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MODELLING THE EFFECTS OF NITROGEN DEPOSITION AND CARBON DIOXIDE ENRICHMENT ON FOREST CARBON BALANCE

TESI DI DOTTORATO

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Modelling the effects of nitrogen deposition and carbon dioxide enrichment on forest carbon balance

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"No começo, pensei que estivesse lutando para salvar seringueiras,
depois pensei que estava lutando para salvar a floresta amazônica.
Agora, percebo que estou lutando pela humanidade"
("At first, I thought I was fighting to save rubber trees,
then I thought I was fighting to save the Amazon rainforest.
Now I realize I am fighting for humanity.")

(Chico Mendes, Brazilian Environmentalist)

« C'era una volta...
- Un re! - diranno subito i miei piccoli lettori.
No ragazzi, avete sbagliato: c'era una volta un pezzo di legno. »
("Centuries ago there lived--
"A king!" my little readers will say immediately.
No, children, you are mistaken. Once upon a time there was a piece of wood")

(Carlo Collodi, incipit de "Le avventure di Pinocchio")

"A model should be as simple as possible, but not simpler than that"

(Albert Einstein)

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ABSTRACT

Atmospheric CO_2 concentration ($[CO_2]$) has increased over the last 250 years, mainly due to human activities. Of total anthropogenic emissions, almost 31% has been sequestered by the terrestrial biosphere. A considerable contribution to this sink comes from temperate and boreal forest ecosystems of the northern hemisphere, which contain a large amount of carbon (C) stored as biomass and soil organic matter. Several potential drivers for this forest C sequestration have been proposed, including increasing atmospheric $[CO_2]$, temperature, nitrogen (N) deposition and changes in management practices. However, it is not known which of these drivers are most important.

The overall aim of this thesis project was to develop a simple ecosystem model which explicitly incorporates our best understanding of the mechanisms by which these drivers affect forest C storage, and to use this model to investigate the sensitivity of the forest ecosystem to these drivers.

I firstly developed a version of the Generic Decomposition and Yield (G'DAY) model to explicitly investigate the mechanisms leading to forest C sequestration following N deposition. Specifically, I modified the G'DAY model to include advances in understanding of C allocation, canopy N uptake, and leaf trait relationships. I also incorporated a simple forest management practice subroutine. Secondly, I investigated the effect of CO_2 fertilization on forest productivity with relation to the soil N availability feedback. I modified the model to allow it to simulate short-term responses of deciduous forests to environmental drivers, and applied it to data from a large-scale forest Free-Air CO_2 Enrichment (FACE) experiment. Finally, I used the model to investigate the combined effects of recent observed changes in atmospheric $[CO_2]$, N deposition, and climate on a European forest stand.

The model developed in my thesis project was an effective tool for analysis of effects of environmental drivers on forest ecosystem C storage. Key results from model simulations include: (i) N availability has a major role in forest ecosystem C sequestration; (ii) atmospheric N deposition is an important driver of N availability on short and long time-scales; (iii) rising temperature increases C storage by enhancing soil N availability and (iv) increasing $[CO_2]$ significantly affects forest growth and C storage only when N availability is not limiting.

ITALIAN ABSTRACT

La concentrazione atmosferica di CO2 ([CO_2]) è aumentata negli ultimo 250 anni, principalmente a causa delle attività umane. Circa il 31% di tutte le emissioni di natura antropogenica viene sequestrato dagli ecosistemi terrestri. Un contributo considerevole a tale sequestro viene dalle foreste temperate e boreali dell'emisfero nord, che immagazzinano una grande quantità di carbone (C) sotto forma di biomassa e sostanza organica del suolo. Sono state proposte varie ipotesi alternative per spiegare tale stoccaggio, incluso l'aumento della [CO_2] in atmosfera, della temperatura e delle deposizioni azotate e cambiamenti nelle pratiche gestionale; resta comunque ancora conosciuta quale di queste ipotesi abbia il maggio effetto.

Scopo di questo progetto di tesi è sviluppare un semplice modello di ecosistema che incorpori esplicitamente le nostre migliori conoscenze dei meccanismi attraverso cui questi fattori influenzano il sequestro di C e usare tale modello per investigare la sensitività dell'ecosistema forestale a tali fattori.

A tal fine, in primo luogo ho sviluppato una versione del modello G'DAY (*Generic Decomposition and Yield*) per indagare esplicitamente i meccanismi per il sequestro di C in seguito alle deposizioni azotate. Ho modificato il modello G'DAY per includervi le ultime conoscenze riguardo l'allocazione di C, l'assorbimento fogliare di azoto e le relazioni tra i principali tratti fogliari. Ho inoltre aggiunto una semplice subroutine per simulate la gestione forestale. In secondo luogo ho indagato l'effetto delle fertilizzazione da CO_2 sulla produttività forestale in relazione alla disponibilità di azoto nel suolo. A questo scopo ho modificato il modello per poter simulate la risposta di breve tempo delle foreste decidue ai fattori ambientali, e l'ho applicato ai dati derivanti da un esperimento di fertilizzazione carbonica di larga scala (FACE, *Free Air Carbon Enrichment*). In fine ho usato il modello per indagare l'effetto combinato dovuto ai cambiamento della [CO_2] atmosferica, delle deposizioni azotate e climatici su una foresta europea.

Il modello sviluppato nel progetto di tesi si è rivelato uno strumento efficace per analizzare gli effetti dei fattori ambientali sull'immagazzinamento di C da parte degli ecosistemi forestali. Risultati chiave includono: (i) la disponibilità di azoto ha un ruolo fondamentale nel sequestro di C degli ecosistemi forestali; (ii) le deposizioni azotate sono importanti cause per l'aumento di disponibilità di azoto a breve e lungo periodo; (iii) l'aumento di temperatura aumenta il sequestro di C aumentando la disponibilità di

N nel suolo; (iv) l'aumento di [CO_2] ha un effetto significativo sulla crescita forestale e il sequestro di C solo quando la disponibilità di azoto non è limitante.

STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled "Modelling the effects of nitrogen deposition and carbon dioxide enrichment on forest carbon balance" has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

The research presented in this thesis did not require approval from the Macquarie University Ethics Review Committee.

Silvia Dezi (41345827)

March 2011

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CHAPTER 1

Introduction and thesis outline

1.1 INTRODUCTION

Atmospheric CO_2 concentration ($[CO_2]$) has increased globally by about 38% over the last 250 years, from 280 ppm in the pre-industrial period (1750) to 385 ppm in 2008 (http://www.globalcarbonproject.org). The rate of growth in $[CO_2]$ is also increasing, despite some year to year variability: the growth rate was larger during the period 2000-2006 (average 1.93 ppm yr^{-1}, or 4.1 PgC yr^{-1}) than it has been since the beginning of continuous direct atmospheric measurements (1960-2005 average: 1.4 ppmyr^{-1}) (IPCC, 2007; Canadell *et al.,* 2007). This increase in global atmospheric $[CO_2]$ is mainly due to human activities: primarily emissions from fossil fuels combustion, gas flaring and cement production, but also emissions due to land use changes and management such as deforestation (Houghton, 2003), biomass burning (Andreae & Merlet, 2001; van der Werf *et al.,* 2004), crop production and conversion of grasslands to croplands (ICPP, 2007).

The annual increase in atmospheric $[CO_2]$ is substantially smaller than the annual anthropogenic emissions, because of natural sinks. Of total combined anthropogenic emissions (fossil fuel plus land use), almost 45% remained in the atmosphere, while oceans are estimated to have taken up approximately 24%. The remaining 31% (2.8 PgC yr^{-1}) was sequestered by the terrestrial biosphere (IPCC, 2007; Canadell *et al.,* 2007). Although the location of this significant terrestrial carbon (C) sink is still debated, a considerable contribution to the sink likely comes from temperate and boreal forest ecosystems of the northern hemisphere, which are estimated to sequester approximately 0.6–0.7 Pg C yr^{-1} (Goodale *et al.,* 2002).

Forest ecosystems contain a large fraction of C stored in land as biomass and soil organic matter (Hyvönen *et al.,* 2007). They also control the main bidirectional C flux between atmosphere and soil. Plants absorb CO_2 from the atmosphere through photosynthesis, releasing oxygen back to the atmosphere. They use the C to produce sugars for their growth, storing it in their leaves, twigs, trunk and root system. Part of the C fixed by the plant is transferred to the soil through above and below ground litter and rhizodeposition. Forest ecosystems release CO_2 back to the atmosphere via plant respiration (autotrophic respiration) on a short time scale and soil decomposition processes (heterotrophic respiration) on longer time scales. The difference between the amount of C absorbed and released during a period of time determines the role of the ecosystem with respect to the C budget: the forest ecosystem is a sink if the difference is positive, while it is a source if the difference is negative. Forest

ecosystems can change from source to sink, or vice versa, depending on different factors.

To be able to predict the future course of the contribution to the global C budget by forest ecosystems, it is necessary to identify the major driving factors causing large-scale forest C sequestration. A wide range of potential drivers has been identified and includes increasing atmospheric [CO_2], rising temperature, increasing nitrogen (N) deposition, and changing forest management practices, all of which affect photosynthesis, plant growth and soil C decomposition (Ciais *et al.,* 2008).

Results from free-air CO_2 enrichment (FACE) experiments have demonstrated a significant stimulatory effect of increased [CO_2] on forest productivity (Norby *et al.,* 2005), leading to more C stored in tree biomass. Some studies on forest growth in CO_2-enriched environments suggest that the potential for a growth response to increasing [CO_2] is limited by the lack of nutrient availability (Oren *et al., 2001*; Luo *et al.,* 2004; de Graaff *et al.,* 2006; Johnson, 2006; Körner, 2006). However, there is some evidence of increased belowground C allocation under elevated [CO_2], with consequent increase in N uptake, even in N-limited ecosystems (Finzi *et al.,* 2007). Moreover, elevated [CO_2] can also affect heterotrophic respiration by decreasing soil decomposition rate, thereby further promoting soil C sequestration (Six *et al.,* 1998; Hyvönen *et al.,* 2007).

Global temperatures are rising. The average global temperature increased by 0.74°C from 1906 to 2006, and eleven of the twelve warmest years since 1850 occurred in the period 1995 – 2006 (IPCC, 2007). Changes in mean air temperature may affect forest productivity and carbon sequestration by increasing plant photosynthetic and autotrophic respiration rates, lengthening growing season (Myneni *et al.,* 1997; Menzel & Fabian, 1999; Saxe *et al.,* 2001; Nemani *et al.,* 2003) and altering soil decomposition rate and nutrient mineralization (Saxe *et al.,* 2001; Davidson & Janssens, 2006).

Over the last 150 years, N deposition has also increased, mainly due to the use of fossil fuels, deforestation and agricultural practices (Mayewski *et al.,* 1990; Galloway *et al.,* 1995; Vitousek *et al.,* 1997; Holland *et al.,* 1999, 2005). The amount of nitrogen deposition varies from 0.1 gN m^{-2} yr^{-1}, in remote forests at high latitude, up to 10 gN m^{-2} yr^{-1}, in industrial central Europe (Jarvis & Fowler, 2001). Although the quantitative impact of N deposition on the terrestrial carbon cycle is strongly debated, N input via atmospheric deposition has been likely a growth promoting factor during recent years, since N is the most significant growth-limiting nutrient in many forests worldwide (LeBauer & Treseder, 2008). Moreover, increased N deposition can increase the rate

of accumulation of soil organic matter (Berg & Matzner, 1997; Harrison *et al.,* 2000; Schulze *et al.,* 2000; Hagedorn *et al.,* 2003). In a recent study, Magnani *et al.* (2007), analysing the C balance across a network of temperate and boreal forests in Europe and North America, demonstrated a strong positive relationship between N deposition and average forest C sequestration (Högberg, 2007). Although the size of the response indicated by this study has been questioned, since it appears to show a very high ratio of C sequestered per unit N deposited (Sutton *et al.,* 2008; de Vries *et al.,* 2008; Hyvönen *et al.,* 2008; Högberg, 2007), there is consensus among scientists that, qualitatively, N deposition is likely to enhance forest C sequestration.

There have been significant improvements in forest management practices in recent years. These include new regeneration methods, changes in species used and modifications to tending, thinning and harvesting regimes. These improvements aim to maximise wood production in combination with soil and water protection and have resulted in enhanced site productivity (Spiecker, 1999; Ciais *et al.,* 2008; Kahle *et al.,* 2008).

Although several studies have investigated the effects of increasing atmospheric $[CO_2]$, temperature, N deposition and changes in management practices on forest growth, there is still no consensus on their relative importance for forest NPP and C sequestration during recent decades, and how that might change in future. Some studies suggest that the major driver of growth increment in Europe is N deposition (Nellemann & Thomsen, 2001; Solberg *et al.,* 2004; Van Oijen *et al.,* 2004, 2008; van Oijen & Jandl, 2004; Mellert *et al.,* 2008) while $[CO_2]$ and temperature have very little effect (Solberg *et al.,* 2009; Laubhann *et al.,* 2009). Rehfuess *et al.* (1999), using a combined (model-statistical-empirical) approach to investigate the relationships between recent changes of growth and nutrition of three European forests, found that the combination of $[CO_2]$ and N deposition increase could account for a 15-20% increase in forest net primary production (NPP), while the rise in temperature was relatively unimportant. Using the complex forest model EFM (Thornley, 1991), parameterized for 22 stands across Europe, Milne & Van Oijen (2005) concluded that the main driver of increased forest growth in the 20th century has been increased N deposition, rather than increased $[CO_2]$ or climate change. Recently, the EU-RECOGNITION project attempted to clarify the causes of the observed forest growth increase using long-term growth studies and models, and came to the conclusion that N availability should be regarded as the main driver for this increase (Kahle *et al.,* 2008; Van Oijen *et al.,* 2008). On the other hand, using the ORCHIDEE model, Ciais *et al.* (2008) concluded that a significant fraction of the trend in European forest NPP may

be explained by changes in climate (temperature and precipitation) and $[CO_2]$. Although Ciais *et al.* (2008) did not consider N limitations in their work, they suggested that N deposition has only a minor role.

Several studies assessing potential climate change effects on future forest production also do not take account of the N deposition effect, identifying the main drivers of forest C accumulation as increased $[CO_2]$ and/or temperature (Loustau *et al.,* 2005; Zaehle *et al.,* 2007; Morales *et al.,* 2007; Kirilenko *et al.,* 2007; Sitch *et al.,* 2008). Other studies find a role for both N deposition and climate: in a tree model study on the effect of N deposition and climate change on growth of different European forests, Laubhann *et al.* (2009) found a positive correlation between growth and both N deposition and temperature.

Thus, there is uncertainty about the direction and magnitude of the effects of these driving factors ($[CO_2]$, temperature, N deposition, and forest management) on forest C sequestration. It is difficult to conduct experiments sufficiently long enough to observe responses on long time scales. Ecosystem models are therefore important tools for identifying and quantifying the mechanisms involved in the response of nutrient-limited forest ecosystems to increased $[CO_2]$, temperature, N deposition and forest management on different time scales.

The overall aim of this thesis project was to develop a simple ecosystem-scale model which explicitly incorporates our best understanding of the impacts of N deposition, $[CO_2]$, temperature and forest management on forest function, and to use it to investigate the sensitivity of the forest system to these factors and their interactions. The model code is presented in Appendix I.

1.2 THESIS OUTLINES

The chapters that constitute the thesis are written as self-contained papers, either published in, or formatted for submission to, scientific journals. A brief synopsis of each of these papers is given below.

Chapter 2 is focused on developing a model that is able to qualitatively describe the effect of N deposition on forest ecosystem C sequestration. To this end, a new version of the Generic Decomposition and Yield (G'DAY) model, originally developed by Comins & McMurtrie (1993), is presented. The new model version takes into account several recent scientific advances, including: advances in understanding of the relationship between C allocation and NPP (Palmroth *et al.,* 2006); experimental

evidence for canopy N uptake (Sievering, 1999; Jenkinson *et al.,* 1999; Sparks, 2009); and leaf trait relationships found by Reich *et al.* (1999). Moreover, it incorporates a simple forest management practice subroutine. Finally, the N leaching formulation was changed so that leaching occurs only for soil nitrogen in the form of nitrate, whilst nitrification is a direct function of soil C:N ratio (Aber *et al.,* 2003).The aim of this part of the project was not to quantify precisely how much C is stored by ecosystems for a given amount of N deposition, but to further develop our understanding of the mechanisms leading to forest C sequestration following N deposition. This chapter has been published in Global Change Biology.

Chapter 3 investigates the effect of CO_2 fertilization on forest productivity with relation to soil N availability feedback, testing the G'DAY model against data from the closed-canopy Sweetgum (*Liquidambar styraciflua* L.) plantation FACE experiment at Oak Ridge National Laboratory (ORNL). In particular the chapter focuses on testing whether G'DAY model can explain several key observations at this experiment: a decline in leaf N concentration over time; a decrease in net primary productivity (NPP) over time; and decreasing stimulation of NPP by elevated [CO_2] over time. To this end the original version of the G'DAY model, developed for evergreen forest stands, was modified to fit the development of the ORNL FACE deciduous plantation. This new model version was then coupled to the Model Any Terrestrial Ecosystem (MATE) model (McMurtrie *et al.,* in preparation), which incorporates the effect of atmospheric [CO_2] and meteorological data (T, PAR, RH, rain) on light use efficiency (LUE). This chapter has been formatted for submission to Global Change Biology.

Chapter 4 investigates the combined effect of recent changes in forest growth environmental drivers, i.e. atmospheric [CO_2], N deposition, and climate variables (temperature, precipitation and radiation) on a pine forest stand near Bordeaux, France, with the aim of quantifying the relative contributions of these changes. The effect of observed changes in atmospheric [CO_2], climate and N deposition over the period 1950-2000 were assessed for gross primary production, net ecosystem production, maximum annual increment and wood and tree C. In order to remove the overwhelming effects of forest age on growth and C sequestration (Pregitzer & Euskirchen, 2004; Magnani *et al.,* 2007), the model was run assuming a wide range of years for forest establishment, thus simulating chronosequences over which outputs could be averaged, as suggested by Magnani *et al.,* 2007). The effects of the environmental factors on chronosequence-scale outputs were examined separately and in combination, using a full factorial design analysis (Box *et al.,* 1978). This chapter has been formatted for submission to Tree Physiology.

1.3 COLLABORATION AND CANDIDATE'S ROLE

The work presented in this thesis has been developed in collaboration with others. The contribution of different parties to the work are as follows.

Work presented in chapter two originated from a discussion with Federico Magnani about the possibility to test his work findings about nitrogen deposition and forest carbon sequestration (Magnani *et al.,* 2007) using a simple forest ecosystem model. I chose the model to use, coded the model, made all the modifications, analysed its behaviour, and wrote the paper that was published in Global Change Biology (Dezi *et al.,* 2010). Belinda Medlyn and Giustino Tonon both made major editorial contributions to this work.

Chapter three originated from a project about the use of forest ecosystem models to reproduce observed forest productivity under elevated CO_2 concentration. I coded the model, analysed its behaviour, and wrote the paper for submission to Global Change Biology. Model modifications to reproduce specific site behaviour were discussed with Belinda Medlyn, Ross McMurtrie and Federico Magnani. Belinda Medlyn and Giustino Tonon provided feedback on analyses and editorial suggestions to the draft prepared by me. Colleen Iversen calculated model parameters and model initial values and collected field data. Richard Norby provided us with the data from ORNL experiment used in this work.

Chapter four originated from the decision to apply the final model version to one of the chronosequence studies from Magnani *et al.* (2007). I coded the model, analysed its behaviour, and wrote the paper for submission to Tree Physiology. Model modifications and analysis were decided with Federico Magnani. Federico Magnani, Giustiono Tonon and Belinda Medlyn provided feedbacks on analysis and editorial suggestions to the draft prepared by me. Denis Loustau provided us the data from "Le Bray" site used in the work, while, Twan van Noije provided us with model N deposition estimates at "Le Bray" site.

1.4 LITERATURE CITED

Aber JD, Goodale CL, Ollonger SV *et al.* (2003) Is nitrogen deposition altering the nitrogen status of north eastern forests? *Biosciences*, **53**, 375-389.

Andreae MO, Merlet P (2001) Emission of trace gases and aerosols from biomass burning. *Global Biogeochemical Cycles*, **15**, 955– 966.

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Review*, **5**, 1-15.

Box GPE, Hunter WG, Hunter JS (1978) Statistics for Experimenters. An Introduction to Design, Data Analysis and Model Building. John Wiley & Sons, New York, 653 pp.

Canadell JG, Le Quéré C, Raupach MR *et al.* (2007) Contributions to accelerating atmospheric CO_2 growth economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866-18870.

Ciais P, Schelhaas MJ, Zaehle S, Piao SL *et al.* (2008) Carbon accumulation in European forests. *Nature geoscience*, **1(7)**, 427-429.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behaviour of plant-soil models. *Ecological Application*, **3(4)**, 666-681.

Davidson EA, Janssens IA (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165-173.

de Graaff MA, van Groeningen KJ, Six J, Hungate BA, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta analysis. *Global Change Biology*, **12**, 2077-2091.

de Vries W, Solberg S, Dobbertin M *et al.* (2008) Ecologically implausible carbon sequestration? *Nature*, **541**, E1-E3.

Dezi S, Medlyn BE, Tonon G, Magnani F (2010) The effect of nitrogen deposition on forest carbon sequestration: a model-based analysis. *Global Change Biology*, **16**, 1470-1486.

Finzi AC, Norby RJ, Calfapietra C *et al.* (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences*, **104(35)**, 14014-14019.

Galloway JN, Schlesinger WH, Levy II HL, Michaels A, Schnoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochemical Cycles*, **9**, 235-252.

Goodale CL, Apps MJ, Birdsey RA *et al.* (2002) Forest carbon sink in North Hemisphere. *Ecological Applications*, **12**, 891-899.

Hagedorn F, Spinnler D, Siegwolf R (2003) Increased N deposition retards mineralization of old soil organic matter. *Soil Biology and Biochemistry*, **35**, 1683-1692.

Harrison AF, Schulze E-D, Gebauer G, Bruckener G (2000) Canopy uptake and utilization of atmospheric pollution nitrogen. In: Schulze E-D, ed. Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies 142. Berlin: Springer-Verlag, 171-188.

Högberg P (2007) Nitrogen impacts on forest carbon. *Nature*, **447**, 781-782.

Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry*, **46**, 7-43.

Holland EA, Braswell BH, Sulzman JM, Lamarque JF (2005) Nitrogen deposition onto the Unites State and Western Europe: synthesis of observations and models. *Ecological Applications*, **15(1)**, 38-57.

Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000. *Tellus,* **55B(2)**, 378-390.

Hyvönen R, Ågren GI, Linder S *et al.* (2007) 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 Phytologist*, **173**, 463-480.

Hyvönen R, Persson T, Andrsson S, Olsson B, Ågren GI, Linder S (2008) Impact of long-term nitrogen addition on carbon stock in trees and soils in northern Europe. *Biogeochemistry*, **89(1)**, 121-137.

Intergovernmental Panel on Climate Change, 2007. Climate Change: The Scientific Basis. Cambridge University Press, Cambridge, UK.

Jarvis PG, Fowler D (2001) Forests and the Atmosphere. In: *Forest Handbook. Vol 1 An Overview of Forest Science* (ed. J Evans) pp 229-281. Blackwell Science, Oxford.

Jenkinson DS, Goulding K, Powlson DS (1999) Nitrogen deposition and carbon sequestration. *Nature*, **400**, 629.

Johnson DW (2006) Progressive N limitation in forests. Review and implications for long-term responses to elevated CO_2. *Ecology* **87(1)**, 64-75.

Kahle HP, Karjalainen T, Schuck A, Agren GI (2008) Causes and Consequences of Forest Growth Trend in Europe. European Forest Institute Research Project 21. Results of the RECOGNITION Project Brill, Leiden, Boston, vol. 21, 261 pp.

Kirilenko AP, Sedjo Ra (2007) Climate changes impacts on forestry. *PNAS*, **104(50)**, 19697-19702.

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist* **172**, 393-411.

Laubhann D, Sterba H, Reinds GJ, de Vries W (2009) The impact of atmospheric deposition and climate on forest growth in European monitoring plots: An individual tree growth model. *Forest Ecology and management*, **258**, 1751-1761.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371-379.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, **54**, 731-739.

Loustau D, Bosc A, Colin A *et al.* (2005) Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiology*, **25**, 813-823.

Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The Human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848-852.

Mayewski PA, Lyons WB, Spencer MJ, Twickler MS, Buck CF, Whitlow S (1990) An ice-core record of atmospheric response to anthropogenic sulphate and nitrate. *Nature*, **346**, 554-556.

Mellert KH, Prietzel J, Straussberger R, Rehfuess KE, Kahle HP, Perez P, Spiecker H (2008) Relationship between long-term trends of air temperature, precipitation, nitrogen nutrient and growth of coniferous stands in Central Europe and Finland. *European Journal of Forest Research*, **127**, 507-524.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.

Milne R, Van Oijen AR (2005) A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. *Annales of Forest Science*, **62**, 911-923.

Morales P, Hickler T, Rowell DP, Smith B, Sykes MT (2007) Changes in European ecosystems productivity and carbon balance driven by regional climate model output. *Global Change Biology*, **13**, 108-122.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981-1991. *Nature*, **386**, 698-702.

Nellemann C, Thomsen MG (2001) Long-term changes in forest growth: potential effects of nitrogen deposition and acidification. *Water, Air and Soil Pollution*, **128**, 197-205.

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Pipper Sc *et al.* (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, **300**, 1560-1563.

Norby RJ, De Lucia EH, Gielen B *et al.* (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *PNAS*, **102(50)**, 18052-18056.

Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature*, **411**, 469-472.

Palmroth S, Oren R, McCarthy HR *et al.* (2006) Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO_2]-induced enhancement. *Proceedings of the National Academy of Sciences of the United States of America*, **103(51)**, 19362-19367.

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forest: biome patterns related to forest age. *Global Change Biology*, **10**, 2052-2077.

Rehfuess KE, Ágren GI, Andersson F *et al.* (1999) Relationships between recent changes of growth and nutrition of Norway spruce, Scots pine and European beech forests in Europe – RECOGNITION. Workinh Paper 19, European Forest Institute, Joensuu, Finland, 94 pp.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80(6)**, 1955-1969.

Saxe H, Cannell MGR, Johnsen Ø, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369-400.

Schulze ED,Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science*, **289**, 2058–2059.

Sievering H (1999). Nitrogen distribution and carbon sequestration. *Nature*, **400**, 629-630.

Sitch S, Huntingford C, Gedney N *et al.* (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Changes Biology*, **14**, 2015-2039.

Six J, Elliott ET, Paustian K, Doran JW (1998).. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Science Society of America Journal* **62**: 1367–1377.

Solberg S, Andreassen K, Clarke N, Torseth K, Tveito OE, Strand GH, Tomter S (2004) The possible influence of nitrogen and acid deposition on forest growth in Norway. *Forest Ecology and Management*, **192**, 241-249.

Solberg S, Dobbertin M, Reinds GJ *et al.* (2009) Analysis of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. *Forest Ecology and Management*, **258**, 1735-1750.

Sparks JP (2009) Ecological ramifications of the direct foliar uptake of nitrogen. *Oecologia* **159**, 1-13.

Spiecker H (1999) Overview of recent growth trends in European forests. *Water, Air and Soil Pollution*, **116**, 33-46.

Sutton MA, Simpson D, Levy PE, Smith RI, Reis S, van Oijen M, de Vries W (2008) Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, **14**, 1-7.

Thornley JHM (1991) A transport-resistance model forest growth and partitioning. *Annals of Botany*, **68**, 211-226.

van der Werf GR, Randerson JT, Collatz GJ *et al.* (2004) Continental-scale partitioning of fire emissions during the 1997 to 2001 El Nino/La Nina period. *Science*, **303**, 73–76.

Van Oijen M, Jandl R (2004) Nitrogen fluxes in two Norway spruce stands in Austria: an analysis by means of process-based modelling. *Austrian Journal of Forest Science*, **121**, 167-182.

Van Oijen M, Cannell MGR, Levy PE (2004) Modelling biogeochemical cycles in forests: state of art and perspectives. In: Andersson F, Birot Y, Päivinen R (Eds.), Towards the Sustainable Use of European's Forests-Forest Ecosystems and Landscape Research: Scientific Challenges and Opportunities. European Forest Institute, 157-169.

Van Oijen M, Agren GI, Chertov O, Kellomäki S, Komarov A, Mobbs DC, Murray MB (2008) Evaluation of past and future changes in European forests growth by means of four process-based models. In: Karjalainen T, Schuck A (Eds.). Causes and

Consequences of Forest Growth in Europe – Results of RECOGNITION Project (Chapter 4.4), 183-199.

Vitousek PM, Aber JD, Howarth RW *et al.* (1997) Human alteration of global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737-750.

Zaehle S, Bondeau A, Carter TR *et al.* (2007) Projected Changes in Terrestrial Carbon Storage in Europe under Climate and Land-use Change, 1990-200. *Ecosystems*, **10**, 380-401.

CHAPTER 2

The effect of nitrogen deposition on forest carbon sequestration: a model-based analysis

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Global Change Biology

The effect of nitrogen deposition on forest carbon sequestration: a model-based analysis

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Abstract

The perturbation of the global nitrogen (N) cycle due to the increase in N deposition over the last 150 years will likely have important effects on carbon (C) cycling, particularly via impacts on forest C sequestration. To investigate this effect, and the relative importance of different mechanisms involved, we used the Generic Decomposition And Yield (G'DAY) forest C–N cycling model, introducing some new assumptions which focus on N deposition. Specifically, we (i) considered the effect of forest management, (ii) assumed that belowground C allocation was a function of net primary production, (iii) assumed that foliar litterfall and specific leaf area were functions of leaf N concentration, (iv) assumed that forest canopies can directly take up N, and (v) modified the model such that leaching occurred only for nitrate N. We applied the model with and without each of these modifications to estimate forest C sequestration for different N deposition levels. Our analysis showed that N deposition can have a large effect on forest C storage at ecosystem level. Assumptions (i), (ii) and (iv) were the most important, each giving rise to a markedly higher level of forest C sequestration than in their absence. On the contrary assumptions (iii) and (v) had a negligible effect on simulated net ecosystem production (NEP). With all five model modifications in place, we estimated that the C storage capacity of a generic European forest ecosystem was at most $121 \, \text{kg C kg}^{-1} \, \text{N}$ deposited. This estimate is four times higher than that obtained with the original version of G'DAY ($27.8 \, \text{kg C kg}^{-1} \, \text{N}$). Thus, depending on model assumptions, the G'DAY ecosystem model can reproduce the range of $dC : dN_{dep}$ values found in the literature. We conclude that effects of historic N deposition must be taken into account when estimating the C storage capacity of a forest ecosystem.

Keywords: allocation, canopy nitrogen uptake, carbon and nitrogen cycles, leaf nitrogen concentration, models, specific leaf area

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Introduction

In the global carbon (C) budget, the terrestrial biosphere is thought to be a significant C sink, sequestering on the order of $2.8 \, \text{Pg C yr}^{-1}$ (Field 2001; Myneni *et al.*, 2001; Canadell *et al.*, 2007). Although the location of the sink is still debated, it appears likely that a considerable contribution to the sink comes from temperate and boreal forest ecosystems of the northern hemisphere; these forests are estimated to sequester approximately $0.6–0.7 \, \text{Pg C yr}^{-1}$ (Goodale *et al.*, 2002). A key scientific challenge is to identify the cause of this sink, in order to be able to predict its future time course.

There are several alternative hypotheses for the cause of the forest sink: these include forest expansion following agricultural abandonment; effects of changes in management practices on established forests; and impacts of increasing atmospheric CO_2 concentration ($[CO_2]$), temperature and nitrogen (N) deposition (Ciais *et al.*, 2008). At present, it is unclear how much each of these mechanisms contributes to the sink, or how that might change in future.

Many scientists have suggested that increasing atmospheric $[CO_2]$ is the primary mechanism, stimulating forest growth and leading to more C stored in wood biomass. However, studies on forest growth in CO_2-enriched environments suggest that the potential capacity for a growth response to increasing $[CO_2]$ may be limited by the lack of nutrient availability for growth (Oren *et al.*, 2001; Luo *et al.*, 2004; de Graaff *et al.*, 2006; Johnson, 2006; Körner, 2006).

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Other researchers have focused on the important role played by N deposition on forest growth (Townsend *et al.*, 1996; Jenkinson *et al.*, 1999; Nadelhoffer *et al.*, 1999; Sievering, 1999; Högberg, 2007; Magnani *et al.*, 2007). Atmospheric N deposition has increased over the last 150 years, mainly due to the use of fossil fuels, deforestation and agricultural practices (Mayewski *et al.*, 1990; Galloway *et al.*, 1995; Vitousek *et al.*, 1997; Holland *et al.*, 1999, 2005). The impact on the terrestrial C cycle is uncertain, and is strongly debated. An early attempt to estimate the impact of N deposition on C sequestration was made by Townsend *et al.* (1996). These authors assumed that C is principally stored in wood, due to its high C : N ratio (ranging from 150 to 300 depending on vegetation type). They then used the NDEP model to estimate a terrestrial C storage ranging from 0.44 to 0.74 Pg C yr^{-1} due to N deposition.

This estimate was contested by Nadelhoffer *et al.* (1999). From ^{15}N studies in nine temperate forests, they found that only a small fraction (20%) of the tracer ended up in the trees, with just 5% allocated to woody biomass, while about 70% entered the forest floor and soil pools. Therefore, they argued that increasing N deposition is not the major contributor to the terrestrial C sink in forested northern temperature regions as suggested by Townsend *et al.* (1996). Instead, they calculated that the contribution of N deposition to forest C uptake was only of the order of 0.25 Pg yr^{-1}, and suggested that there must be other factors accounting for the terrestrial sink. In their calculations, Nadelhoffer *et al.* (1999) also assumed fixed C : N ratios for all biomass pools.

Nadelhoffer *et al.*'s (1999) conclusions were in turn questioned, by both Jenkinson *et al.* (1999) and Sievering (1999). These authors pointed out that Nadelhoffer's group had simulated atmospheric deposition by adding ^{15}N-tracer to forest soil in all the experiments, while much of the atmospheric N deposition is actually intercepted and absorbed by the forest canopy. They argued that, if the direct canopy uptake is taken into account, the N allocated to wood biomass would be doubled or tripled (10–15%) and the C sink increased by 50–100% over that estimated by Nadelhoffer *et al.* (1999) (Sievering, 1999).

More recently, Magnani *et al.* (2007), analysing measurements of average C sequestration in chronosequences of a number of temperate and boreal forests in Europe and North America, demonstrated a strong positive relationship between N deposition and average forest C sequestration (Högberg, 2007). These results have also been questioned, since they appear to show a very high ratio of C sequestered per unit N deposited (Högberg, 2007; Hyvönen *et al.*, 2008; de Vries *et al.*, 2008; Sutton *et al.*, 2008).

Thus, there is much uncertainty and debate about the impact of atmospheric N deposition on forest C sequestration. One step towards resolving this issue is to develop better ecosystem models, which incorporate our best understanding of the impacts of N deposition on forest function, and to use these models to advance our understanding of the sensitivity of the forest system to N deposition.

The key aim of this paper is to develop a model that is able to qualitatively describe the effect of N deposition on forest C. The model takes into account several recent scientific advances, including: advances in understanding of the relationship between allocation and net primary production (NPP) (Palmroth *et al.*, 2006); experimental evidence for canopy N uptake (CNU) (Jenkinson *et al.*, 1999; Sievering, 1999; Sparks, 2009); and leaf trait relationships found by Reich *et al.* (1999). We do not claim to quantify precisely how much C is stored by ecosystems for a given amount of N deposition. Instead, we aim to further develop our understanding of the mechanisms leading to forest C sequestration following N deposition.

There are many different connections between the C and N cycles in forest ecosystems. An increase in N deposition may lead to an increase in photosynthesis per unit land area by increasing both foliar biomass and the concentration of photosynthetic enzymes, if other nutrients are not limiting (Oren *et al.*, 1988; Katz *et al.*, 1989b). The canopy seems to be able to absorb a certain percentage of atmospheric N deposition (Sievering, 1999; Sievering *et al.*, 2007), directly increasing the photosynthetic rate. On the other hand, an increase in tissue N concentration also leads to an increase in respiration rate (Pregitzer *et al.*, 1998; Reich *et al.*, 1998), and to a faster turnover of leaves (Reich *et al.*, 1999). Increasing N availability also causes a shift in the allocation of plant C away from roots and their symbiotic mycorrhizal fungi, both short-lived, towards aboveground structures with a high C : N ratio, which may lead to an increase in C sequestration in forest wood biomass (Berg & Matzner, 1997; Högberg, 2007). Apart from its direct effects on biomass accumulation, this shift will results in lower fine root litter deposition. The ensuing reduction in soil C sequestration will be counter-balanced by the retardant effect on the decomposition of plant litter and soil organic matter (SOM; Berg & Matzner, 1997; Högberg, 2007).

In this context, the use of a forest ecosystem model that explicitly includes the effect of N deposition on ecosystem dynamics is an important and helpful tool to investigate these connections between the C and N cycles and to obtain more realistic predictions of future forest C balance. Here, we present a new version of the Generic Decomposition and Yield (G'DAY) model

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developed by Comins & McMurtrie (1993). To focus on the effect of N deposition on net forest ecosystem production, we started from the model version of McMurtrie *et al.* (2001), which incorporates explicitly the dynamics of the SOM C and N pools, and we introduced the following new model assumptions: (1) all dead stems are exported each year from the ecosystem as forest management practice; (2) C allocation is a function of NPP (Palmroth *et al.*, 2006); (3) foliar litterfall and specific leaf area (SLA) are functions of leaf N concentration (Reich *et al.*, 1999; Burton *et al.*, 2000); (4) there is direct CNU (Sievering *et al.*, 2007); and (5) leaching occurs only for soil N in the form of nitrate, while nitrification is a direct function of soil C:N ratio (Aber *et al.*, 2003). We estimated the sensitivity of model estimates of net ecosystem production (NEP) to each assumption, both individually and in all combinations, using a full factorial design analysis (Box *et al.*, 1978). We then tried to explain the model sensitivities using the nitrogen-use efficiency (NUE) analysis of Halliday *et al.* (2003).

Materials and methods

The model

G'DAY is a process-based model that simulates C and N dynamics in a forest ecosystem (Comins & McMurtrie, 1993). The model is fully described elsewhere (Comins & McMurtrie, 1993; Medlyn *et al.*, 2000); here we give a brief overview of the original model, and then describe in detail the modifications we have made.

G'DAY is composed of two submodels, representing plant and soil components. The plant submodel simulates the dynamics of the C and N contents of three pools: foliage, wood (stem, branches and coarse roots) and fine roots. The wood N content is divided into an immobile component, held in structural compounds, and a mobile (nonstructural) component that can be retranslocated to support new woody tissue. The soil submodel, as in the CENTURY soil model (Parton *et al.*, 1987, 1993), consists of four litter pools (structural and metabolic, above- and belowground) and three SOM pools (active, slow and passive) of C and N content. The integrated model simulates plant C assimilation, plant N uptake, C and N allocation among plant pools, tissue senescence, N retranslocation, litter and SOM decomposition, soil mineralization and immobilization, N input by atmospheric deposition and biological fixation, and N loss by leaching and gaseous emission.

