	0.96557	29.105	-30.18	0.95754

Table A1.7Clear cut cycle for tree species. After the clear cut the same species is assumed to be replanted.

Species	Cycle (yr)
Scots pine	85
Larch	70
Douglas fir	85
Norway spruce	60
Birch	75
Ash	75
Alder	80
Poplar	75
Oak	105
Northern red oak	85
Beech	135

Table A1.8 Thinning percentages for tree species (after Jansen et al., 1996). Percentages are given for a five year cycle. Thinning starts at the moment more than 25 ton.ha^{-1} dry mass of wood is present for the trees. When the number of management occurrences is higher than here given the last thinning percentage is used.

Scots pine	Larch	Douglas fir	Norway spruce	Birch	Ash	Alder	Poplar	Oak	Northern red oak	Beech
3.57	5.77	35.56	13.46	9.09	20.83	3.85	20.83	10.47	25.86	4.41
18.48	20.62	20.23	17.75	7.69	31.86	10.58	31.86	15.67	16.48	9.84
16.15	31.83	17.28	18.41	18.85	19.57	11.03	19.57	13.74	13.6	17.05
26.79	22.72	14.74	27.24	12.56	16.86	17.55	16.86	22.61	11.68	19.13
20.43	18.57	12.63	18.35	10.87	14.87	16.68	14.87	18.87	37.24	19.41
17.71	15.2	10.69	15.14	10.4	13.39	15.92	13.39	17.38	15.11	19.18
15.02	12.27	9.16	13.19	9.52	11.67	15.04	11.67	15.59	13.42	17.82
12.81	9.88	7.8	12.52	8.65	10.46	13.98	10.46	14.19	11.33	15.43
10.91	8.23	6.62	11.37	7.95	9.35	13.05	9.35	13.43	10.14	18.2
9.33	6.7	5.7	10.12	7.41	8.11	11.62	8.11	12.42	8.71	16.89
7.98	5.61	4.75	9.31	6.99	6.93	10.97	6.93	11.56	7.91	15.51
6.79	4.89	4.14	8.41	6.65	6.4	9.81	6.4	10.73	7.44	14.62
5.71	4.35	3.36	7.53	6.37	5.5	8.94	5.5	10.01	6.79	13.43
5.15	4.13	2.86		5.93	4.97	7.97	4.97	9.01	6.2	12.68
4.62	4.18	2.78		5.76	4.64	7.58	4.64	8.5	5.84	11.8
4.42		2.47		5.07	4.2	6.71	4.2	8.03	5.33	10.89
4.21		2.43						7.65	5.03	10.2
4.16								7.12	4.93	9.46
								6.79		8.67
								6.78		8.07
								6.35		7.63
								6.09		6.89
										6.52
										6.18
										5.65
										5.35
										4.86

Table A1.9 Threshold values for available biomass (Ba) for grazers

Functional type	organ	Ba (ton.ha^{-1})
Herbs	Root	1.0
	Wood	0.01
	Leaves	0.5
Dwarf shrubs	Root	1.0
	Wood	0.2
	Leaves	0.5
Shrubs	Root	1.0
	Wood	0.2
	Leaves	0.1
Pioneer tree	Root	1.0
	Wood	0.2
	Leaves	0.1
Climax tree	Root	1.0
	Wood	0.2
	Leaves	0.1

Table A1.10 Amount of biomass to be eaten per grazer (Be), the factor for calculating the amount of manure (fm) and the N-content of the manure (Ncm).

grazer	Be (ton.ha^{-1})	fm	Ncm
Domestic cattle	2.288	0.65	0.007
'wild'cattle	2.490	0.65	0.007
Young cattle	2.450	0.65	0.007
European bison	4.500	0.65	0.007
pony	1.462	0.65	0.007
horse	1.900	0.65	0.007
sheep	0.480	0.65	0.021
moose	2.007	0.65	0.007
Roe deer	0.240	0.65	0.007
Red deer	0.670	0.65	0.007
Fallow deer	0.513	0.65	0.007
moufflon	0.422	0.65	0.007
Wild boar	0.522	0.65	0.007
goose	0.0028	0.65	0.044
rabbit	0.0032	0.65	0.007

Table A1.11 Biomass preference factor for grazers (fBp)

*f*Bp Domestic cattle	'wild' cattle	Young cattle	European bison	pony	horse	sheep	moose	Roe deer	Red deer	Fallow deer	moufflon	Wild boar	goose	rabbit
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0	0.0
0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.01	0.01	0.01	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.03	0.01	0.01	0.05	0.10	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.06	0.01	0.01	0.05	0.15	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.01	0.01	0.01	0.06	0.01	0.01	0.04	0.15	0.01	0.01	0.01	0.01	0.01	0.0	0.01
0.74	0.50	0.74	0.78	0.84	0.89	0.20	0.28	0.43	0.53	0.21	0.45	0.11	1.00	0.75
0.0	0.01	0.0	0.00	0.01	0.0	0.20	0.00	0.08	0.13	0.0	0.0	0.02	0.0	0.10
0.0	0.03	0.0	0.01	0.0	0.0	0.12	0.10	0.24	0.12	0.45	0.0	0.0	0.0	0.02
0.10	0.15	0.10	0.02	0.05	0.03	0.13	0.10	0.10	0.08	0.14	0.25	0.17	0.0	0.04
0.11	0.26	0.11	0.02	0.05	0.03	0.13	0.10	0.10	0.09	0.15	0.25	0.17	0.0	0.04

Data used for the validation of SUMO

Rothamstead Parkgrass

The initial biomass per organ for SUMO is given in Table A2.1, the deposition of nitrogen en sulphur is given in Fig. A2.1.

Table A2.1. Initial biomass per functional type and organ for the Parkgrass site at Rothamstead (UK).

functional type	roots	wood	leaves
herbs and grasses	4	0.1	4
dwarf shrubs	0.1	0.1	0.1
shrubs	0.000001	0.000001	0.000001
tree 1	0.000001	0.000001	0.000001
tree 2	0.000001	0.000001	0.000001