In a previous study, McMurtrie *et al.* (2001) assumed that the C:N of the substrate entering the three soil pools decreases linearly between given minimum and maximum values, as soil inorganic N (N_{inorg}) decreases

from a critical value (N_{crit}) to zero. We have retained this assumption, replacing the minimum and maximum values of SOM C:N ratio with values more suitable for a forest soil (Nalder & Wein, 2006).

We assumed that N taken up by the plant depends on soil inorganic N (as in Comins & McMurtrie, 1993) but is also a saturating function of root biomass, as in Dewar & McMurtrie (1996a, b).

The following modifications were then made to the model.

Forest management. It is known that forest management of established forests, afforestation and natural regeneration following agricultural abandonment are significant processes in controlling the C sink in the northern hemisphere (Houghton *et al.*, 1999; Caspersen *et al.*, 2000; UN ECE/FAO, 2000; Fang *et al.*, 2001; Magnani *et al.*, 2009). Changes in local forest management may therefore have an important effect on the global C balance (Schulze *et al.*, 2000; Magnani *et al.*, 2007, 2009). To investigate this potential effect, and its interaction with increasing N deposition, we introduce into the model a simple representation of forest management. Forest age class distribution was not explicitly modelled, but all developmental stages were supposed to be evenly represented at the scale of interest, making it possible to consider natural mortality and management a continuous rather than discrete event.

In the absence of forest management, we assumed a constant tree mortality rate as a result of self-thinning and stand-replacing disturbances, with dead wood entering the litter pools. To simulate forest management, we assumed natural mortality to be replaced by silvicultural practices (thinnings and maturity harvests), with the only difference that dead woody stems (a constant fraction of total woody biomass) are exported from the system. Branches and coarse roots of harvested trees are assumed to enter the surface and soil structural litter pools, respectively, and decompose over time.

A fixed value of 2.5% was assumed for annual harvesting (and natural mortality), irrespective of site fertility and yield class. Although lower mortality rates are generally observed as a result of competition and self-thinning, the figure represents a conservative estimate when also the effects of stand-replacing disturbance (windstorms, pests, etc.) and harvest at maturity are considered (Eriksson, 1976).

The annual export of a fixed percentage of wood represents a C sink for the forest system. The amount of N in stems exported is very low due to the high C:N ratio of stemwood (Kostiainen *et al.*, 2004). Hence, introducing the assumption of forest management

should increase the overall ecosystem ability to sequester C per unit of N entering the system ($dC:dN_{dep}$). We also expect that the export of woody stems should decrease heterotrophic respiration and shift the $C:N$ ratio of soil pools with consequences for soil N dynamics and N uptake.

Allocation as a function of NPP. Following photo synthesis, C products can be transported to the different parts of the plant (roots, stem and leaves) and used for respiration or for growth. Although the mechanisms of plant allocation between organs are not well understood, they do appear to follow an optimization principle, in which the plant is assumed to try to obtain all the resources it needs for growth with the lowest energetic cost (Aber & Melillo, 2001). For example, under conditions of good light and no water stress, nutrient availability determines the amount of C allocated to roots, with a greater proportion of NPP going to the roots on infertile sites than in fertile sites (Santantonio, 1989; Landsberg & Waring, 1997). In a review of existing literature, Litton *et al.* (2007) found that increased nutrient availability increased parti tioning to aboveground NPP and decreased partiti oning to total belowground C flux.

Here, we have used a function relating allocation to NPP, developed by Palmroth *et al.* (2006), based on measurements of aboveground production and soil efflux in forest CO_2 enrichment experiments. After rearrangement, this function links root allocation to NPP, as follows:

$$\eta_r = \frac{1}{1 + \dfrac{1}{\alpha\left(Y_0 + Q\exp(-BNPP)\right)}}, \qquad (1)$$

where η_r is the root allocation coefficient (dimensionless), α is the carbon-use efficiency (NPP:GPP ratio, dimensionless), assumed constant for a given forest type (DeLucia *et al.*, 2007) and Y_0, Q and B are parameters describing the relationship between total belowground C allocation and NPP (in $kg\,C\,m^{-2}\,yr^{-1}$) as in Palmroth *et al.* (2006). This relationship suggests that, as tree production increases, the percentage of available C allocated to the root system decreases. In a system where the production is limited only by N availability, Eqn (1) results in a negative relationship between η_r and NPP.

Allocation to stemwood is assumed to be proportional to foliage allocation

$$\eta_w = d\eta_f, \qquad (2)$$

where η_f and η_w are the allocation coefficients to foliar and wood, and d is an empirical parameter, here set equal to 4 (Iivonen *et al.*, 2006).

Equations for foliage allocation can then be calculated from the requirement that

$$\eta_r + \eta_f + \eta_w = 1. \qquad (3)$$

Dependence of SLA and leaf mortality on leaf N concentration. Reich *et al.* (1999) showed that there is a convergence in interspecific leaf trait relationships across diverse biomes. Testing 100 species in six different biomes, they found significant relationships between leaf N concentration (v_f), SLA and leaf life span in the pooled data. These relationships indicated that leaf life span decreases, and SLA increases, with increasing leaf N concentration.

Based on this work, we introduced expressions for SLA and leaf mortality as functions of leaf N concentration. We replotted data reported in Reich *et al.* (1999) to obtain the following relationships:

$$SLA = 767 v_f^{1.0889}, \qquad (4)$$

where SLA is the specific leaf area (in $m^2\,kg^{-1}\,C$) and v_f is the leaf N concentration (in $kg\,N\,kg^{-1}\,C$), and

$$\gamma_f = \frac{v_f^{1.424}}{0.0108}, \qquad (5)$$

where γ_f is the leaf mortality (in $year^{-1}$).

The increase in SLA with v_f [Eqn (4)] makes productivity more sensitive to v_f, because of the enhanced leaf area, and therefore intercepted radiation, in addition to the direct physiological effect of v_f on photosynthetic production. Conversely, Eqn (5) represents a negative feed-back between v_f and plant productivity, because leaf mortality increases as v_f increases, reducing photosynthetic area.

CNU. Reactive N can be taken up directly by the canopy via stomata leaf cuticle and bark (Katz *et al.*, 1989a, b; Sparks, 2009) and can amount to a substantial fraction of atmospheric N deposition (De Vries *et al.*, 2001) and forest N requirements (Harrison *et al.*, 2000). N deposition is variable in time, space and composition (Sievering *et al.*, 2007). In general, the greater the atmospheric input, the greater the net canopy effects (Lovett, 1992), but there appears to be a maximum level of N utilization and retention by forest ecosystems (Aber *et al.*, 2003; Gaige *et al.*, 2007). Different studies show that canopy N absorption varies depending upon season, whether deposition is in the form of ammonia or nitrate, and according to the age of the stand (Tomaszewski *et al.*, 2003; Klopatek *et al.*, 2006; Gaige *et al.*, 2007). In their study, Sievering *et al.* (2007) found that 80% of the growing-season total deposition intercepted by the canopy was retained by foliage and branches. This CNU constituted about 1/3 of the canopy growing season new N demand at this conifer

forest site. Studies with 15-N tracer confirm the retention of wet N deposition by forest canopies (Garten *et al.*, 1998; Wilson & Tiley, 1998; Gaige *et al.*, 2007).

In our model, we assumed that the CNU was equal to the product of a CNU efficiency (CNU_e), the vegetation cover fraction (*c*) and the total N deposition (N_{in}):

$$CNU = CNU_e \cdot c \cdot N_{in}$$

CNU_e was estimated to be equal to 0.8 (Sievering *et al.*, 2007) and *c* was here given a representative value of 0.6 (Chopping *et al.*, 2008). Although strictly valid only in the case of wet deposition, the resulting N deposition absorption percentage of 48% appears to be consistent with independent estimates using budget model (De Vries *et al.*, 2001). N_{in} was set to $0.4\,g\,N\,m^{-2}\,yr^{-1}$, as in McMurtrie *et al.* (2001), for the low N deposition simulations and then was increased to 1, 2 or $3\,g\,N\,m^{-2}\,yr^{-1}$.

It is still unclear whether N taken up by the canopy is directly assimilated by leaves and used immediately in the process of photosynthesis (Katz *et al.*, 1989b). There is evidence that part of the canopy N retention is absorbed by branches and twigs rather than foliage (Katz *et al.*, 1989a; Boyce *et al.*, 1996; Wilson & Tiley, 1998; Harrison *et al.*, 2000; Sievering *et al.*, 2007). To take into account this uncertainty about the fate of N once absorbed, we simulated two different hypothetical scenarios: in (a) the N taken up is all added directly to the N concentration of the foliage to stimulate the photosynthesis ($CNU + N_f$); or alternatively, in (b) the N taken up is added to the N taken up by roots and then allocated to the different parts of the plant ($CNU + U_r$). We compared these two scenarios to the scenario (c) where there was assumed to be no CNU ($CNU = 0$). In each case, the quantity of N input to the soil was set equal to the difference between N_{in} and CNU.

Leaching. In the original version of G'DAY (Comins & McMurtrie, 1993), inorganic N in the soil is simulated as a single pool, with no difference between ammonium and nitrate forms of N. The loss rate of N through leaching and gaseous emissions was assumed to be proportional to the inorganic N pool (McMurtrie *et al.*, 2001). It is known that the main form of N lost by leaching is nitrate, because of its greater mobility in soil (Addiscott *et al.*, 1991; Aber & Melillo, 2001). To investigate the effect of a more realistic description of N leaching on ecosystem productivity, we represented the soil inorganic N as two pools, an ammonium and a nitrate pool, and divided the net mineralization influx between these pools, based on the soil C : N ratio as in Aber *et al.* (2003). We modelled the N loss through leaching and gaseous emissions as a constant fraction

of the nitrate inorganic N pool only, as such losses are mostly from that form of N (Addiscott *et al.*, 1991).

Simulations

We ran a series of simulations to study the influence of each modification to the model on simulated NEP, as follows:

(1) We first investigated the impact of forest management on NEP. To do this, we ran the original model version and varied only the forest management assumption. In these simulations, SLA, leaf mortality and allocation coefficients were held constant, the original leaching formulation was used and no CNU was assumed.

(2) Second, we investigated the impact of the relationships between allocation patterns and NPP [Eqns (1)–(3)] and between leaf N, SLA and leaf mortality [Eqns (4) and (5)]. Using the model version from (1) with management applied, we began with a base-case simulation where allocation, SLA and leaf mortality were held constant (referred to below as the '*all const*' case). We then ran a similar simulation, but with allocation driven by NPP [Eqns (1)–(3)] and litterfall and SLA functions of leaf N concentration [Eqns (4) and (5)]. This case is referred to as the '*all var*' case. The other intermediate cases between these two combinations were also investigated.

(3) Third, we investigated the effect of CNU on the NEP. To do this, we set the model from (2) in the '*all var*' case. Then we compared three different assumptions regarding CNU: (i) no CNU ($CNU = 0$); (ii) the N taken up is all added to the N concentration of the foliage ($CNU + N_f$); (iii) the N taken up is added to the N taken up by roots and then allocated to the different parts of the plant ($CNU + U_r$).

(4) Fourth, we investigated the difference between our new formulation for N losses and the previous leaching formulation. Here, we used the version of the model with management, '*all var*' and $CNU + N_f$ as our base case.

(5) Finally, we investigated the overall effect of the new version of the model, for different rates of N deposition (ranging from 0.4 to $3\,g\,N\,m^{-2}\,yr^{-1}$) on NEP after 100 years from the N deposition increased. We performed two sets of simulations: one with the basic model as in McMurtrie *et al.* (2001) ('*all const*', $CNU = 0$, without management and the old leaching formulation), and a second with the model with all new features ('*all var*', $CNU + N_f$, with management and the new leaching formulation).

For all simulations, we ran the model to reach the equilibrium state (defined as that state for which the

difference between successive annual values of all output variables is $<10^{-11}$) under the baseline climate, and then we imposed a step increase in the N input rate, from 0.4 to $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$.

Although the parameters used in the simulation are not site specific, they can be considered representative of a European temperate stand of Norway spruce [*Picea abies* (L.) Karst.]. We supposed that the site is N-limited but not water-limited. A list of the parameters used is given in the supporting information Appendix S1. The model was run with a weekly time step using constant mean annual climate data.

Sensitivity analysis

The simulations were run under constant environmental conditions (averaging out the annual climatic cycle). To investigate the effect of environmental factors on the model results, a sensitivity analysis was carried out. The factors analysed were the two input meteorological data [photosynthetically active radiation, (PAR) and the soil temperature] and the variable characterizing soil [soil silt plus clay fraction (T)]. The sensitivity of the model to each of these input variables was explored by varying each by a constant amount above and below the value used in simulations (Table 1). The output variable considered was the NEP 100 years after the step increase in N deposition, for four different values of N input rate (0.4, 1, 2 and $3 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$). The range of the environmental factors chosen for the sensitivity analysis are representative of environmental conditions across Europe. In particular, the radiation range was obtained

from the JRC European solar radiation map (Šúri *et al.*, 2007), which represents the yearly sum of global irradiation incident on optimally inclined south-oriented photovoltaic modules, averaged over the period 1981–1990.

Factorial analysis

To better understand the interactions among the five new sets of relationships introduced in G'DAY, we also implemented the full factorial design model analysis as described by Box *et al.* (1978), Henderson-Sellers (1993) and Henderson-Sellers & Henderson-Sellers (1996). For this methodology, simulations must be run for all combinations of factors at each of the perturbation levels. Hence for n factors each with two levels, 2^n simulation runs are required. In our study the factors considered are the five new relationships introduced to the model, and the two levels represent: the cases '*all const*' and '*all var*' for SLA, litterfall and allocation; CNU = 0 and CNU + N_f for the CNU; the original and new formulations of leaching; and the inclusion or not of forest management. The model output used for this analysis was the NEP 100 years after the step increase in N deposition.

The outputs are evaluated to estimate the effect of each factor. Several alternative algorithms can be used for this purpose. Here, we used the alternative method given by Box *et al.* (1978, p. 322). The standard errors of effects were calculated using higher-order interactions (Box *et al.*, 1978, p. 327) and the relative importance of the single or combination of effects was assessed by the

Table 1 Net ecosystem production, 100 years following a step increase in nitrogen deposition from $0.4 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$, for different values of N_{in}, PAR, soil temperature (T_{soil}), and soil texture parameter (T)

Nin ($\mathrm{g \, N \, m^{-2} \, yr^{-1}}$)	0.4	1	2	3	
PAR ($MJ \, m^{-2} \, yr^{-1}$)					
1800	−23	−20	−17	−16	%
2250	**0.30**	**0.39**	**0.52**	**0.61**	$\mathrm{kg \, C \, m^{-2} \, yr^{-1}}$
2700	20	17	15	13	%
T_{soil} ($^\circ$C)					
5	−1	−2	−3	−2	%
10	**0.30**	**0.39**	**0.52**	**0.61**	$\mathrm{kg \, C \, m^{-2} \, yr^{-1}}$
15	1	3	4	3	%
T (−)					
0.3	0	1	2	2	%
0.5	**0.30**	**0.39**	**0.52**	**0.61**	$\mathrm{kg \, C \, m^{-2} \, yr^{-1}}$
0.7	0	−1	−2	−2	%

The central bold numbers refer to the values of PAR, T_{soil} and T used for the simulations ran in this study (from Figs 1–7) and to the corresponding NEP. The other values are the percentage change with respect to the bold values. The simulations were run with SLA, leaf mortality and allocation variable, the new leaching formulation, CNU + N_f and stem wood biomass export of 2.5% $\mathrm{yr^{-1}}$ as forest management.

normal probability method (Daniel, 1976; Box *et al.*, 1978; Henderson-Sellers, 1993).

NUE and N uptake

To identify the major physiological process or processes that drive NEP following increased N deposition, we applied the analysis of Halliday *et al.* (2003). This analysis expresses NPP as the product of N uptake and NUE, and thus identifies whether changes in NPP are due principally to changes in N uptake or to changes in NUE. In our study, we applied this analysis in two steps. First we decomposed NEP into the terms NPP and heterotrophic respiration (R_h). Then we expressed NPP as the product of N uptake and NUE, and calculated the changes in each of these terms.

Results

Forest management

Before investigating the effect of increased N deposition rate on the managed and unmanaged systems, we investigated the effect of introducing a management assumption into the model. To this end, we ran the model to equilibrium for the system without management and then introduced the management assumption. For this simulation, SLA, leaf mortality and allocation were kept constant (the case *'all const'*), and we assumed the original leaching formulation, no CNU (CNU = 0), and a constant incoming N deposition rate of $0.4\,g\,N\,m^{-2}\,yr^{-1}$.

The effect of forest management on NEP is shown in Fig. 1. Following the introduction of forest management, it can be observed a sharp increase in NEP, reaching a maximum ($1.7\,kg\,C\,m^{-2}\,yr^{-1}$) after 11 years, followed by a progressive decline (Fig. 1a). NPP also increased following the introduction of forest management, from $1.6\,kg\,C\,m^{-2}\,yr^{-1}$ at equilibrium to a maximum of $3.2\,kg\,C\,m^{-2}\,yr^{-1}$ after 13 years, and then progressively declined over time (Fig. 1b). R_h, on the other hand, decreased following the introduction of forest management (Fig. 1b). The overall increase in NEP is due to the combination of the effects on NPP and R_h.

The constant removal of stems (material with high C : N ratio) from the ecosystem, in addition to representing a sink at forest ecosystem level, appears to have a twofold effect. In the short term, the prevailing effect is a reduction in the average C : N ratio of litter entering the soil, which leads in turn to an increase in net N mineralization. As a consequence, the amount of inorganic N available for plant growth increases and so does productivity. By removing stems, on the other
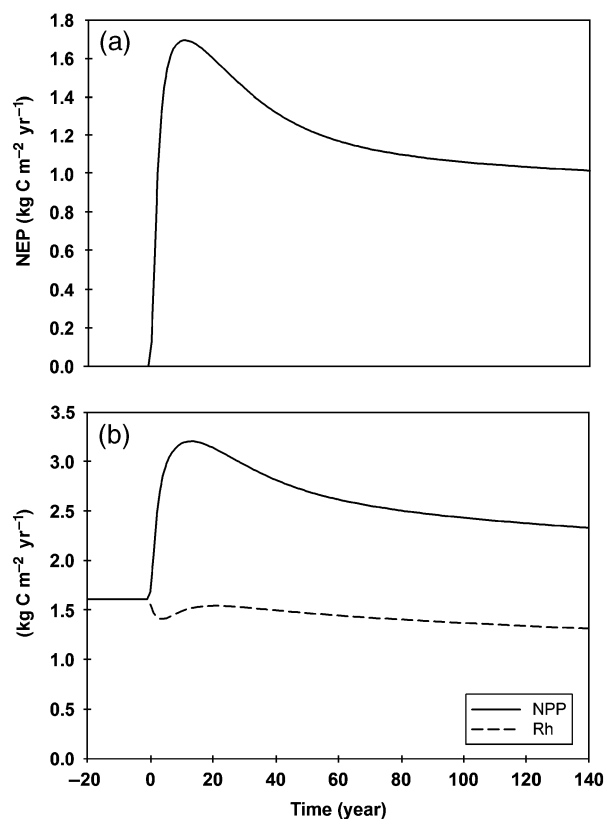
Fig. 1 Effect of introducing forest management at year 0 on net ecosystem production (a), net primary production and heterotrophic respiration (b). The simulations were run with specific leaf area (SLA), leaf mortality and allocation constant, the original leaching formulation, canopy nitrogen uptake (CNU) = 0 and a rate of input nitrogen deposition of $0.4\,g\,N\,m^{-2}\,yr^{-1}$.

hand, management decreases the input of biomass to the soil, and thus decreases the rate of decomposition and soil respiration. As a result of both processes, NEP is higher for the managed system than for the unmanaged system.

In the long run, however, the N released is locked up in standing biomass and partly exported from the system as timber. Moreover, the reduction in C and N soil pools and SOM decomposition translates in a slow decline in net N mineralization rate. Plant N uptake and NPP also decline slowly over time as a result. Eventually, the managed system reaches a new equilibrium state with higher NEP, but lower inorganic N, NPP and R_h compared with the equilibrium state of the unmanaged system (see starting point in Fig. 2).

The effect of an increase in N deposition rate on both managed and unmanaged forest ecosystem is shown in Fig. 2. For these simulations, we ran the model to reach the equilibrium state with and without management, with SLA, leaf mortality and allocation kept constant
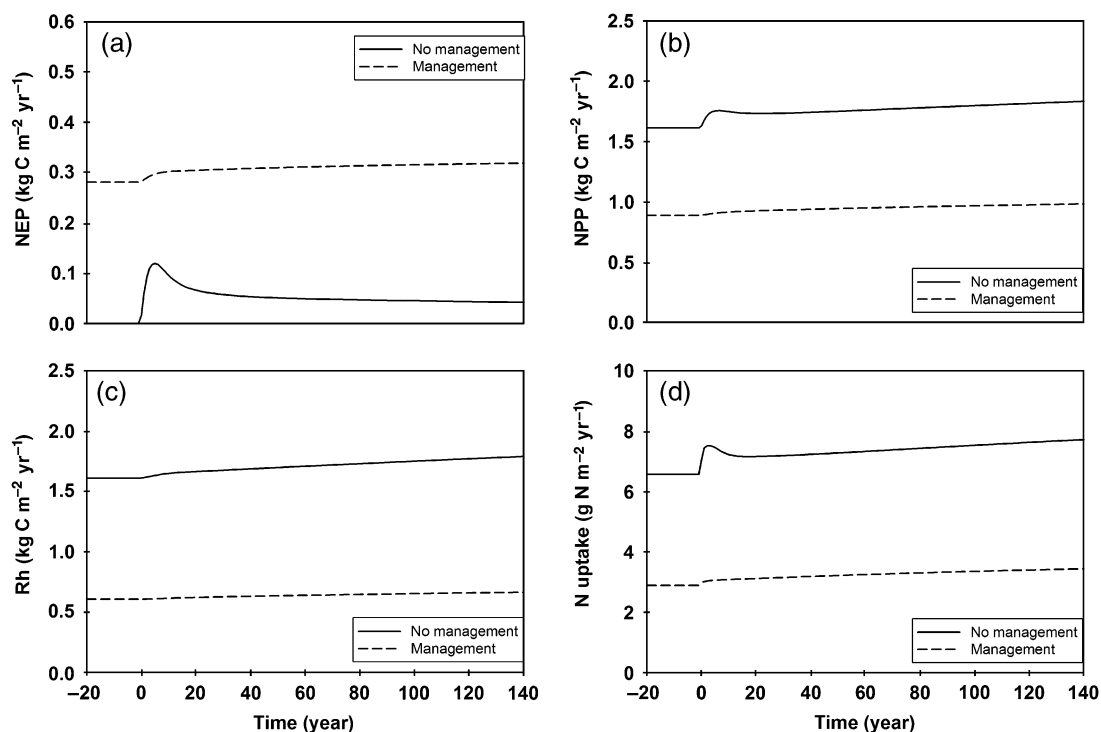
Fig. 2 Effect of forest management on net ecosystem production (a), net primary production (b), heterotrophic respiration (c) and nitrogen uptake (d). The simulations were run with specific leaf area (SLA), leaf mortality and allocation constant, the original leaching formulation, canopy nitrogen uptake (CNU) = 0 and a step increase in nitrogen deposition at time 0 from 0.4 to $2\,g\,N\,m^{-2}\,yr^{-1}$.

(the case 'all const'), the original leaching formulation, no CNU (CNU = 0) and a step increase in external nitrogen deposition at time 0 from 0.4 to $2\,g\,N\,m^{-2}\,yr^{-1}$.

Following the step increase in deposition rate there was an increase in NEP, which was sharper for the case without forest management, where NEP increased from 0 to $0.12\,kg\,C\,m^{-2}\,yr^{-1}$ in 6 years, than for the case with forest management, where NEP increased from 0.28 to $0.3\,kg\,C\,m^{-2}\,yr^{-1}$ over the same period of time (Fig. 2a).

In both cases, both NPP (Fig. 2b) and R_h (Fig. 2c) increased following the step change in N input rate. For the no-management case, the NPP increased by 9% after 7 years, while in the long term the rate of increase in NPP was linear. R_h increased at a slower linear rate throughout the simulation. In the case of managed stand, NPP increased by just 2.4% after 7 years, while in the long term the rate of increase was linear and approximately half that in the unmanaged stand. R_h increased at a very slow, linear rate.

The lower values of NPP overall in the with-management simulation, as explained above, are due to the lower amount of inorganic N available for plant growth, resulting from the smaller soil pools and the export of N due to the constant removal of dead stems from the system.

As N deposition increases, N uptake, leaf N concentration and photosynthesis increase in both cases, but the absolute increase is lower in the management scenario because of the stronger competition by soil microbes for inorganic N under these more N-limited conditions.

The higher overall values of R_h in the no-management case are caused by the increased amount of C in soil pools associated with dead trees. In both cases, the increase in N deposition rate enhances R_h because of the gradual increase in litter production. This increase is steeper in the no-management case because of the additional contribution from stems.

Although both NPP and R_h are greater in the no-management simulation, the difference between the two (i.e. NEP) is higher in the simulation with management. In the absence of management, NEP at equilibrium must be zero by definition, as a result of the build-up of soil C. The positive NEP at equilibrium in the management simulation equals the export of C biomass through harvesting.

Following a step increase in N deposition, both managed and unmanaged systems become positive C sinks (NEP > 0), but while the C sink increases over time in the managed forest system, it progressively declines towards zero in the unmanaged forest system. In both cases, the system is returning to equilibrium. In the unmanaged forest system, equilibrium NEP is zero

regardless of the N deposition rate, whereas the equilibrium NEP in the managed system increases with increasing N deposition, due to the higher stem production being exported.

SLA, leaf mortality and allocation

Figure 3 shows the simulated NEP in response to a step increase in atmospheric N deposition from 0.4 to $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ at time 0. There are eight different simulations resulting from eight different combinations of constant and/or variable allocation, leaf mortality and SLA. In all of these simulations, we assumed that forest management removes 2.5% of stem wood biomass per year, there is no CNU and leaching follows the original formulation.

Figure 3 shows a greater response of NEP to increased N deposition for the '*all var*' simulation than for the '*all const*' simulation for the entire simulation period (from 0 to 140 years). In both of these simulations there is a gradual increase in NEP, from $0.28 \, \mathrm{kg \, C \, m^{-2} \, yr^{-1}}$ with low N input, to $0.32 \, \mathrm{kg \, C \, m^{-2} \, yr^{-1}}$ in the '*all const*' simulation and to $0.37 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ in the '*all var*' simulation, after 140 years of high N input.

Since NPP grows at a slightly greater rate than R_{h}, NEP shows a slow, linear annual increase of $0.31 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ for the '*all var*' simulation and $0.11 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$ for the '*all const*' simulation.
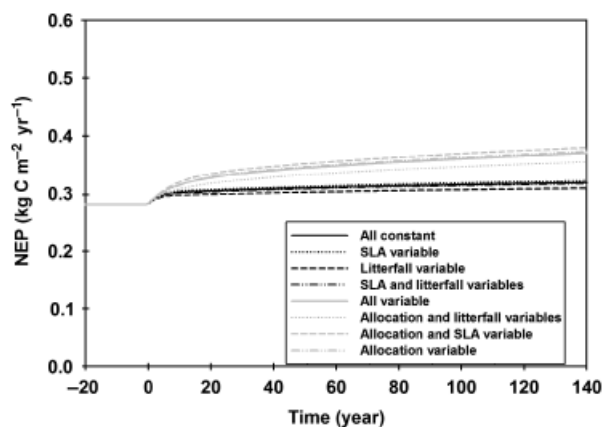
Fig. 3 Net ecosystem exchange in response to a step increase in atmospheric nitrogen deposition from 0.4 to $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ at year 0 for all eight different combinations of constant and/or variable allocation, leaf mortality and specific leaf area (SLA). In all simulations we assumed as forest management to export 2.5% of stem wood biomass per year, no canopy nitrogen uptake and the old formulation of nitrogen leaching. The black lines refer to the combinations with a variable allocation while the grey ones refer to the simulations with a constant value for allocation equal to the values at equilibrium.

This slightly higher increase in NEP in response to N deposition in the '*all var*' simulation is due to the increase in SLA and foliar biomass (C_{f}), and thus in leaf area index (LAI), which enhance NPP, and to a decrease in root biomass (C_{r}), which decreases R_{h} as compared with '*all const*' simulation. The increase in SLA is a consequence of the positive relationship between SLA and leaf N concentration, while the changes in foliage and root biomass are related to the new allocation function. When allocation coefficients are held constant, on the contrary, the increase in NPP due to the increase in SLA is offset by the decrease in C_{f} due to the increase in litterfall. Therefore, as indicated by the other simulations in Fig. 3, the difference between the '*all const*' and the '*all var*' cases is due primarily to the change in the allocation relationship, with a small effect of the change in SLA formulation. All cases in which allocation coefficients are held constant, even if the SLA and mortality change, show similar values for NEP.

CNU

To investigate the effect of CNU, three different simulations were performed. The baseline simulation was the '*all var*' case from the previous analysis, with SLA, leaf mortality and allocation being assumed to vary, a stem wood biomass export of $2.5\% \, \mathrm{yr^{-1}}$ as forest management, the original leaching formulation and a step increase of external N deposition at time 0, from 0.4 to $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$.

Figure 4 shows the model response for the three different hypotheses of (a) no CNU, (b) N taken up is added to the N taken up by roots and then allocated to the different parts of the plant ($CNU + U_{\mathrm{r}}$) and (c) N taken up is all added to the N concentration of the foliage and directly stimulates photosynthesis ($CNU + N_{\mathrm{f}}$). In both cases (b) and (c) we can distinguish a short- and a long-term response. In the short term, the transient response of the system is described by a fast increase in the NEP, followed by a smooth decrease. In the long term, there is a quasi-equilibrium response where NEP continues to increase, but at a slower linear rate. The short-term response is more marked and slightly faster in the case of $CNU + N_{\mathrm{f}}$, increasing by about 85% in 17 years, than in the case of $CNU + U_{\mathrm{r}}$, increasing by about 63% in 23 years, with the former always greater than the latter. Both simulations always give a value of NEP that is higher than in the $CNU = 0$ case, where NEP increases by only 17% over the first 23 years.

In both cases (b) and (c), photosynthesis (GPP) shows a faster initial increase than in case (a) because of the higher amount of N in leaves derived from canopy
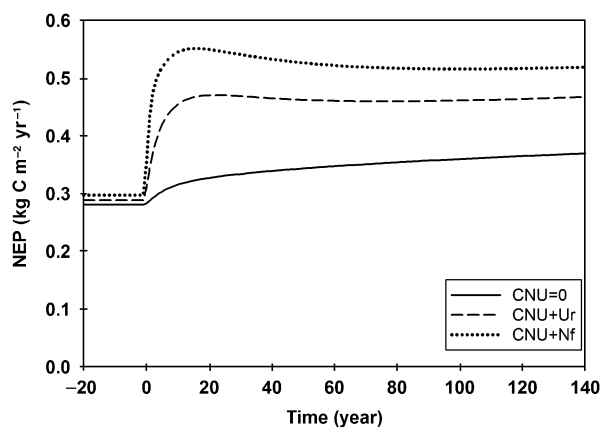
Fig. 4 Net ecosystem exchanges for the three different hypotheses of canopy nitrogen (N) uptake: (i) no canopy N uptake (CNU = 0), (ii) N taken up by the canopy is added to the N taken up by roots and then allocated to the different parts of the plant (CNU + U_r), (iii) N taken up by the canopy is added to the foliage N concentration (CNU + N_f). The simulations were run with specific leaf area (SLA), leaf mortality and allocation variable, a stem wood biomass export of 2.5% yr^{-1} as forest management, the old leaching formulation and a step increase of external nitrogen deposition at time 0 from 0.4 to $2 gN m^{-2} yr^{-1}$.

uptake and instantaneously available. This rapid increase in GPP, along with the time-lag in respiration rate, explains the rapid increase and decrease in NEP.

After a transient period of about 70 years for case (b) and 90 years for case (c), a quasi-equilibrium state is reached, where the annual rates of increase in NEP are 0.17 and $0.1 g C m^{-2} yr^{-1}$, respectively. The damped response for case (b) compared with case (c) occurs because less N is routed to the foliage, reducing the amount that is instantly available for photosynthesis.

Leaching

Figure 5 shows the difference in model behaviour with the original and new leaching formulations. Here, our baseline case had SLA, leaf mortality and allocation variable ('*all var*'), a stem wood biomass export of 2.5% yr^{-1} as forest management, CNU allocated to foliage (CNU + N_f) and a step increase in external N deposition at time 0 from 0.4 to $2 gN m^{-2} yr^{-1}$.

Although there was no observable difference in the NEP value or trend between the two formulations (the two lines overlap, Fig. 5a), the N losses for leaching and gas emissions were less for the new formulation than for the original one (Fig. 5b). This reduction in N loss occurs because, in the new formulation, only the nitrate component is lost. Even if the C:N ratio of the soil is such that all mineral N is in the nitrate form, there is still
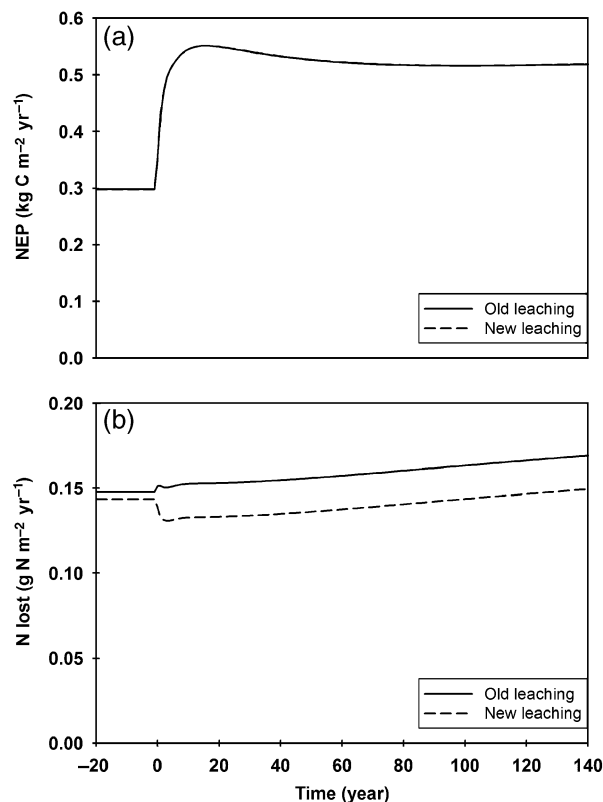
Fig. 5 Model response to the new and old leaching formulations in terms of net ecosystem production (a) and nitrogen losses for leaching and gas emissions (b). The simulations were run with specific leaf area (SLA), leaf mortality and allocation variable, a stem wood biomass export of 2.5% yr^{-1} as forest management, CNU + N_f and a step increase in external nitrogen deposition at time 0 from 0.4 to $2 gN m^{-2} yr^{-1}$.

a small quantity of N from deposition that is in the ammonium form in soil and so is not lost by the ecosystem.

The transient initial decrease in N loss in the new formulation occurs because of an initial decrease in the nitrate N pool. This initial decrease is mainly related to an instantaneous decrease in net mineralization flux following the step increase in N deposition.

The reduction in N lost by leaching does not lead to a perceptible change in NEP because the reduction is very small ($0.02 gN m^{-2} yr^{-1}$) compared with the total amount of N added to the system ($2 gN m^{-2} yr^{-1}$). From our analysis, the reduction in N leached should result in a change in NEP of 0.01%, a change too small to be visible in Fig. 5a.

N deposition rate

The model response to different rates of N addition was investigated (Fig. 6). Two different model formulations:
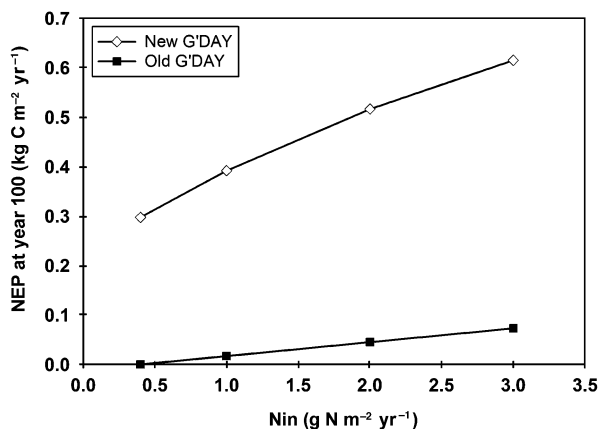
Fig. 6 Net ecosystem production of the new and old version of Generic Decomposition And Yield (G'DAY) for different rates of nitrogen deposition (0.4, 1, 2 and $3 \, g \, N \, m^{-2} \, yr^{-1}$). The two different model formulations were: specific leaf area (SLA), leaf mortality and allocation variable, new leaching formulation, $CNU + N_f$, and a stem wood biomass export of $2.5\% \, yr^{-1}$ as forest management (new); SLA, leaf mortality and allocation constant, old leaching formulation, no canopy nitrogen uptake and no forest management (old). The values of NEP refer to 100 years after the beginning of the increase in external nitrogen deposition rate vs. the different nitrogen addition rates, while the NEP for $0.4 \, g \, N \, m^{-2} \, yr^{-1}$ is the value at the steady state.

Table 2 Values of specific leaf area (SLA), nitrogen leaf concentration (v_f), allocation (η_f, η_r, η_w) and leaf mortality (γ_f), calculated with our new version of G'DAY, for different nitrogen deposition rates (N_{in}), 100 years following a step increase in N deposition rate

N_{in} ($g \, N \, m^{-2} \, yr^{-1}$)	0.4	1	2	3
SLA ($m^2 \, kg \, C^{-1}$)	6.89	7.52	8.51	9.37
v_f ($kg \, N \, kg \, C^{-1}$)	0.013	0.014	0.016	0.017
η_f (−)	0.12	0.13	0.15	0.16
η_r (−)	0.4	0.34	0.26	0.22
η_w (−)	0.48	0.53	0.59	0.62
γ_f ($year^{-1}$)	0.19	0.22	0.26	0.29
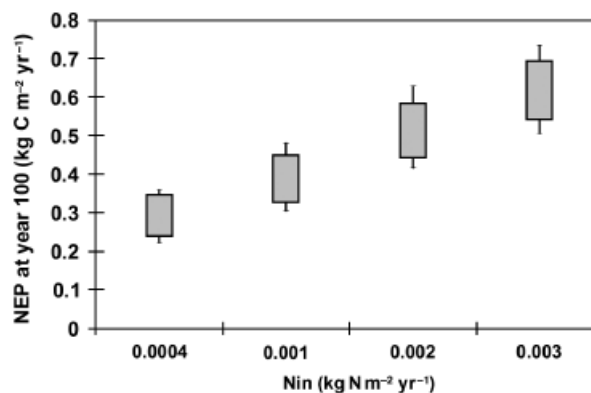
Fig. 7 Results of the sensitivity analysis of the model to environmental factors for all the different combinations of values of soil temperature (5, 10, 15 °C), soil texture parameter T (0.3, 0.5, 0.7), PAR (1800, 2250, 2700 $MJ \, m^{-2} \, yr^{-1}$), and nitrogen deposition (0.4, 1, 2, 3 $g \, N \, m^{-2} \, yr^{-1}$). The simulations were run with specific leaf area (SLA), leaf mortality and allocation variable, a stem wood biomass export of $2.5\% \, yr^{-1}$ as forest management, the new leaching formulation and $CNU + N_f$.

the new model final formulation, with SLA, leaf mortality and allocation variable (the case '*all var*'), the new leaching formulation, $CNU + N_f$, and a stem wood biomass export of $2.5\% \, yr^{-1}$ as forest management, was compared with the original model formation with SLA, leaf mortality and allocation constant (the case '*all const*'), the original leaching formulation, no CNU and no forest management. Figure 6 shows the NEP after 100 years from the beginning of the increase in external N deposition rate vs. the different N addition rates: 0.4 (the equilibrium state), 1, 2 and $3 \, g \, N \, m^{-2} \, yr^{-1}$.

For all the different N input rates, the new model formulation shows higher values of NEP compared with the original model formulation. The higher NEP values are principally due to the assumption of forest management, with the assumptions regarding CNU and the variability of C allocation also contributing (see 'Factorial analysis'). The modelled values of SLA, leaf N concentration, allocation and leaf mortality, for the four different N input rates are shown in Table 2.

Sensitivity analysis

Figure 7 shows the NEP simulated by the model after 100 years from the N deposition rise, for four different values of N input rates (0.4, 1, 2 and $3 \, g \, N \, m^{-2} \, yr^{-1}$). The

new formulation of the model (the case '*all var*', the new leaching formulation, $CNU + N_f$, a stem wood biomass export of $2.5\% \, yr^{-1}$ as forest management) was run. For each value of N input rate, we ran 27 simulations, corresponding to all possible combinations of three different values of the three environmental variables analysed: the PAR, the soil temperature and the soil texture parameter (Table 1).

As shown in Table 1, the forest system is more sensitive to the PAR than to the other climatic conditions. Also the effect of N deposition is important, while the effects of variations in soil temperature and soil texture on the system are negligible.

An increase in PAR and soil temperature drives an increase of NEP, while an increase in the soil texture parameter T leads to a decrease in NEP. Therefore, the maximum values for NEP after 100 years from the N deposition rate rise (0.36, 0.48, 0.63 and $0.73 \, kg \, C \, m^{-2}$

corresponding to the N input rates of 0.4, 1, 2 and $3\,g\,N\,m^{-2}\,yr^{-1}$, respectively) are reached with maximum values of PAR and soil temperature in the coarsest textured soils, while the minimum values (0.22, 0.31, 0.42 and $0.51\,kg\,C\,m^{-2}$ corresponding to the N input rates of 0.4, 1, 2 and $3\,g\,N\,m^{-2}\,yr^{-1}$) are those with minimum values of PAR and soil temperature in the finest texture soils.

Factorial analysis

Table 3 shows the effects of all combinations of the new relationships introduced in the model. The five assumptions are: SLA and litterfall depend on leaf N concentration (1), root allocation depends on NPP (2), canopy N is assumed, with all the N taken up going into the leaves ($CNU + N_f$) (3), new leaching is modelled (4), forest management is assumed (5). For the single factor effects, the assumption regarding management (5) has the greatest effect, followed by the assumptions regarding CNU (3), and allocation (2). All the two- and three-way interactions between these three factors also had distinguishable effects. The other two assumptions had negligible effects, both when considered alone or in combination with other assumptions.

NUE and N uptake

Figure 8 shows the percentage change over time of NEP and its component terms, compared with their initial equilibrium values. Here, we investigate the full new formulation of the model (the case *'all var'*, the new leaching formulation, $CNU + N_f$, and a stem wood biomass export of $2.5\%\,yr^{-1}$ as forest management).

The rise in N deposition rate has a strong positive effect on NEP, NPP and R_h (Fig. 8a). NEP increases by 80% with respect to the steady state value, while NPP and R_h increase by about 35% and 20%, respectively. From Fig. 8a, it emerges that the marked increase in NEP is mainly due to the increase in productivity (NPP), while its transient short-term shape is mainly due to the time lag in soil respiration.

Figure 8b shows the percentage change with time of NPP, N uptake and NUE, compared with their initial equilibrium values. As the N deposition rate increases, the N uptake, considered to be the sum of N uptake from roots and CNU, increases instantly manly due to the assumption of CNU. After a few years, as the mineralization flux increases, the N taken up by roots also increases, giving rise to the slowly rising shape of N uptake. In contrast, NUE shows a sharply transient negative response in the

Table 3 Estimated effects of all combinations of new assumptions introduced into the model

Effects	Estimated effects ± standard error (10^{-3})
Average	161.3 ± 0.08
1	−1.39 ± 0.17
2	46.91 ± 0.17
3	60.02 ± 0.17
4	0.92 ± 0.17
5	220.72 ± 0.17
12	0.51 ± 0.17
13	−0.55 ± 0.17
14	−0.008 ± 0.17
15	−1.06 ± 0.17
23	11.6 ± 0.17
24	−0.21 ± 0.17
25	38.6 ± 0.17
34	−0.48 ± 0.17
35	58.63 ± 0.17
45	1.61 ± 0.17
123	0.19 ± 0.17
124	−0.0003 ± 0.17
125	0.6 ± 0.17
134	0.0048 ± 0.17
135	−0.52 ± 0.17
145	−0.02 ± 0.17
234	−0.04 ± 0.17
235	11.82 ± 0.17
245	0.1 ± 0.17
345	−0.24 ± 0.17
1234	0.009 ± 0.17
1235	0.23 ± 0.17
1245	−0.01 ± 0.17
1345	0.0004 ± 0.17
2345	−0.06 ± 0.17
123 456	0.004 ± 0.17

The magnitude of the effects was evaluated using the method given by Box *et al.* (1978, p. 322), while the standard errors of effects were calculated using higher-order interactions (Box *et al.*, 1978, p. 327). The relative importance of the single or combination of effects was assessed by the normal probability method (Daniel 1976; Box *et al.*, 1978; Henderson-Sellers, 1993). The five assumptions are: (1) SLA and litterfall depend on leaf nitrogen concentration; (2) root allocation depends on NPP; (3) canopy nitrogen uptake is assumed, with all the nitrogen taken up going into the leaves ($CNU + N_f$); (4) the new formulation for leaching is used; (5) forest management is assumed.

first few years after the increase of N deposition, followed by a progressive decline. This pattern is a consequence of both the instantaneous increase in N uptake in year 1, and of the lag in the response of NPP, due to the time needed to increase the canopy under elevated N input.
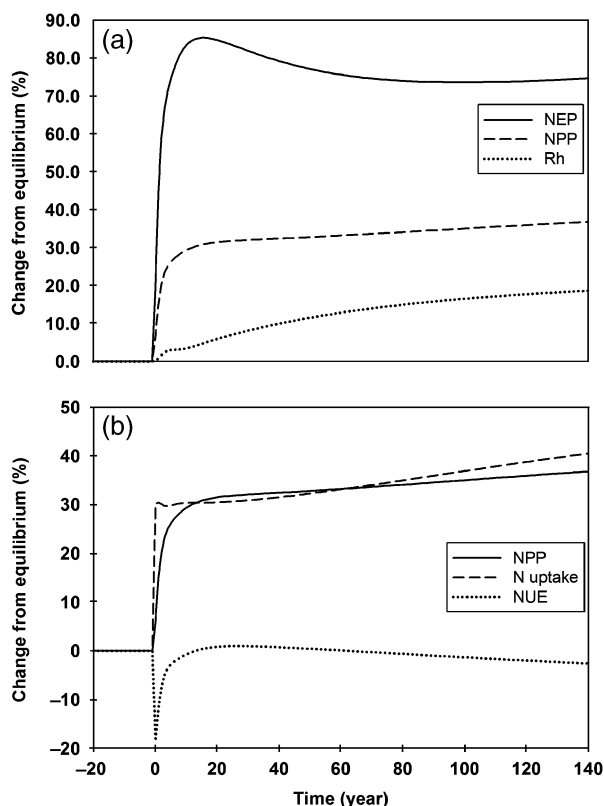
Fig. 8 Percentage changes of net ecosystem production (NEP) and factors related to the change in net primary production (NPP) and heterotrophic respiration (R_h) (a), and factors related to change in NPP, N uptake and NUE (b). Values of all variables are relative to their value for the initial equilibrium state. The simulations were run with specific leaf area (SLA), leaf mortality and allocation variable, a stem wood biomass export of 2.5% yr^{-1} as forest management, the new leaching formulation and CNU + N_f, and a step increase in external nitrogen deposition at time 0 from 0.4 to 2 g N m^{-2} yr^{-1}.

Discussion

Of all the new model assumptions considered in the study, the inclusion of forest management appears to be the most important. The constant removal of woody biomass increases the capacity of the ecosystem to store C, and makes it more sensitive to changes in the rate of N deposition than in the case of unmanaged forest.

Our study shows that management practice can strongly affect C storage capacity of the system by changing C and N soil dynamics, and that this effect is variable over time.

The predicted short-term impact of forest management is consistent with results from sawdust amendment studies (Fisher *et al.*, 2000). The truly long-term effects of forest management on growth and soil processes are more difficult to ascertain: whether un-managed old-growth forest can be considered at

equilibrium under current conditions is a matter of debate, as they have been recently found to be substantial C sinks, although not as strong as younger managed forests (Luyssaert *et al.* 2008).

Based on model simulations, knowledge of the management history of a given forest ecosystem is very important to model correctly the response of the system to an increase in N deposition rate, especially in reference to the northern temperate zone where most forests are, or have been, managed. If anything, the relevance of forest management under conditions of increasing N deposition could have been underestimated, because of the simplifying assumption of a constant mortality rate, irrespective of site fertility and yield class; shorter rotation periods and more substantial harvests are generally observed under conditions of high fertility and fast growth (Eriksson, 1976), resulting in a greater export of C from the forest and a higher NEP.

A second important contribution to the higher simulated net C uptake of the ecosystem came from the introduction of the assumption regarding variable allocation patterns.

It is known that C in plants is allocated to different organs depending on the availability of the resources and the age of the stand (Aber & Melillo, 2001; Litton *et al.*, 2007). In this framework, if the forest ecosystem is growing in an environment in which the only limiting resource is the availability of N, as in the case of our simulations, a change in N availability would lead to a change in allocation patterns. A less limiting N environment is associated with a higher percentage of C being allocated to the foliage and stems than to roots. This in turn leads to a higher NEP, because of the higher C : N ratio and lower turnover rate of stems.

The importance of a variable allocation pattern emerged also from a study on the response of three ecosystem models (Century, BGC and Hybrid) to N enrichment, where Levy *et al.* (2004) found that the most sensitive parameter in those models was the allocation to the fine roots, whose increase was associated with a reduction in $\Delta C_{\mathrm{total}} : \Delta N_{\mathrm{deposition}}$ in all cases. Similarly, Milne & van Oijen (2005) highlighted the dangers of using a simple model with constant allocation coefficients when modelling impacts of N deposition. In agreement with the study by Milne & van Oijen (2005), we also found a small decrease in the amount of fine roots following a step increase in N-deposition under the assumption of no management; in contrast, in the with-management case, the amount of fine roots was quite constant, despite a decrease in root allocation, in good agreement with experimental evidence (e.g. Iivonen *et al.*, 2006). In our results, after 100 years from the rise of N-deposition from 0.4 to 1 g N m^{-2} yr^{-1}, we found a decrease in η_r of 16.5% and an increase in η_f and η_w of 11.2%.

In accordance with the suggestion by Santantonio (1989) and Litton *et al.* (2007) that a change in root allocation is at expense of wood allocation, in the case of the rise in N deposition from 0.4 to $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$, we found that while the percentage of NPP allocated to foliage increased from 12% to 14%, the percentages of NPP allocated to wood and root changed from 48% to 59% and from 40% to 26%, respectively.

The model formulation we chose for allocation (Palmroth *et al.*, 2006) relates η_r directly to NPP. We preferred this approach to that taken in other models (e.g. Thornley, 1991; Landsberg & Waring, 1997; Milne & van Oijen, 2005), in which root allocation is an explicit function of age and environmental factors, because it of the advantage of its simplicity and of its empirical foundation.

The third important model assumption that we introduced regards the CNU.

Although it is not yet clear to what extent plants absorb N from atmospheric deposition through their leaves or bark (Katz *et al.*, 1989a, b), and what is the fate of the N once taken up, it is important to note that this process has the potential to considerably increase the capacity of the forest ecosystem to store C. If all the N absorbed by the canopy is delivered directly to photosynthetically active foliage, there is an instantaneous increase in photosynthesis and GPP. As autotrophic respiration is assumed to be a constant fraction of GPP, and R_h lags environmental changes, this increase in GPP translates to an immediate increase in NEP. Even under the assumption that the N taken up by the canopy is used indirectly, adding it to the root uptake and then assigned to the different parts of the plant, we observed a substantial increased in NEP.

From this study, adding $0.4 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ at equilibrium, it results that CNU ($0.19 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$) supplies 8% additional N compared with the root N uptake (results not shown). These estimates are in agreement with the results of Sievering *et al.* (2000), who, for a similar N deposition input ($0.53 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$), found a CNU of $0.1–0.5 \, \mathrm{g \, N \, m^{-2}}$ over the growing season, equivalent to 10–20% of N root uptake over several years time. We also found that this percentage increases with increasing N deposition rate, representing 48% of total N uptake for an input of $3 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ (results not shown), and that, in accordance with Rennenberg & Gessler (1999), the increase in CNU results in a decline of N uptake by the roots, which is reduced from 2.4 to $1.5 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ 100 years after a step increase in N deposition from 0.4 to $3 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$.

From our simulation also it results that supplying 0.19 and $0.96 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$ (corresponding to N deposition rate of 0.4 and $2 \, \mathrm{g \, N \, m^{-2} \, yr^{-1}}$, respectively) by CNU enhances forest C sequestration by 6% and 40%, respectively (Fig. 5). Model simulations seem to confirm that

the N absorbed by canopy can have a large effect on the capacity of the forest to store C (Sievering *et al.*, 2007). This calls for a renewed effort towards a better quantification and understanding of this often neglected ecological process.

Unfortunately at the moment, it is difficult to make other comparisons between our results and the outcomes of experimental studies, for several reasons. (i) In fertilization experiments, N is usually added to the soil, bypassing the possible effect of canopy uptake (Nadelhoffer *et al.*, 1999; Pregitzer *et al.*, 2008). (ii) In studies of CNU, the authors have been largely interested in the percentage contribution of CNU to the annual N required by leaves for their growth, rather than the total N uptake and its effect on productivity (Boyce *et al.*, 1996; Wilson & Tiley, 1998; Harrison *et al.*, 2000; Ignatova & Dambrine, 2000; Sievering *et al.*, 2007). (iii) There is also a great difference in techniques used by different authors, making it difficult to compare results from different experiments.

Because of the uncertainty regarding the fate and amount of N taken up by the canopy, and the evidence from some studies (Katz *et al.*, 1989a, b; Boyce *et al.*, 1996; Wilson & Tiley, 1998; Harrison *et al.*, 2000; Sievering *et al.*, 2007), that braches, twigs and stems can also play an important rule in N deposition assimilation, the most realistic representation of CNU would be somewhere in between the two assumptions investigated in this study, with a fraction of the N from deposition taken up by the canopy becoming immediately available for photosynthesis and the rest being allocated to the different parts of the tree.

Our study has shown, in accordance with Sparks (2009), the importance of CNU as a pathway of N flux into foliage, in addition to N soil-derived uptake and reallocation. We believe this to be the first time that this mechanism has been implemented in an ecosystem model to assess the ecosystem C balance. Having demonstrated the potential relevance of the process for a proper representation of forest C–N interactions, a more detailed representation would be now advisable, considering the effect of LAI on wet and dry deposition, possible saturation effects and their relationship with canopy closure, and the effects of meteorological conditions (rain, fog, ...) and plant internal N status on gaseous and wet uptake (Simpson *et al.*, 2003).

Introducing direct effects of the leaf N concentration on SLA and turnover into the model did not greatly affect the estimated NPP of the ecosystem. An increase in leaf N concentration was accompanied by an increase in SLA, but also by an increase in turnover. The two effects, one tending to increase the photosynthetic capacity of the system and the other one tending to decrease this capacity, balanced each other out after a

very short time, without affecting the C storage capacity of the system. Including assumptions about management practice, variable C allocation, and the capacity of the leaves to directly take up N, made the model more sensitive to the input of N, increasing the estimated capacity of the ecosystem to store C in response to increased N availability. Using our new version of the model, we found that the ecosystem C storage capacity was enhanced by $121 \, \text{kg} \, \text{C} \, \text{kg}^{-1} \, \text{N}$ deposited. This estimate is more than four times the value obtained with the version of G'DAY of McMurtrie *et al*. (2001) ($27.8 \, \text{kg} \, \text{C} \, \text{kg}^{-1} \, \text{N}$) and represents an upper boundary estimate of $dC : dN_{dep}$ ratio of the ecosystem. Following the initial step increase the estimated ecosystem $dC : dN_{dep}$ ratio appears to be little variable over time. The same happens when the rate of N deposition is altered, and when different assumptions are taken into account. Therefore, we can consider these two values as the upper and lower value for the C storage by forest ecosystem under N deposition. Keeping in mind that this is intended as a qualitative, rather than a quantitative study, we have demonstrated that the G'DAY ecosystem model can reproduce the range of $dC : dN_{dep}$ values found in literature (Nadelhoffer *et al*., 1999; Högberg, 2007; de Vries *et al*., 2008; Magnani *et al*., 2008; Sutton *et al*., 2008), depending on the assumptions introduced about management and ecological processes. That being so, a revision of our current understanding of C–N interactions in forest ecosystems and of their representation in global models appears urgent, also taking into account the effects of ecosystem history and forest management, in order to model accurately the C sequestration capacity of forest ecosystems.

Conclusions

N and C cycles are closely related and interact in many complex ways. To better understand their relationship it is important to represent as well as possible the direct and indirect effects of N deposition on forest C cycle.

The model described in this paper appears to be a helpful tool for this purpose. It is able to consider and analyse these interactions and to predict their implications, highlighting a strong relationship between NEP and N deposition, mediated by CNU, C allocation and forest management. Simulations with this model show that assessment of the C exchange of a forest ecosystem without taking into account effects of N deposition can easily lead to an underestimate of the C storage capacity of the forest ecosystem. For this purpose, it is critical to know about forest management and N deposition history, but other effects such as the dependence of SLA and litterfall on foliar N concentration appear to be negligible.

The qualitative analysis undertaken in this paper provides important insights into identification of the keys areas of uncertainty regarding forest ecophysiological processes considered by the model. In particular the present study shows that C allocation and CNU can have a critical role in determining the C storage capacity of forest ecosystems. More knowledge of these processes would be needed for further model development.

Although the model is also able to reproduce the all range of values for C storage per N deposition found in literature, we should stress here that this analysis is a qualitative analysis, related to an ideal forest ecosystem with no age or environmental effects, other than the N deposition. It is beyond the scope of this paper to give a quantitative answer to the debate that is currently under way about the correct value of C : N ratio to use when estimating forest C storage in response to N deposition (Högberg, 2007; de Vries *et al*., 2008; Magnani *et al*., 2008, Sutton *et al*., 2008).

A step forward in our analysis to better understand the relationship between N deposition and NEP would be to validate modelled simulation results against experimental data for a given forest or chronosequence.

Further model developments may also include: (i) improvements in the formulation of CNU, encompassing the dependence on LAI and the N deposition saturation; (ii) explicit incorporation of the effect on GPP of environment (as temperature, vapour pressure deficit and soil water content); (iii) inclusion of the N soil saturation effect on leaching and soil respiration.

References

Aber JD, Goodale CL, Ollonger SV *et al*. (2003) Is nitrogen deposition altering the nitrogen status of north eastern forests? *Biosciences*, **53**, 375–389.

Aber JD, Melillo JM (2001) *Terrestrial Ecosystems*, 2nd edn. Academic Press.

Addiscott TM, Whitmore AP, Powlson DS (1991) *Farming, Fertilizers and the Nitrate Problem*. CBA International, Wallingford, San Diego.

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Review*, **5**, 1–15.

Box GPE, Hunter WG, Hunter JS (1978) *Statistics for Experimenters. An Introduction to Design, Data Analysis and Model Building*. John Wiley & Sons, New York.

Boyce RL, Friedland AJ, Chamberlain CP, Poulson SR (1996) Direct canopy nitrogen uptake from N-15-labeled wet deposition by mature red spruce. *Canadian Journal of Forest Research*, **26**, 1539–1547.

Burton AJ, Pregitzer KS, Hendrick RL (2000) Relationship between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. *Oecologia*, **125**, 389–399.

Canadell JG, Le Quéré C, Raupach MR *et al.* (2007) Contributions to accelerating atmospheric CO_2 growth economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866–18870.

Caspersen JP, Pacala SW, Jenkins JC *et al.* (2000) Contributions of land-use history to carbon accumulation in US forests. *Science*, **290**, 1148–1151.

Chopping M, Moisen GG, Su L, Laliberte A, Rango A, Martonchik JV, Peters DPC (2008) Large area mapping of southwestern forest crown cover, canopy height, and biomass using the NASA Multiangle Imaging Spectro-Radiometer. *Remote Sensing of Environment*, **112**, 2051–2063.

Ciais P, Schelhaas MJ, Zaehle S *et al.* (2008) Carbon accumulation in European forests. *Nature Geoscience*, **1**, 425–429.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behaviour of plant–soil models. *Ecological Application*, **3**, 666–681.

Daniel C (1976) *Application of Statistics to Industrial Experimentation*. John Wiley & Sons, New York.

de Graaff MA, van Groeningen KJ, Six J, Hungate BA, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta analysis. *Global Change Biology*, **12**, 2077–2091.

DeLucia EH, Drake JE, Thomas RB, Gonzalez-Meler MA (2007) Forest carbon use efficiency: is respiration a constant fraction of gross primary production? *Global Change Biology*, **13**, 1157–1167.

De Vries W, Reinds GJ, van der Salm C *et al.* (2001) *Intensive Monitoring of Forest Ecosystems in Europe*. Technical Report (2001). EC, UN/ECE, Brussels, Ginevra.

De Vries W, Solberg S, Dobbertin M *et al.* (2008) Ecologically implausible carbon sequestration? *Nature*, **541**, E1–E3.

Dewar RC, McMurtrie RE (1996a) Analytical model of stemwood growth in relation to nitrogen supply. *Tree Physiologist*, **16**, 161–171.

Dewar RC, McMurtrie RE (1996b) Sustainable stemwood yield in relation to the nitrogen balance of forest plantations: a model analysis. *Tree Physiologist*, **16**, 173–182.

Eriksson H (1976) *Yield of Norway spruce in Sweden.* Royal College of Forestry, Department of Forest Yield Research, Report 41, 291 pp.

Fang J, Chen A, Peng C, Zhao S, Ci L (2001) Changes in forest iomass carbon storage in China between 1949 and 1998. *Science*, **292**, 2320–2322.

Field CB (2001) Plant physiology of the "missing sink" carbon sink. *Plant Physiology*, **125**, 25–28.

Fisher RF, Binkley D, Pritchett WL (2000) *Ecology and Management of Forest Soils*. John Wiley and Son, New York.

Gaige E, Dail DB, Hollinger DY *et al.* (2007) Changes in canopy processes following whole-forest canopy nitrogen fertilization of a mature spruce-hemlock forest. *Ecosystems*, **10**, 1133–1147.

Galloway JN, Schlesinger WH, Levy II HL, Michaels A, Schnoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochemical Cycles*, **9**, 235–252.

Garten CT, Schwab AB, Shirshac TL (1998) Foliar retention of 15N tracers: implications for net canopy exchange in low- and high-elevation forest ecosystems. *Forest Ecology and Management*, **103**, 211–216.

Goodale CL, Apps MJ, Birdsey RA *et al.* (2002) Forest carbon sink in North Hemisphere. *Ecological Applications*, **12**, 891–899.

Halliday JC, Tate KR, McMurtrie RE, Scott NA (2003) Mechanisms for changes in soil carbon storage with pasture to *Pinus radiata* land-use change. *Global Change Biology*, **4**, 1294–1308.

Harrison AF, Schulze E-D, Gebauer G, Bruckener G (2000) Canopy uptake and utilization of atmospheric pollution nitrogen. In: *Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecological Studies*, **142** (ed. Schulze E-D), pp. 171–188. Springer-Verlag, Berlin.

Henderson-Sellers A (1993) A factorial assessment of the sensitivity of the BATS land-surface parameterization scheme. *Journal of Climate*, **6**, 227–247.

Henderson-Sellers B, Henderson-Sellers A (1996) Sensitivity evaluation of environmental models using fractional factorial experimentation. *Ecological Modelling*, **86**, 291–295.

Högberg P (2007) Nitrogen impacts on forest carbon. *Nature*, **447**, 781–782.

Holland EA, Braswell BH, Sulzman JM, Lamarque JF (2005) Nitrogen deposition onto the Unites State and Western Europe: synthesis of observations and models. *Ecological Applications*, **15**, 38–57.

Holland EA, Dentener FJ, Braswell BH, Sulzman JM (1999) Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry*, **46**, 7–43.

Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land-use change. *Science*, **285**, 574–578.

Hyvönen R, Persson T, Andersson S, Olsson B, Ågren GI, Linder S (2008) Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry*, **89**, 121–137.

Ignatova N, Dambrine E (2000) Canopy uptake of N deposition in spruce (*Picea abies* L. Karst) stands. *Annals of Forest Science*, **57**, 113–120.

Iivonen S, Kaakinen S, Jolkkonen A, Vapaavuori E, Linder S (2006) Influence of long-term nutrient optimization on biomass, carbon and nitrogen acquisition and allocation in Norway spruce. *Canadian Journal of Forest Research*, **36**, 1563–1671.

Jenkinson DS, Goulding K, Powlson DS (1999) Nitrogen deposition and carbon sequestration. *Nature*, **400**, 629.

Johnson DW (2006) Progressive N limitation in forests. Review and implications for long-term responses to elevated CO_2. *Ecology*, **87**, 64–75.

Katz C, Oren R, Schulze E-D, Milburn JA (1989a) Uptake of water and solutes through twigs of *Picea abies* (L.) Karst. *Trees*, **3**, 33–37.

Katz C, Oren R, Schulze E-D, Steudle E (1989b) Uptake of water and solutes through bark and needle surfaces. In: *Forest Decline and Air Pollution: A study of spruce (Picea abies (L.) Karst.) on Acid Soils. Ecological Studies Series*, Vol. 77 (eds Schulze E-D, Lange OL, Oren R), pp. 218–221. Springer Verlag, Berlin.

Klopatek JM, Barry MJ, Johnson DW (2006) Potential canopy interception of nitrogen in the Pacific Northwest, USA. *Forest Ecology and Management*, **234**, 344–354.

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist*, **172**, 393–411.

Kostiainen K, Kaakinen S, Saranpää P, Sigurdsson BD, Linder S, Vapaavuori EM (2004) Effects of elevated $[CO_2]$ on stem wood properties of mature Norway spruce grown at different soil nutrient availability. *Global Change Biology*, **10**, 1526–1538.

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Levy PE, Wendler R, van Oijen M, Cannel MGR, Millard P (2004) The effect of nitrogen enrichment on the carbon sink in coniferous forests: uncertainty and sensitivity analyses of three ecosystem models. *Water, Air and Soil Pollution*, **4**, 67–74.

Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Global Change Biology*, **13**, 2089–2109.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, **54**, 731–739.

Lovett GM (1992) Atmospheric deposition and canopy interactions of nitrogen. In: *Atmospheric Deposition and Forest Nutrient Cycling* (eds Johnos DW, Lindberg SE), pp. 152–166. Springer-Verlag, New York, pp. 207–213.

Luyssaert S, Schultz ED, Börner A *et al.* (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–215.

Magnani F, Dewar RC, Borghetti M (2009) Leakage and spillover effects of forests management on carbon storage: theoretical insights from a simple model. *Tellus*, **61B**, 385–393.

Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–852.

Magnani F, Mencuccini M, Borghetti M *et al.* (2008) Magnani et al. reply. *Nature*, **451**, E3–E4.

1486 S. D E Z I *et al.*

Mayewski PA, Lyons WB, Spencer MJ, Twickler MS, Buck CF, Whitlow S (1990) An ice-core record of atmospheric response to anthropogenic sulphate and nitrate. *Nature*, **346**, 554–556.

McMurtrie RE, Medlyn BE, Dewar RC (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 Physiology*, **21**, 831–839.

Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys MP (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research*, **30**, 873–888.

Milne R, van Oijen M (2005) A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. *Annals of Forest Science*, **62**, 1–13.

Myneni RB, Dong J, Tucker CJ *et al.* (2001) A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Science*, **26**, 14784–14789.

Nadelhoffer KJ, Emmett BA, Gundersen P *et al.* (1999) Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, **398**, 145–148.

Nalder IA, Wein RW (2006) A model for the investigation of long-carbon dynamics in boreal forests of western Canada I. Model development and validation. *Ecological Modelling*, **192**, 37–66.

Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature*, **411**, 469–472.

Oren R, Schulze E-D, Werk KS, Meyer J (1988) Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. VII. Nutrient relations and growth. *Oecologia*, **77**, 163–173.

Palmroth S, Oren R, McCarthy HR *et al.* (2006) Aboveground sink strength in forests controls the allocation of carbon below ground and its $[CO_2]$-induced enhancement. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 19362–19367.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Parton WJ, Scurlock JMO, Ojima DS *et al.* (1993) Observations and modelling of biomass and soil organic matter dynamic for the grassland biome worldwide. *Global Biogeochemistry Cycles*, **7**, 785–809.

Pregitzer KS, Burton AJ, Lessard VC, Zak DR, Talhelm AF (2008) Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. *Global Change Biology*, **14**, 142–153.

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR (1998) Variation in sugar maple root respiration with root diameter distribution and soil depth. *Tree Physiology*, **18**, 665–670.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.

Reich PB, Walters MB, Ellsworth DS, Vose JM, Volin JC, Gresham C, Bowman WD (1998) Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia*, **114**, 471–482.

Rennenberg H, Gessler A (1999) Consequences of N depositions to forest ecosystems: recent results and future research needs. *Water, Air and Soil Pollution*, **116**, 47–64.

Santantonio D (1989) Dry-matter partitioning and fine-root production in forests–new approaches to a difficult problem. In: *Biomass Production by Fast-Growing Trees* (eds Pereira JS, Landsberg JJ), pp. 57–72. Kluwer Academic Publishers, Norwell, MA.

Schulze ED, Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science*, **289**, 2058–2059.

Sievering H (1999) Nitrogen distribution and carbon sequestration. *Nature*, **400**, 629–630.

Sievering H, Fernandez I, Lee J, Hom J, Rustad L (2000) Forest canopy uptake of atmospheric nitrogen deposition at eastern US conifer site: carbon storage implications? *Global Biogeochemical Cycles*, **14**, 1153–1159.

Sievering H, Tomaszewski T, Torizzo J (2007) Canopy uptake of atmospheric N deposition at conifer forest: part I – canopy N budget, hotosynthetic efficiency and net ecosystem exchange. *Tellus B*, **59**, 483–492.

Simpson D, Fagerli H, Jonson JE, Tsyro S, Wind P, Tuovinen JP (2003) *Transboundary Acidification, Eutrophication and Ground Level Ozone in Europe. Part 1.* Unified EMEP Model Description. EMEP Status Report 2003. Norwegian Meteorological Institute, 104 pp.

Sparks JP (2009) Ecological ramifications of the direct foliar uptake of nitrogen. *Oecologia*, **159**, 1–13.

Šúri M, Huld TA, Dunlop ED, Ossenbrink HA (2007) Potential of solar electricity generation in the European Union member states and candidate countries. *Solar Energy*, **81**, 1295–1305, Available at: http://re.jrc.ec.europa.eu/pvgis/

Sutton MA, Simpson D, Levy PE, Smith RI, Reis S, van Oijen M, de Vries W (2008) Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, **14**, 1–7.

Thornley JHM (1991) A transport-resistance model forest growth and partitioning. *Annals of Botany*, **68**, 211–226.

Tomaszewski T, Boyce RL, Sievering H (2003) Canopy uptake of atmospheric nitrogen and new growth nitrogen requirement at Colorado subalpine forest. *Canadian Journal of Forest Research*, **33**, 2221–2227.

Townsend AR, Braswell BH, Holland EA, Penner JE (1996) Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecological Applications*, **6**, 806–814.

UN ECE/FAO (2000) *Forest Resources of Europe, CIS, North America, Australia, Japan and New Zealand*. Report No. 17. United Nations, Geneva.

Vitousek PM, Aber JD, Howarth RW *et al.* (1997) Human alteration of global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.

Wilson EJ, Tiley C (1998) Foliar uptake of wet-deposited nitrogen by Norway spruce: an experiment using N-15. *Atmospheric Environment*, **32**, 513–518.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Parameter values used in the model for a representative European temperate stand of Norway spruce (*Picea abies* (L.) Karst.).

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2.9 APPENDIX S

Parameter values used in the model for a representative European temperate stand of Norway spruce (*Picea abies* (L.) Karst.).

Parameter	Definition	Value	Units	Reference
w	C content of dry matter	0.49	-	Medlyn et al. 2000
f	NPP/GPP ratio	0.53	-	DeLucia et al. 2007
k	Light extinction factor	0.5	-	Comins & McMurtrie 1993
PAR	Incident photosynthetic active radiation	2250	MJ m^{-1} yr^{-1}	This study
ε_0	Potential PAR utilisation efficiency	2.73	gC MJ^{-1}	Landsberg et al. 2003
ρ	Ratio of root nitrogen concentration to foliar nitrogen concentration	0.6	-	Newman & Hart 2006
d	η_w/η_f	4	-	Iivonen et al. 2006
B	Exponential coefficient in η_r equation	2.309	m^2 yr kgC^{-1}	Palmroth et al. 2006
Q	Coefficient in η_r equation	9.499	-	Palmroth et al. 2006
$Y0$	Constant in η_r equation	0.138	-	Palmroth et al. 2006
γ_r	Constant root mortality	0.667	yr^{-1}	Withington et al. 2006
T	Soil texture parameter	0.5	-	Comins & McMurtrie 1993
$Tsoil$	Soil temperature	10	°C	This study
CNU_e	Canopy nitrogen uptake	0.8	-	Sievering et al. 2007
c	Fractional canopy cover	0.6	-	Chopping et al. 2008
f_{BR}	Fraction of wood carbon in branches (average for American conifers)	0.14	-	Jenkins et al. 2003
f_{CR}	Fraction of wood carbon in coarse roots (average for American conifers)	0.18	-	Jenkins et al. 2003
N_{crit}	Critical inorganic N value for soil variable N/C scenario	0.002	kgN m^{-2}	McMurtrie et al. 2001
v_{f_max}	Maximum foliar N/C above which N is not limiting	0.04	kgN kgC^{-1}	Comins & McMurtrie 1993
v_{f_min}	minimum foliar N/C	0.001	kgN kgC^{-1}	This study
v_u	N/C ratio for surface structural litter	1/150	kgN kgC^{-1}	Comins & McMurtrie 1993
v_v	N/C ratio for soil structural litter	1/150	kgN kgC^{-1}	Comins & McMurtrie 1993
v_{newa}	Intercept of relationship between v_{new} and v_f	0	kgN kgC^{-1}	Medlyn et al. 2000
v_{newb}	Slope of relationship between v_{new} and v_f	0.16773	-	Medlyn et al. 2000
v_{swa}	Intercept of relationship between v_{sw} and v_f	0	kgN kgC^{-1}	Medlyn et al. 2000
v_{swb}	Slope of relationship between v_{sw} and v_f	0.05624	-	Medlyn et al. 2000
v_{a_max}	Maximum for newly active soil pool SOM	1/8	kgN kgC^{-1}	Nalder & Wein 2006
v_{a_min}	Minimum for newly active soil pool SOM	1/16	kgN kgC^{-1}	Nalder & Wein 2006
v_{s_max}	Maximum for newly slow soil pool SOM	1/12	kgN kgC^{-1}	Nalder & Wein 2006
v_{s_min}	Minimum for newly slow soil pool SOM	1/40	kgN kgC^{-1}	Nalder & Wein 2006
v_{p_max}	Maximum for newly passive soil pool SOM	1/6	kgN kgC^{-1}	Nalder & Wein 2006
v_{p_min}	Minimum for newly passive soil pool SOM	1/20	kgN kgC^{-1}	Nalder & Wein 2006

Parameter	Definition	Value	Units	Reference
v_{a_max}	Maximum for newly active soil pool SOM	1/8	kgN kgC^{-1}	Nalder & Wein 2006
v_{a_min}	Minimum for newly active soil pool SOM	1/16	kgN kgC^{-1}	Nalder & Wein 2006
v_{s_max}	Maximum for newly slow soil pool SOM	1/12	kgN kgC^{-1}	Nalder & Wein 2006
v_{s_min}	Minimum for newly slow soil pool SOM	1/40	kgN kgC^{-1}	Nalder & Wein 2006
v_{p_max}	Maximum for newly passive soil pool SOM	1/6	kgN kgC^{-1}	Nalder & Wein 2006
v_{p_min}	Minimum for newly passive soil pool SOM	1/20	kgN kgC^{-1}	Nalder & Wein 2006
λ_{loss}	Constant rate of N lost through leaching and gaseous emission	0.1	yr^{-1}	McMurtrie et al 2001
λ_u	Constant rate of N uptake by plant roots	1.9	yr^{-1}	McMurtrie et al 2001
k_r	Value of root C at which 50% of the available N is taken up	0.05	kgC m^{-2}	Dewar & McMurtrie 1996
Lfl	Lignin/biomass ratio in leaf litter	0.25	-	Eliasson et al. 2005
Lrl	Lignin/biomass ratio in root litter	0.127+0.393* Lfl	-	Newman & Hart 2006

2.10 CORRIGENDUM

p.18: The text "the effect of N deposition on forest C" should be replaced with "the effect of N deposition on N limited forest C sequestration."

p. 19: The sentence *"In a previous study McMurtrie et al. (2001) assumed that the C:N of the substrate entering the three soil pools decreases linearly between given minimum and maximum values, as soil inorganic N (N_{inorg}) decreases from a critical value (N_{crit}) to zero."* should be *"In a previous study McMurtrie et al. (2001) assumed that the N:C of the substrate entering the three soil pools decreases linearly between given maximum and minimum values, as soil inorganic N (N_{inorg}) decreases from a critical value (N_{crit}) to zero."*

p. 19: "the substrate entering the three soil pools the substrate entering the three soil pools decreases linearly between given minimum and maximum values, as soil inorganic N (Ninorg) decreases from a critical value (Ncrit) to zero." should read "the partly decomposed substrate entering the soil pools from litter pools the substrate entering the three soil pools decreases linearly between given minimum and maximum values, as soil inorganic N (Ninorg) decreases from a critical value (Ncrit) to zero, while the decomposition rate of the litter pools depends on the C:N of the litter."

p. 19: The statement *"(as in Comins & McMurtrie, 1993)"* should read *"(as in McMurtrie et al., 2001)"*

p.21: The following text should be added at the end of "CNU" section: "Although it is known that leaf N partitioning occurs between photosynthetic and not photosynthetic components (Field & Mooney, 1986; Evans, 1989; Evans & Seemann, 1989; Hikosaka, 2004; Eichelmen *et al.,* 2005), the level of detail of this partition makes it unsuitable for inclusion in a relatively simple forest ecosystem model as G'DAY."

p. 24: The statement *"the rate of increase in NPP was linear"* should read *"the rate of increase in NPP was constant"*

p. 25: The text "due to the higher stem production being exported." should be replaced with "due to the higher stem production being exported and that we are not considering the fate of this exported C wood."

p. 28, Table 3: *"123456"* should be *"12345"*

p. 29: *"it of the advantage"* should be removed

p. 30: After the sentence "(iii) There is also a great difference in techniques used by different authors, making it difficult to compare results from different experiments." the following text should be added: "However, comparing the values of leaf N concentration for low level of N deposition, under the assumption of canopy nitrogen uptake, we found a good correspondence with the vales observed by Calanni *et al.* (1999). In fact, simulating a step increase of N deposition from 0.4 to 1 gN m^{-2} yr^{-1} the foliar N concentration increases from 0.013 to 0.0145 kgN kgC^{-1}, in good agreement with the avarege value of 0.0148 kgN/kgC found by Calanni *et al.* (1999) for the N deposition rate range of 0.4-0.8 gN m^{-2} yr^{-1}."

p. 30: The sentence "We believe this to be the first time that this mechanism has been implemented in an ecosystem model to assess the ecosystem C balance" should be replaced with "Canopy N uptake has been modelled previously using transport-resistance approaches to reproduce the instantaneous bi-directional exchange of N between leaves and atmosphere (Sutton *et al.*, 1998, 2009; Flechard *et al.*, 1999; Riedo *et al.*, 2002). However, the fine temporal scale and the level of detail of these models make them unsuitable for inclusion in a relatively simple forest ecosystem model as G'DAY. Despite the ability of these models to provide detailed hourly estimates of canopy N exchange, they are not complete ecosystem models, as they do not represent all the plant and soil feedbacks. We can therefore state that this is the first time that the canopy N uptake has been explicitly considered in a forest ecosystem model."

p. 31: *"the keys area"* should be *"the key area"*

p. 31: *"the all range of values"* should be *"the range of values"*

p. 31: After the text "depending on the assumptions introduced about management and ecological processes." the following sentence should be added: "For example, from the sensitivity analysis (Table 1), using a value for PAR equal to 1800 MJ m^{-2} yr^{-1}, for Tsoil equal to 15°C and for T equal to 0.3, the modelled dC:dN ratio goes up to 177, which is within the range reported in Magnani *et al.* 2008".

p. 32: The reference "Calanni J, Berg M, Wood M, Mangis D, Boyce R, Weathers W, Sievering H (1999) Atmospheric nitrogen deposition at a conifer forest: response of free amino acids in Engelmann spruce needles. *Environmental Pollution*, **105**, 79-89." shoul be added.

p. 32: The reference "Eichelmann H, Oja V, Rasulov B, Padu E, *et al.* (2005) Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. *Plant Cell and Environment*, **28**, 389–401." Should be added

p. 32: The reference "Evans JR (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia*, **78**, 9–19." should be added

p. 32: The reference "Evans JR, Seemann JR (1989) The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences and control. In: Briggs WR (ed) *Photosynthesis.* Alan R. Liss, New York, pp 183–205" should be added

p. 32: The reference "Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 25–55" should be added

p. 32: The reference "Flechard CR, Fowel D, Sutton MA, Cape JN (1999) A dynamic chemical model of bi-directional ammonia exchange between semi-natural vegetation and the atmosphere. *Quarterly Journal of the Royal Meteorological Society*, **125 (559)**, 2611-2641." should be added

p. 32: The reference "Hikisaka K (2004) Interspecific difference in the photosynthesis-nitrogen relationship: patterns, physiological causes, and ecological importance. *Journal of Plant Research*, **117**, 481–494." should be added

p. 33: The reference "Riedo M, Milford C, Schmid M, Sutton MA (2002) Coupling soil-plant-atmosphere exchange of ammonia with ecosystem functioning in grasslands. *Ecological Modelling*, 158, 83-110." should be added

p. 33: The reference "Sutton MA, Burkhardt JK, Guerin D, Nemitz E, Foeler D (1998) Development of forest resistance models to describe measurements of bi-directional ammonia surface-atmosphere exchange. *Atmospheric Environmental*, **32(3)**, 473-480." should be added

p. 33: The reference: "Sutton MA, Nemitz E, Milford C, Campbell C *et al.* (2009) Dynamics of ammonia exchange with cut grassland: synthesis of results and conclusions of the GRAMINAE Integrated Experiment. *Biogeosciences*, **6**, 2907-2934." should be added

p. 33: The reference *"Thornley JHM (1991) A transport-resistance model forest growth and partitioning. Annals of Botany, **68**, 211-226."* should be *"Thornley JHM (1991) A transport-resistance model of forest growth and partitioning. Annals of Botany, **68**, 211-226."*

CHAPTER 3

Model analysis of feedbacks between atmospheric CO$_2$ concentration and N availability in a forest free-air CO2 enrichment experiment

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3.1 ABSTRACT

Global average atmospheric CO_2 concentration ($[CO_2]$) has increased steadily since the industrial revolution and is predicted to further double by the end of this century. Free-Air CO_2 Enrichment (FACE) experiments demonstrate that nitrogen availability plays a crucial role in determining the forest ecosystem response to this increase in atmospheric $[CO_2]$.