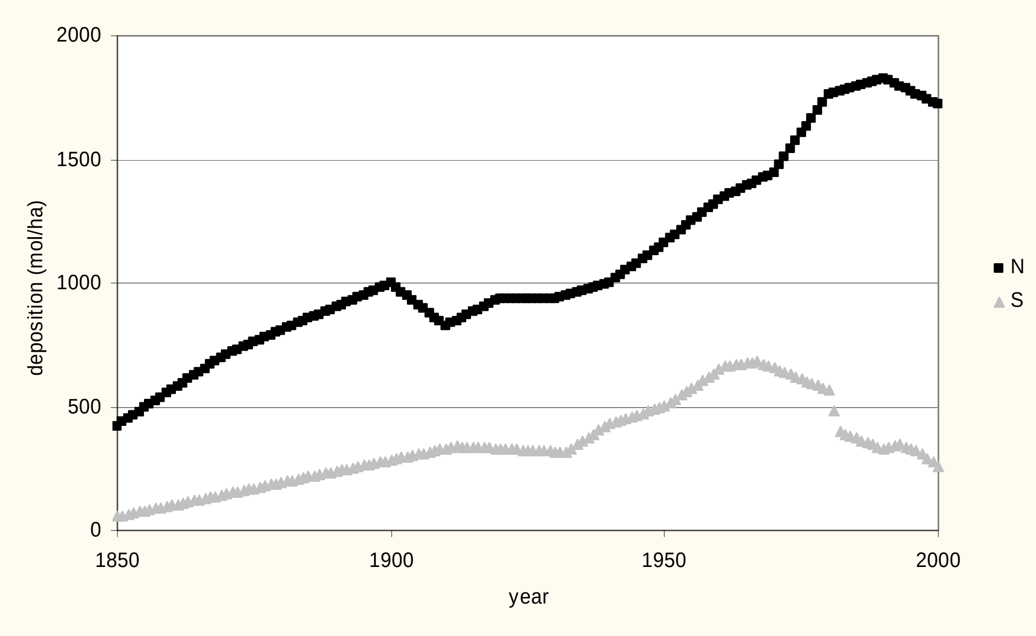

Fig. A2.1. Nitrogen (N) en Sulphur (S) deposition for Parkgrass Rothamstead (UK).

Wageningen

The initial biomass for SUMO is given in Table A2.2, the deposition of nitrogen en sulphur is given in Figs. A2.2 and A2.3.

Table A2.2. Initial biomass per functional type and organ for the grassland site near Wageningen.

functional type	roots	wood	leaves
herbs and grasses	4	0.1	4
dwarf shrubs	0.1	0.1	0.1
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

Fig. A2.2. Constructed 'historic' nitrogen deposition for the sites in The Netherlands where SUMO was validated on.

Fig. A2.3. Constructed 'historic' sulphur deposition for the sites in The Netherlands where SUMO was validated on.

The deposition data are reconstructed from measurements and historic emissions. Deposition rates are estimated for 5*5 km grids and subsequently appointed to the sites SUMO was validated on.

Strabrechtse heide

The initial biomass for SUMO is given in Table A2.3, the deposition of nitrogen en sulphur is given in Figs A2.2 and A2.3. The initial biomass for all the different stages after turf stripping are the same, since they are only used to initialise the model SMART2. As soon as the turf stripping takes place at different years in the past the biomass accumulation starts, which is compared to the measured biomass.

Table A2.3. Initial biomass per functional type and organ for each heathland site at Strabrechtse heide.

functional type	roots	wood	leaves
herbs and grasses	1	0.1	1
dwarf shrubs	3	2	3
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

Sellingen

The initial biomass for SUMO is given in Table A2.4, the deposition of nitrogen en sulphur is given in Figs A2.2 and A2.3. The initial biomasses are for all the sites this chronosequence is composed of the same, the runs just start at different points in time.

Table A2.4. Initial biomass per functional type and organ for the grassland site near Sellingen for all age classes.

functional type	roots	wood	leaves
herbs and grasses	0.1	0.1	0.1
dwarf shrubs	0.1	0.1	0.1
shrubs	0.1	0.1	0.1
tree 1	0.2	0.1	0.2
tree 2	0.2	0.1	0.2

Data used for analysing the effect of decreasing nitrogen deposition

Zeesserveld

The initial biomass for SUMO is given in Table A3.1, the deposition of nitrogen en sulphur for both scenarios is given in Fig. A3.1.

Table A3.1. Initial biomass per functional type and organ for the pine forest site Zeesserveld.

functional type	roots	wood	leaves
herbs and grasses	1	0.1	1
dwarf shrubs	0.1	0.1	0.1
shrubs	1	1	1
tree 1 (birch)	1	1	1
tree 2 (pine)	1	1	1

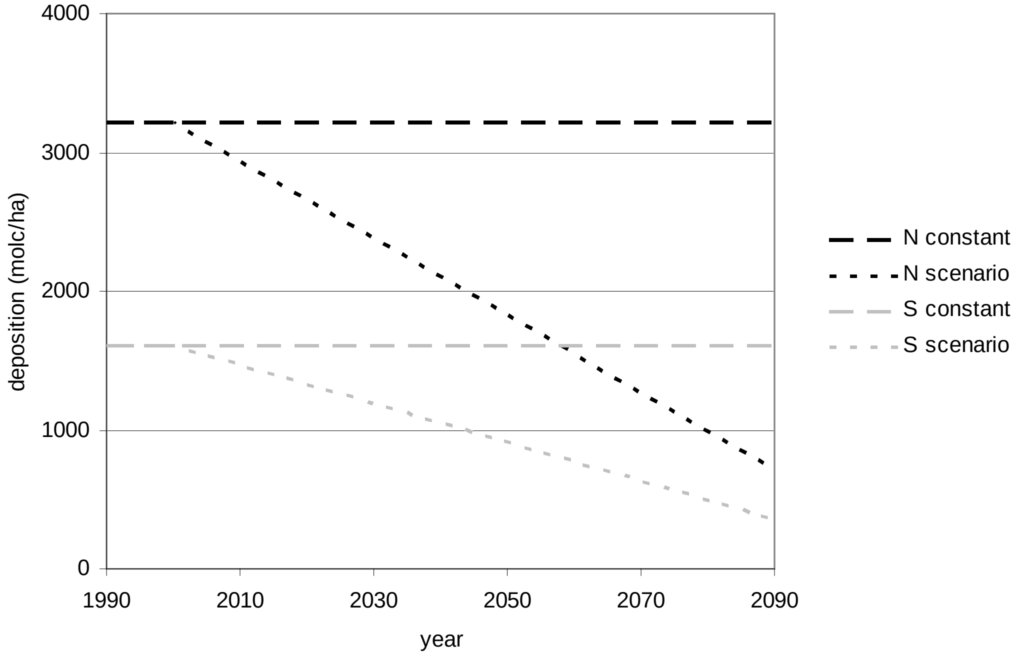

Fig. A3.1. Deposition scenarios of nitrogen (N) and sulphur (S) used for the simulation of Zeesserveld, Edesche heide and Renkum.

Edesche heide

The initial biomass for SUMO is given in Table A3.2, the deposition of nitrogen en sulphur is given in Fig. A3.1.

Table A3.2. Initial biomass per functional type and organ for the heathland site Edesche heide.

functional type	roots	wood	leaves
herbs and grasses	1	0.1	1
dwarf shrubs	3	2	3
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

Renkum

The initial biomass for SUMO is given in Table A3.3, the deposition of nitrogen en sulphur is given in Fig. A3.1.