We investigated the interaction between soil nitrogen (N) availability and the $[CO_2]$ effect on forest productivity by applying a forest ecosystem model to a large-scale forest FACE experiment where N availability has been observed to constrain the $[CO_2]$ response. We applied the Generic Decomposition And Yield (G'DAY) forest carbon-nitrogen (C-N) cycling model to data from the Oak Ridge National Laboratory's FACE experiment and investigated whether the model could simulate key C-N interactions observed in this experiment.

It was found that the model could reproduce the observed decline in NPP at ambient $[CO_2]$, which was caused by declining soil N availability as the stand aged. However, the model failed to reproduce the observed stimulation in productivity at elevated $[CO_2]$. Analysis of the mechanisms involved indicated that likely reasons for the model failures were (i) the initialization of soil pools and (ii) incorrect parameterization and/or formulation of the soil N uptake as function of depth. These values are not directly observable and their estimation poses a challenging problem. Further studies applying inverse techniques could potentially improve simulation results, and therefore our understanding of C-N feedbacks under rising atmospheric $[CO_2]$.

3.2 INTRODUCTION

Global average atmospheric CO_2 concentration ($[CO_2]$) increased from 280 ppm before the industrial revolution to 381 ppm in 2006 (Canadell *et al.,* 2007a), and it is predicted to further double by the end of this century (IPCC, 2007). Forests, absorbing CO_2 through photosynthesis and releasing it through plant respiration and soil decomposition, control the major terrestrial bidirectional carbon (C) transfer between atmosphere and soil, and play an important role in the global C budget (IPCC, 2007; Canadell *et al.,* 2007b, Hyvönen *et al.*, 2007; Sitch *et al.,* 2008).

Using data from four Free-Air CO_2 Enrichment (FACE) experiments, Norby *et al.* (2005) showed that the short-term (four to five years) NPP response to the atmospheric $[CO_2]$ predicted for the latter half of the century is conserved across a broad range of

productivity, with an average stimulation of 23 ± 2 %. Nonetheless, there is evidence that the CO_2 stimulation is limited under conditions of low nutrient availability, especially nitrogen (N) (Oren *et al.,* 2001; Luo *et al.,* 2004; Reich *et al.,* 2006). As many temperate forests are N-limited, the ability of ecosystems to absorb additional C in future is very likely to be constrained by levels of N availability and fixation (Reich *et al.,* 1997). Therefore, a good understanding of the relationship between atmospheric [CO_2] and soil N availability is necessary to better predict future forest ecosystem behaviour.

Increased C uptake and its storage in a forest ecosystem growing under elevated [CO_2] may increase ecosystem demand for N. On a long time scale, this increased N demand may result in a progressive N immobilisation in plant litter, biomass and soil organic matter (Luo *et al.,* 2004). However the experimental evidence for progressive nitrogen limitation (PNL) remains equivocal, either because experiments were not run long enough to show it, or because of mechanisms that can delay N limitation (Luo *et al.,* 2006a; McKinley *et al.,* 2009). Such mechanisms can include enhanced N uptake. In a recent meta-analysis of CO_2 enrichment experiments, Luo *et al.* (2006a, b) reported an increase in the total ecosystem N pool under elevated [CO_2]. Similarly, Finzi *et al.* (2007), reviewing forest FACE experiments, reported an increase in N uptake in N limited sites under elevated [CO_2]. Both observations may be related to a shift in C allocation towards fine root system under conditions of decreased nutrient availability (Santantonio, 1989; Litton *et al.,* 2007), as suggested by some CO_2 enrichment studies, where an increase in fine root production has been observed (Pregitzer *et al.,* 2000; Finzi *et al.,* 2007; Stover *et al.,* 2007; Iversen *et al.,* 2008; Iversen, 2010). This increase in fine root production could enhance N uptake from parts of soil not previously explored by roots. It has also been observed that both stomatal conductance and N concentration are reduced in elevated [CO_2] (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007).

Given the uncertainty of the direction and magnitude of the feedbacks between C and N availability, and the difficulty in conducting experiments sufficiently long to observe responses on long time scales, ecosystem models can represent important tools to identify and understand those mechanisms involved in the response of nutrient-limited forest ecosystems to increased [CO_2] on different time scales.

To this end, Comins and McMutrie (1993) developed the integrated plant-soil G'DAY (Generic Decomposition and Yield) model, which reproduces the dynamics of C and N in forest ecosystems. The G'DAY model predicts that the response of net primary productivity to a step change in [CO_2] differs in magnitude and sign depending on

observation timescales: a positive transient response on short time scale is followed by a slight decrease and a subsequent small increase on long time scale (Comins & McMurtrie, 1993; Kirschbaum *et al.,* 1994, 1998; McMurtrie & Comins, 1996; Medlyn & Dewar, 1996; McMurtrie & Dewar, 1999; Medlyn *et al.,* 2000; Pepper *et al.,* 2005; Pepper *et al.,* 2007). The model also predicts that this response will vary depending on the N:C ratio of newly formed soil organic matter at elevated $[CO_2]$ concentration (McMurtrie & Comins, 1996). This ratio could vary because of decreased foliage N concentration under elevated $[CO_2]$, and/or because of the reduced soil N availability at high $[CO_2]$, (Medlyn *et al.,* 2000; Pepper *et al.,* 2007). Applying the model to a Norway spruce site, McMurtrie *et al.* (2000) also found that the only way to overcome soil N limitation on the long term CO_2 fertilization effect is by increases in N acquisition.

Although the G'DAY model represents a useful theoretical tool to investigate the effect of elevated $[CO_2]$ on forest C cycle, until now, the model has not explicitly been tested against data from CO_2 enrichment experiments. The aim of this paper is to parameterize the G'DAY model for the closed-canopy forest FACE experiment at Oak Ridge National Laboratory (ORNL) and to test whether this C-N cycling model can explain the results observed at the study site.

At the ORNL experiment site, a ten year old Sweetgum (*Liquidambar styraciflua* L.) plantation was fertilised with elevated $[CO_2]$ from 1998 to 2007. Although a large increase in NPP under elevated $[CO_2]$ was observed during the first five years of the experiment, the NPP response progressively declined over time to values similar to those for ambient $[CO_2]$ at the end of the experiment (Norby *et al.,* 2010).

The decrease in productivity over time, and the reduction over time of the fertilizing effect of CO_2, have been attributed to increasing N limitation as the forest matures. Leaf N concentration, which was lower under elevated $[CO_2]$, decreased over the course of the experiment for both elevated and ambient $[CO_2]$ treatments. A slight reduction over time of the specific leaf area (SLA) was also observed in both treatments (Norby *et al.,* 2010).

In this paper we focused on testing whether the G'DAY model can explain the decline in leaf N concentration over time and whether the accumulation of N in litter and wood, during plantation development, can explain the decrease in NPP and the decreasing stimulation by CO_2. The original version of G'DAY model, developed for evergreen forest stands, was modified to enable simulation of the development of the ORNL FACE deciduous plantation. This new model version was then coupled to the Model Any Terrestrial Ecosystem (MATE) model (McMurtrie *et al.* in preparation), that

incorporates the effect of atmospheric [CO_2] and meteorological data (T, PAR, RH, rain) on light use efficiency (LUE).

We ran the model testing two alternative representations for SLA: either (1) SLA was assumed to be constant and to have the same value for elevated and ambient [CO_2] treatments, for the entire period of the simulation; or (2) SLA was assumed to vary with leaf N concentration. Finally we discussed the capacity of this C-N cycling model to reproduce and explain experimental results.

3.3 MATERIALS AND METHODS

3.3.1 STUDY SITE

The study site is a Sweetgum (*Liquidambar styraciflua* L.) plantation established in 1988 at the Oak Ridge National Environmental Research Park in Roane County, TN (35°54_N, 84°20_W). The soil, classified as Aquic Hapludult, has a silty clay loam texture and is moderately well drained (van Miegroet *et al.,* 1994; Norby *et al.,* 2001). One year old, bare-rooted seedlings were planted at a spacing of 2.3 x 1.2 m (Norby *et al.,* 2004). The canopy has been closed since 1996 and the trees are in the linear growth phase (Norby *et al.,* 2001). Wullschleger et al. (2002) stated that "A survey of the site in 1998 indicated that the 10-yr-old plantation had a basal area of about 29 m^2 ha^{-1}, with an average height of 12 m and a leaf area index of 5.5 m^2 m^{-2}". The mean annual temperature is 13.9 °C (1962-1993) and the mean annual precipitation is 1371 mm (Norby *et al.,* 2001).

3.3.2 THE EXPERIMENT

The free-air CO_2 enrichment (FACE) experiment was established with the aims of understanding how the eastern deciduous forest will be affected by CO_2 enrichment of the atmosphere, and quantifying feedbacks from the forest to the atmosphere (http://face.ornl.gov/index.html). The experimental plots comprise five 25 m diameter circular rings within the sweetgum plantation, enclosing 80-90 trees per ring (Sholtis *et al.,* 2004). FACE apparatus was installed in four of the rings based on the design, equipment and software of Hendrey *et al.* (1999). Each ring consists of 24 vent pipes spaced 3.3 m apart, suspended from 12 aluminium towers. Pure CO_2 is mixed with a turbulent air-stream in a plenum and released through vertical vent pipes, according to wind direction, and regulated to maintain the target [CO_2] near the top of the canopy (Wullschleger *et al.,* 2002; Norby *et al.*, 2005). Two of these rings are treated with

elevated [CO_2]. The other two rings, exposed to ambient CO_2 concentration, and the fifth ring, without FACE apparatus, serve as control. The CO_2 treatment commenced in April 1998 and has been maintained for 24 h per day every year, during the growing season (April-November). The treatment set point, in 1998, was a constant [CO_2] of 565 ppm (about 200 ppm above the global [CO_2]). To better represent the diurnal variation in [CO_2], the protocol was adjusted in 1999 and 2000 with a dual set point (565 ppm day and 645 ppm night).

A complete description of the site and of ORNL FACE has been given by (Norby *et al.*, 2001, 2002, 2004). Operating, meteorological conditions and measurement results are documented at http://public.ornl.gov/face/ORNL/ornl_home.shtml and at http://face.ornl.gov.

3.3.3 KEY EXPERIMENTAL RESULTS

The major results on impacts of CO_2 enrichment on C and N cycling from this experiment can be summarised as follows.

(1) Net primary production (NPP, kgC m^{-2} yr^{-1}) at the site was estimated as the sum of annual C increase in wood, leaves, coarse and fine roots and the major inputs of detritus (litterfall and fine root turnover) (Norby *et al.,* 2005). The annual increments of stems and coarse woody roots were estimated by applying a site-specific allometric equation that incorporated basal area, height, taper and wood density to reduce the possible alterations deriving from elevated [CO_2] (Norby *et al.,* 2001, 2005). The annual leaf increment was zero, as is normal for deciduous trees, while litterfall was estimated using litter baskets (Norby *et al.,* 2003). The contribution of fine root production to NPP, measured directly by using minirhizotrons and in-growth cores, averaged 16% (Norby *et al.,* 2004, 2005, 2008).

Comparison of NPP between elevated and ambient [CO_2] plots shows that although CO_2 enrichment consistently stimulated net primary production during the first years of the experiment (ca +33%), its fertilizing effect progressively declined over time to +9% at the end of the experiment (Norby *et al.,* 2010). Although the decline in NPP was observed in both treatments, it was more consistent at elevated [CO_2] (Norby *et al.,* 2010).

(2) Leaf N content per unit leaf mass was measured from the leaves sampled in the plots (Norby & Iversen, 2006). Leaf N concentration was found to be consistently reduced in the trees treated with elevated [CO_2] (Norby *et al.,* 2010). In both

treatments, leaf N concentration declines over time with the same rate of about 1.1 gN kgC^{-1} per year from 1998 to 2007 (Norby *et al.,* 2010).

3.3.4 THE MODEL

G'DAY (Generic Decomposition and Yield) model is a process-based model that simulates C and N dynamics in a forest ecosystem (Comins & McMurtrie, 1993). The model is composed of two sub-models representing plant-system production and soil organic matter decomposition, respectively. The plant sub-model consists of three pools: foliage, wood (stem, branches and coarse roots) and fine roots. The soil sub-model, as in the CENTURY soil model (Parton *et al.,* 1987, 1993), consists of four litter pools (structural and metabolic, both above and below ground), three soil organic matter pools (active, slow and passive) of C and N content, and a pool for available inorganic N. A full description of the model is given elsewhere (Comins & McMurtrie, 1993; Medlyn *et al.,* 2000; McMurtrie *et al.,* 2001); here we focus on the modifications made to allow simulation of the ORNL FACE experiment.

Following McMurtrie *et al.* (2001), we assumed that the N:C ratio of substrate entering the three soil pools increases linearly with increasing inorganic N until a critical value of inorganic N (N_{crit}), after which the N:C ratio is constant. The minimum and maximum values of the three soil pool N:C ratios were taken from Nalder & Wein (2006).

Observations at ORNL FACE experiment site have suggested that the increased demand for available N at elevated [CO_2] was satisfied through a deeper exploration of soil profile by increased root biomass (Norby & Iverson, 2006). In the previous version of G'DAY there was no dependence of N uptake on root biomass. Here, we modified the N uptake formulation and assumed that N taken up by the plant is a saturating function of root biomass, as in Dewar & McMurtrie (1996a, b):

$$N_u = \lambda_u N_{ino} \frac{C_r}{\left(C_r + k_r\right)} \tag{1}$$

where N_u (kgN m^{-2}) is the root N uptake, λ_u (yr^{-1}) is a constant, N_{ino} (kgN m^{-2}) is the available inorganic N, C_r (kgC m^{-2}) is the root C and k_r (kgC m^{-2}) is the value of C_r at which 50% of N_{ino} is taken up.

No effect of soil moisture on the system was considered.

The original G'DAY model employed a very simple representation of LUE, assuming it depended only on leaf N concentration and atmospheric [CO_2] (Comins & McMurtrie,

1993). To better capture effects of daily environmental variability, and to take advantage of extensive physiological data available from the experiment, we incorporated a new sub-model MATE (Model Any Terrestrial Ecosystem, McMurtrie *et al.,* in preparation) to estimate daily LUE. This model integrates the leaf-level photosynthetic rate obtained from the Farquhar & von Caemmerer (1982) model over the whole canopy, using an algorithm proposed by Sands (1995) (see Appendix).

The original version of G'DAY was developed for evergreen forest stands. To apply the model to a deciduous stand, such as the Sweetgum plantation at Oak Ridge, it was necessary to add phenological development and modify the representation of C and N allocation processes. In deciduous trees, plant growth processes (i.e. photosynthesis, autotrophic respiration, etc.) are not constant throughout the year but take place during the growing season, defined as the time between bud burst and senescence. To adjust the model to reproduce deciduous stand dynamics, we needed to identify the growing season and to relate plant growth processes to this time interval. Here we made use of the time course of the measured LAI to indentify the growing season period. We set the first day of growing season (and therefore of photosynthesis, autotrophic respiration, etc.) as the first day of the year for which LAI is greater than zero. We then set the senescence period as beginning on the day LAI reaches its maximum value (LAI_{max}) and ending on the day LAI returns to zero. LAI values vary slightly year to year without any clear trend over time and with no apparent effect of treatment (Norby *et al.,* 2001, 2010).

While photosynthesis was simulated throughout the growing season on a daily time step, allocation of C and N to the different plant pools required calculations on both a daily and an annual time step. During each year, we assumed that all C assimilated during the growing season was placed in a storage pool. At the end of the year, the stored C was divided between foliage, wood (stem, branch and coarse root) and fine root. The absolute amount of C allocated to foliage was held constant (H_f), as indicated by the data (Norby *et al.,* 2005, 2008), and the remaining amount of C was divided between wood (H_w) and roots (H_r) according to annual C allocation coefficients estimated from measurements (Norby *et al.,* 2005, 2008). The values of H_f and the H_w:H_r ratio were found to be different for ambient and elevated treatments (see Table 1).

In the same way, we assumed that all N taken up by roots during the year, plus that retranslocated from senescent foliage, was placed in a storage pool and then divided between the three plant pools at the end of each year. The fraction of stored N going to each pool was estimated from leaf N concentration. We assumed that the N:C ratio of

fine roots is constant (0.2 $kgN\ kgC^{-1}$), as indicated by measurements (Norby *et al.,* 2008), and that the N:C ratios of the mobile and structural components of wood N are functions of leaf N concentration (Medlyn *et al.,* 2000). If U_N is the total amount of N available for the plant at the end of the year (root uptake plus leaf re-translocation), we have:

$$U_N = N_f + N_w + N_r = v_f H_f + v_f v_{wnewb} H_w + v_r H_r \tag{2}$$

so that:

$$v_f = \frac{U_N - v_r H_r}{H_f + v_{wnewb} H_w} \tag{3}$$

where v_f and v_r ($kgN\ kgC^{-1}$) are the leaf and fine root N:C ratios, and v_{wnewb} (dimensionless) is the slope of the relationship between the N:C ratio of new wood and the N:C ratio of foliage.

The amounts of N allocated to the plant pools (A_i) are then given by:

$$A_f = v_f H_f \tag{4}$$

$$A_{wm} = \left(v_{wnewb} - v_{wmb}\right) v_f H_w \tag{5}$$

$$A_{ws} = v_{wmb} v_f H_w \tag{6}$$

$$A_r = v_r H_r \tag{7}$$

where v_{wmb} (dimensionless) is the slope of the relationship between the N:C ratio of the non-structural component of the new wood and the N:C ratio of foliage. Measurements indicate there is no N retranslocation from wood (Norby, personal communication).

The C and N in each of these plant storage pools were then allocated during the next year to foliage, wood and fine root pools on a daily time step. The daily allocation of C and N to foliage during the growing season was assumed to follow the time course of LAI:LAI$_{max}$ ratio. The daily amounts of C and N lost by litterfall during senescence were also determined from the time course of LAI:LAI$_{max}$ ratio. In this way we have a constant value of leaf N:C ratio throughout the year. The daily allocation of C to wood was also set to follow the time course of LAI:LAI$_{max}$ ratio during the growing season, while the amount of N allocated daily to the mobile and structural pools of wood was proportional to leaf N concentration as in Medlyn *et al.* (2000). Mortality of trees was estimated from data and set equal to 1.1 and 1.2 % for ambient and elevated CO_2

respectively (Norby, personal communication). The daily allocation of C and N to fine root pools was assumed to occur at a constant rate over the full year, as were the C and N losses, so that root N concentration was kept constant throughout the year as indicated by measurements (Norby & Iversen, 2006).

There is evidence from measurements of changes in SLA over time (Norby, personal communication). To investigate the importance of these changes, we incorporated two alternative hypotheses about SLA into the model. In the first hypothesis, SLA is held constant and assumed not to differ between elevated and ambient treatments. In the second hypothesis, SLA is assumed to vary with leaf N concentration (Norby *et al.,* 2010). The relationship between SLA and leaf N concentration was obtained by plotting measured data from both treatments (Norby, personal communication). We obtained:

$$SLA = 514.3v_f + 8.2 \tag{8}$$

where SLA is in $m^2\,kgC^{-1}$ and v_f in $kgN\,kgC^{-1}$.

3.3.5 MODEL SIMULATIONS

Simulations for the Oak-Ridge site were run in three steps. In an attempt to initialize the values of C and N soil pools at the beginning of the treatments (1998), we simulated the site history. Before the plantation was established in 1988 the site was a grassland, so we first ran a simulation with the model parameterized for a grassland, using a 30 year meteorological data sequence from the site, repeated until pools equilibrated. We then ran a second simulation, initialised with the soil pool values obtained from the grassland equilibrium simulation, to reproduce the development of the young sweetgum stand from 1988 to 1997.

At this point we ran the main simulation for the mature stand. To better fit the shape of measured values of NPP (Norby *et al.,* 2008, 2010) we changed the initial values of soil C pools and soil organic and inorganic N pools. For this purpose we kept the C:N ratios of soil pools equal to the values obtained from the young stand simulation and changed initial soil C values and initial soil inorganic N value. We ran four simulations, two for the elevated plots and two for the ambient plots. The two simulations for each treatment related to the assumption of constant or variable SLA.

A sensitivity analysis of simulated NPP to the main parameters characterizing plant physiology at ambient and elevated [CO_2] was also carried out. Starting from the baseline case of simulated NPP at ambient [CO_2], with constant SLA, four different simulations were run. We first ran the model for elevated [CO_2] but parameterized

exactly as for the ambient [CO_2] simulation. The second simulation was run as previously, but using the root life span parameter estimated for the elevated [CO_2] treatment. In the third simulation we changed also the NPP:GPP ratio to that estimated for the elevated [CO_2] treatment. Finally the estimated annual C wood allocation for the elevated [CO2] treatment was added to the previous simulation.

We ran the simulations on a daily time step, using the daily meteorological data of air and soil temperature, relative humidity, precipitation, photosynthetically active radiation and atmospheric [CO_2] measured for the period 1999-2007 at the plots (http://public.ornl.gov/face/index.shtml). The annual values of N deposition, equally distributed throughout the year, were measured at Walker Branch Watershed station, Anderson County, Tennessee, USA (http://nadp.sws.uiuc.edu/).

3.3.6 MODEL PARAMETERISATION

We parameterized the model for Oak Ridge using experimental data. Where parameter values were not available from measurements, we took values from the literature. Some parameters were found to differ between elevated and ambient treatments, while others were the same. A list of all parameters used is given in Table 1.

The grass to-equilibrium simulation was parameterized with default values typical for grassland, taken from Pepper *et al.* (2005). For the young forest stand we initialised the stand with values found in literature and used the same parameter values as for the main ambient simulation.

The daily values of LAI (total one-sided leaf area per unit ground area) used to estimate the allocation coefficients for foliage and wood, were calculated for each plot for every day of the growing season from measurements of absorbed PAR and litterfall as described in Norby *et al.* (2003).

The value of N uptake rate coefficient λ_u was tuned to obtain a good match between the net primary production of the last year of the simulation for the young stand and the measured value at the beginning of the treatment. The nitrogen uptake parameter, k_r (Eqn (1)) was estimated from values of N uptake and root biomass measured at both ambient and elevated [CO_2] from 2001 to 2007 (Fig. 1).

3.3.7 STATISTICAL ANALYSIS

The correspondence between simulated and observed data was tested applying linear regression analysis. The simultaneous F-test for slope = 1 and intercept = 0 was

performed to identify bias (Dent & Blackie, 1979; Mayer *et al.,* 1994). Small values of F-test mean that the model is a good fit. Model performance in reproduced observed data was also tested using the model efficiency index (EF, Loague & Green, 1991; Mayer & Butler, 1993). This test directly relates model predictions to observed data and represents an assessment of how well the 1:1 line explains the variance in simulated vs observed correlation. The goodness of model fit decreases as the EF value decreases from one (perfect fit), with negative values representing a poor fit.

3.4 RESULTS

3.4.1 AMBIENT [CO_2]

SIMULATION WITH CONSTANT SLA

Figure 2 shows simulated and observed net primary production, leaf N concentration, SLA and LAI of the ambient [CO_2] grown plots over time. In this simulation SLA is kept constant and equal to 24.2 m^2 kgC^{-1}. The initial values of soil N (organic and inorganic) and C pools are reported in Table 2.

Observed NPP in the ambient [CO_2] treatment increased from 0.83 kgC m^{-2} yr^{-1} in 1998 to a plateau of around 1 kgC m^{-2} yr^{-1} in 2001-2003. From 2003 to 2006 NPP decreased progressively to a lower value of productivity than at the beginning of experiment, with a stabilisation in 2007 (Fig. 2a, 3a).

Modelled NPP follows a very similar trend to observed NPP for the ambient [CO_2] treatment. It increases during the first two years, from 0.83 kgC m^{-2} yr^{-1} in 1998 to 1.06 kgC m^{-2} yr^{-1} in 2000, and then decreases progressively to the value of 0.72 kgC m^{-2} yr^{-1} in 2007 (Fig. 2a). In Figure 4a we plot observed NPP against simulated NPP. Although there is some scatter of data around the regression line (R^2=0.62, Fig. 4a, Table 3), the agreement between observed and simulated data seems very good. This is also confirmed by the low F-test result and the positive EF index value (F=0.02, EF=0.62, Table 3).

Simulated leaf N concentration increases from 0.04 kgN kgC^{-1} in 1998 to 0.05 kgN kgC^{-1} in 1999. From 1999 it decreases steadily, reaching the value of 0.025 kgN kgC^{-1} in 2007 (Fig. 2b). The peak in leaf N concentration in 1999 is the consequence of the higher amount of N taken up during 1998 and allocated to foliage in 1999, since the amount of C allocated to the foliage system is constant. Comparing observed and simulated leaf N concentration, it is evident that, although the regression indicates a quite good correlation between observed and simulated data (R^2=0.69, Fig. 4b, Table

3), there is a low correspondence of data with the line 1:1 (F=68.3 p<0.001, EF=-5.44, Table 3). While the model underestimates low leaf N concentration values, it slightly overestimates high values (Fig. 4b).

Figures 2c and 2d show a good accordance between simulated and observed SLA and LAI. This agreement is expected, because SLA and foliage biomass are held constant at measured average values in this simulation.

SIMULATION WITH VARIABLE SLA

Figure 3 shows simulated and observed net primary production, leaf N concentration, SLA and LAI of the plots treated with ambient [CO_2] over time. In this simulation SLA is variable as in Eqn (8). The initial values of soil N (organic and inorganic) and C pools are reported in Table 2.

As for the case with SLA constant, simulated NPP increases initially, from 0.83 kgC m^{-2} yr^{-1} in 1998 to 1.01 kgC m^{-2} yr^{-1} in 2000. After 2000, simulated NPP decreases progressively to the value of 0.69 kgC m^{-2} yr^{-1} in 2007 (Fig. 3a).

Comparing observed NPP with simulated NPP it emerges that, although the best fit line does not follow the 1:1 line as well as the case assuming constant SLA (Fig. 4), the smaller scatter of data and the statistical analysis (R^2=0.81, EF=0.76, Fig. 4c, Table 3) indicate that the model is slightly better at predicting NPP with the assumption of variable SLA than in the previous case.

After increasing from 0.04 kgN kgC^{-1} in 1998 to 0.08 kgN kgC^{-1} in 1999, simulated leaf N concentration decreases almost constantly, reaching the value of 0.017 kgN kgC^{-1} in 2007 (Fig. 3b). The peak in leaf N concentration in 1999 is the consequence of the higher amount of N taken up during 1998 and allocated to foliage in 1999, since the amount of C allocated to the foliage system is constant. Comparing observed and simulated leaf N concentration, it is evident that, although the regression indicates a quite good correlation between observed and simulated data (R^2=0.68, Fig. 4d, Table 3), there is no correspondence of data with the line 1:1 (F=393 p<0.001, EF=-36.7, Table 3). The model predicts a much wider range of leaf N concentration values than that observed (Fig. 4d).

Simulated SLA and LAI, being linear functions of leaf N concentration (Eqn (8)), show the same trend as leaf N concentration. They increase from 1998 to 1999, and then decrease progressively over time, in disagreement with observed data (Fig. 3c and 3d).

3.4.2 ELEVATED [CO_2]

SIMULATION WITH CONSTANT SLA

Figure 5 shows simulated and observed net primary production, leaf N concentration, SLA and LAI of the enriched CO_2 plots over time. In this simulation, SLA is kept constant and equal to 24.2 $m^2\,kgC^{-1}$. The initial values of soil N (organic and inorganic) and C pools are the same as in the case of ambient [CO_2] and SLA constant (Table 2).

Observed NPP increased until 2001, when it reached a maximum value of 1.38 $kgC\,m^{-2}\,yr^{-1}$. After 2001, NPP decreased progressively to 0.7 $kgC\,m^{-2}\,yr^{-1}$ in 2006, a lower value than at the beginning of experiment. This low productivity was also measured during 2007 (Fig. 5a and 6a).

Simulated net primary production shows a decrease in 1999 followed by an increase during 2000, reaching a value slightly higher than that of 1998. From 2000 NPP decreases progressively from 1.09 $kgC\,m^{-2}\,yr^{-1}$ to 0.68 $kgC\,m^{-2}\,yr^{-1}$ in 2007 (Fig. 5a). Simulated NPP is always lower than observed NPP. This difference is maximum for the period from 2001 to 2004 and decreases at the end of simulated time interval. The regression curve is not parallel to the 1:1 line, there is some scatter around the line (R^2=0.61, Fig. 7a) and EF is negative (Table 3).

After an increase in 1999, simulated leaf N concentration decreases almost steadily, reaching the value of 0.015 $kgN\,kgC^{-1}$ in 2007 (Fig. 5b). The regression line of observed against simulated leaf N concentration does not follow the 1:1 line, showing a poor correspondence between simulated and observed data, confirmed by the high F-test result and negative EF value (F=105 p<0.001, EF=-9.8, Fig. 7b, Table 3). While the model underestimates low leaf N concentration values, it slightly overestimates high values (Fig. 7b).

As expected, Figures 5c and 5d show a good accordance between simulated and observed SLA and LAI.

SIMULATION WITH VARIABLE SLA

Figure 6 shows simulated and observed net primary production, leaf N concentration, SLA and LAI of the enriched CO_2 plots over time. In this simulation, SLA is variable as in Eqn (8). The initial values of soil N (organic and inorganic) and C pools are the same as in the case of elevated [CO_2] and SLA constant (Table 2).

Simulated net primary production decreases from 1998 to 1999 and increases during 2000. From 2000 onwards, NPP decreases progressively to 0.64 kgC m^{-2} yr^{-1} in 2007 (Fig. 6a).

Although the shape of the time course of simulated NPP is similar to that of observed NPP, the simulated values are always lower than observed values. The regression curve is not parallel to the 1:1 line and EF is negative (Table 3, Fig. 7c).

Simulated leaf N concentration, as in the previous cases, increases during the first year of simulation, from 0.036 kgN kgC^{-1} in 1998 to 0.07 kgN kgC^{-1} in 1999. From 1999 leaf N concentration decreases progressively over time, reaching the value of 0.008 kgN kgC^{-1} in 2007 (Fig. 6b). Comparing observed and simulated leaf N concentration, it is evident that, there is no correspondence of data with the line 1:1 (F=407 p<0.001, EF=-41.2, Table 3, Fig. 7d): the model, once more, predicts a much wider range of leaf N concentration values than that observed. (Fig. 7d).

Simulated SLA and LAI, being linear functions of leaf N concentration (Eqn (8)), show the same trend as leaf N concentration. They increase from 1998 to 1999, and then decrease progressively, in disagreement with observed data (Fig. 6c, 6d).

3.4.3 NITROGEN UPTAKE, INORGANIC NITROGEN AND ROOT BIOMASS

Figure 8 shows simulated and observed N uptake and root biomass and simulated soil available inorganic N of the ambient and enriched CO_2 plots over the period 1998 to 2007. The initial values of soil N (organic and inorganic) and C pools are reported in Table 2. Given the better fit of model results assuming a constant SLA value, these simulations were run just with this assumption.

Observed N uptake by the root system increases during the first half of the experiment and then progressively decreases with some fluctuations at both ambient and elevated atmospheric [CO_2]. Observed N uptake is higher at elevated [CO_2] than at ambient [CO_2] during all years of the experiment but the difference between the two treatments is not constant: it reaches its maximum during the first years of the experiment (+50%) and then decreases to 10% at the end of the experiment (Fig. 8a).

In contrast, simulated N uptake from soil by the root system decreases progressively at both ambient and elevated atmospheric [CO_2]. At elevated [CO_2], N uptake stabilises during the last years of simulation, but at ambient [CO_2], N uptake shows a slight increase during this period (Fig. 8a).

This decrease in simulated N uptake over time can be attributed to a decrease in soil inorganic N availability. Inorganic N markedly decreases during 1998 – 2000 and then stabilises (Fig. 8c). Although inorganic N is always higher for ambient than for elevated $[CO_2]$, the trend in inorganic N is the same for both treatments.

Observed root biomass is consistently higher at elevated $[CO_2]$ than at ambient $[CO_2]$. The difference between the two treatments in maximum during the third year of the experiment and than decreases progressively (Fig. 8b). Simulated root biomass is predicted to increase from 1998 to 2000 and then decrease, for both treatments. The initial increase is much higher in the elevated $[CO_2]$ treatment (Fig. 8b).

3.4.4 SENSITIVITY ANALYSIS

Figure 11 shows the sensitivity analysis of NPP (kgC m^{-2} yr^{-1}) for the main parameters characterizing plant physiology at ambient and elevated $[CO_2]$. The NPP values represent the output of four different simulations run using the model parameterized as for the case at ambient $[CO_2]$ and then changing one by one parameters to values from the elevated $[CO_2]$ treatment: first the root life span, then the NPP:GPP ratio and finally the annual C wood allocation. Values of simulated NPP are from 1998 to 2007. The simulations were run under the assumption that SLA is constant.

The analysis shows that when the model is parameterized as for the ambient $[CO_2]$ treatment but running with high $[CO_2]$, it predicts an increase in NPP of about 13% compared to the NPP at ambient $[CO_2]$. This increase in NPP is similar when root life span is changed to the high $[CO_2]$ value, but decreases slightly to10% when the NPP:GPP ratio for elevated $[CO_2]$ is used. However, when the annual C wood allocation for elevated $[CO_2]$ is used, the model predicts a decrease in NPP compared to ambient $[CO_2]$ (-2%). The model is thus very sensitive to this parameter. This sensitivity occurs because a higher fraction of C going to the root system (1-aw, Table1) translates to a higher amount of N going to the root system (N:C ratio is constant, see material and methods, the model) and therefore a smaller amount of N going to the above ground plant fraction than for the ambient $[CO_2]$ case.

3.5 DISCUSSION

3.5.1 AMBIENT $[CO_2]$ SIMULATIONS

The model predicts an overall decline over time of sweetgum plantation net primary production at ambient $[CO_2]$, in good agreement with data. The decline over time of

modelled NPP is a consequence of the decrease in leaf N concentration, that in turn is a consequence of reduced soil N availability. This is in agreement with the results from several studies which show a progressive N limitation of the system regardless of the initialization state of the model (Comins & McMurtrie, 1993; McMurtrie *et al.,* 2000, 2001; Medlyn *et al.,* 2000).

Annual plant available N is given by the sum of N taken up by roots and that retranslocated within the foliage, both of which decrease over time. The reduction in modelled root N uptake is a consequence of a movement of C and N into long residence time SOM pools, which causes a decrease in net N mineralization. Retranslocation is assumed to be a constant fraction of N resorbed from foliage before the fall, so the decrease in retranslocation over time is a consequence of decreased amount of N in foliage. This simulated decrease in leaf N concentration, despite the initial increase and the following faster decrease, is in reasonable agreement with the observed data trend (Norby *et al.,* 2010).

The reduction in modelled leaf N concentration, after the marked increase during 1999, is observed in simulations with both SLA assumptions, constant and variable. However, under the assumption of variable SLA, the maximum value for leaf N concentration is considerably higher than with the constant SLA assumption, and the decrease over time is faster. Although modelled NPP with this assumption seems to better fit measured NPP, we consider the assumption of variable SLA definitely incorrect because of the large difference between observed and modelled leaf N concentration.

Although there is evidence of a positive correlation between SLA and leaf N concentration across different species (Reich *et al.,* 1999) and observations from Oak Ridge experiment show a decrease in N concentration and SLA, it may be that the relationship between these two parameters is poor within a single species. A full investigation of the relationship between leaf N concentration, SLA and photosynthesis would be desirable.

Currently it is assumed that the maximum rate of electron transport (J_{max}) and the maximum rate of Rubisco activity (V_{cmax}) vary linearly with leaf N per unit area, based on photosynthesis measurements from August 1999 and 2007 (see appendix). However, changes in SLA might modify these relationships (Peterson *et al.,* 1999). A path analysis of the dependence of J_{max} and V_{cmax} on leaf N per unit area, leaf N per unit mass and SLA, based on all photosynthesis measurements would be useful to determine how SLA should be incorporated into the photosynthesis model. If J_{max} and

V_{cmax} are related to SLA as well as to leaf N, that may change the outcome when SLA is variable.

3.5.2 EFFECT OF ELEVATED [CO_2]

The model fails to simulate the initial stimulatory effect of elevated [CO_2] on forest production. The model predicts reduced net primary production at elevated [CO_2] (Fig. 9), in complete disagreement with experimental data, which show an average enhancement of NPP by about 23% (Norby *et al.,* 2005). The model results also differ from previous model studies showing enhanced NPP in response to elevated [CO_2] (Comins & McMurtrie, 1993; Kirschbaum *et al.,* 1994, 1998; McMutrie & Comins, 1996; Medlyn & Dewar, 1996; McMurtrie & Dewar, 1999; Medlyn *et al.,* 2000, Pepper *et al.,* 2005, Pepper *et al.,* 2007).

The main reason for this model outcome is the simulated decrease in leaf N concentration. The leaf N concentration in elevated [CO_2] is lower than in ambient [CO_2], not just because of the dilution effect due to higher canopy biomass in elevated [CO_2], but also because the increase in root biomass results in a decreased fraction of N uptake being allocated to foliage. Since modelled N uptake is similar in ambient and elevated [CO_2], and total N allocated to wood plus root is higher in elevated [CO_2], the N allocated to foliage is reduced. This is also confirmed by the sensitivity analysis of NPP to the main parameters characterizing plant physiology at ambient and elevated [CO_2]. This analysis shows that the lowest response of NPP at elevated [CO_2] is correlated to the highest fraction of C allocated to the root system (1-aw, Table 1) and then to a higher amount of N (Fig. 11) allocated to this pool compared at elevated [CO_2]. This reduction in N allocated to foliage enhances the dilution effect and decreases leaf N concentration to such a degree that it offsets the direct stimulatory effect of increased atmospheric [CO_2] on photosynthesis.

To test this conclusion, we forced the model with measured leaf N concentrations. We first used observed ambient leaf N concentration and different [CO_2], and then used observed ambient and elevated leaf N concentration and different [CO_2]. We found that, on average, NPP at elevated [CO_2] was higher than NPP at ambient [CO_2] for both these sets of simulations (around +15% for the first and +6% for the second set). Although the increase in production simulated by the model in these two cases was less than the value of 23±2 % estimated by Norby *et al.* (2005), the outcome highlights that the main problem with current simulations is the strong decrease in leaf N concentration.

The model allocates a greater amount of N to root system as a consequence of increased fine root production in elevated [CO_2], which is in accordance with experimental evidence (Norby & Collen, 2006; Iversen *et al.,* 2008). Despite the increase in root biomass at elevated [CO_2], the model simulates similar N uptake by roots in ambient and elevated [CO_2], in disagreement with data (Norby *et al.,* 2005; Finzi *et al.,* 2007). This discrepancy may be caused by an incorrect formulation of the N uptake function or by an incorrect parameterization of the N uptake function used in the paper (Eqn (1)), where N_{ino} represents the total amount of inorganic N in the soil available for plant uptake, and root biomass represents an assessment of the portion of soil volume explored, in which N_{ino} is contained. Therefore increased root biomass translates into increased soil volume explored and increased N uptake. This relationship between root biomass and N uptake continues until the whole soil volume has been explored. With the current parameterization of this function (Table 1), almost all soil volume is already explored by roots at ambient [CO_2]. Therefore, although fine root biomass at elevated [CO_2] increases to more than twofold fine root biomass at ambient [CO_2], soil volume explored only increases from 90% to 94-95% (Fig. 10). This small increase in percentage of explored soil volume does not result in increased N uptake, because inorganic N decreases more rapidly in elevated than in ambient [CO_2].

We examined the model sensitivity to the parameterisation of this function. Using a higher value of the k_r coefficient used in N uptake function, we found a stronger effect of fine root increase on N uptake. However, we also found a decrease in N uptake and in NPP compared with the previous case due to a decrease in the percentage of soil volume explored by root (from 39% at minimum to 55% at maximum root biomass for k_r = 0.15). Although an increase in λ_u can counter-act the decrease in N uptake at high k_r, since λ_u is a multiplicative term in the N uptake formulation, this analysis does not add any further information about the reasons for the disagreement between observed and simulated N uptake in relation to root biomass.

Given the parameterization of root N uptake formulation and the consequent lack of effect of increased root biomass, the main reason for the decrease in simulated N uptake is the decrease in inorganic N, which occurs because of a reduction in net N mineralization. This outcome disagrees with experimental data, which shows an increase in N uptake and a constant N mineralization rate at elevated [CO_2] (Finzi *et al.* 2007). In simulations at both [CO_2] levels, net N mineralization decreases as a consequence of a shift of soil N towards long residence time soil organic matter pools. This shift happens mainly during first 5 years of simulation, after which the system

equilibrates. To explore this result, we ran further simulations with the values of this equilibrium state as initial values for C and N soil pools. Using the new initial values, the model simulated lower values for NPP and N uptake. Running several simulations for different initial values of soil pools, we found that the magnitude and the overall time course of model outputs are very sensitive to the initial condition of simulation, expecially regarding the active and slow soil pools, while they seem to be insensitive to initial values of the passive soil pool (Fig. 12). Further studies on a new improved formulation for N availability and root N uptake as a function of depth is needed to improve the model's ability to simulate outcomes of this experiment.

Although the initial values of the total soil C and N used in the simulations are lower than the measured values, that has no effect on the results of our analysis. This is because the passive soil pool has a turnover life of 200-1500 years (Parton *et al,.* 1987), considerably longer than the 10 years of simulation. Therefore allocating a higher amount of C and N to this pool would increase the soil C and N amounts towards the measured value without changing the results of the analysis. This is also confirmed by the sensitivity analysis of the model for different initial values of soil pools (Fig. 12).

Estimation of appropriate initial conditions and parameter values pose challenging problems when applying models to experimental data, especially with respect to soil organic matter models. Initial values for soil pools are not directly observable, and it is difficult to partition C and N between the different model soil pools. Inappropriate adjustment of these values can lead to important errors in model results (Bruun & Jensen, 2002; Orescanin *et al.,* 2009; Yeluripati *et al.,* 2009). Using inverse or statistical analysis techniques can help to select more appropriate parameters to optimize the model and to estimate the distribution of SOM and N within soil pools (Bruun & Jensen, 2002; Calvello & Finno, 2004; Wang *et al.,* 2006; Orescanin *et al.,* 2009; Yeluripati *et al.,* 2009).

To improve the ability of the model to simulate the Oak Ridge FACE experiment, we would focus on (i) a better formulation for N availability and the N uptake as function of depth and (ii) initialization of soil C and N pools, potentially using model inversion.

3.6 CONCLUSIONS

Soil N availability is likely to play a crucial rule in determining forest ecosystem response to increasing atmospheric [CO_2]. To reliably predict forest ecosystem

responses to future atmospheric $[CO_2]$, it is important to understand and represent as well as possible feedbacks between the C and N cycles.

In this paper we compared the integrated plant-soil G'DAY model, which reproduces the dynamic of C and N in forest ecosystems with data from the closed-canopy forest FACE experiment at Oak Ridge National Laboratory (ORNL).

The model successfully reproduced the observed decline in NPP at ambient $[CO_2]$. However, it failed to reproduce the observed effect of elevated $[CO_2]$ on forest production, simulating net primary production values that were lower than at ambient atmospheric $[CO_2]$. In accordance with observations, it predicted a decline in observed leaf N concentration at both $[CO_2]$, but the magnitude of the predicted decline was much greater than observed.

Although the model failed to simulate the observed transient $[CO_2]$ response in this experimental system, the model did capture the observed longer-term reduction in the $[CO_2]$ effect on productivity, indicating that it is still valid to use the model for simulating long-term responses to gradually increasing $[CO_2]$.

From the analysis of the mechanisms involved, it emerged that likely reasons for the model failures were (i) initialization of soil pools, and (ii) incorrect parameterization and/or formulation of the soil N uptake as function of depth. These values are not directly observable and their estimation poses a challenging problem. Further studies applying inverse techniques can help to improve simulation results.

Table 3-1 Parameter values used in the model for the sweetgum (*Liquidambar styraciflua* L.) plantation at 1988 at the Oak Ridge National Environmental Research Park, TN.

Symbol & Definition		Value aCO₂	Value eCO₂	Units	Reference
W	C content of dry matter	0.467		-	This study
F	NPP/GPP ratio	0.52	0.49	-	Norby et al. 2002
K	Light extinction factor	0.5		-	Comins & McMurtrie 1993
γ_r^{-1}	Constant root life span	0.783	1.1640	yr	This study
T	Soil texture parameter	0.5		-	Comins & McMurtrie 1993
f_BR	Fraction of wood carbon in branches (average for American conifers)	0.0941		-	This study
f_CR	Fraction of wood carbon in coarse roots (average for American conifers)	0.071	0.070	-	This study
N_{crit}	Critical inorganic N value for soil variable N/C scenario	0.002		kgN m⁻²	McMurtrie et al. 2001
v_{f_min}	minimum foliar N/C	0.0151	0.0121	kgN kgC⁻¹	This study
v_u	N/C ratio for surface structural litter	1/150		kgN kgC⁻¹	Comins & McMurtrie 1993
v_v	N/C ratio for soil structural litter	1/150		kgN kgC⁻¹	Comins & McMurtrie 1993
v_{newa}	Intercept of relationship between v_{new} and v_f	0		kgN kgC⁻¹	This study
v_{newb}	Slope of relationship between v_{new} and v_f	0.0736	0.0827	-	This study
v_{swa}	Intercept of relationship between v_{sw} and v_f	0		kgN kgC⁻¹	This study
v_{swb}	Slope of relationship between v_{sw} and v_f	0.0559	0.0629	-	This study
v_{a_max}	Maximum for newly active soil pool SOM	1/8		kgN kgC⁻¹	Nalder & Wein 2006
v_{a_min}	Minimum for newly active soil pool SOM	1/16		kgN kgC⁻¹	Nalder & Wein 2006
v_{s_max}	Maximum for newly slow soil pool SOM	1/12		kgN kgC⁻¹	Nalder & Wein 2006
v_{s_min}	Minimum for newly slow soil pool SOM	1/40		kgN kgC⁻¹	Nalder & Wein 2006
v_{p_max}	Maximum for newly passive soil pool SOM	1/6		kgN kgC⁻¹	Nalder & Wein 2006
v_{p_min}	Minimum for newly passive soil pool SOM	1/20		kgN kgC⁻¹	Nalder & Wein 2006
λ_{loss}	Constant rate of N lost through leaching and gaseous emission	0.3899	0.32	yr⁻¹	This study
λ_u	Constant rate of N uptake by plant roots	9.7	6.0	yr⁻¹	This study
k_r	Value of root C at which 50% of the available N is taken up	0.0105		kgC m⁻²	This study
Lfl	Lignin/biomass ratio in leaf litter	0.279	0.286	-	This study
Lrl	Lignin/biomass ratio in root litter	0.127+0.393* Lfl		-	Newman & Hart 2006
H_f	NPP allocated to leaf annually	0.216	0.233	kgC m⁻²yr⁻¹	This study
aw	$H_w/(H_w+H_r)$	0.85	0.73	-	This study

Table 3-2 Initial values for C (in kg C m^{-2}) and N (inorganic and organic, in kg N m^{-2}) in soil, for ambient and elevated [CO_2] simulations, with constant and variable SLA.

	Constant SLA	Variable SLA
C in the active pool (kg Cm^{-2})	0.43	0.65
C in the slow pool (kg Cm^{-2})	2.1	0.7
C in the passive pool (kg Cm^{-2})	0.5	0.6
N in the active pool (kg Nm^{-2})	0.039	0.059
N in the slow pool (kg Nm^{-2})	0.086	0.029
N in the passive pool (kg Nm^{-2})	0.05	0.06
N in the inorganic soil pool (g Nm^{-2})	0.623	0.628

Table 3-3 Statistical analysis of model validation results. Linear regression parameters, simultaneous F-test for slope = 1 and intercept = 0 and model efficiency index (EF) were reported for both *NPP* and leaf N concentration (v_f), under the assumptions of constant and variable SLA, at both ambient and elevated [CO_2].

Treatment	Assumption	Variable	Linear regression			F[a]	EF
			R^2	Slope	Intercept		
Ambient	Constant SLA	*NPP*	0.62	1.05	-0.05	0.02[ns]	0.62
		v_f	0.69	0.25	0.02	68.3[3]	-5.44
	Variable SLA	*NPP*	0.81	1.25	-0.2	0.81[ns]	0.76
		v_f	0.68	0.12	0.03	393[3]	-36.8
Elevated	Constant SLA	*NPP*	0.61	1.27	0.01	8.5[1]	-0.34
		v_f	0.65	0.23	0.02	105[3]	-9.8
	Variable SLA	*NPP*	0.82	1.24	0.02	17.8[2]	-0.08
		v_f	0.64	0.11	0.03	407[3]	-41.2

[a] Simultaneous F-statistic for slope = 1 and intercept = 0.

[ns] not significant; [1] $P < 0.025$; [2] $P < 0.0025$; [3] $P < 0.001$;

Figure 3-1 Observed root C (C_r) : root N uptake (N_u) ratio vs C_r for both the ambient and elevated [CO_2] treatments from 2001 to 2007. The k_r parameter (Eqn (1)) is equal to the half-saturation (Half sat) constant in the Michaelis-Menten equation relating N_u to C_r (regression line, Eqn (1)), where $MaxN_u$ is the maximum value of available N that the root system can uptake and both ambient and elevated [CO_2] data are considered together.
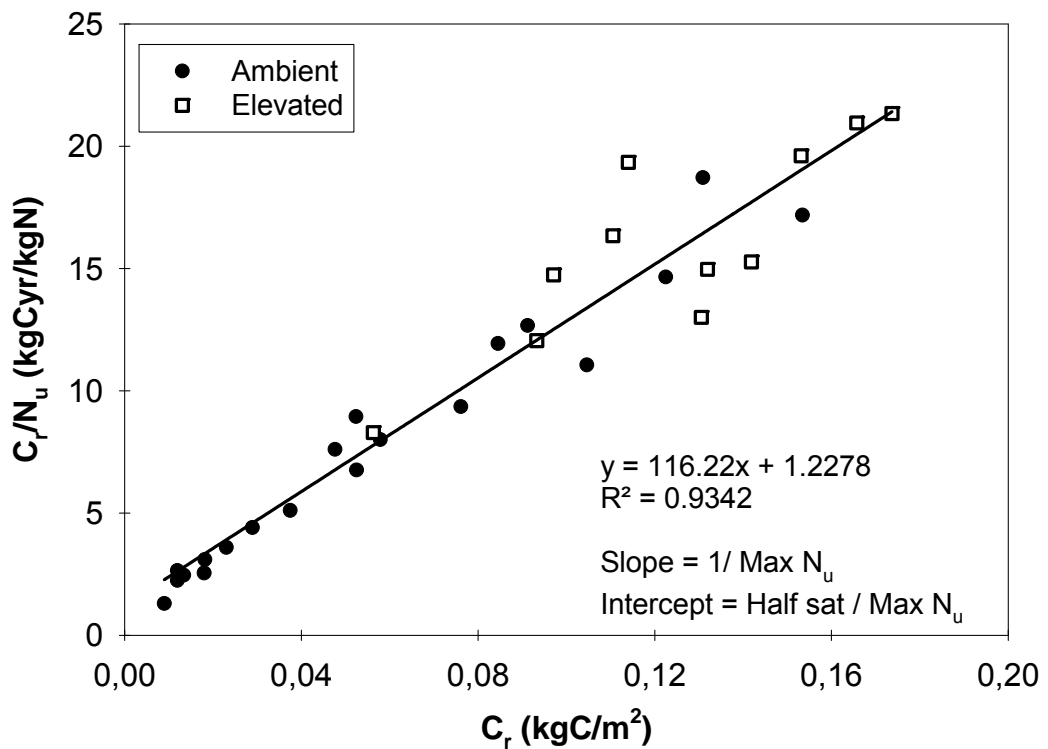
Figure 3-2 NPP, leaf N concentration, SLA and LAI simulated and observed ± SEM, from 1998 to 2007, for the ambient [CO_2] treatment. The simulation was run under the assumption that SLA is constant and equal to 24.2 $m^2 kgC^{-1}$.
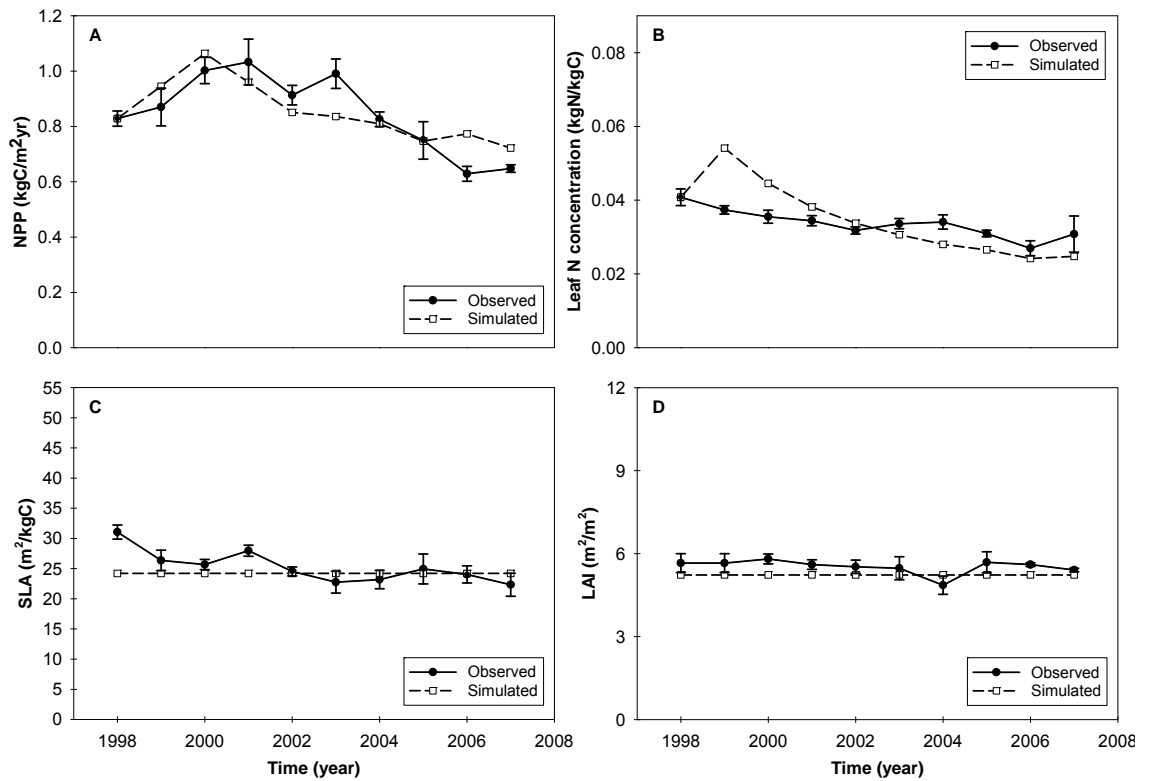
Figure 3-3 NPP, leaf N concentration, SLA and LAI simulated and observed ± SEM, from 1998 to 2007, for the ambient [CO_2] treatment. The simulation was run under the assumption that SLA varies according to Eqn (8).
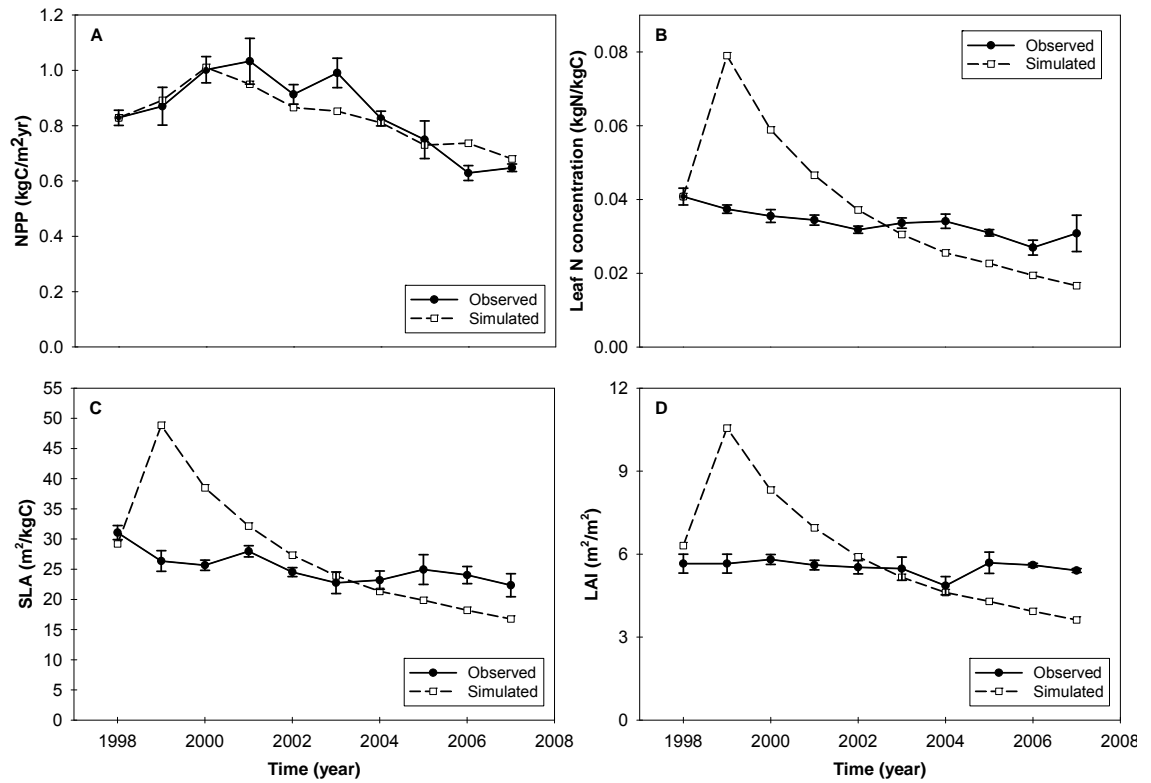
Figure 3-4 Net primary production and leaf N concentration observed against net primary production and leaf N concentration predicted by the model regression scatter plots in the two cases of constant (a, b) and variable (c, d) SLA, for the ambient [CO_2] treatment. Regression equations are shown in the graphs.
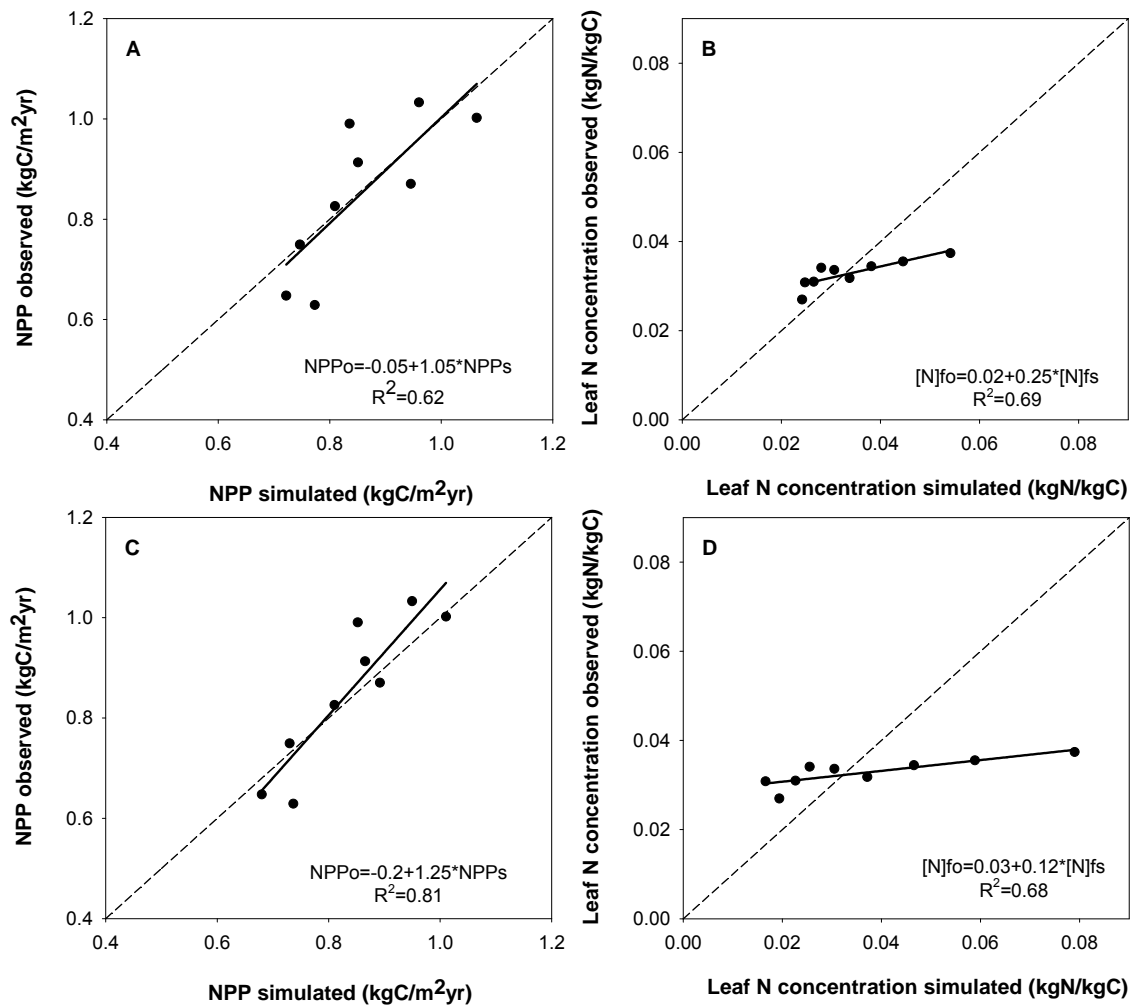
Figure 3-5 NPP, leaf N concentration, SLA and LAI simulated and observed ± SEM, from 1998 to 2007, for the elevated [CO_2] treatment. The simulation was run under the assumption that SLA is constant and equal to 24.2 $m^2 kgC^{-1}$.
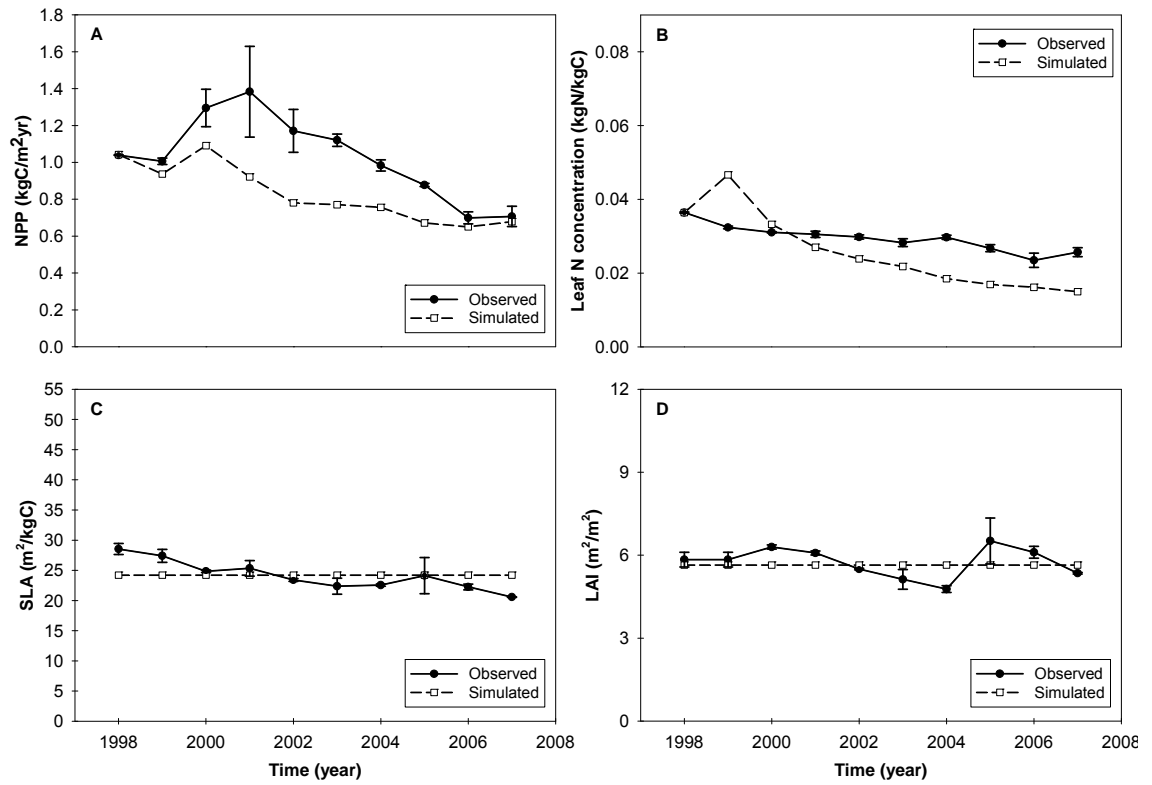
Figure 3-6 NPP, leaf N concentration, SLA and LAI simulated and observed ± SEM, from 1998 to 2007, for the elevated [CO_2] treatment. The simulation was run under the assumption that SLA varies according to Eqn (8).
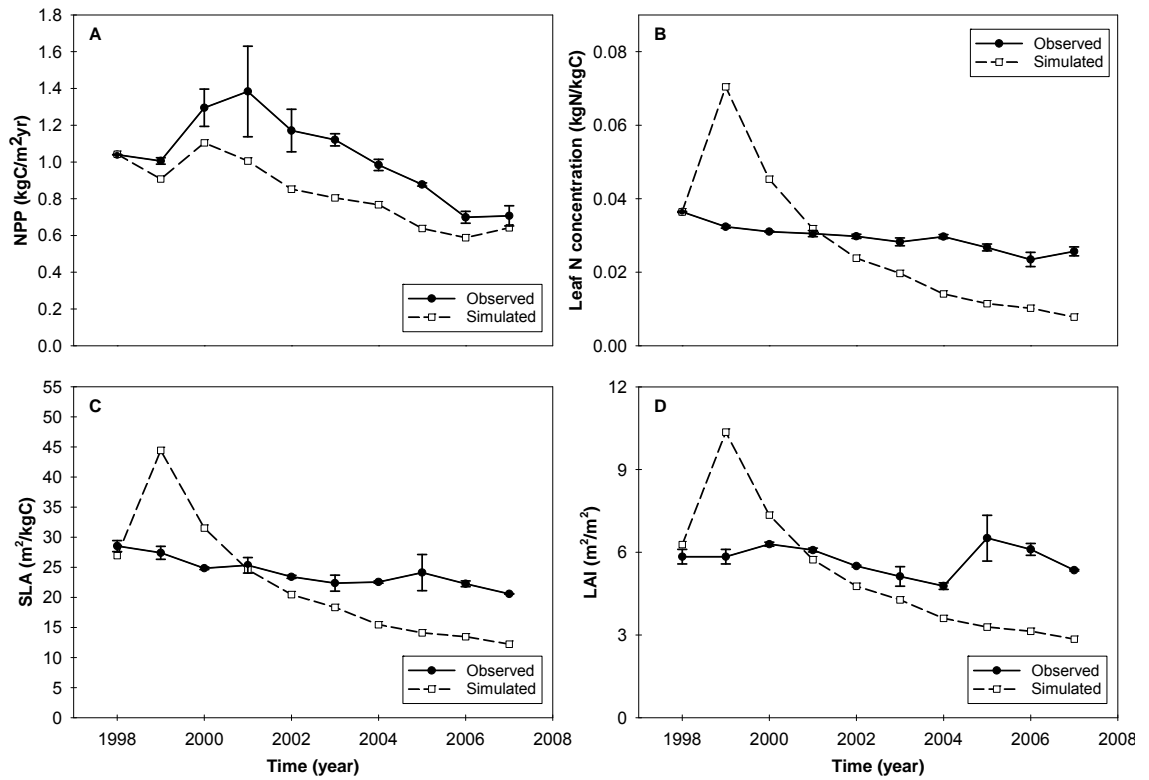
Figure 3-7 Net primary production and leaf N concentration observed against net primary production and leaf N concentration predicted by the model regression scatter plots in the two cases of constant (a, b) and variable (c, d) SLA, for the elevated [CO_2] treatment. Regression equations are shown in the graphs.
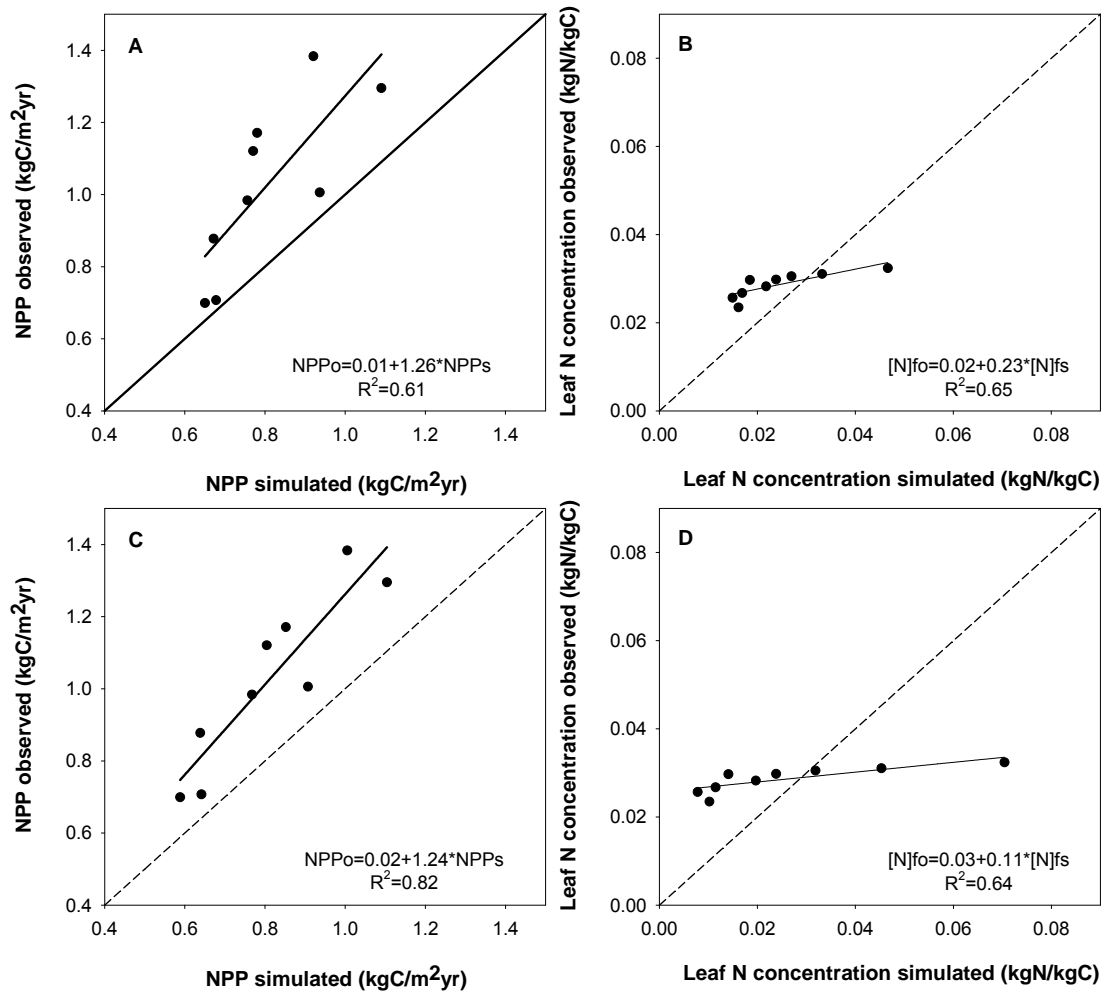
Figure 3-8 Simulated and observed (± SEM) N uptake (A) and root biomass (B) and simulated inorganic N available for plants (C) from 1998 to 2007, for the ambient and elevated [CO_2] treatments. The simulation was run under the assumption that SLA is constant and equal to 24.2 $m^2 kgC^{-1}$.
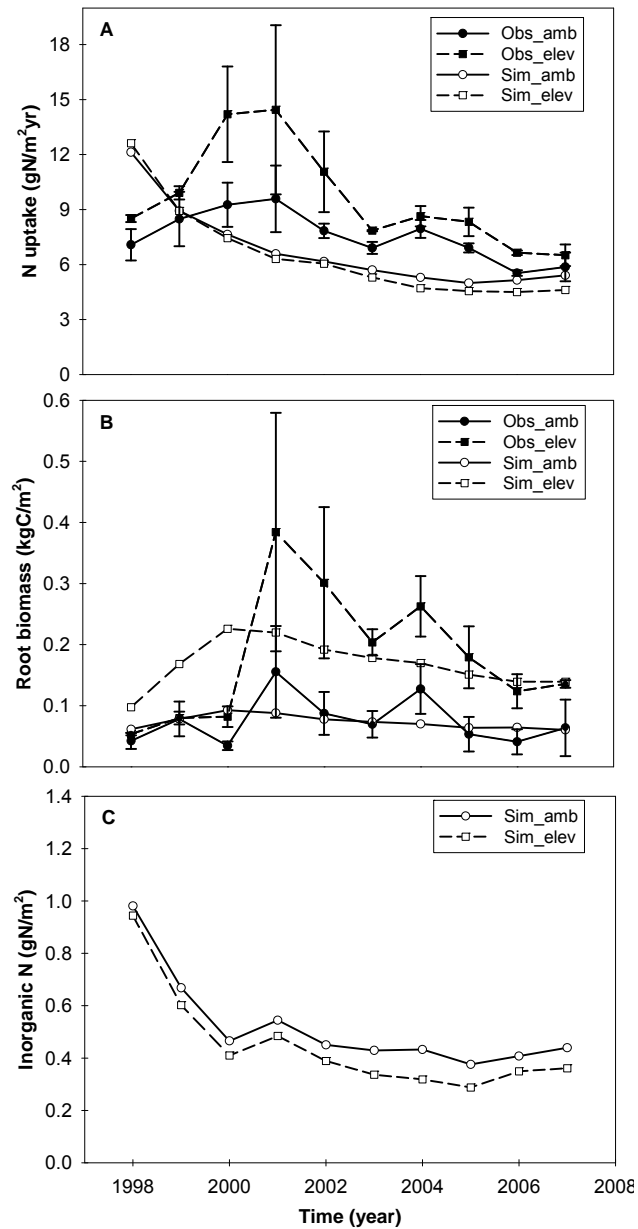
Figure 3-9 Simulated and observed elevated to ambient [CO_2] treatment ratios for net primary production (A) and leaf N concentration (B) from 1998 to 2007. The simulation was run under the assumption that SLA is constant and equal to 24.2 $m^2 kgC^{-1}$.
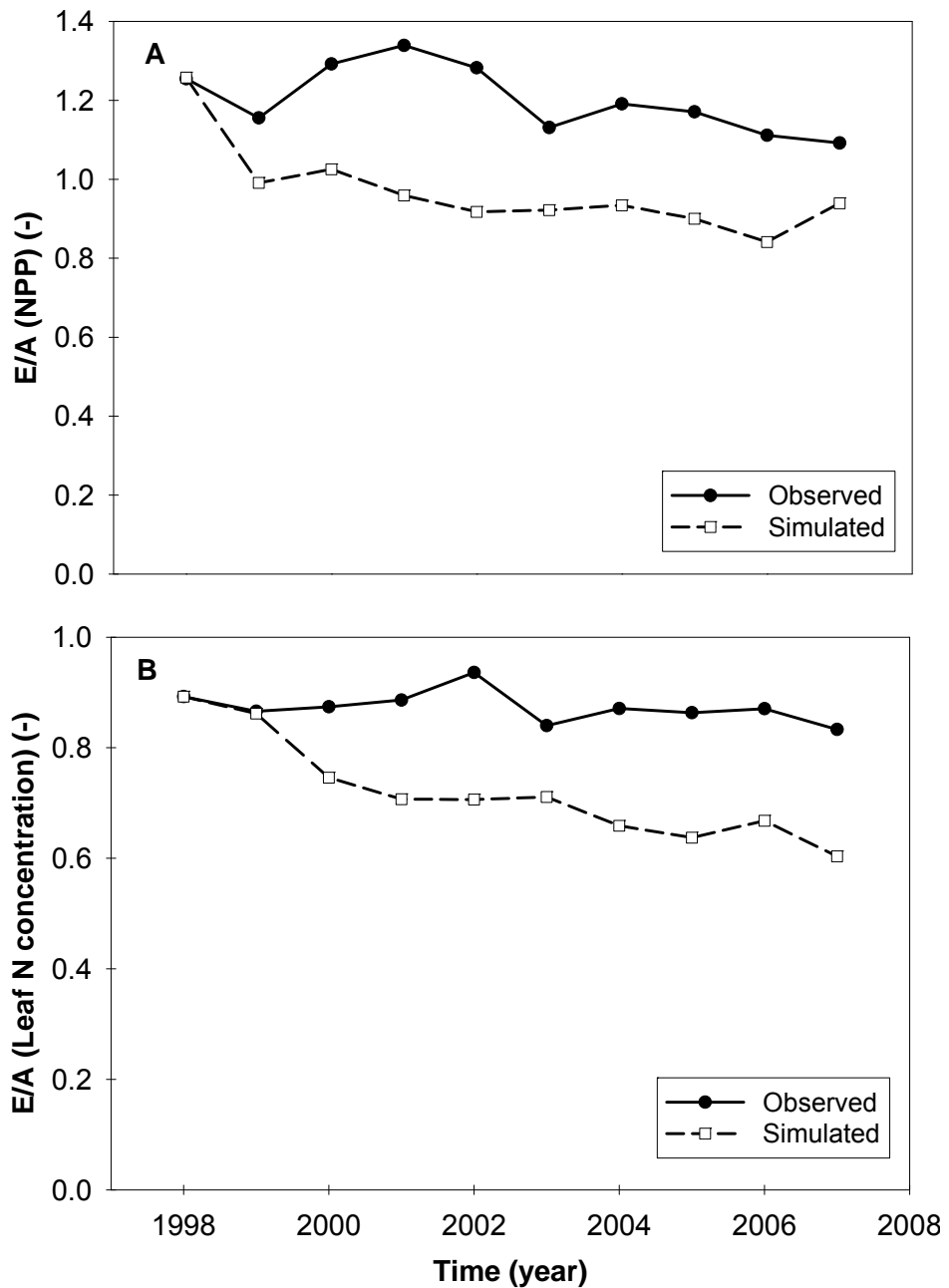
Figure 3-10 Simulated N uptake (A) and $C_r{:}(C_r{+}k_r)$ ratio (B) vs root C (C_r) for the ambient and elevated [CO_2] treatments. The simulation was run under the assumption that SLA is constant and equal to 24.2 $m^2 kgC^{-1}$.
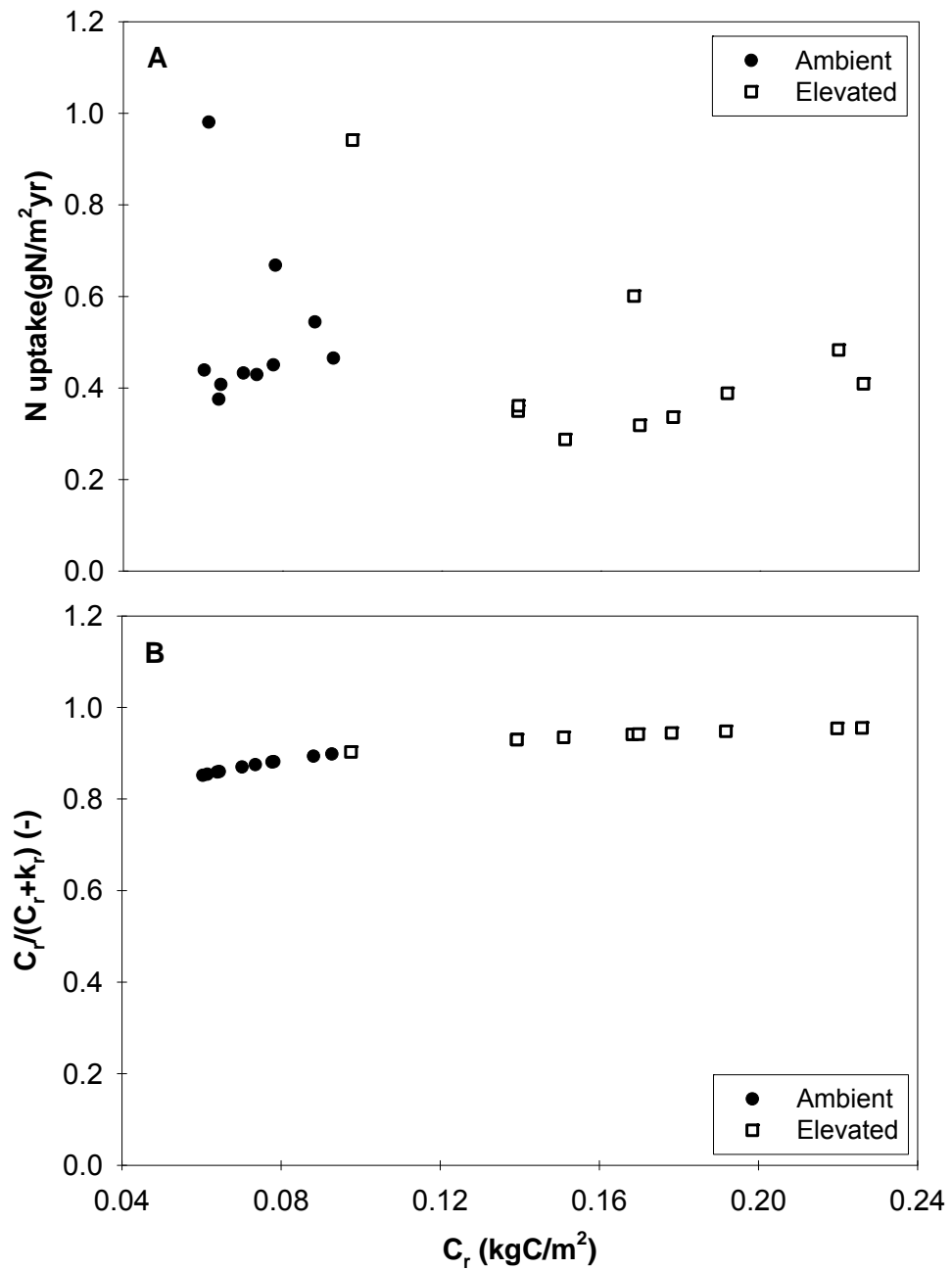
Figure 3-11 Sensitivity analysis of NPP (kgC m^{-2} yr^{-1}) for the main parameters characterizing plant physiology at ambient and elevated [CO_2]. The NPP values represent the output of four different simulations run using the model parameterized as for the case at ambient [CO_2] (NPPa) and then changing one by one parameters to values from the elevated [CO_2] treatment (NPPe): first the [CO_2] (+[CO_2]e), than the root life span (+g_r), than the NPP:GPP ratio (+f) and finally the annual C wood allocation (+a_w). Values of simulated NPP are from 1999 to 2007. The simulations were run under the assumption that SLA is constant and equal to 24.2 m2 kgC-1.
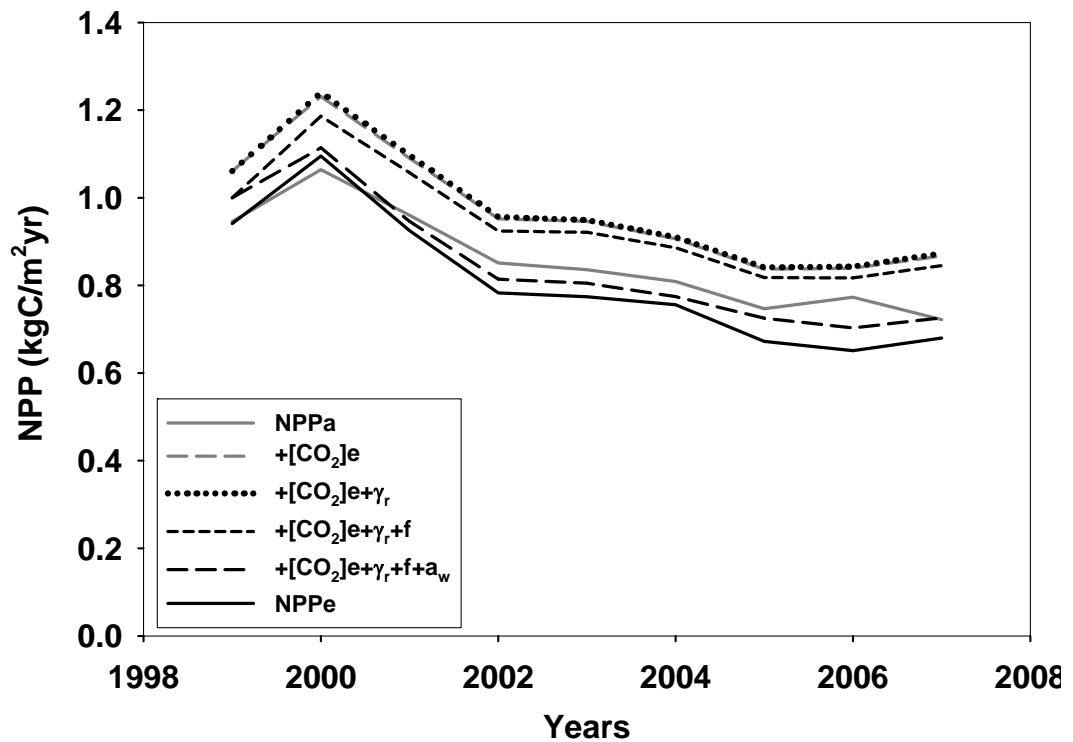
Figure 3-12 Sensitivity analysis of NPP (kgC m^{-2} yr^{-1}) for different soil pool initializations.The NPP values represent the output of six different simulations run using the model parameterized at ambient [CO_2]. In the first simulation the model was initialized using the soil C and N (organic and inorganic) pools values reported in Table 3.2 (base). In the other simulations the model was initilizated using a doubled amount of both C and N in the active, slow and passive and inorganic N pools, respectively. Finally a simulation was run initializing the model with a doubled amount of C and N in all the soil pools. Values of simulated NPP are from 1998 to 2007. The simulations were run under the assumption that SLA is constant and equal to 24.2 m2 kgC-1.
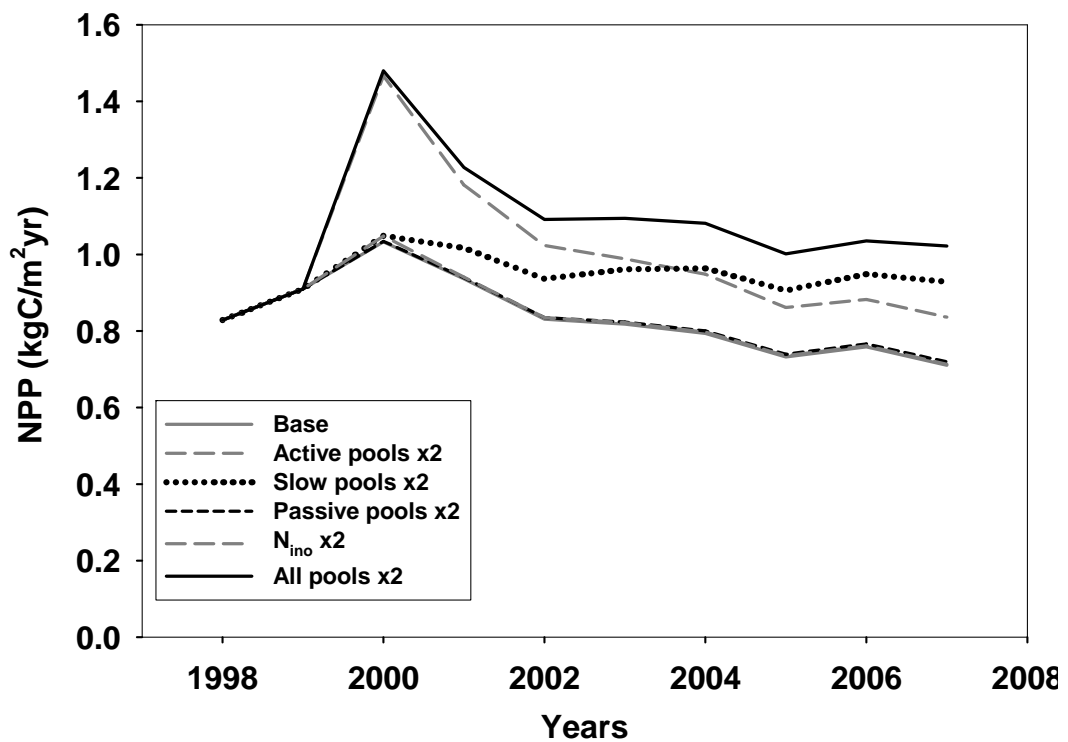
3.7 APPENDIX: THE MATE MODEL