Table A3.3. Initial biomass per functional type and organ for the grassland site near Renkum.

functional type	roots	wood	leaves
herbs and grasses	3.0	0.1	3.0
dwarf shrubs	0.1	0.1	0.1
shrubs	0.1	0.1	0.1
tree 1	0.1	0.1	0.1
tree 2	0.1	0.1	0.1

Literature data used for the calculation of the relation between NPP and temperature

Table A4.1 Data collected on NPP and average annual temperature from forest sites

Vegetation type	NPP (ton.ha^{-1}.yr^{-1})	annual temp. (°C)	Country	source
Trees in general	0	-5.3	Alaska	Gough & Hobbie (2003)
larix	10.32	-3.5	China	Ni et al. (2001)
Abies-Picea	8.47	4	China	Ni et al. (2001)
Pinus sylvestris var. Mongolica	6.66	-2.5	China	Ni et al. (2001)
mixed coniferous-broad-leaf	9.94	4	China	Ni et al. (2001)
Deciduous broad-leaf	10.9	11.5	China	Ni et al. (2001)
picea mariana	3.91	-3.3	China	Ruess et al. (2003)
deciduous	0.3458	-7	China	Shaver et al. (2001)
Pinus contorta var. Latifolia	7.8	1.4	Canada	http://daac.ornl.gov/NPP/
Pinus contorta var. Latifolia	9.6	1.4	Canada	http://daac.ornl.gov/NPP/
Pinus contorta var. Latifolia	11.9	1.4	Canada	http://daac.ornl.gov/NPP/
Pinus contorta var. Latifolia	11.9	1.4	Canada	http://daac.ornl.gov/NPP/
Picea abies	2.91	2	Flakaliden, Sweden	
Pinus sylvestris	8.6	3.8	Jadraas, Sweden	
Picea abies	4.41	0	Kuusamo, Finland	
Pinus sylvestris	10.18	0.6	Russia	
Pinus sylvestris	16.95	-0.6	Russia	
Picea; Ledum;	1.26	-3.4	USA	Osnabruck data'
Picea mariana	2.63	-3.4	USA	Osnabruck data
Pinus sylvestris	13.6	-2.1	Finland	Osnabruck data
Picea abies; Juniperus;	5.98	-1.2	USSR	Osnabruck data
Picea excelsa; Vaccinium;	4.4	0	Finland	Osnabruck data
Picea abies	3.39	2.2	USSR	Osnabruck data
Picea abies	5.26	2.2	USSR	Osnabruck data
Picea abies	6.04	2.2	USSR	Osnabruck data
Picea abies	7.33	2.2	USSR	Osnabruck data
Picea abies	7.31	2.2	USSR	Osnabruck data
Picea abies	5.26	2.2	USSR	Osnabruck data
Picea abies	4.15	2.2	USSR	Osnabruck data
Pinus sylvestris	6.53	2.9	Finland	Osnabruck data
Picea abies; Vaccinium;	6.44	3.4	USSR	Osnabruck data
Pinus sylvestris	4.78	3.7	Finland	Osnabruck data
Pinus sylvestris	8.42	3.7	Finland	Osnabruck data
Picea; Tsuga; Abies; Thuya;	19.81	4	Canada	Osnabruck data
Picea; Pinus; Tsuga;	9.01	4	Canada	Osnabruck data
Picea; Tsuga; Abies;	7.66	4	Canada	Osnabruck data
Picea; Tsuga; Acer; Abies;	17.41	4	Canada	Osnabruck data
Populus tremuloides	19.2	4.2	Canada	Osnabruck data
Populus tremuloides Populus grandidentata	19.01	4.2	Canada	Osnabruck data

Vegetation type	NPP (ton.ha^{-1}.yr^{-1})	annual temp. (°C)	Country	source
Quercus; Betula; Populus tremuloides; P.grandidentata	5.68	4.2	Canada	Osnabruck data
Abies alba; Oxalis; Pleurozium	22.61	5.1	Romania	Osnabruck data
needle/leaf	17.75	5.3	USA	Osnabruck data
Abies amabilis	18.27	5.4	USA	Osnabruck data
Abies amabilis	16.78	5.4	USA	Osnabruck data
Acer; Betula; Populus; Quercus; Tilia	15.47	5.5	Sweden	Osnabruck data
Betula spp.	9.66	5.5	Sweden	Osnabruck data
Quercus robur; Corylus; Betula	14.46	5.5	Sweden	Osnabruck data
Fagus sylvatica; Abies; Pulmonaria;	18.51	5.7	Romania	Osnabruck data
Picea abies	16.99	5.9	Germany	Osnabruck data
Picea abies	18.72	5.9	Germany	Osnabruck data
Picea abies	14.95	5.9	Germany	Osnabruck data
Fagus sylvatica; Deschampsia	12.29	6	Sweden	Osnabruck data
Fagus sylvatica; Deschampsia	12.29	6	Sweden	Osnabruck data
Quercus robur; Tilia; Acer;	19.49	6	USSR	Osnabruck data
Quercus robur; Tilia; Acer; Euonymus;	19.28	6	USSR	Osnabruck data
Fagus sylvatica	20.17	6.1	Germany	Osnabruck data
Fagus sylvatica	13.73	6.1	Germany	Osnabruck data
Fagus sylvatica	24.48	6.3	Germany	Osnabruck data
Nardus; Festuca; Sauguisorba;	16.21	6.3	USSR	Osnabruck data
Fagus sylvatica; Luzula	14.93	6.5	Germany	Osnabruck data
Fagus sylvatica; Lamium galeobdolon; Oxalis acetosella; Stellaria nemoreum	17.81	6.5	Sweden	Osnabruck data
Fagus sylvatica; Mercuralis perennis	19.01	6.5	Sweden	Osnabruck data
Picea abies; Oxalis; Rubus	16.29	6.5	Sweden	Osnabruck data
Quercus alba; Prunus	14.8	6.9	USA	Osnabruck data
Picea	31.01	7	Germany	Osnabruck data
Fagus sylvatica; Mercurialis; Allium;	19.01	7	Sweden	Osnabruck data
Fagus; Stelloria;	17.81	7	Sweden	Osnabruck data
Picea abies; Oxalis; Rubus	16.29	7	Sweden	Osnabruck data
Fagus sylvatica; Anemone; Carex;	18.74	7.1	Denmark	Osnabruck data
Quercus robur; Tilia cordata; Sorbus aucuparia; Ulmus glabra	15.2	7.5	Sweden	Osnabruck data
Pseudotsuga menziessii; Tsuga heterophylla	2.13	7.5	USA	Osnabruck data
Quercus robur; Tilia; Carpinus;	11.31	7.8	Poland	Osnabruck data
Quercus petraea; Betula; Fraxinus;	12.61	7.8	UK	Osnabruck data
Pinus sylvestris; Ilex aquifolium; Fagus sylvatica	35.12	8	Spain	Osnabruck data
Picea abies	28.46	8.2	Japan	Osnabruck data
Pseudotsuga; Polystichum	10.29	8.5	USA	Osnabruck data
Quercus robur; Fraxinus excelsior; Corylus avelana; Carpinus betulus	11.81	8.6	Belgium	Osnabruck data
Populus hybrid	26	8.6	Germany	Osnabruck data
Quercus petraea; Fagus; Sorbus	22.4	8.6	Netherlands	Osnabruck data
Quercus; Fraxinus; Tilia; Ulmus	35.77	9	Czechoslovakia	Osnabruck data

Vegetation type	NPP (ton.ha^{-1}.yr^{-1})	annual temp. (°C)	Country	source
Pseudotsuga menziessii; Tsuga heterophylla	18	9.8	USA	Osnabruck data
Pseudotsuga menziesii	18	9.8	USA	Osnabruck data
Quercus alba; Q. coccinea; Pinus rigida	12.61	9.8	USA	Osnabruck data
Quercus petraea; Q. cerris; Cornus; Acer;	14.29	9.9	Hungary	Osnabruck data
Quercus petraea; Q. cervis	10.78	9.9	Hungary	Osnabruck data
Quercus castaneifolia; Zelkova; Parrotia	17.16	10	USSR	Osnabruck data
Fagus sylvatica	5.56	10.2	France	Osnabruck data
Fagus sylvatica; Brachypodium	8.8	10.2	France	Osnabruck data
Larix leptolepsis; Morus; Pranus;	17.14	10.2	Japan	Osnabruck data
Quercus pedunculifolia; Acer; Brachypodicum;	12.55	10.2	Romania	Osnabruck data
Ilex; Sassafras; Nyssa; Prunus; Pyrus	11.01	10.3	USA	Osnabruck data
Tsuga heterophylla	36.21	10.3	USA	Osnabruck data
Quercus pubescens; Cotinus; Galium;	8.76	10.6	Romania	Osnabruck data
Eucalyptus obliqua	24.23	11	Australia	Osnabruck data
Quercus; Hickory	8	12.8	USA	Osnabruck data
Quercus; Carya; Pinus	19.03	13.3	USA	Osnabruck data
Cercis; Pinus; Liriodendron	8.19	13.3	USA	Osnabruck data
Quercus spp.; Liriodendron tulipifera	16.69	13.3	USA	Osnabruck data
Liriodendron tulipifera; Quercus	13.81	13.3	USA	Osnabruck data
Pinus taeda	13.81	13.6	USA	Osnabruck data
Pinus taeda	11.6	15.6	USA	Osnabruck data
Forest	15.87	17.2	USA	Osnabruck data

‘Osnabruck data set: Esser (1998).

Table A4.2 Data collected on NPP and average annual temperature from non- forest sites

Vegetation type	comments	NPP (ton.ha^{-1}.yr^{-1})	annual temp. (°C)	country	source
arctic tundra	(shrubs + grasses	1.1083	-7		Shaver et al. (2001)
arctic tundra	shrubs + grasses the year 1999	1.45	-5.3		Gough & Hobbie (2003)
Grassland		3.52	-3.6	USA	Osnabruck data
Grassland		2.48	-3.6	USA	Osnabruck data
Grassland		1.33	-3.4	USA	Osnabruck data
Grassland		1.47	-3.4	USA	Osnabruck data
Grassland		5.66	-3.4	USA	Osnabruck data
heathland		4	-3.4	USA	Osnabruck data
grassland	(Xilin river basin)	8.01	0.3	Mongolia	
heathland		2.17	0.5	Austria	Osnabruck data
heathland		9.71	2	Austria	Osnabruck data
Dwarf shrubs	Loiseleuria procumbens	6.34	2.2	Austria	Osnabruck data
Wetland	alpine tundra	3.49	2.5	Norway	Osnabruck data
Grassland	Tullgarnsnaset (T Stockholm)	3.77	5	Sweden	
Grassland	Bromus riparius; Carex prumilis; Festuca sulcata	8.74	5.7	USSR	Osnabruck data
grassland	salt marsh	8.61	5.9	Sweden	Osnabruck data
Grassland	Zoysia japonica	10	6.2	Japan	Osnabruck data
grassland		16.21	6.3	USSR	Osnabruck data
Grassland	prairie-forest	14.8	6.9	USA	Osnabruck data
Grassland		6.02	7.2	USA	Osnabruck data
Grassland	Filipendula ulmaria; Carex	7.2	7.3	Sweden	Osnabruck data
Grassland	Ossekampen; max production above ground, T from KNMI average Dutch T in de Bilt	6.145	9.8	Netherlands	unpublished
grassland		12.46	17.3	USA	Osnabruck data
grassland		22.61	17.3	USA	Osnabruck data
grassland		12.57	17.3	USA	Osnabruck data
grassland	Swamp	29.33	20	USA	Osnabruck data
grassland	Swamp	52.57	24	USA	Osnabruck data

Data derived for the impacts of CO_2, temperature and nutrients for all included tree species in SUMO.

Table A5.1 Values of β for all functional type/species used in SUMO to describe the effect of CO_2 concentration on forest growth, based on literature (see Appendix 6)

Species/functional type	Source	β	s.d.	n
Herbs and grasses	Average of all herbs and grasses and dwarf shrubs	0.53	-	
dwarf shrubs	Average of all herbs and grasses and dwarf shrubs	0.53	-	
Shrubs	Based on the average of all C3 trees	0.59	-	
Quercus rubra	Literature	0.86	1.04	6
Fagus sylvatica	Literature	1.01	0.82	5
Pseudotsuga meziesii	Literature	0.04	-	1
Quercus robur	Literature	0.51	0.18	4
Pinus sylvestris	Literature	0.30		
Larix decidua	Literature	0.18	-	1
Popules spec	Literature	0.52	0.31	4
Betula pendula	Literature	0.12	0.03	2
Fraxinus excelsior	Literature	0.41	-	1
Picea abies	Literature	0.27	0.28	4
Alnus glutinosa	Literature	0.67	0.06	2
Salix spec	Average of the Salix species	0.70	0.84	21
Abies alba	Literature	0.45	0.55	4
Picea stichensis	Literature	0.32	0.30	3
Pinus halepensis	As pinus sylvestris	0.30		
Pinus pinaster	As pinus sylvestris	0.30		
Pinus mugo	As pinus sylvestris	0.30		
Pinus nigra	As pinus sylvestris	0.30		
Quercus cerris	As Quercus robur	0.51		
Quercus ilex	As Quercus robur	0.51		
Quercus pyrenaica	As Quercus robur	0.51		
Quercus suber	Literature	0.85	-	1
Quercus petrea	Literature	1.08	-	1

Table A5.2 Values of NPP$_{max}$ for all functional type/species used in SUMO to describe the effect of temperature on forest growth.