The MATE (Model Any Terrestrial Ecosystem) model (McMurtrie, in preparation) was used in this study as the light use efficiency (LUE) sub-model in G'DAY. MATE calculates daily values of LUE as a function of the environmental factors (temperature, atmospheric [CO_2], soil moisture, vapour pressure deficit) and physiological factors (leaf nitrogen concentration) that limit photosynthesis. In the original version of G'DAY, these effects were represented by multiplier functions, with values between 0 and 1, applied directly to gross primary production.

In MATE, the Farquhar & von Caemmerer (1982) model is used to calculate the rate of leaf photosynthesis. The rate of photosynthesis is given by the minimum of the rate of carboxylation when Rubisco activity is limiting (A_c) and that when RUBP regeneration is limiting (A_j):

$$A = \min(A_c, A_j) \tag{A1}$$

Here A_c (μmol CO_2 m^{-2} s^{-1}) is given by

$$A_c = V_{cmax} \frac{\left(C_i - \Gamma^*\right)}{\left(C_i + k_m\right)} \tag{A2}$$

where V_{cmax} (μmol CO_2 m^{-2} s^{-1}) is the maximum rate of Rubisco activity, C_i (μmol mol^{-1}) is the intercellular [CO_2], Γ^* (μmol mol^{-1}) is the CO_2 compensation point in the absence of mitochondrial respiration, and K_m (μmol mol^{-1}) is the effective Michaelis-Menten constant for Rubisco catalytic activity for CO_2; while A_j (μmol CO_2 m^{-2} s^{-1}) is given by

$$A_j = \frac{J_{max}}{4} \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} \tag{A3}$$

where J_{max} (μmol CO_2 m^{-2} s^{-1}) is the maximum rate of electron transport.

V_{cmax}, J_{max} and K_m have temperature dependences as given by Medlyn *et al.* (2002a and b).

J_{max25} and Vc_{max25}, the values of J_{max} and V_c at 25°C, are functions of leaf nitrogen content per area (v_f', gN m^{-2}):

$$J_{max25} = av_f' + b \tag{A4}$$

$$V_{cmax25} = cv_f' + d \tag{A5}$$

where a, b, c, d are empirical parameters that were fitted to site specific data.

C_i, the intercellular $[CO_2]$, is calculated as the product of C_a (atmospheric $[CO_2]$, μmol mol^{-1}) and the ratio of C_i:C_a. The C_i:C_a ratio is estimated by combining the Ball Berry model (Eqn (A6)) for stomatal conductance, with the equation for CO_2 diffusion into the leaf (Eqn (A7)), as follows. According to the Ball-Berry model,

$$g_{sw} = g_i f_w A \frac{RH}{C_a} \tag{A6}$$

where g_s (mol m^{-2} s^{-1}) is the stomatal conductance, g_i (dimensionless) is a slope parameter, f_w (dimensionless) is a factor describing the effect of soil moisture on stomatal conductance, with values from zero to 1, A (μmol CO_2 m^{-2} s^{-1}) is the rate of leaf photosynthesis and RH (dimensionless) is the relative humidity. The diffusion equation can be expressed as:

$$A = \frac{g_{sw}}{1.6}\left(C_a - C_i\right) \tag{A7}$$

where 1.6 accounts for the different diffusivities of water vapour and CO_2 in air. Combining Eqns (A6) and (A7) gives the following expression for the $C_i : C_a$ ratio:

$$\frac{C_i}{C_a} = 1 - \frac{1.6}{g_i f_w RH} \tag{A8}$$

The value for leaf photosynthesis estimated through this set of equations is then integrated using the method of Sands (1995) to estimate the daily value of LUE integrated over the canopy.

Briefly, using Sands' (1995) model, the LUE is given by:

$$LUE = \alpha \pi g \tag{A9}$$

where α (mol mol^{-1}) is the quantum efficiency of photosynthesis and g is given by the integral (Sands 1995):

$$g\left(q,\theta\right) = \frac{2}{\pi} \int_0^{\pi/2} \frac{2\,q\,sinx}{1 + q\,sinx\sqrt{\left(1+q\,sinx\right)^2 - 4\,\theta\,q\,sinx}} \tag{A10}$$

where θ (dimensionless) is the shape of light-response curve and q is given by

$$q = \frac{\pi\,k\,\alpha\,Q\,\gamma}{2\,h\,A} \tag{A11}$$

where k (dimensionless) is the light extinction coefficient; Q (MJ m^{-2} day^{-1}) is total daily irradiance above the canopy; γ (μmol PAR MJ^{-1}) converts total solar irradiance into photosynthetically active radiation (PAR) and h (s day^{-1}) is the day-length.

All the calculations to estimate LUE are performed twice, using mean meteorological data for the morning and afternoon periods, and the average of the morning and afternoon LUE is used in the simulation to calculate canopy photosynthesis.

3.8 REFERENCES

Ainsworth EA, Long SP (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 properties and plant production to rising CO_2. *New Phytologist*, **165**, 351-372.

Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO_2]: mechanisms and environmental interactions. *Plant, Cell, Environment*, **30**, 258-270.

Bruun S, Jensen LS (2002) Initialisation of soil organic matter pools of the Daisy model. *Ecological Modelling*, **153(3)**, 291-295.

Calvello M, Finno RJ (2004) Selecting parameters to optimize in model calibration by inverse analysis. *Computers and Geotechnics*, **31(5)**, 410-424.

Canadell JG, Le Quéré C, Raupach MR *et al.* (2007) Contributions to accelerating atmospheric CO_2 growth economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866-18870.

Canadell JG, Pataki DE, Gifford R *et al.* (2007) Saturation of the Terrestrial Carbon Sink. In: Canadell JG, Pataki D, Pitelka L (Eds), Terrestrial Ecosystems in a Changing World, The IGBP Series, Springer-Verlag, Berlin Heidelberg, New York, 59-78.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behaviour of plant-soil models. *Ecological Application*, **3(4)**, 666-681.

Dent JB, Blackie MJ (1979) *Systems Simulation in Agriculture*. Applied Science Publishers, London, UK.

Dewar RC, McMurtrie RE (1996a) Analytical model of stemwood growth in relation to nitrogen supply. *Tree Physiologist* **16**, 161-171.

Dewar RC, McMurtrie RE (1996b) Sustainable stemwood yield in relation to the nitrogen balance of forest plantations: a model analysis. *Tree Physiologist* **16**, 173-182.

Farquhar GD, Von Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In Physiological plant ecology II: water relations and carbon assimilation. Edited by Lange O, Noble P, Osmond CB, Zieger. Encycl. Plant Physiol. 12B, 549-587.

Finzi AC, Norby RJ, Calfapietra C *et al.* (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences*, **104(35)**, 14014-14019.

Hendrey GR, Ellsworth DS, Lewin KF, Gross C (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biology*, **5**, 1738-1756.

Hyvönen R, Ågren GI, Linder S *et al.* (2007) 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 Phytologist*, **173**, 463-480. [IPCC] Intergovernmental Panel on Climate Change (2007) Fourth Assessment Report: Climate Change 2007. Cambridge (United Kingdom): Cambridge University Press.

Iversen CM, Ledford J, Norby RJ (2008) CO_2 enrichment increases carbon and nitrogen input from fine roots in deciduous forest. *New Phytologist*, **179**, 837-847.

Iversen CM (2010) Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist*, **186**, 346-357.

Kirschbaum MUF, King DA, Comins HN *et al.* (1994) Modelling forest response to increasing CO_2 concentration under nutrient-limited conditions. *Plant, Cell, Environment*, **17**, 1081-1099.

Kirschbaum MUF, Medlyn BE, King DA *et al.* (1998) Modelling forest-growth response to increasing CO_2 concentration in relation to various factors affecting nutrient supply. *Global Change Biology*, **4**, 23-41.

Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Global Change Biology*, **13**, 2089-2109.

Loague K, Green RE (1991) Statistical and graphical methods for evaluating solute transport models: Overview and application. *Journal of Contaminant Hydrology*, **7**, 51-73.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience,* **54**, 731-739.

Luo YQ, Field CB, Jackson RB (2006a) Does nitrogen constrain carbon cycling, or does carbon input stimulate nitrogen cycling? *Ecology*, **87**, 3-4.

Luo YQ, Hui DF, Zhang DQ (2006b) Elevated CO_2 stimulates net accumulation of carbon and nitrogen inland ecosystems: a meta-analysis. *Ecology*, **87**, 53-63.

Mayer DG, Butler DG (1993) Statistical validation. *Ecological Modelling*, **68**, 21-32.

Mayer DG, Stuart MA, Swain AJ (1994) Regression of Real-World Data on Model Output: An Appropriate Overall Test of Validity. *Agricultural Systems*, **45**, 93-104.

McKinley DC, Romero JC, Hungate BA, Drake B, Megonigal JP (2009). Does deep soil N availability sustain long-term ecosystem response to elevated CO_2? *Global Change Biology*, **15**, 2035-2048.

McMurtrie RE, Comins HN (1996) The temporal response of forest ecosystems to doubled atmospheric CO_2 concentration. *Global Change Biology*, **2**, 49-57.

McMurtrie RE, Comins HN (1999) Ecosystem modelling of the CO_2-response of forest on sites limited by nitrogen and water. In: *Carbon dioxide and environmental stress* (eds Luo Y, Mooney HA), pp 347-369. Academic Press, San Diego, California.

McMurtrie RE, Dewar RC, Medlyn BE, Jeffrey MP (2000) Effects of elevated [CO_2] on forest growth and carbon storage: a modelling analysis of the consequences of changes in litter quality/quantity and root exudation. *Plant and Soil*, **224**, 135-152.

McMurtrie RE, Medlyn BE, Dewar RC (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 Physiology*, **21**, 831-839.

Medlyn BE, Dewar RC (1996) A model of the long-term response of carbon allocation and productivity of forests to increased CO_2 concentration and nitrogen deposition. *Global Change Biology*, **2**, 367–376.

Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys MP (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research*, **30**, 873-888.

Medlyn BE, Loustau D, Delzon S (2002a) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Aït.). *Plant, Cell and Environment*, **25**, 1155-1165.

Medlyn BE, Dreyer E, Ellsworth D et al (2002b) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell and Environment*, **25**, 1167-1179.

Nalder IA, Wein RW (2006) A model for the investigation of long-carbon dynamics in boreal forests of western Canada I. Model development and validation. *Ecological Modelling*, **192**, 37-66.

Norby RJ, Todd DE, Fults J, Johnson DW (2001) Allometric determination of tree growth in a CO_2-enriched sweetgum stand. *New Phytologist*, **150**, 477–487.

Norby RJ, Hanson PJ, O'Neill EG *et al.* (2002) Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. *Ecological Applications*, **12**, 1261-1266.

Norby RJ, Sholtis JD, Gunderson CA, Jawdy SS. (2003) Leaf dynamics of a deciduous forest canopy: no response to elevated CO_2. *Oecologia*, **136(4)**, 574-584.

Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neil EG (2004) Fine-root production dominates response of a deciduous forest at atmospheric CO_2 enrichment. *PNAS*, **101(26)**, 9689-9693.

Norby RJ, De Lucia EH, Gielen B *et al.* (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *PNAS*, **102(50)**, 18052-18056.

Norby RJ, Iversen CM (2006) Nitrogen uptake, distribution, turnover, and efficiency of use in a CO_2-enriched sweetgum forest. *Ecology*, **87**, 5-14.

Norby, R.J., and M.L. Tharp (2008) ORNL FACE Leaf Area Index (LAI) Data. Carbon Dioxide Information Analysis Center *(http://cdiac.ornl.gov)*, U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, TN.

Norby RJ, Warren MJ, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO_2 enrichment of forest productivity constrained by limited nitrogen availability. *PNAS*, **107(45)**, 19368-19373.

Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature*, **411**, 469-472.

Orescanin B, Rajkovic B, Zupanski M, Zupanski D (2009) Soil model parameter estimation with ensemble data assimilation. *Atmospheric Science Letters*, **10**, 127-131.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173-1179.

Parton WJ, Scurlock JMO, Ojima DS *et al.* (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, **7**, 785-809.

Pepper DA, Del Grosso SJ, McMurtrie RE, Parton WJ (2005) Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO_2], temperature and nitrogen input. *Global Biogeochemical Cycles*, **19**, GB1004, doi:10.1029/2004GB002226.

Pepper DA, Eliasson PE, McMurtrie RE, Corbeels M, Ågren GI, Strömgren M, Linder S (2007) Simulated mechanisms of soil N feedback on the forest CO_2 response. *Global Change Biology*, **13**, 1265-1281.

Peterson A, Ball JT, Luo Y et al. (1999) The photosynthesis – leaf nitrigen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biology*, **5**, 331-346.

Pregitzer KS, Zak DR, Maziasz J, DeForest J, Curtis PS (2000) Interactive effects of atmospheric CO_2 and soil-N availability on fine roots of Populus tremuloides. *Ecological Applications*, **10**, 18-33.

Reich PB, Grigal DF, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*, **78(2)**, 335-347.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80(6)**, 1955-1969.

Reich PB, Hobbie SE, Lee T *et al.* (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO_2. *Nature*, **440**, 922-925.

Sands PJ (1995) Modelling canopy production II. From Single-leaf Photosynthetic Parameters to Daily to Canopy Photosynthesis. *Australian Journal of Plant Physiology*, **22**, 601-14.

Santantonio D (1989) Dry-matter partitioning and fine-root production in forests -- new approaches to a difficult problem. In: Pereira, J.S., Landsberg J.J. (Eds), Biomass Production by Fast-Growing Trees, Kluwer Academic Publishers, Norwell, MA, 57-72.

Sholtis JD, Gunderson CA, Norby RJ, Tissue DT (2004) Persistent stimulation of photosynthesis by elevated CO_2 in a sweetgum (*Liquidambar styraciflua*) forest stand. *New Phytologist*, **162**, 343-354.

Sitch S, Huntingford C, Gedney N *et al.* (2008) Evaluation of the terrestrial carbon cycle future plant geography and climate-carbon cycle feedbacks using five Dynamics Global Vegetation Models (DGVMs). *Global Change Biology*, **14**, 2015-2039.

Stover DB, Day FP, Butnor JR *et al.* (2007) Effect of elevated CO_2 on coarse-root biomass in Florida scrub detected by ground-penetrating radar. *Ecology*, **88**, 1328-1334.

van Miegroet H, Norby RJ, Tschaplinski TJ (1994) Nitrogen fertilization strategies in a short-rotation sycamore plantation. *Forest Ecology and Management,* **64**, 13–24.

Wang YP, McMurtrie R, Medlyn B, Pepper D (2006) Issues in modelling plant ecosystem responses to elevated CO_2: interactions with soil nitrogen. In: Morison, J.I.L., Morecroft M.D. (Eds), Plant Growth and Climate Change, Blackwell Publishing LtD, Oxford, UK, 165-186kl..

Wullschleger SD, Gunderson CA, Hanson PJ, Wilson KB, Norby RJ (2002) Sensitivity of stomatal and canopy conductance to elevated CO_2 concentration – interacting variables and perspectives of scale. *New Phytologist*, **153**, 485-496.

Yaluripati JB, van Oijen M, Wattenbach M, Neftel A, Ammann A, Parton WJ, Smith P (2009) Bayesian calibration as a tool for initialising the carbon pools of dynamic soil models. *Soil Biology & Biochemistry*, **41**, 2579-2583.

CHAPTER 4

Comparative effect of historical changes in N deposition, Atmospheric [CO$_2$] and climate on a maritime pine plantation: an ecosystem model based analysis

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4.1 ABSTRACT

During recent decades forest growth rates have increased in several European regions. Increasing atmospheric $[CO_2]$, temperature, nitrogen (N) deposition and changes in management practices have been suggested as potential causes for this increase. However, in order to predict future dynamics of forest growth and carbon (C) sequestration it is of fundamental importance to understand the specific role of these factors and their interactions.

We investigated the combined effect of recent changes in forest growth environmental drivers (atmospheric $[CO_2]$, N deposition, and climate variables) on a maritime pine stand in France. To this end, we used a modified version of the Generic Decomposition And Yield (G'DAY) forest C-N cycling model, which incorporates explicitly N deposition effects on forest ecosystems, coupled to the Model Any Terrestrial Ecosystem (MATE) model, which describes the effects of atmospheric $[CO_2]$ and meteorological data (temperature, radiation, relative humidity and rain) on light use efficiency. The coupled model was parameterized using data from a maritime pine (*Pinus pinaster* Ait.) stand in "Le Bray", France. The confounding effects of age on tree growth and C sequestration were removed by averaging across simulated forest chronosequences.

We found that enhanced N availability could explain the observed increase in forest growth rates. Specifically, increasing N deposition was found to greatly increase N availability both through direct canopy uptake, which produces a short term stimulation effect on forest growth, and through stimulation of net soil N mineralization, which produces a long term effect on forest growth. In addition, increased temperature was found to enhance N availability, but at a lower rate than N deposition. Finally the observed increase in atmospheric $[CO_2]$ was found to be important only when N was not limiting, i.e. in recent decades.

4.2 INTRODUCTION

During recent decades, forest growth rates have increased across Europe (Spiecker *et al.,* 1996, 1999; Ciais *et al.,* 2008; Kahle *et al.,* 2008; Bedison & McNeil, 2009; Thomas *et al.,* 2010). Ciais *et al.* (2008) estimated that net primary production of European forest, on average, has increased by 67% over the last 50 years.

There are several possible causes for this increase: changes in forest management practices; climate change, including increased temperature and longer growing seasons; increased atmospheric CO_2 concentration ($[CO_2]$); and increased nitrogen (N)

deposition may all have had a role in the increase in forest growth rate (Spiecker *et al.,* 1996, 1999; Ciais *et al.,* 2008). The factors act individually and also interactively. To date, it is not clear how much each of these factors contributes to the increase in forest growth rate. However, it is important to quantify the role of each of these factors in order to be able to predict how growth rate might change in future (Spiecker *et al.,* 1996; Ciais *et al.,* 2008; Canadell *et al.,* 2007a,b).

Improvements in forest management practices, such as new regeneration methods, changes in species mixtures, and modifications to tending, thinning and harvesting regimes, aim to maximise wood production while maintaining soil and water protection function. These improvements have resulted in enhanced site productivity in recent years (Spiecker, 1999; Ciais *et al.,* 2008; Kahle *et al.,* 2008).

 Annual average land temperature over Europe up to 2008 has increased by about 1.3°C above pre-industrial levels (EEA 2009). Increases in mean air temperature affect forest productivity by increasing plant photosynthetic and autotrophic respiration rates, lengthening the growing season (Myneni *et al.,* 1997; Menzel & Fabian, 1999; Saxe *et al.,* 2001; Nemani *et al.,* 2003) and altering soil decomposition and nutrient mineralization rates (Saxe *et al.,* 2001; Davidson & Janssens, 2006).

Global average atmospheric [CO_2] increased from 280 ppm before the industrial revolution to 381 ppm in 2006 (Canadell *et al.,* 2007a), and it is predicted to further double by the end of this century (IPCC, 2007). Results from free-air CO_2 enrichment (FACE) experiments have demonstrated a significant stimulatory effect of CO_2 on forest productivity (Norby *et al.,* 2005), leading to more carbon (C) being stored in woody biomass. However, studies of forest growth in CO_2-enriched environments have also suggested that the potential for a plant growth response to increasing [CO_2] may be limited by low nutrient availability (Oren *et al.,* 2001; Luo *et al.,* 2004; de Graaff *et al.,* 2006; Johnson 2006; Körner, 2006). On the other hand, there is also evidence of increasing belowground C allocation under elevated [CO_2], with consequent increase in N uptake, even in N-limited ecosystems (Finzi *et al.,* 2007).

N input via atmospheric deposition has likely been a growth promoting factor during recent years, because N is the most significant growth-limiting nutrient in many forests worldwide (LeBauer & Treseder, 2008). Moreover, increased N deposition can also increase soil organic matter accumulation rates by reducing mineralization rates (Berg & Matzner, 1997; Harrison *et al.,* 2000; Schulze *et al.,* 2000; Hagedorn *et al.,* 2003). In a recent study, Magnani *et al.* (2007) demonstrated a strong positive relationship between N deposition and average forest C sequestration (Högberg, 2007). Although

the numeric values of these results have been questioned, because they appear to show a very high ratio of C sequestered per unit N deposited (Sutton *et al.,* 2008; de Vries *et al.,* 2008; Hyvönen *et al.,* 2008; Högberg, 2007), scientists nevertheless agree that N deposition is likely to enhance forest C sequestration.

Several studies have investigated the effect of environmental factors (climate, N deposition and $[CO_2]$) on forest growth, but there is still no consensus on their relative importance for C sequestration during recent decades. Some studies suggest that the major driver of growth increment in Europe is N deposition (Nellemann & Thomsen, 2001; Solberg *et al.,* 2004; Van Oijen *et al.,* 2004, 2008; van Oijen & Jandl, 2004; Mellert *et al.,* 2008) while rising $[CO_2]$ and temperature have very little effect (Solberg *et al.,* 2009; Laubhann *et al.,* 2009). Rehfuess *et al.* (1999) used a combined (model-statistical-empirical) approach to investigate the relationships between recent changes of growth and nutrition of Norway spruce, Scots pine and European beech forests. They found that the combination of $[CO_2]$ and N deposition increase could account for a 15-20% increase in forest net primary production (NPP), while the rise in temperature was relatively unimportant. Using the complex forest model EFM (Thornley, 1991), parameterized for 22 stands across Europe, Milne & Van Oijen (2005) concluded that the main driver of increased forest growth in the 20th century has been increased N deposition, rather than increased $[CO_2]$ or climate change. Recently, the EU-RECOGNITION project attempted to clarify the causes of the observed forest growth increase using long-term growth studies and models, and came to the conclusion that N availability should be regarded as the main driver for this increase (Kahle *et al.,* 2008; Van Oijen *et al.,* 2008).

On the other hand, using the ORCHIDEE model, Ciais *et al.* (2008) concluded that a significant fraction of the trend in European forest NPP may be explained by changes in climate (temperature and precipitation) and $[CO_2]$. Although Ciais *et al.* (2008) did not consider N limitations in their work, they suggested that N deposition has only a minor role.

Several studies assessing potential climate change effects on future forest production also do not take account of the N deposition effect, identifying the main drivers of forest C accumulation as increased $[CO_2]$ and/or temperature (Loustau *et al.,* 2005; Zaehle *et al.,* 2007; Morales *et al.,* 2007; Kirilenko *et al.,* 2007; Sitch *et al.,* 2008). Other studies find a role for both N deposition and climate: in a tree model study on the effect of N deposition and climate change on growth of different European forests, Laubhann *et al.* (2009) found a positive correlation between growth and both N deposition and temperature.

In a recent study, however, Dezi *et al.* (2010) demonstrated that several key components of the response of forest ecosystems to N deposition have not been taken into account in previous modelling studies. Therefore a novel study is needed, taking into account the latest ecological evidence to investigate the effect of global change components on forest growth and C sequestration rates over the last decades.

In a review of the impact of elevated $[CO_2]$, N deposition, increased temperature and management on C sequestration in temperate and boreal forest ecosystems, Hyvönen *et al.* (2007) observed a lack of relationship between net ecosystem exchange (NEE) and N deposition. They concluded that to account for effects of N deposition, all stand factors need to be included. However, Magnani *et al.* (2007) subsequently showed that the main confounding factor is forest age and that it is possible to account for this confounding factor by using data from chronosequences. Once the age effect was corrected for, a strong relationship between average NEE and N deposition was found. Therefore, in the present study, we opted to use a chronosequence approach in order to avoid confounding due to age effects when evaluating results.

 We investigated the combined effect of recent changes in forest growth environmental drivers, i.e. atmospheric $[CO_2]$, N deposition, and climate variables (temperature, precipitation and radiation) on a maritime pine plantation. We used a coupled ecosystem model, the Generic Decomposition and Yield (G'DAY) model, developed by Comins & McMurtrie (1993). We used a version of the model modified by Dezi *et al.* (2010) to explicitly consider forest management and N deposition effects on forest ecosystems. Data from "Le Bray" maritime pine stand near Bordeaux, France, were used to parameterize the model. The "Le Bray" site was chosen because it is one of the chronosequence studies from Magnani *et al.* (2007). The effect of observed changes in atmospheric $[CO_2]$, climate and N deposition over the period 1950-2000 were assessed for gross primary production, net ecosystem production, maximum annual increment and wood and tree C. In order to factor out the overwhelming effects of forest age on growth and C sequestration (Pregitzer & Euskirchen, 2004; Magnani *et al.,* 2007), the model was run assuming a wide range of years for forest establishment, thus simulating chronosequences over which outputs could be averaged. The effects of the environmental factors on chronosequence-scale outputs were examined separately and in combination, using a full factorial design analysis (Box *et al.,* 1978).