Tree species/functional type	NPP$_{max}$ (ton.ha^{-1}.yr^{-1})
Herbs and grasses	14'
Dwarf shrubs	13
Shrubs	15
Quercus rubra	20'
Fagus sylvatica	28
Pseudotsuga meziesii	23
Quercus robur	19
Pinus sylvestris	16
Larix decidua	18'
Popules spec	16'
Betula pendula	15'
Fraxinus excelsior	28
Picea abies	19
Alnus glutinosa	18'
Salix spec	18'
Abies alba	23
Picea stichensis	28
Pinus halepensis	20'
Pinus pinaster	20'
Pinus mugo	20'
Pinus nigra	23
Quercus cerris	10
Quercus ilex	16'
Quercus pyrenaica	16'
Quercus suber	16'
Quercus petrea	15'

' NPPs that were changed in the parameterization

Table A5.3 Values of minimum and maximum element contents for all functional type/species used in SUMO to describe the effect of nutrient availability on forest growth

functional type/tree species	N_{min}	N_{max}	K_{min}	K_{max}	Mg_{min}	Mg_{max}	Ca_{min}	Ca_{max}
herbs & grasses	0.011	0.025	0.005	0.01	0.001	0.003	0.003	0.015
dwarf shrubs	0.0085	0.023	0.004	0.009	0.001	0.003	0.002	0.014
shrubs	0.0085	0.023	0.005	0.01	0.001	0.003	0.003	0.015
Quercus rubra	0.01	0.018	0.003	0.0142	0.0012	0.0035	0.0046	0.0158
Fagus sylvatica	0.01	0.025	0.0005	0.0128	0.0008	0.0031	0.005	0.0177
Pseudotsuga meziesii	0.008	0.025	0.001	0.0114	0.0005	0.0022	0.004	0.0058
Quercus robur	0.009	0.025	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Pinus sylvestris	0.009	0.0193	0.001	0.0076	0.0006	0.0018	0.0016	0.0069
Larix decidua	0.005	0.02	0.001	0.0075	0.0011	0.002	0.0048	0.0178
Popules spec	0.008	0.018	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Betula pendula	0.008	0.025	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Fraxinus excelsior	0.008	0.023	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Picea abies	0.01	0.0163	0.001	0.0083	0.0006	0.0018	0.0023	0.0105
Alnus glutinosa	0.008	0.023	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Salix spec	0.008	0.018	0.001	0.0142	0.0012	0.0035	0.0046	0.0158
Abies alba	0.008	0.0161	0.00005	0.0087	0.0007	0.003	0.005	0.0163
Picea stichensis	0.005	0.0201	0.001	0.0108	0.0006	0.0014	0.0022	0.007
Pinus halepensis	0.0096	0.0161	0.001	0.0083	0.0016	0.0032	0.0033	0.0072
Pinus pinaster	0.0088	0.0137	0.001	0.0074	0.0015	0.0031	0.0017	0.0039
Pinus mugo	0.008	0.0268	0.001	0.0108	0.0016	0.0032	0.0065	0.0113
Pinus nigra	0.007	0.0193	0.001	0.0076	0.0006	0.0018	0.0016	0.0069
Quercus cerris	0.008	0.0229	0.001	0.0116	0.001	0.0029	0.0006	0.00137
Quercus ilex	0.008	0.02	0.001	0.0092	0.0009	0.0023	0.0033	0.0095
Quercus pyrenaica								
Quercus suber	0.008	0.0196	0.001	0.0104	0.0014	0.0028	0.0035	0.009
Quercus petrea	0.008	0.0224	0.001	0.00139	0.0009	0.0025	0.0045	0.0125

Overview of β values in the relationship between CO_2 concentration and biomass growth

Table A6.1 Estimated β values in the formula: β =((G/G0)-1)/ln(Ca/Ca,0), where Ca,0: ambient CO_2 *concentration, Ca: raised* CO_2 *concentration and G/G0: biomass growth factor. Data are collected from literature, given are the sources and in the case of a review article the original source if known.*

Species	$C_{a,0}$	C_a	G/G_0	Original author	in:	Remarks	β
abies alba	365	500	1		(Hättenschwiler, 2001)		0.00
abies alba	365	660	1.47		(Hättenschwiler, 2001)		0.80
abies alba	365	660	0.97		(Hättenschwiler, 2001)		-0.05
abies alba	365	660	1.62		(Hättenschwiler, 2001)		1.04
Acer pseudoplatanus	365	500	1.1		(Hättenschwiler, 2001)		0.32
Acer pseudoplatanus	365	500	1.27		(Hättenschwiler, 2001)		0.87
Acer pseudoplatanus	365	660	1.03		(Hättenschwiler, 2001)		0.06
Acer pseudoplatanus	365	660	1.51		(Hättenschwiler, 2001)		0.85
all species	330	660	1.37		(Poorter, 1993)		0.53
Alnus glutinosa	330	660	1.44		(Poorter, 1993)		0.63
Alnus glutinosa	330	660	1.49	Norby 1987	(Poorter, 1993)		0.71
avg C3 trees	330	660	1.41		(Poorter, 1993)	weighted average	0.59
Avg wild plants	330	660	1.35		(Poorter, 1993)	weighted average	0.50
Betula pendula	350	700	1.1	Petterson & MacDonald 1993	(Kittel et al., 1995)		0.14
Betula pendula	350	700	1.07	(Lee & Jarvis, 1995)			0.10
Fagus sylvatica	365	500	1.74		(Hättenschwiler, 2001)		2.34
Fagus sylvatica	365	500	1.19		(Hättenschwiler, 2001)		0.59
Fagus sylvatica	365	660	1.74		(Hättenschwiler, 2001)		1.24
Fagus sylvatica	365	660	1.17		(Hättenschwiler, 2001)		0.28
Fagus sylvatica	350	700	1.41	(Lee & Jarvis, 1995)			0.59
Fraxinus excelsior	360	700	1.27	(Broadmeadow & Jackson, 2000)			0.41
Larix decidua	367	566	1.08		(Hättenschwiler, 2001)	Needle biomass	0.18
Picea abies	350	700	1.14		(Laitat et al., 2000)	aboveground biomass	0.20
Picea abies	350	467	1		(Laitat et al., 2000)	aboveground biomass	0.00

Species	$C_{a,0}$	C_a	G/G_0	Original author	in:	Remarks	β
Picea abies	350	583	1.34		(Laitat et al., 2000)	aboveground biomass	0.67
Picea abies	280	490	1.12		(Hättenschwiler & Körner, 1996)		0.21
picea sitchensis	350	700	1.14	(Lee & Jarvis, 1995)		5 year old seedlings	0.20
picea sitchensis	350	700	1.46	(Lee & Jarvis, 1995)		juvenile clonal 3 years old	0.66
picea sitchensis	350	700	1.07	(Lee & Jarvis, 1995)		mature 3 years	0.10
Pinus sylvestris	360	700	1.2	(Broadmeadow & Jackson, 2000)		seedlings	0.30
popules spec	330	660	1.3	Radaglou & Jarvis 1990	(Poorter, 1993)		0.43
popules spec	330	660	1.15	Radaglou & Jarvis 1990	(Poorter, 1993)		0.22
popules spec	330	660	1.33	Radaglou & Jarvis 1990	(Poorter, 1993)		0.48
popules spec	330	660	1.66	Radaglou & Jarvis 1990	(Poorter, 1993)		0.95
Populis euramericana	350	540	1.18	(Calfapietra et al., 2003)			0.42
Populis nigra	350	540	1.29	(Calfapietra et al., 2003)			0.67
Populus alba	350	540	1.2	(Calfapietra et al., 2003)			0.46
Populus tremuloides	350	750	1	Brown & Higginbotham 1986	(Kittel et al., 1995)		0.00
Populus tremuloides	389	496	1.1	Brown & Higginbotham 1986	(Kittel et al., 1995)		0.41
Pseudotsuga menziesii	330	660	1.03	Hollinger 1987	(Poorter, 1993)	weighted average	0.04
Quercus petrea	360	700	1.72	(Broadmeadow & Jackson, 2000)		seedlings	1.08
Quercus robur	365	500	1.20		(Hättenschwiler, 2001)		0.64
Quercus robur	365	500	1.20		(Hättenschwiler, 2001)		0.64
Quercus robur	365	660	1.15		(Hättenschwiler, 2001)		0.25
Quercus robur	365	660	1.31		(Hättenschwiler, 2001)		0.52
Quercus rubra	350	700	3	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	2.89
Quercus rubra	350	700	1.4	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	0.58
Quercus rubra	350	700	1.2	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	0.29
Quercus rubra	300	500	1.1	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	0.20
Quercus rubra	300	500	1.1	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	0.20

Species	$C_{a,0}$	C_a	G/G_0	Original author	in:	Remarks	β
Quercus rubra	300	500	1.5	Bazzaz & Miao 1993	(Kittel et al., 1995)	seedlings	0.98
Quercus suber	350	700	1.59	(Silva et al., 2004)		4 year old seedlings	0.85
Salix phylicifolia	300	500	3.8	Sionit et al. 1984	(Kittel et al., 1995)		3.30
Salix phylicifolia	300	700	1	Sionit et al. 1984	(Kittel et al., 1995)		0.00
Salix phylicifolia	300	700	1.7	Sionit et al. 1984	(Kittel et al., 1995)		0.58
Salix phylicifolia	300	700	1.8	Sionit et al. 1984	(Kittel et al., 1995)		0.66
Salix phylicifolia	300	700	1.3	Sionit et al. 1984	(Kittel et al., 1995)		0.25
Salix phylicifolia	300	1000	1	Sionit et al. 1984	(Kittel et al., 1995)		0.00
Salix phylicifolia	300	1000	1.7	Sionit et al. 1984	(Kittel et al., 1995)		1.37
Salix phylicifolia	300	1000	2.5	Sionit et al. 1984	(Kittel et al., 1995)		1.77
Salix phylicifolia	300	1000	2.7	Sionit et al. 1984	(Kittel et al., 1995)		2.01
Salix x dasyclados	300	500	1.5	Silvola & Ahlholm 1992	(Kittel et al., 1995)		0.98
Salix x dasyclados	300	700	1.2	Silvola & Ahlholm 1993	(Kittel et al., 1995)		0.24
Salix x dasyclados	300	700	1.1	Silvola & Ahlholm 1994	(Kittel et al., 1995)		0.12
Salix x dasyclados	300	700	1.5	Silvola & Ahlholm 1995	(Kittel et al., 1995)		0.59
Salix x dasyclados	300	700	1.5	Silvola & Ahlholm 1996	(Kittel et al., 1995)		0.59
Salix x dasyclados	300	1000	1	Silvola & Ahlholm 1997	(Kittel et al., 1995)		0.00
Salix x dasyclados	300	1000	1	Silvola & Ahlholm 1998	(Kittel et al., 1995)		0.00
Salix x dasyclados	300	1000	1.5	Silvola & Ahlholm 1999	(Kittel et al., 1995)		0.42
Salix x dasyclados	300	1000	1.4	Silvola & Ahlholm 2000	(Kittel et al., 1995)		0.33
Salix x dasyclados	300	500	1.5	Silvola & Ahlholm 2001	(Kittel et al., 1995)		0.98
Salix x dasyclados	300	500	0.9	Silvola & Ahlholm 2002	(Kittel et al., 1995)		-0.20
Salix x dasyclados	300	500	1.1	Silvola & Ahlholm 2003	(Kittel et al., 1995)		0.20
Taxus tabaccatta	365	500	0.13		(Hättenschwiler, 2001)		-2.75
Taxus tabaccatta	365	500	0.97		(Hättenschwiler, 2001)		-0.11
Taxus tabaccatta	365	660	0.14		(Hättenschwiler, 2001)		-1.45
Taxus tabaccatta	365	660	1.16		(Hättenschwiler, 2001)		0.27