4.3 MATERIALS AND METHODS

4.3.1 THE MODEL

The G'DAY (Generic Decomposition and Yield) model, as modified by Dezi *et al.* (2010), was used to represent tree and soil C and N dynamics. Within the G'DAY model, we implemented the MATE (Model Any Terrestrial Ecosystem) submodel (McMurtrie *et al.,* in preparation) to estimate daily light use efficiency (LUE) as affected by atmospheric $[CO_2]$ and environmental factors.

Briefly, G'DAY is a process-based model that simulates C and N dynamics in a forest ecosystem (Comins & McMurtrie, 1993). The model is composed of two sub-models, one that simulates plant production and one that simulates soil organic matter decomposition. The plant sub-model consists of three pools: foliage, wood (stem, branches and coarse roots) and fine roots. The soil sub-model, which is similar to the CENTURY soil model (Parton *et al.,* 1987, 1993), consists of four litter pools (structural and metabolic, above and below ground) and three soil organic matter pools (active, slow and passive) of C and N content. The N:C ratio of the substrate entering the three soil pools is assumed to be a saturating function of the soil inorganic N content (N_{inorg}), as N_{inorg} increases from zero to a critical value (N_{crit}) (McMurtrie *et al.,* 2001). A full description of the model is given elsewhere (Comins & McMurtrie, 1993; Medlyn *et al.,* 2000; McMurtrie *et al.,* 2001).

Several new assumptions were introduced to the model by Dezi *et al.* (2010) in order to simulate the effects of N deposition on forest C sequestration. These assumptions were: (i) prescribed forest thinning was assumed to result in the annual removal of a constant fraction of total woody biomass from the system, while the branches and the coarse roots of harvested trees were assumed to enter the surface and soil structural litter pools, respectively, and decompose over time; (ii) C root allocation was assumed to depend on NPP (Palmroth *et al.,* 2006) so that as tree production increases, the percentage of available C allocated to the root system decreases; (iii) foliar litterfall and specific leaf area (SLA) were assumed to increase with increasing leaf N concentration (Burton *et al.,* 2000; Reich *et al.,* 1999); (iv) leaves could directly absorb a fraction of the N deposition retained by the canopy (Sievering *et al.,* 2007) equal to the product of the canopy nitrogen uptake efficiency and the vegetation cover fraction; (v) the inorganic N soil pool was divided in two pools, namely nitrate and ammonium components; only the nitrate form could be lost from the system by leaching. The N taken up by the plant was assumed to depend on both soil inorganic N pools (Comins

& McMurtrie, 1993) and to be a saturating function of root biomass as in Dewar & McMurtrie (1996a, b).

For this paper, a few additional modifications are made to the model.

(1) A more realistic representation of silvicultural practices is introduced. Forest thinning is simulated as a periodic rather than annual event, applying prescribed export fractions derived from local Growth & Yield tables (Lemoine & Décourt, 1969). In order to simulate final harvests, all stems are assumed to be exported from the system following a clear-cut, while branches, leaves, fine and coarse roots remain in the system and enter the decomposition pools. Immediately after the clear-cut, the plantation of a new stand is simulated by setting C and N contents of foliage and roots to very low levels, with woody pools remaining at zero. For the current study, we assumed a rotation length of 50 years (Lemoine & Décourt, 1969). (2) C partitioning to foliage is assumed to be conservative and equal to 26 % of NPP, as shown by Litton *et al.* (2007). C root allocation is assumed to be a function of NPP as in Dezi *et al.* (2010), the remaining fraction being allocated to wood.

(3) N-induced changes in SLA and foliage mortality were demonstrated to be of minor importance by Dezi *et al.* (2010), so a constant value for leaf turnover and SLA is assumed in the present study.

(4) The representation of stand water balance and of the effects of soil moisture on litter and soil decomposition rate are taken from Corbeels *et al.* (2005a, b), with the exception that soil moisture is represented using only two layers, the top soil layer and the total root zone, rather than three.

(5) Finally, in order to incorporate the effects of atmospheric [CO_2] and other environmental variables on forest C sequestration, we use the MATE (McMurtrie *et al.* in preparation) plant model to calculate LUE of the stand as a function of meteorological data, atmospheric [CO_2] and leaf N concentration. This model calculates leaf photosynthesis based on the Farquhar & von Caemmerer (1982) model, and uses this value to estimate daily canopy-scale LUE according to the algorithm developed by Sands (1995).

4.3.2 EXPERIMENTAL SITE

The study site is a maritime pine (*Pinus pinaster* Ait.) plantation established in 1970 at "Le Bray", 20 km southwest of Bordeaux, France (44°42' N, 0°43' W). The understory consists mainly of *Molinia coerulea* (L.) Moench. The soil is a sandy humic podzol with

a cemented Bh horizon limiting the depth of the root zone at 75 cm and a permanent water table that fluctuates between 20 and 150 cm below the soil surface (Loustau & Granier, 1993).

The mean annual temperature is 12.5 °C and mean annual precipitation is 932 mm (Loustau & Granier, 1993; Granier & Loustau, 1994). Although the site is subject to summer drought, growth rates are relatively high, with a mean height of about 25 m at 50 years (Lemoine & Decourt, 1969; Delzon & Loustau, 2005). The stand, originating from direct sowing, covers an area of 16 ha and its elevation is 60 m a.s.l.. In 1997 the density of the pines was 621 trees per hectare (Loustau & Granier, 1993; Porté *et al.,* 2002) and leaf area index (LAI) ranged from 2.6 to 3.1 m^2 m^{-2}. In 1996-1999 the mean net ecosystem production (NEP) of the stand, estimated from eddy covariance measurements, was 530 gC m^{-2} yr^{-1} (Berbigier *et al.,* 2001) and the mean above ground net primary production (ANPP), estimated by allometric equations, was 390 gC ha^{-1} yr^{-1} (Bosc *et al.,* 2003; Porté, 1999; Porté *et al.,* 2002).

Since 1987, the site has been intensively studied for C and water relations, energy fluxes, tree transpiration, allometric relationships, resulting in a collection of available physiological data suitable for model parameterisation (Berbigier *et al.,* 1991; Granier & Loustau, 1994; Berbigier & Bonnefond, 1995; Loustau *et al.,* 1992a, 1992b, 1997, 1998; Porté & Loustau, 1998; Bosc, 1999; Porté *et al.,* 2002).

The silvicultural practices applied to this stand are characterized by a medium-term rotation cycle (ca. 50 years) with clear-cut harvesting and frequent thinning (ca every 5-7 years) (Lemoine & Décourt, 1969; Brin *et al.,* 2008).

A complete description of the site was given by Diawara *et al.* (1991).

4.3.3 PARAMETERISATION

Model simulations were driven by daily meteorological data of precipitation, global radiation, and maximum and minimum temperatures recorded on site from 1951 to 2000 (Fig. 1). Missing values of radiation and temperature were filled with the mean values between the previous and subsequent days. For precipitation, gaps were filled by averaging all values of precipitation registered that same day of year, for all 50 years. Daily soil temperatures were calculated using the 15-day moving average of mean daily air temperature. The values of temperature for morning (AM) and afternoon (PM) periods used in MATE were calculated as in McMurtrie *et al.* (1990). To estimate the values of vapour pressure deficit (VPD) for AM and PM periods we used the model

proposed by Kimball *et al.* (1997), which gives minimum daily humidity estimates using daily air temperature, annual precipitation and daily potential evapotranspiration.

The values of atmospheric [CO_2] (Fig. 2a) were derived from measurements at Mauna Loa, Hawaii, USA (http://cdiac.ornl.gov/). The values of N deposition (Fig. 2b) were simulated for the "Le Bray" site using the models EDGAR_HYDE, for the period 1949-1959, and TM4 RETRO, for the period 1960-2000 (van Noije, personal communication). A list of the principal model parameters used for this site are given in Table 1.

In the version of the plant model MATE used in this study, stomatal conductance was estimated using the Leuning model (1995), as modified by Medlyn *et al.* (2005). In this model, neglecting the effects of stomatal opening at the light compensation point, the intercellular [CO_2] (C_i) to atmospheric [CO_2] (C_a) ratio is calculated as:

$$\frac{C_i}{C_a} = 1 - \frac{1.6\left(1 + VPD/b\right)}{g_i} \tag{1}$$

where Ci and Ca are expressed in μmol mol^{-1}, VPD is vapour pressure deficit in kPa, g_i (dimensionless) is the slope parameter for the Leuning model (1995), b (kPa^{-1}) is a constant representing stomatal sensitivity to VPD and the 1.6 factor corrects for the difference in diffusivity between CO_2 and water.

The site-specific dependence of stomatal conductance on soil moisture was taken from Granier & Loustau (1994). Computed values of C_i were then used as input to the Farquhar photosynthesis model (Farquhar *et al.,* 1982). The species-specific coefficients for the relationships between leaf N concentration per area and the maximum values of electron transport and Rubisco activity rates at 25°C, used in MATE, are from Medlyn *et al.* (2002).

In Dezi *et al.* (2010) two possible pathways for N taken up by canopy were explored: (a) the N taken up is all added directly to the nitrogen concentration of the foliage to stimulate the photosynthesis; or alternatively, (b) it is added to the N taken up by roots and then allocated to the different parts of the plant. Given the uncertainty regarding the fate and amount of nitrogen taken up by the canopy the more conservative second assumption was used.

In Dezi *et al.* (2010), foliar litterfall and SLA were simulated as functions of N concentration, following Reich *et al.* (1999). Since there was no evidence that turnover rate and SLA changed with N concentration in maritime pine, in this study the foliage

turnover rate and SLA were held constant at 0.5 yr^{-1} and 21.13 m^2 kgC^{-1} respectively (this study). Values for root N uptake rate and N leaching rate were tuned to fit data (Table 1).

A rotation length of 50 years was assumed (Brin *et al.,* 2008), with imposed thinnings at an age of 24, 30, 35, 40 and 45 years (of intensity equal to 15, 14, 12, 5 and 5% respectively; Lemoine & Décourt, 1969). We assumed no natural tree mortality between thinnings.

4.3.4 SIMULATIONS AND ANALYSIS

Simulations for "Le Bray" maritime pine plantation consisted of two steps: (1) a simulation that led the system to the equilibrium condition, defining the common starting point for the (2) combination of simulations to investigate the effect of rising atmospheric [CO_2], N deposition and climate change (incident radiation, precipitation, temperature and humidity) on production and C sequestration of the plantation.

We initialised the model to equilibrium by repeating the first half of the available meteorological data set (i.e. from 1951 to 1975). In this simulation we kept N deposition rate and atmospheric [CO_2] constant and equal to 0.4 gN m^{-2} yr^{-1} and 280 ppm respectively, values characteristic of the start of the industrial revolution period. We used the values of litter and soil pools from this simulation to initialize the model for the analysis.

Direct meteorological measurements were used for the period 1976-2000 to reproduce the effects of any recent changes in climatic conditions at the site.

In order to account for the effects of forest age on growth and C sequestration rates, and highlight the impact of environmental factors alone, model results were averaged over an entire chronosequence, i.e. a number of stands of age ranging from 0 (regenerating stand, just after a clear-cut) to 50 (mature stand, just before harvesting). For this purpose, we simulated the dynamics over four rotations (i.e. covering a period of 200 years) of stands first established in 1801, 1811, 1821, 1831, 1841 or 1850. Model simulations were repeated for all combinations of the three varying environmental drivers (atmospheric [CO_2], N deposition and climate; hereafter referred to as the CO_2, N_d and CC driver respectively) that can affect forest C sequestration. Changes in environmental drivers over the period of simulations are presented in Figures 1 and 2.

In this way, both *synchronic* and *diachronic* analyses of model results could be performed. In this study, a *synchronic* analysis compares for a specific year a number

of stands of different age, grown under the same site and environmental conditions, while a *diachronic* analysis describes the development of an individual stand over time. The combined effects of varying age and environmental conditions overlap in the diachronic analysis (see Fig. 4). In the synchronic analysis, the effects of age can be removed by averaging results for one specific year (i.e., 1950, 1960, 1970, 1980, 1990 or 2000) across age classes.

In order to disentangle the effects of recent changes in each environmental driver considered, model results were then analyzed through a full factorial design model analysis, as described by Box *et al.* (1978), Henderson-Sellers (1993) and Henderson-Sellers & Henderson-Sellers (1996). Given three factors (atmospheric $[CO_2]$, N deposition and climate change) and two levels (either constant or observed natural trend), 2^3 simulations were required. The model outputs considered for this analysis were: gross primary production (GPP, kgC m^{-2} yr^{-1}), net ecosystem production (NEP, kgC m^{-2} yr^{-1}), wood C (Cw, kgC m^{-2}), total ecosystem C (Ctot, kgC m^{-2}) and mean annual increment (MAI, kgC m^{-2} yr^{-1}). To remove the age effect on this analysis, the average values of GPP, NEP, Cw and Ctot at year 2000, for the 6 different establishment years, were used for the analysis, while the maximum value across the age sequence was used for MAI.

4.4 RESULTS

4.4.1 VARIATION IN GROWTH RATE WITH ESTABLISHMENT YEAR

In model simulations with all three global environmental drivers (CO_2, N_d and CC) changing, the model predicted a clear difference in wood C accumulation among stands with different establishment years (Fig. 3, where the age of the stand after germination is reported on the abscissa). The three simulations shown in Figure 3 correspond to stands planted in 1900, 1950 and 1980. The wood C of all three stands increases over time, but the more recently the stand was planted, the higher the amount of C stored in wood for the same stand age.

At an age of 20 years, the stands planted in 1900, 1950 and 1980 stored in wood 1.3, 2.0 and 3.9 kgC m^{-2}, respectively. Growth rate was also higher for the most recently planted stand. While the stand planted in 1900 stored C in woody organs at a rate of 66 gC m^{-2} yr^{-1}, for the stands planted in 1950 and 1980 the rates were 146 and 257 gC m^{-2} yr^{-1}, respectively.

Results were then averaged across simulated forest chronosequences in order to remove the variable effects of age on forest response to environmental drivers.

4.4.2 CHRONOSEQUENCE ANALYSIS

A forest chronosequence is a set of stands of different ages, grown on sites with the same characteristics and under the same environmental conditions. Therefore, a forest chronosequence represents a substitute for the temporal development of the stand and can be used to remove the effects of age on stand response to long term changes in environmental drivers. In the present study, forest chronosequences were simulated by combining results from 6 simulations, representing 6 stands of different ages, assuming the same site characteristics and environmental conditions (see Material and Methods).

The pattern of wood biomass over time for the 6 simulated stands grown under the observed trend in the CO_2, N_d and CC drivers is presented in Figure 4a. From these simulations it is evident that wood C increased from the beginning of the 1900s, with an accelerating trend towards the end of the century. The last 50 years of the same simulations are presented in more detail in Figure 4b. The vertical boxes indicate the years for which values of GPP, NEP, Cw, Ctot were averaged across the 6 stands of a chronosequence. In the case of MAI, the maximum value over the chronosequence was evaluated.

Hereafter we will always refer to average values of GPP, NEP, Cw, Ctot and maximum MAI, from which age effects have been removed, for all the analyses.

4.4.3 TEMPORAL RESPONSE TO CLIMATE CHANGE, N DEPOSITION AND ATMOSPHERIC [CO_2]

To investigate the effects of the CO_2, N_d and CC drivers on the forest ecosystem at "Le Bray", the average values of NEP, GPP, MAI, Cw and Ctot from 1950 to 2000 were considered. Starting from the baseline case (none), which was run with pre-industrial constant values of all the drivers, simulations with all combinations of constant and increasing natural trends of the CO_2, N_d, and CC drivers are presented in Figure 5. It is important to stress that only the last 50 years of simulation are shown and that in each figure all the different simulations have a common origin. The split into different groups is due to the effects of the environmental drivers.

Figure 5a represents the effects of environmental drivers on average NEP over time. The variability of NEP over time within each curve is a consequence of the inter-annual

variability in the climatic pattern used. The decrease in NEP in 1980, for all cases not driven by the observed trend in CC, is likely due to the short term variability in the climate pattern used for the baseline case and to the sampling frequency used for setting up the chronosequences. This conclusion seems to be confirmed by the lack of decline in NEP in 1980 when the model is driven by the observed trend in CC.

Using a 25-year repeated meteorological data set, we would expect to have the same model response for the periods 1950-1975 and 1975-2000 in the baseline case. However, using a sampling frequency of 10 years, it follows that there is a mismatch between the years used for representing the period 1950-1970 (corresponding to the years 0, 10 and 20 of the data set) and those used for representing the period 1980-2000 (corresponding to the years 5, 15 and 25 of the data set). This mismatch would explain the different model response during the two periods in the base line case and in all cases without the CC driver.

In our model simulations, N deposition strongly enhances the capacity of the system to store C, as shown by the fact that all the combinations with the N_d driver lie in the upper part of the graph and keep increasing over time (Fig. 5a). The combinations without the N_d driver all have similar values of NEP in the year 2000, but those which include the observed N_d driver trend show different values. The combinations with the N_d driver but without the CC driver show a stabilization of NEP in the last period of the simulation, while the combinations with the CC driver show a continuation of the enhancement of NEP through to the end of the simulation.

These differences are confirmed by the analysis of GPP in Figure 5b, where the simulations with the N_d driver but without the CC driver show a decrease in GPP during the last years of simulation, when N deposition rate levels off, while in the simulations with both N_d and CC drivers (N_dCC), GPP keeps increasing. This effect of CC may be a consequence of increased temperatures, which stimulate N mineralization rates in the soil. Although a higher N mineralization is associated with more heterotrophic respiration (R_h), it also means that a greater amount of N is available in the soil for plant uptake, so stimulating leaf N content, LAI and therefore GPP.

 Figure 5b shows an increase in productivity for each of the environmental drivers considered and for their combinations. The effect of the CO_2 and CC drivers, without N_d (CO_2CC), is evident only in the last 25 years of the simulations, when the increase in atmospheric [CO_2] and temperature is maximum. On the contrary, the effect of N_d is evident throughout the simulated period, resulting in an increase of GPP over the control from 30% in 1950 to 62% in 2000 (considering only the N_d driver). Increasing N

deposition rate also seems to enhance the CO_2 driver effect on GPP, while the main effect of the CC driver is the interaction with the N_d driver effect towards the end of the simulation period.

Figure 5c shows maximum MAI over time, for the 8 environmental driver combinations. The effect of CO_2 and CC and their combination is to slightly increase maximum MAI at the end of the simulation period. In contrast, the N_d driver enhances maximum MAI throughout the simulation; this enhancement is already evident in 1950 and increases over time. As with GPP, simulations with the N_d driver but without the CC driver seem to stabilize at the end of the simulation period, due to the stabilization in N deposition rates, whereas maximum MAI continues to increase in simulations including the CC driver. .

The resulting effects of the environmental drivers on wood and total C over time are shown in Figure 6. As with C fluxes, the N_d driver is the most important factor increasing C stocks, both for wood and total ecosystem C. Once more, the effects of the CC and CO_2 drivers and of the CO_2CC combination are evident only at the end of simulation period, slightly increasing the amount of C stored. The combination of the CC and CO_2 drivers with the N_d driver strongly enhances this effect.

For the baseline case, wood and total ecosystem C remain constant at values of about 0.8 and 5.9 kgC m^{-2} yr^{-1}, respectively, throughout the simulation period. In contrast, in the case with all environmental drivers applied (All), wood C increases from 1.7 kgC m^{-2} yr^{-1} in 1950 to 3.9 kgC m^{-2} yr^{-1} in 2000 (Fig. 6a), and total C increases from 7.4 to 10.1 kgC m^{-2} yr^{-1} during the same period (Fig. 6b).

4.4.4 AVERAGE RESPONSE TO CLIMATE CHANGE, N DEPOSITION AND ATMOSPHERIC [CO_2] OVER THE PERIOD 1950 - 2000

Simulated values of NEP, GPP and maximum MAI, averaged over the period 1950-2000, for all the combination of environmental drivers are shown in Figure 7. The results are expressed as the percentage change from the baseline simulation, run with pre-industrial constant values of all the environmental drivers.

The CO_2 driver increases NEP and the CC driver reduces it; overall, the CO_2CC combination has very little effect on NEP over the 50 years considered. The N_d driver can increase NEP by about 800%; this seems large but it should be stressed that NEP assumes very low values, so that even small absolute changes result in great percentage changes. As in the case without the N_d driver, the effect of the combination

of N_d and CC (N_dCC) is to decrease the NEP response compared with N_d alone, while the combination of N_d and CO_2 ($N_d CO_2$) increases it. Finally, the joint effect of all environmental drivers is to increase NEP by about 840 % compared with the baseline case.

All environmental drivers and their combinations increase GPP. The greatest GPP response is observed when all environmental drivers are applied (+60%), while the $N_d CO_2$ and N_dCC combinations and the N_d driver alone increased GPP by 54%, 52% and 49%, respectively. The smallest effect on GPP was observed in the case of the CO_2 driver alone, with GPP increasing by just 2% over 50 years.

Maximum MAI increased under all environmental driver combinations compared with the baseline scenario. As for GPP, the greatest positive effect was observed when all environmental drivers are considered. Of the three drivers, the most important is the N_d driver, which magnifies the positive effect on maximum MAI of both the CO_2 and CC drivers, while the CO_2 driver alone seems to have a negligible effect on maximum MAI.

Simulated values of wood and total carbon stocks, averaged over the period 1950-2000, for all the combination of environmental drivers are shown in Figure 8. The results are expressed as the percentage change from the baseline simulation, ran with pre-industrial constant values of all the environmental drivers.

The CC and CO_2 drivers each had a relatively small effect on both C_w and C_{tot}, while the N_d driver had a much larger effect, increasing C_w and C_{tot} on average by 170% and 38%, respectively, compared with the baseline case. The larger increase in C_w relative to C_{tot} in response to N deposition is due to the higher C:N ratio of wood compared with the C:N ratio of the entire ecosystem, and to the fact that C_w does not represent the main component of C_{tot}. Therefore an increase in N taken up by the plant translates into a greater percentage increase of C stored in wood than in the ecosystem as a whole.

The $N_d CO_2$ combination has a slightly greater effect on C_w and C_{tot} than the N_dCC combination. This reflects the NEP behaviour under the same driver combinations.

For both C_w and C_{tot} the greatest response is observed when all drivers are applied, while the lowest response is observed when only the CO_2 driver is considered.

4.4.5 FACTORIAL ANALYSIS

The effects of all combinations of the three environmental drivers on NEP, GPP, C_w, C_{tot} and maximum MAI, once the age effect has been removed, are summarized in Table 2. The three environmental drivers considered are: observed atmospheric $[CO_2]$ trend (CO_2), observed N deposition rate (N_d) and observed climate change (CC). For all variables, the single driver with the greatest effect is the change in N deposition rate. For NEP, the second most important driver is the increase in atmospheric $[CO_2]$, followed by climate change, while for the other variables the CC driver is more important than the CO_2 driver. Of all the two-way and three-way interactions, only the N_dCC interaction was significant; interactive effects between the other driver combinations were negligible.

4.5 DISCUSSION

Model results show a strong effect of time of stand establishment on growth stand dynamics. Stands planted more recently grow faster than stands planted in the past because increased temperature, atmospheric $[CO_2]$ and N deposition stimulate photosynthesis and modify resource allocation. These results are in agreement with the observations of an increase in site quality and growth over recent decades (Spiecker, 1999, 2002; Lebourgeois *et al.*, 2000). An increase in site quality will also influence tree growth rhythm (Peschel, 1938), so that recently established stands may grow faster and reach maximum current annual increment earlier than stands established in the past (Spiecker, 2002). Although the amount of simulated C in wood is higher than that reported in this studies due to other limiting factors as a result of long-term N fertilization (see discussion below about MAI), model results seem to agree with the observed pattern in stand growth.

Given the strong overlap between age dynamics and changes in environmental factors (climate change, $[CO_2]$ and N deposition) in their effects on forest ecosystem growth and C storage capacity, in order to investigate climate-growth relations it was necessary to remove the effects of any age-related changes (Pregitzer & Euskirchen, 2004; Magnani *et al.*, 2007). In this study, we removed confounding age effects by simulating forest chronosequences. After removal of this confounding effect, forest dynamics over recent decades were found to be driven mainly by the increase in N deposition. This finding is in agreement with the experimental results of Mellert *et al.* (2008) that increased N nutrition was the most important driving factor (compared to

precipitation and air temperature) of growth acceleration of Scots pine during the period 1950-2000 in Central Europe, where N deposition rate was generally high.

Atmospheric N deposition affects forest ecosystems via two main mechanisms. Part of the N deposited is intercepted by the canopy and absorbed by leaves, thus directly affecting forest trees (Katz *et al.,* 1989a, b; Wilson & Tiley, 1998; de Vries *et al.,* 2001; Harrison *et al.,* 2000; Sievering *et al.*, 2007; Sparks, 2009). The N deposited that is not retained by leaves reaches the soil and largely accumulates in soil organic matter, changing the soil C:N ratio and so influencing the conversion by the microbial community of soil and litter organic N into the inorganic N required by trees. This process of net N mineralization is generally considered to be the rate-limiting step in plant N uptake (Bending & Read, 1996, 1997; Colpaert & Van Laere, 1996; Nave *et al.*, 2009a). This long-term stimulation of N mineralization is an indirect effect of N deposition on forest trees.

In our simulations, the relative contribution of N deposition to total N taken up by trees changed with time. As N deposition increased from 0.2 to 1.3 gN m^{-2} yr^{-1} from 1800 to 1974, the contribution of N deposition to total N uptake increased from 10% to 31%. Between 1974 and 2000, the N deposition rate decreased to 1.0 gN m^{-2} yr^{-1}, and the contribution to total N uptake decreased to 21%. These values are in agreement with the estimated contribution from N deposition to total N requirements for forest growth of 15% estimated by Nave et al. (2009a), for a N deposition rate of 0.75 gN m^{-2} yr^{-1}.

In our model, about 48% of N deposition is assumed to be retained and absorbed by the canopy. Thus, the direct contribution of N deposition, as canopy N uptake, to annual N requirements for stand growth amounts to 5-15%. These values are in agreement with experimental measurements of the contribution of canopy N uptake to total annual N requirement, which range from 2 to 42% (Boyce *et al.,* 1996; Wilson & Tiley, 1998; Harrison *et al.,* 2000). However, given the simplified formulation used in the model to estimate canopy N uptake, the uncertainty in canopy nitrogen uptake efficiency and the important effect that this mechanism may have on forest growth and C storage (Dezi *et al.,* 2010), further studies towards a better quantification and understanding of this often neglected ecological process are desirable. In particular, research should focus on replacing the the dependence on the constant vegetation cover fraction c with the dependence on LAI effect on wet and dry deposition, possible saturation effects and their relationship with canopy closure, meteorological conditions and plant internal N status on wet and dry deposition, and the inclusion of the N soil saturation effect on leaching and soil respiration.

In contrast with canopy nitrogen uptake, which closely follows the trend in N deposition rate, net N mineralization continues to increase over time, despite the decrease in N deposition in recent decades, and therefore it can be regarded as a long-lasting indirect effect of N deposition on forest growth. In the simulation with only the N deposition driver, net N mineralization increases from 3 gN m^{-2} yr^{-1} in 1950 to around 4 gN m^{-2} yr^{-1} in 2000 due to the stimulatory effect of N deposition. This represents a 33% increase during the period 1950-2000, or 82% if considering the entire period of simulation (1810-2000). Such percentages are of the same order of magnitude as the value estimated by Nave *et al.* (2009b), who carried out a meta-analysis of the responses of soil C storage, soil C:N ratio, and net N mineralization to different types of N inputs in northern temperate forests.

The contribution of net N mineralization to total annual N uptake decreases until 1974 and then slightly increases, being always higher than 70%.

Our model simulations therefore indicate that the main mechanism through which N deposition interacts with forest ecosystems, increasing forest growth and C sequestration, is through the long-term increase in net N mineralization.

Adding climate change effects to N deposition, we found an acceleration in the rise of net N mineralization during the last 50 years, as it was found to increase from 3 gN m^{-2} yr^{-1} in 1950 to around 4.8 gN m^{-2} yr^{-1} in 2000. The effect of this larger increase in net N mineralization is to further stimulate tree growth from 1980 onward, corresponding to a recorded temperature increase of about 1.8 °C from 1980 to 2000. This increase in growth translates into a parallel increase in litter production, representing a positive feedback for mineralization. The enhancement of decomposition rate by temperature increases the release of nutrient available for plant uptake, as found by Jarvis & Linder (2000) for a boreal forest and by Rustad *et al.* (2001) in a meta-analysis of ecosystem responses to experimental warming. This extra input of N due to increased temperature translates in turn into an increase in foliar N concentration, photosynthesis, tree growth and C accumulation.

Although net N mineralization also increased after 1980 in the simulation with only the observed trend in climate change applied, the rate of increase was lower than in presence of N deposition, therefore highlighting an interaction between temperature and N deposition, also confirmed by factorial analysis. This indirect temperature effect, of enhancing soil N availability, is in agreement with several studies that identify changes in N supply, and not only N deposition, as the main nutritional factor that may

have induced changes in site index and height growth in European stands during recent decades (Mellert *et al.,* 2004, 2008; Kahle *et al.,* 2008).

Increases in mean air temperature affect forest productivity directly by lengthening the growing season (Myneni *et al.,* 1997; Menzel & Fabian, 1999; Saxe *et al.,* 2001; Nemani *et al.,* 2003) and indirectly by altering soil decomposition and nutrient mineralization rates (Saxe *et al.,* 2001; Davidson & Janssens, 2006). In our simulation the direct effect of increased temperature on photosynthesis is modelled as an increase in LUE. However, given the model formulation of LUE, which includes also the effect of increased leaf N concentration, it is not possible at this stage to discriminate between the two effects of temperature on LUE and ecosystem C sequestration (i.e. directly and through changes in net N mineralization). Further model analyses would help to discriminate between the two mechanisms.

Studies on forest growth in CO_2-enriched environments show that lack of nutrients limits the enhancement effect of [CO_2] on forest productivity (Oren *et al.,* 2001; Luo *et al.,* 2004; de Graaff *et al.,* 2006; Johnson, 2006; Körner, 2006). In accordance with these studies, we found that increasing [CO_2] significantly affects forest growth and C storage substantially in simulations when the observed N deposition trend is also applied.

A small increase in forest growth was also observed in the simulation when increasing [CO_2] and temperature were considered together. This result is a consequence of the increased N availability for plant growth due to faster N mineralization.

The difference in the intensity of forest growth increase between the two simulations is because of the higher N availability due to N deposition than to increased temperature.

This result is in agreement also with the suggestion by Mellert *et al.* (2008) that atmospheric [CO_2] was only of a secondary importance for accelerating growth, based on the consideration that there was spatial variation of tree growth changes in Europe, and that growth increases were mainly restricted to those stands where N nutrition improved.

It should be stressed, however, that the CO_2 effect is possibly underestimated in our model results. This underestimation is due to the allocation formulation we used for our simulations. While we kept constant the fraction of C allocated to canopy, we varied the fraction to root system in accordance with Dezi *et al.* (2010) using the coefficients suggested in Palmroth *et al.* (2006) for the ambient [CO_2] treatment. A higher belowground allocation fraction is commonly observed in elevated [CO_2], suggesting

that there should be a relationship between allocation coefficients and $[CO_2]$, which is not captured in these simulations. Allocation patterns could have differed under the lower atmospheric $[CO_2]$ assumed at the beginning of the simulation period. Use of allocation fractions estimated for current ambient $[CO_2]$ at earlier, lower $[CO_2]$ may mean the model overestimates past C allocation to the root system, and therefore overestimates past forest growth and productivity. A lower past growth rate would have resulted in a higher difference between baseline and CO_2 treatments, meaning that this effect is likely underestimated in the model results presented here. Further studies on the relationship between atmosphere [CO2] and belowground C allocation are needed to improve the model's outcomes.

Although the stand age effects on changes in C allocation over lifetime of the forest are not explicit in the model, it is realistically considered through the NPP-driver patter as reported by Litton *et al.* (2007, Fig. 8) and Ryan *et al.* (2004). Moreover, we found that the percentage of C allocated to the root system decreased over time to a maximum of 0.73 to 0.63 (corresponding to a value of GPP of 870 gC m^{-2} yr_{-1}), in agreement with the values found by Litton *et al.* (2007).

Another important limitation on our results is the inability of the soil C submodel to take into account the effects of pH on soil decomposition. A low or high soil pH would likely decrease soil organic matter decomposition rates and therefore increase soil C:N ratio. Including such an effect in our simulations would have resulted in a higher soil C:N ratio. Measured soil C:N ratio at "Le Bray" site was above 25, while simulated soil C:N ratio was around 20. Since N deposition effect is more pronounced on soil having C:N above 25 (Solberg *et al.,* 2009), the exclusion of pH effects on decomposition could have led to an underestimation of N deposition effects on forest growth analysis.

Although there are no data available on long-term changes in forest productivity at the "Le Bray" site, an acceleration in height growth rate up to 60% was observed for an even-aged stand of common beech (*Fagus sylvatica* L.) in north-east France at the end of 20th century (Bontemps *et al.,* 2009). An increase in basal area of about 50 % was also observed in a Corsican pine (*Pinus nigra* Arnold ssp. *Laricio* var. *Corsicana*) plantation in western France from 1921-1991 (Lebourgeois *et al.,* 2000). In both cases N deposition was proposed as one of the most likely drivers.

Although changes in MAI will be greater than for either height and basal area, as discussed in RECOGNITION project, estimation of MAI changes (around +100%, during the period 1950-2000) from our study is likely higher than observed on the ground. This over-estimation may be due to other limiting factors as a result of long-

term N fertilization, such as phosphorous (P) availability, as suggested by the significant P x N interaction observed by Trichet *et al.* (2009) in their fertilization experiment on Maritime pine (*Pinus pinaster*) close to "Le Bray". These limiting factors are not considered at present in the G'Day model,

Finally we want to stress that our model results are not directly applicable for assessing future forest growth rate and C sequestration capacity, given the uncertain effects of government measures on N deposition and climate change in future. However we can infer that although N deposition rates are predict to decrease in near future, the fertilizing effect due to N deposition would continue for some decades.

4.6 CONCLUSIONS

Forest ecosystems are an important component of the terrestrial C sink. The rate of forest growth has increased over the last decades. Using a model that explicitly incorporates N deposition, atmospheric $[CO_2]$ and climate change effects, we found that the main driver for the observed increase in forest growth is enhanced N availability, in agreement with recent results from the RECOGNITION project. Model simulations allowed us also to discriminate between the different mechanisms responsible for such an increase in N availability, and their relative importance. Atmospheric N deposition is found to be the main source for the increase in N availability, both through direct canopy uptake over a short time scale and through indirect effects on net N mineralization over long time scales. Increased temperature was also found to enhance N availability, but at a lower rate than N deposition. Finally $[CO_2]$ effects were found to be important only when N was not limiting, as a result of either N deposition or higher temperatures and faster N mineralization rates. A step forward in our analysis to enhance the impact of the present study relative to previous one (e.g. RECOGNITION, Kahle *et al.,* 2008) would be to validate modelled simulation results against experimental data on long-term changes in forest productivity.

Table 4-1 Parameter values used in the model for the maritime pine (*Pinus pinaster* Ait.) plantation of Le Bray.

Symbol	Definition	Value	Units	Reference
w	C content of dry matter	0.53	-	This study
f	NPP/GPP ratio	0.53	-	DeLucia et al. 2007
k	Light extinction factor	0.467	-	This study
ρ	Ratio of root nitrogen concentration to foliar nitrogen concentration	0.6	-	Newman & Hart 2006
d	η_w/η_f	1.17	-	This study
B	Exponential coefficient in η_r equation	2.309	$m^2 \, yr \, kgC^{-1}$	Palmroth et al. 2006
Q	Coefficient in η_r equation	9.499	-	Palmroth et al. 2006
$Y0$	Constant in η_r equation	0.138	-	Palmroth et al. 2006
γ_r	Constant root mortality	1.39	yr^{-1}	This study
T	Soil texture parameter	0.1	-	This study
CNU_e	Canopy nitrogen uptake	0.8	-	Sievering et al. 2007
c	Fractional canopy cover	0.6	-	Chopping et al. 2008
f_BR	Fraction of wood carbon in branches (average for American conifers)	0.26	-	This study
f_CR	Fraction of wood carbon in coarse roots (average for American conifers)	0.21	-	This study
N_{crit}	Critical inorganic N value for soil variable N/C scenario	0.002	$kgN \, m^{-2}$	McMurtrie et al. 2001
v_{f_max}	Maximum foliar N/C above which N is not limiting	0.04	$kgN \, kgC^{-1}$	Comins & McMurtrie 1993
v_{f_min}	minimum foliar N/C	0.001	$kgN \, kgC^{-1}$	This study
v_u	N/C ratio for surface structural litter	1/150	$kgN \, kgC^{-1}$	Comins & McMurtrie 1993
v_v	N/C ratio for soil structural litter	1/150	$kgN \, kgC^{-1}$	Comins & McMurtrie 1993
v_{newa}	Intercept of relationship between v_{new} and v_f	0	$kgN \, kgC^{-1}$	Medlyn et al. 2000
v_{newb}	Slope of relationship between v_{new} and v_f	0.16773	-	Medlyn et al. 2000
v_{swa}	Intercept of relationship between v_{sw} and v_f	0	$kgN \, kgC^{-1}$	Medlyn et al. 2000
v_{swb}	Slope of relationship between v_{sw} and v_f	0.05624	-	Medlyn et al. 2000
v_{a_max}	Maximum for newly active soil pool SOM	1/8	$kgN \, kgC^{-1}$	Nalder & Wein 2006
v_{a_min}	Minimum for newly active soil pool SOM	1/16	$kgN \, kgC^{-1}$	Nalder & Wein 2006
v_{s_max}	Maximum for newly slow soil pool SOM	1/12	$kgN \, kgC^{-1}$	Nalder & Wein 2006
v_{s_min}	Minimum for newly slow soil pool SOM	1/40	$kgN \, kgC^{-1}$	Nalder & Wein 2006
v_{p_max}	Maximum for newly passive soil pool SOM	1/6	$kgN \, kgC^{-1}$	Nalder & Wein 2006
v_{p_min}	Minimum for newly passive soil pool SOM	1/20	$kgN \, kgC^{-1}$	Nalder & Wein 2006
λ_{loss}	Constant rate of N lost through leaching and gaseous emission	0.32	yr^{-1}	This study
λ_u	Constant rate of N uptake by plant roots	6.0	yr^{-1}	This study
k_r	Value of root C at which 50% of the available N is taken up	0.05	$kgC \, m^{-2}$	Dewar & McMurtrie 1996
Lfl	Lignin/biomass ratio in leaf litter	0.25	-	Eliasson et al. 2005
Lrl	Lignin/biomass ratio in root litter	0.127+0.393* Lfl	-	Newman & Hart 2006

Table 4-2 Dimensionless estimated effects of all combinations of the three environmental drivers on GPP, NEP Cw and Ctot and maximum MAI age effect removed. The magnitude of the effects was evaluated using the method given by Box *et al.* (1978, p. 322), while the standard errors of effects were calculated using higher-order interactions (Box *et al.,* 1978, p. 327). The relative importance of the single or combination of effects was assessed by the normal probability method (Henderson-Sellers, 1993; Box *et al.,* 1978; Daniel, 1976). The three environmental drivers are: observed atmospheric [CO_2] (CO_2), observed N deposition rate (N) and observed trend of climate change (CC).