Graphs of the carbon sequestration per latitude for all four scenarios

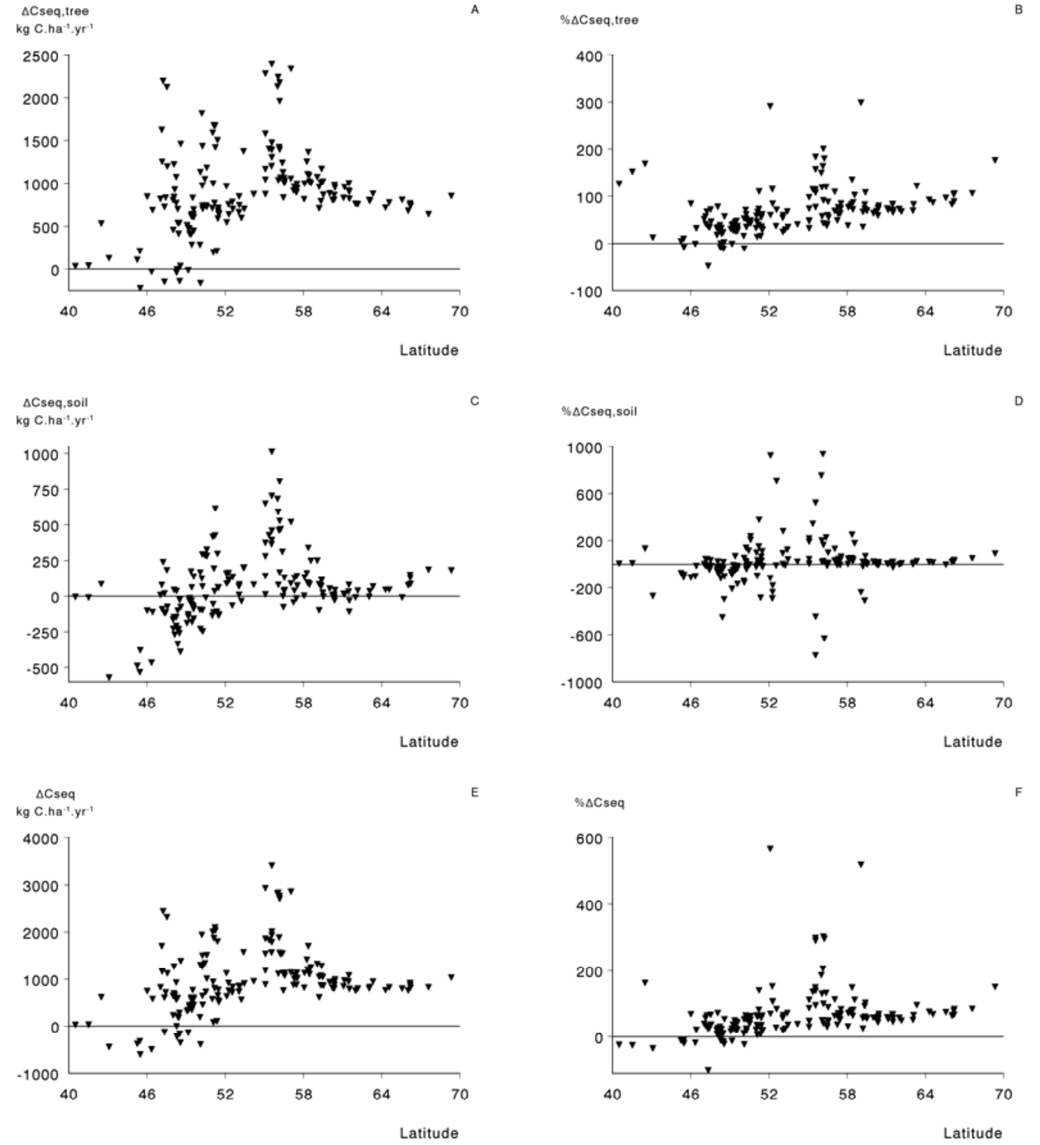

Figure A.7.1 Biomass change of European forests in 2070 compared to the reference run as a result of an increasing CO_2 *concentration, climate change (mainly temperature) and a changing nitrogen deposition as a function of latitude. Results include the difference in C sequestration in tree (A), soil (C) and both tree and soil (E) and the relative difference in C sequestration (relative to the NPP in the reference run) for tree (B), soil (D) and both tree and soil (F).*

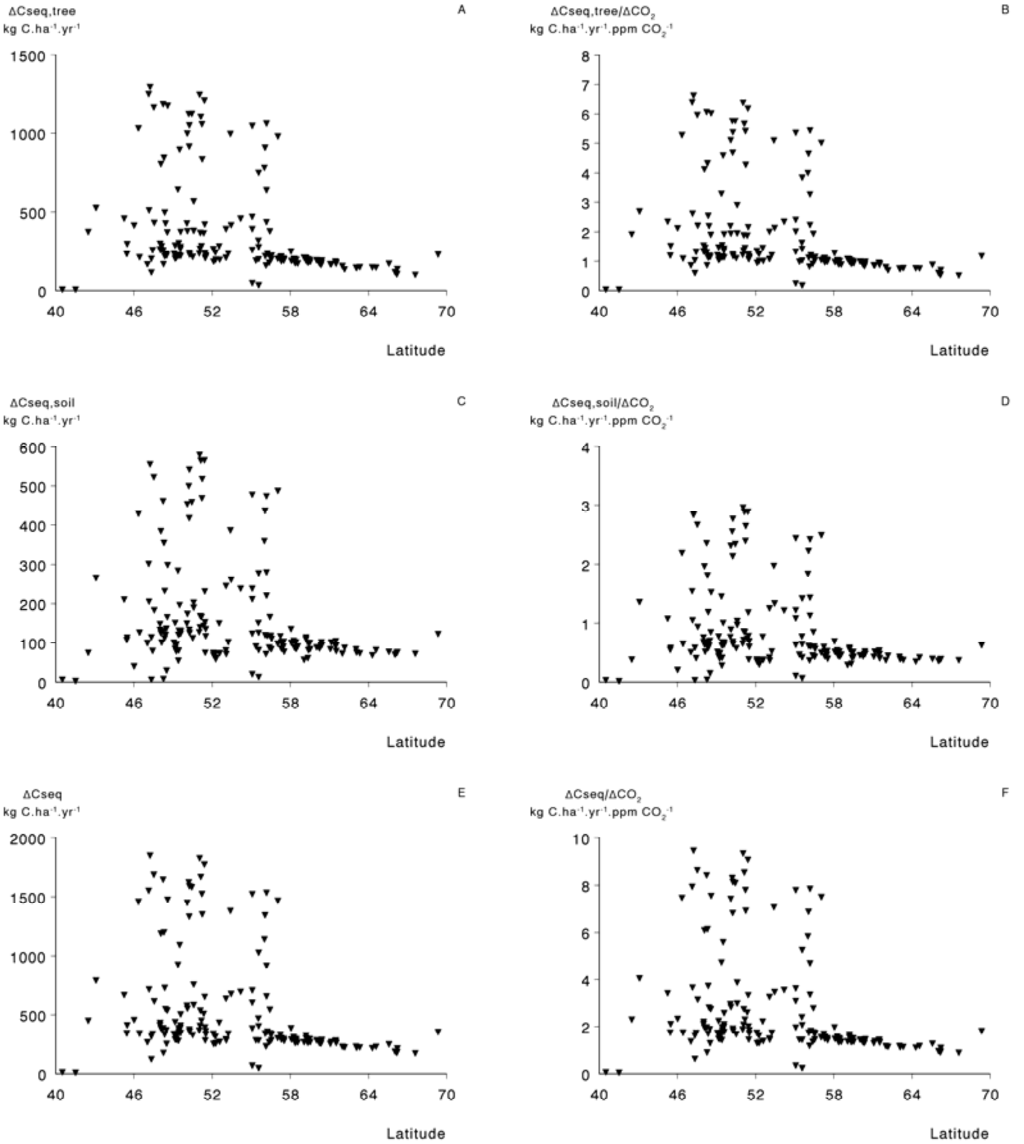

Figure A.7.2 Biomass change of European forests in 2070 compared to the reference run as a result of an increasing CO_2 concentration as a function of latitude. Results include the difference in total C sequestration in tree (A), soil (C) and both tree and soil (E) and the difference in total C sequestration per ppm CO_2 difference for tree (B), soil (D) and both tree and soil (F).

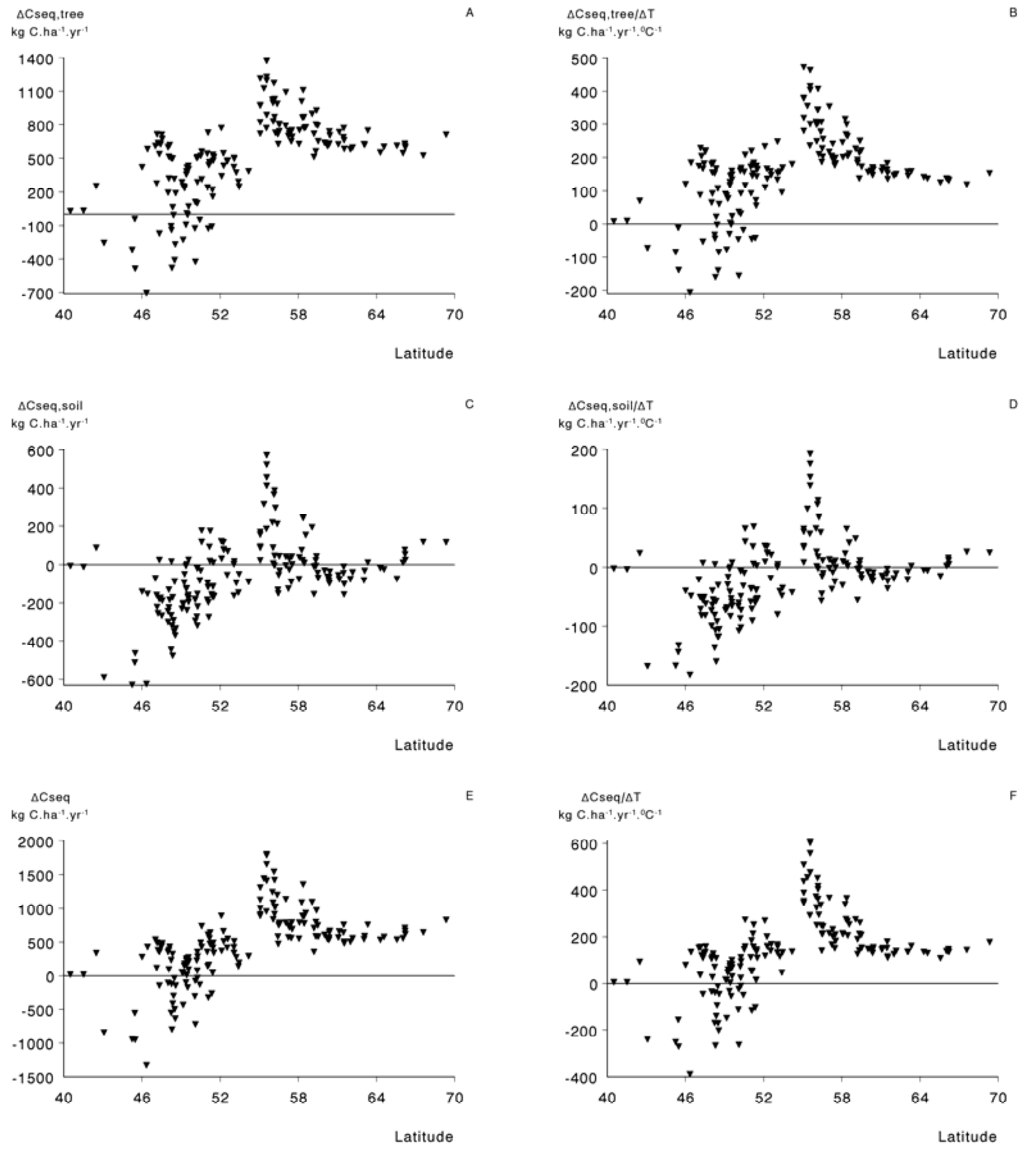

Figure A.7.3 Biomass change of European forests in 2070 compared to the reference run as a result of climate change (specifically temperature) as a function of latitude. Results include the difference in total C sequestration in tree (A), soil (C) and both tree and soil (E) and the difference in total C sequestration per °C difference for tree (B), soil (D) and both tree and soil (F).

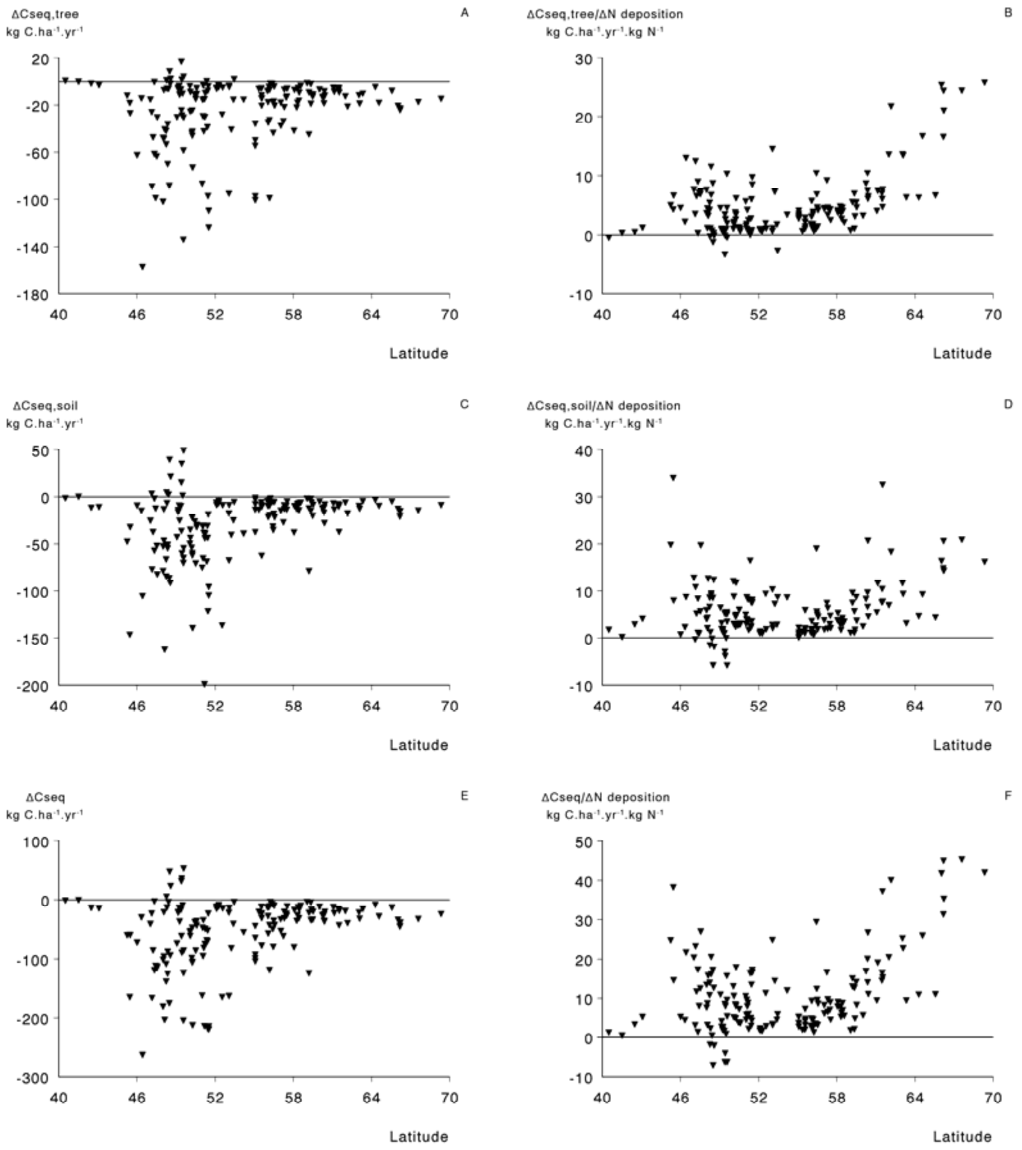

Figure A.7.4 Biomass change of European forests in 2070 compared to the reference run as a result of a change in N deposition, according to the Gothenburg protocol, as a function of latitude. Results include the difference in total C sequestration in tree (A), soil (C) and both tree and soil (E) and the difference in total C sequestration per kg N difference for tree (B), soil (D) and both tree and soil (F).