Effects	Estimated effects ± standard error (10^{-2})				
	NEP	**GPP**	**Cw**	**Ctot**	**Maximum MAI**
average	7.64 ± 0.32	109.24 ± 0.27	219.07 ± 4.39	781.09 ± 5.2	11.285 ± 0.24
CO_2	1.76 ± 0.64	6.33 ± 0.55	29.12 ± 8.78	21.55 ± 10.49	1.71 ± 0.49
N	14 ± 0.64	51.55 ± 0.55	241.97 ± 8.78	353.69 ± 10.49	12.49 ± 0.49
CC	0.45 ± 0.64	11.13 ± 0.55	38.22 ± 8.78	41.19 ± 10.49	2.44 ± 0.49
CO_2N	1.27 ± 0.64	3.04 ± 0.55	17.55 ± 8.78	20.98 ± 10.49	0.97 ± 0.49
CO_2CC	0.32 ± 0.64	0.86 ± 0.55	3.48 ± 8.78	3.91 ± 10.49	0.25 ± 0.49
CCN	0.91 ± 0.64	1.09 ± 0.55	13.94 ± 8.78	5.33 ± 10.49	0.86 ± 0.49
CO_2CCN	0.17 ± 0.64	0.16 ± 0.55	1.57 ± 8.78	1.62 ± 10.49	0.05 ± 0.49

Figure 4-1 Yearly observed average air temperature, total photosynthetically active radiation (PAR) and precipitation for Le Bray site from 1950 to 2000.
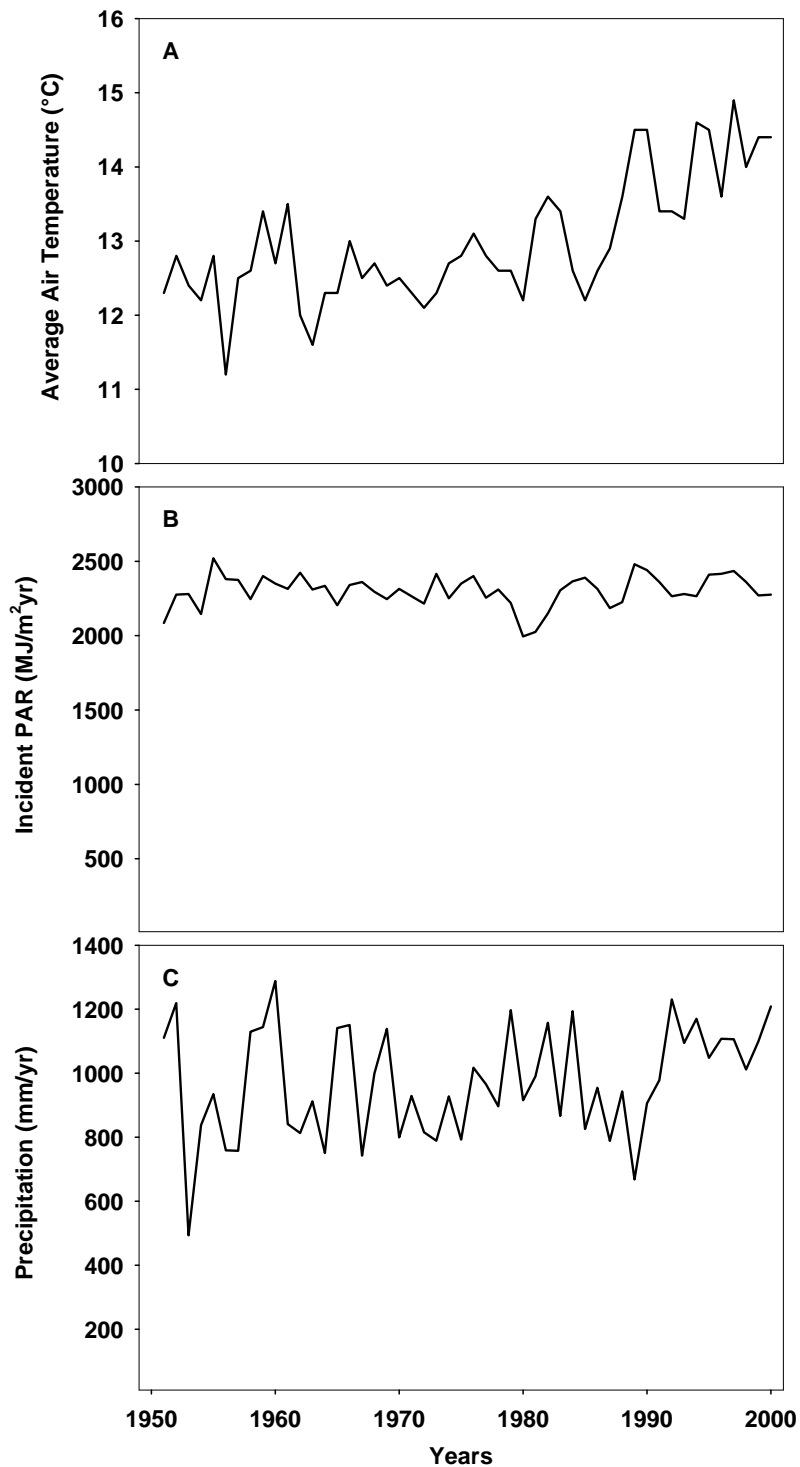
Figure 4-2 Yearly atmospheric [CO_2] and total N deposition from 1800 to 2000. The values of atmospheric [CO_2] are derived from in situ air samples collected at Mauna Loa, Hawaii, USA (http://cdiac.ornl.gov/). The values of N deposition were simulated for the Le Bray site using the models EDGAR_HYDE, for the period 1949-1959, and TM4 RETRO, for the period 1960-2000 (Twan van Noije, personal comunication).
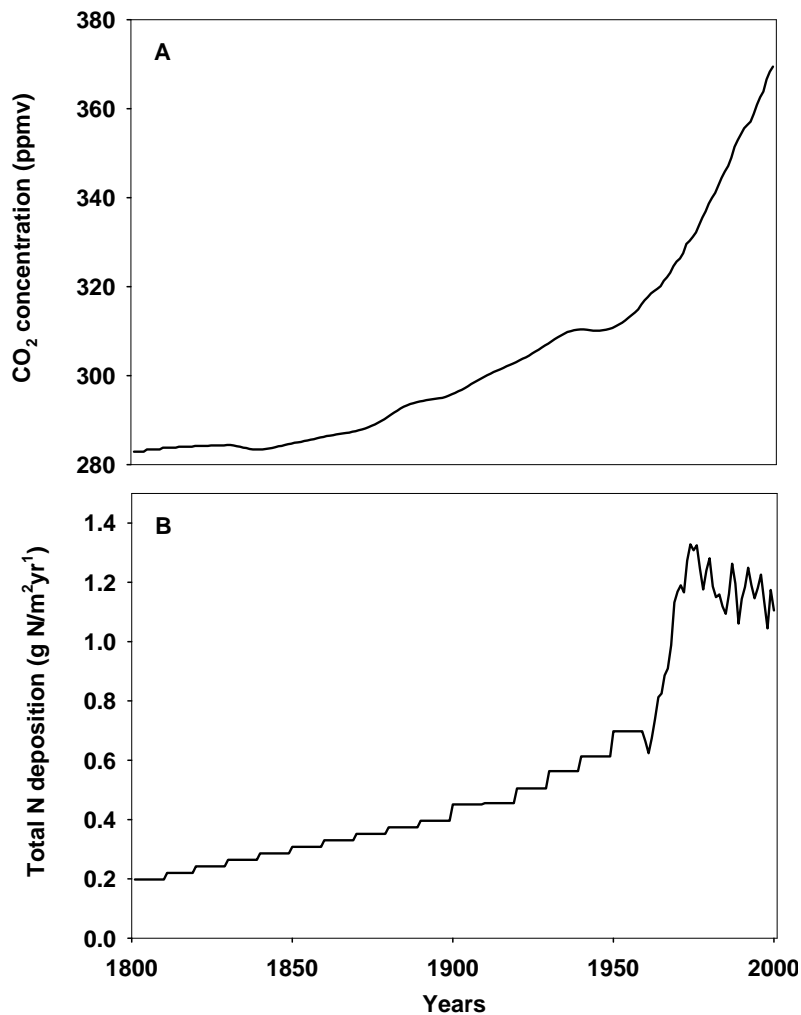
Figure 4-3 Wood C over time for three stands established in 1900, 1950 and 1980, plotted against stand age. The simulations were driven with observed trends in atmospheric [CO_2], N deposition and climate.
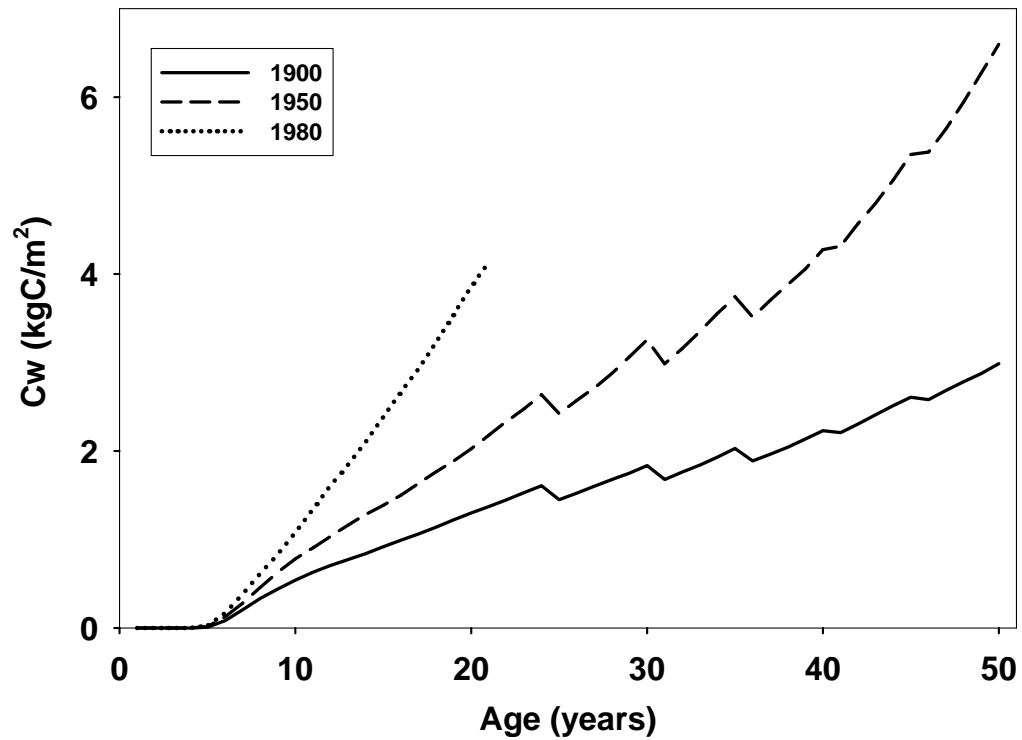
Figure 4-4 Wood C of 6 simulated stands established in 1801, 1811, 1821 1831, 1841 and 1850. The simulations were run considering the same observed trend of climate change, atmospheric [CO$_2$] and N deposition for all the stands, from 1801 to 2000 (A) and from 1950 to 2000 (B). The vertical boxes in B indicate the years when chronosequence data were grouped for the age-effect removal analysis.
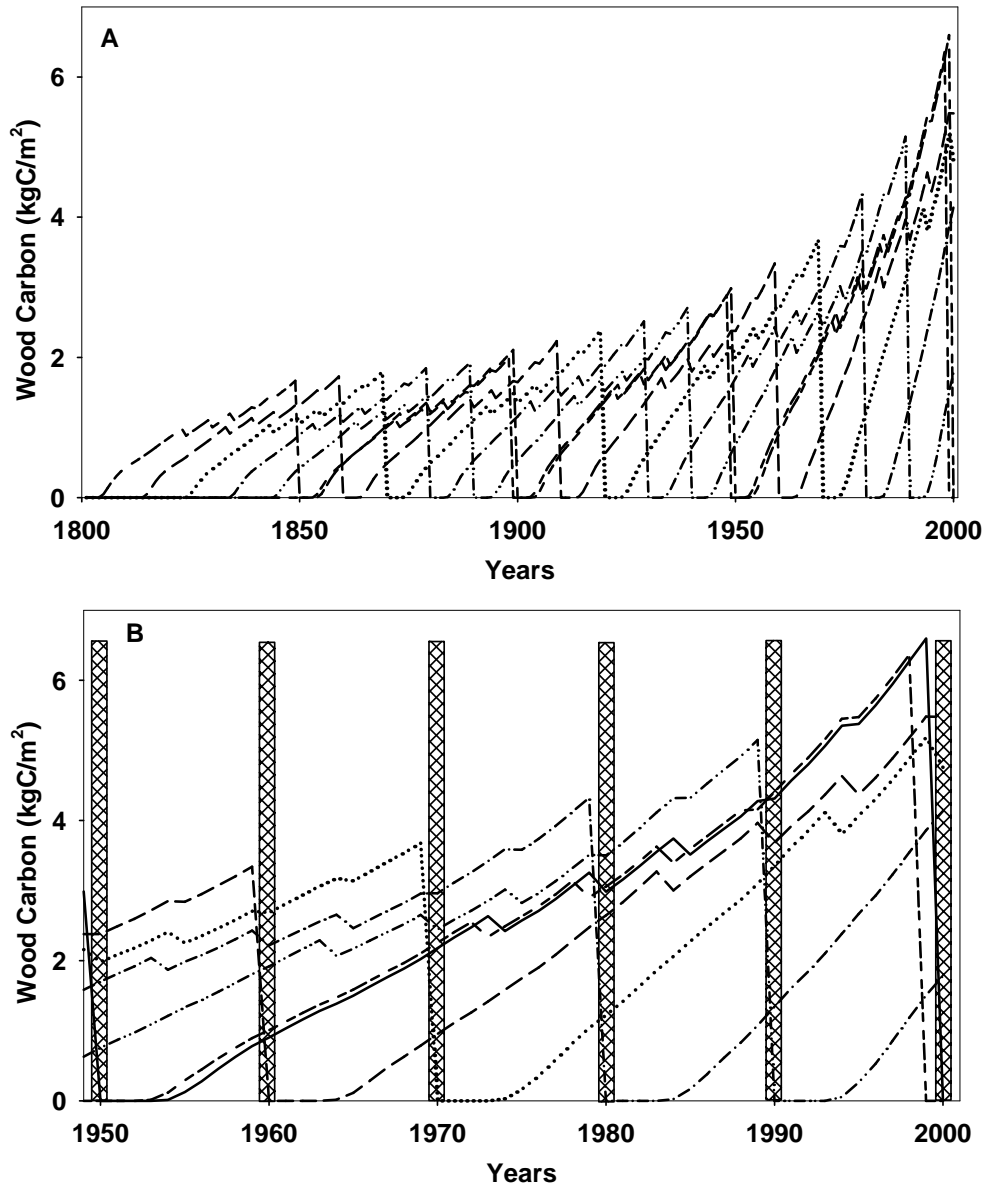
Figure 4-5 Simulated average net ecosystem production (A), average gross primary production (B) and maximum mean annual increment (C) for the Le Bray maritime pine stand, for the different environmental driver combinations applied from 1950 to 2000. The variables were averaged for 6 specific years (i.e., 1950, 1960, 1970, 1980, 1990 or 2000) across age classes to remove the effects of age. The environmental drivers are: observed atmospheric [CO_2] (CO2), N deposition (N_d) rate and climate change (CC) trends.
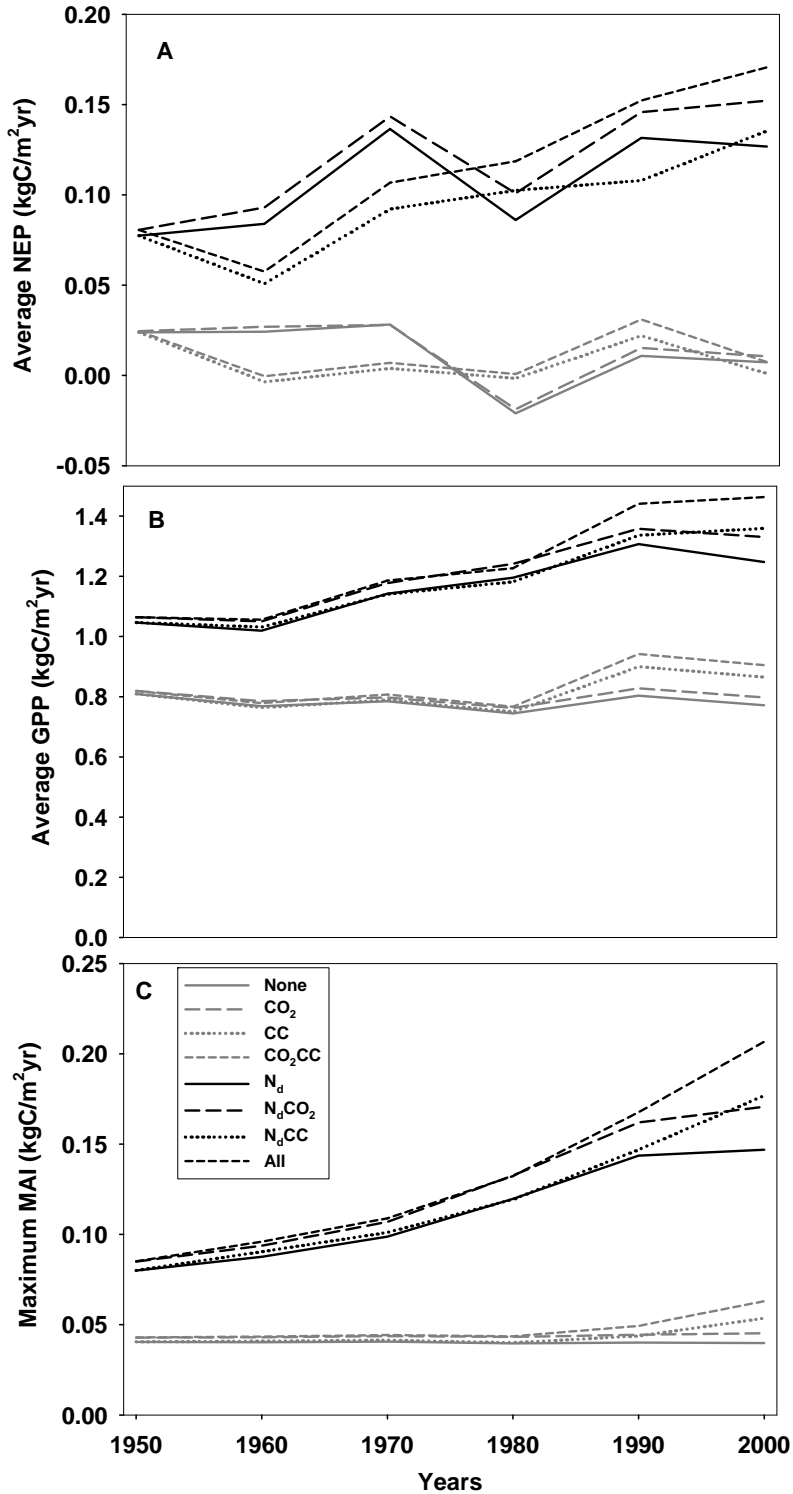
Figure 4-6 Average wood (A) and average total (B) C for the Le Bray maritime pine stand, for the different environmental driver combinations applied from 1950 to 2000. The variables were averaged for 6 specific years (i.e., 1950, 1960, 1970, 1980, 1990 or 2000) across age classes to remove the effects of age. The environmental drivers are: observed atmospheric $[CO_2]$ (CO2), N deposition (N_d) rate and climate change (CC) trends.
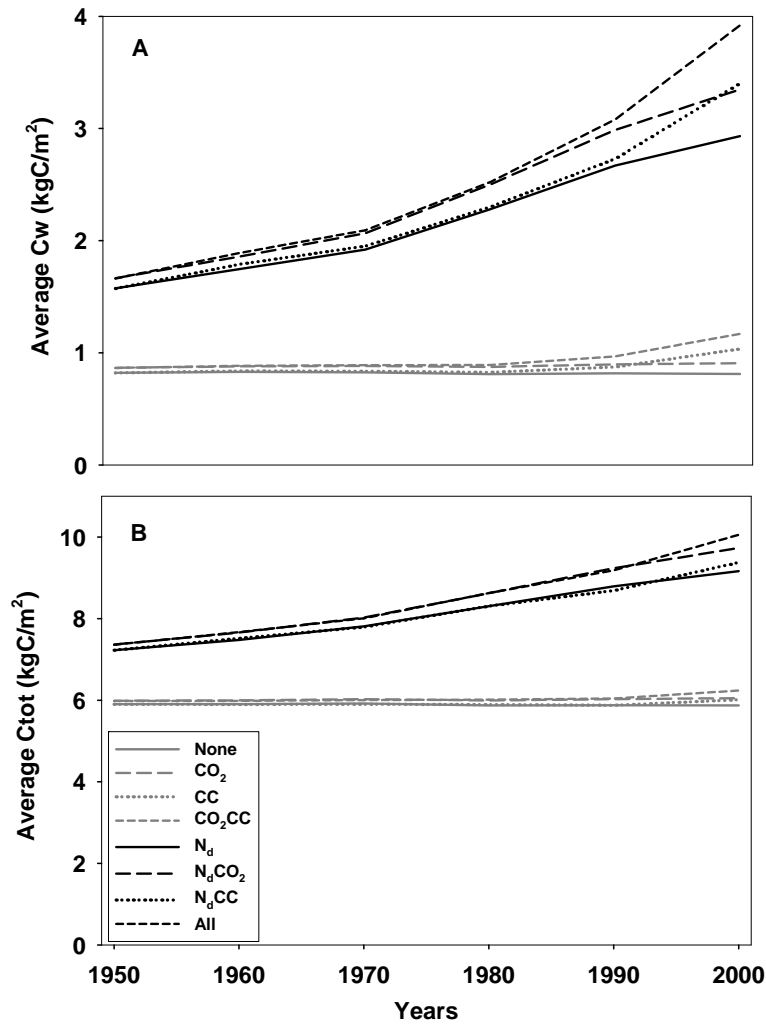
Figure 4-7 Net ecosystem production (black), gross primary production (light gray) and maximum mean annul increment (dark grey) for the Le Bray maritime pine stand, for the different environmental driver combinations averaged over the period 1950-2000. The results are expressed as percentage difference from the baseline case with constant driver values applied. The environmental drivers are: observed atmospheric $[CO_2]$ (CO2), N deposition (N_d) rate and climate change (CC) trends.
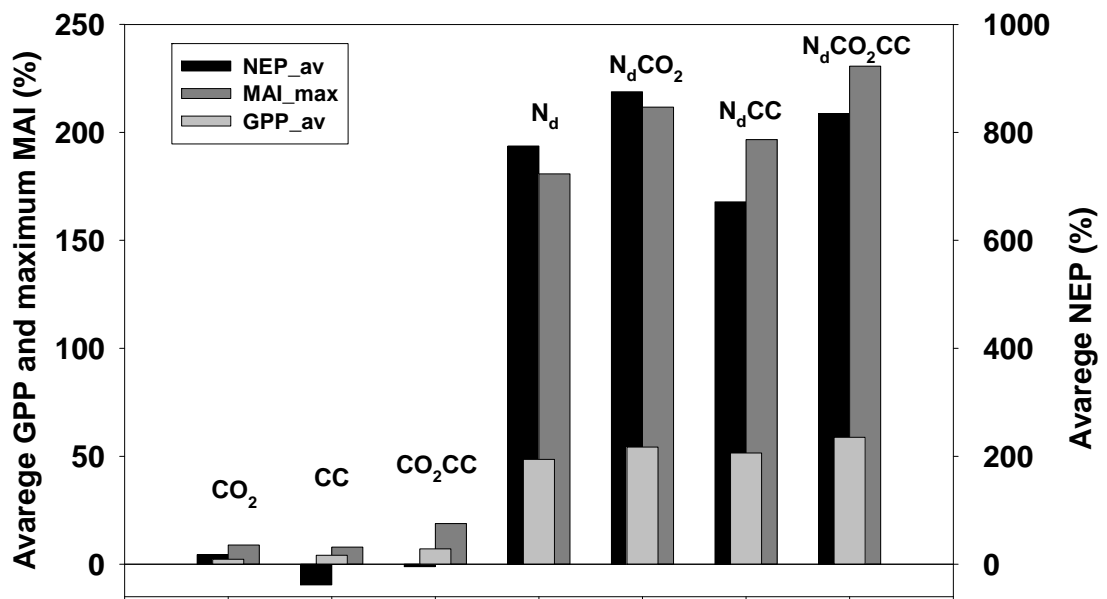
Figure 4-8 Wood (black) and total (grey) C for the Le Bray maritime pine stand, for the different treatments combinations averaged over the period 1950-2000. The results are expressed as percentage difference from the baseline case with constant driver values applied. The environmental drivers are: observed atmospheric $[CO_2]$ (CO2), N deposition (N_d) rate and climate change (CC) trends.
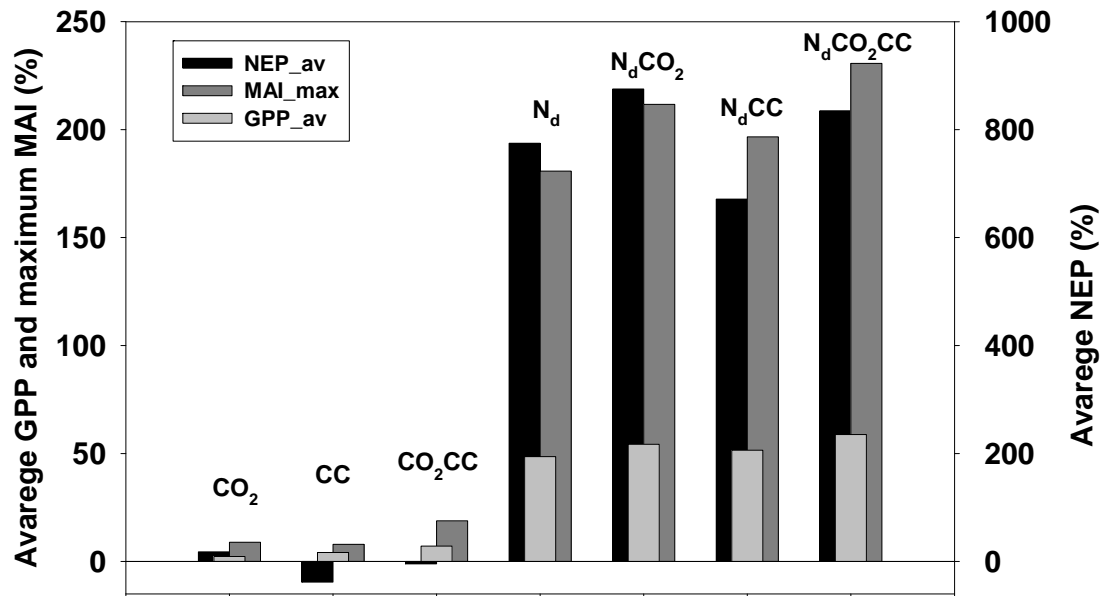
4.7 REFERENCES

Bedison JE, McNeil BE (2009) Is the growth of temperate forest trees enhanced along an ambient nitrogen deposition gradient? *Ecology*, **90**, 1736-1742.

Bending GD, Read DJ (1996) Nitrogen mobilization from protein-polyphenol complex by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry*, **28**, 1603-1612.

Bending GD, Read DJ (1997) Lignin and soluble phenolic degradation by ectomycorrhizal and ericoid mycorrhizal fungi. *Mycological Research*, **101**, 1348-1354.

Berbigier P, Loustau D Diawara A (1991) Etude microclimatique de l'effet de la sécheresse sur l'évaporation d'une platation de Pin maritime à sous-bois de Molinie. *Annales Des Sciences Forestieres*, **22**, 157-177.

Berbigier P, Bonnefond JM (1995) Measurement and modelling of radiation transmission within a stand of maritime pine (*Pinus pinaster* Aït.). *Annales Des Sciences Forestieres*, **52**, 23-42.

Berbigier P, Bonnefond JM, Mellmann P (2001) CO_2 and water vapour fluxes for 2 years above Euroflux forest site. *Agricultural and Forest Meteorology*, **108**, 183-197.

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environmental Review*, **5**, 1-15.

Bontemps JD, Hervé JC, Dhôte JF (2009) Long-term changes in forest productivity: a consistent assessment in even-aged stands. *Forest Science*, **55**, 549-564.

Bosc A (1999) Etude expérimentale du fonctionnement hydrique et carboné des organs aériens du Pin maritime (*Pinus pinaster* Aït.). Ph.D. Université Victor Segalen Bordeaux 2.

Bosc A, de Grandcourt A, Loustau D (2003) Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree. *Tree Physiology*, **23**, 227-236.

Boyce RL, Friedland AJ, Chamberlain CP, Poulson SR (1996) Direct canopy nitrogen uptake from N-15-labeled wet deposition by mature red spruce. *Canadian Journal of Forest Research*, **26**, 1539-1547.

Box GPE, Hunter WG, Hunter JS (1978) Statistics for Experimenters. An Introduction to Design, Data Analysis and Model Building. John Wiley & Sons, New York, 653 pp.

Brin A, Meredieu C, Dominique P, Brustel H, Jactel H (2008) Changes in quantitative patterns of dead wood in maritime pine plantations over time. *Forest Ecology and Management*, **256**, 913-921.

Burton AJ, Pregitzer KS, Hendrick RL (2000) Relationship between fine root dynamics and nitrogen availability in Michigan northern hardwood forests. *Oecologia*, **125**, 389-399.

Canadell JG, Le Quéré C, Raupach MR *et al.* (2007a) Contributions to accelerating atmospheric CO_2 growth economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866-18870.

Canadell JG, Pataki DE, Gifford R *et al.* (2007b) Saturation of the Terrestrial Carbon Sink. In: Canadell JG, Pataki D, Pitelka L (Eds), Terrestrial Ecosystems in a Changing World, The IGBP Series, Springer-Verlag, Berlin Heidelberg, New York, 59-78.

Ciais P, Schelhaas MJ, Zaehle S, Piao SL *et al.* (2008) Carbon accumulation in European forests. *Nature geoscience*, **1(7)**, 427-429.

Colpaert JV, Van Laere A (1996) A comparison of the extracellular enzyme activities of two ectomycorrhizal and a leaf-saprotrophic basidiomycete colonizing beech leaf litter. *New Phytologist*, **134**, 133-141.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behaviour of plant-soil models. *Ecological Application*, **3(4)**, 666-681.

Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005a) A processed-based model of nitrogen cycling in forest plantation Part I. Structure, calibration and analysis of the decomposition model. *Ecological Modelling*, **187**, 246-448.

Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005b) A processed-based model of nitrogen cycling in forest plantation Part II. Simulating growth and nitrogen mineralisation of *Eucalyptus globulus* plantations in south-western Australia. *Ecological Modelling*, **187**, 449-474.

Daniel C (1976) Application of Statistics to Industrial Experimentation. John Wiley & Sons, New York, 294 pp.

Davidson EA, Janssens IA (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440***,* 165-173.

Delzon S, Loustau D (2005) Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agricultural and Forest Meteorology* **129**, 105-119.

de Graaff MA, van Groeningen KJ, Six J, Hungate BA, van Kessel C (2006) Interactions between plant growth and soil nutrient cycling under elevated CO_2: a meta analysis. *Global Change Biology*, **12**, 2077-2091.

de Vries W, Reinds GJ, van der Salm C *et al.* (2001) Intensive Monitoring of Forest Ecosystems in Europe. Technical Report (2001). EC, UN/ECE, Brussels, Ginevra.

de Vries W, Solberg S, Dobbertin M *et al.* (2008) Ecologically implausible carbon sequestration? *Nature*, **541**, E1-E3.

Dewar RC, McMurtrie RE, (1996a) Analytical model of stemwood growth in relation to nitrogen supply. *Tree Physiologist* **16**, 161-171.

Dewar RC, McMurtrie RE, (1996b) Sustainable stemwood yield in relation to the nitrogen balance of forest plantations: a model analysis. *Tree Physiologist* **16**, 173-182.

Dezi S, Medlyn BE, Tonon G, Magnani F (2010) The effect of nitrogen deposition on forest carbon sequestration: a model-based analysis. *Global Change Biology*, **16**, 1470-1486.

Diawara A, Loustau D. Berbigier P (1991) Comparison of two methods for estimating the evaporation of a Pinus Pinaster (Ait) stand: Sap flow and energy balance with sensible heat flux measurements by eddy covariance method. *Annales Des Sciences Forestieres*, **54**, 49-66.

EEA (European Environmental Agency) (2009) CSI 012 - Global and European temperature - Assessment published Mar 2009

Farquhar GD, Von Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In Physiological plant ecology II: water relations and carbon assimilation. Edited by Lange O, Noble P, Osmond CB, Zieger. Encycl. Plant Physiol. 12B, 549-587.

Finzi AC, Norby RJ, Calfapietra C *et al.* (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences*, **104(35)**, 14014-14019.

Granier A, Loustau D (1994) Measuring and modelling the transpiration of maritime pine canopu from sapflow data. *Agricultural and Forest Meteorology* **71**, 61-81.

Hagedorn F, Spinnler D, Siegwolf R (2003) Increased N deposition retards mineralization of old soil organic matter. *Soil Biology and Biochemistry*, **35**, 1683-1692.

Harrison AF, Schulze E-D, Gebauer G, Bruckener G (2000) Canopy uptake and utilization of atmospheric pollution nitrogen. In: Schulze E-D, ed. Carbon and nitrogen cycling in European forest ecosystems. Ecological Studies 142. Berlin: Springer-Verlag, 171-188.

Henderson-Sellers A (1993) A factorial assessment of the sensitivity of the BATS land-surface parameterization scheme. *Journal of Climate*, **6**, 227-247.

Henderson-Sellers B, Henderson-Sellers A (1996) Sensitivity evaluation of environmental models using fractional factorial experimentation. *Ecological Modelling*, **86**, 291-295.

Högberg P (2007) Nitrogen impacts on forest carbon. *Nature*, **447**, 781-782.

Hyvönen R, Ågren GI, Linder S *et al.* (2007) 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 Phytologist*, **173**, 463-480.

Hyvönen R, Persson T, Andersson S, Olsson B, Ågren GI, Linder S (2008) Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. Biogeochemistry 89(1), 121-137.

Intergovernmental Panel on Climate Change, 2007. Climate Change: The Scientific Basis. Cambridge University Press, Cambridge, UK.

Jarvis P, Linder S (2000) Constraints to growth of boreal forests. *Nature*, **405**, 904-905.

Johnson DW (2006) Progressive N limitation in forests. Review and implications for long-term responses to elevated CO_2. *Ecology* **87(1)**, 64-75.

Kahle HP, Karjalainen T, Schuck A, Agren GI (2008) Causes and Consequences of Forest Growth Trends in Europe. European Forest Institute Research Project 21. Results of the RECOGNITION Project Brill, Leiden, Boston, vol. 21, 261 pp.

Katz C, Oren R, Schulze E-D, Milburn JA (1989a) Uptake of water and solutes through twigs of Picea abies (L.) Karst. *Trees* **3**, 33-37.

Katz C, Oren R, Schulze E-D, Steudle E (1989b) Uptake of Water and solutes through bark and needle surfaces. In Schulze E-D, Lange OL, Oren R (eds) Forest Decline and Air Pollution: A study of spruce (*Picea abies* (L.) Karst.) on acid soils. In: *Ecological Studies Series* Vol 77, pp 218-221, Springer Verlag, Berlin.

Kimball JS, Running SW, Nemani R (1997) An improved method for estimating surface humidity from daily minimum temperature. *Agricultural and Forest Meteorology*, **85**, 87-98.

Kirilenko AP, Sedjo Ra (2007) Climate changes impacts on forestry. *PNAS*, **104(50)**, 19697-19702.

Körner C (2006) Plant CO_2 responses: an issue of definition, time and resource supply. *New Phytologist* **172**, 393-411.

Laubhann D, Sterba H, Reinds GJ, de Vries W (2009) The impact of atmospheric deposition and climate on forest growth in European monitoring plots: An individual tree growth model. *Forest Ecology and management*, **258**, 1751-1761.

Lebourgeois F, Becker M, Chevalier R, Dupouey JL, Gilbert JM (2000) Height and radial growth trends of Corsican pine in western France. *Canadian Journal of Forest Research*, **30**, 712-724.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371-379.

Lemoine B, Décourt N (1969) Tables de production pour le pin maritime dans le sud-ouest de la France. *Revue Forestière Française* **21**, 5-17.

Leuning R (1995) A critical appraisal of a couple stomatal-photosynthesis model for C_3 plants. *Plant, Cell & Environmental*, **18**, 339-357.

Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Global Change Biology*, **13**, 2089-2109.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, **54**, 731-739.

Loustau D, Berbigier P, Granier A (1992a) Interception, throughfall and stemflow in a Maritime pine stand .II. An application of the Gash's model. *Journal of Hydrology*, **138**, 469-485.

Loustau D, Berbigier P, Granier A, El Jadj Moussa F (1992b) Interception, throughfall and stemflow in a Maritime pine stand. I. Variability of throughfall and stemflow. *Journal of Hydrology*, **138**, 449-467.

Loustau D, Granier A (1993) Environmental control of water flux through Maritime pine (*Pinus Pinaster* Ait.). In: Borghetti M, Grace J, Raschi A, ed. Water Transport in Plants under Climatic Stress. Cambridge University Press, 205-218.

Loustau D, Berbigier P, Kramer K (1997) Sensitivity of the water balance of southwestern France Maritime pine forest to climate. In: Mohren GMJ, Kramer K, Sabaté S (Ed), Impacts of Global Change on Tree Physiology and Forest. Kluwer Academic Publishers, Dordrecht, pp 193-207.

Loustau D, Domec JC, Bosc A (1998) Interpreting the variability of xylem sap flux density within the trunk of Maritime pine (*Pinus pinaster* Aït.): application for calculating the water flux at the tree and stand level. *Annales des Sciences Forestières*, **55**, 29-46.

Loustau D, Bosc A, Colin A *et al.* (2005) Modeling climate change effects on the potential production of French plains forests at the sub-regional level. *Tree Physiology*, **25**, 813-823.

Magnani F, Mencuccini M, Borghetti M *et al.* (2007) The Human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848-852.

McMurtrie RE, Rook DA, Kelliher FM (1990) Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen. *Forest Ecology and Management*, **30**, 381–413.

McMurtrie RE, Medlyn BE, Dewar RC (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 Physiology*, **21**, 831-839.

Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys MP (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research*, **30**, 873-888.

Medlyn BE, Loustau D, Delzon S (2002) Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Aït.). *Plant, Cell and Environment*, **25**, 1155-1165.

Medlyn BE, Berbigier P, Clement R *et al.* (2005) Carbon balance of coniferous forests growing in contrasting climates: Model-based analysis. *Agricultural and Forest Meteorology*, **131**, 97-124.

Mellert KH, Prietzel J, Straussberger R, Rehfuess KE (2004) Long-term nutritional trends of conifer stands in Europe: results from RECOGNITION project. *European Journal of Forest Research*, **123**, 305-319.

Mellert KH, Prietzel J, Straussberger R, Rehfuess KE, Kahle HP, Perez P, Spiecker H (2008) Relationship between long-term trends of air temperature, precipitation, nitrogen nutrient and growth of coniferous stands in Central Europe and Finland. *European Journal of Forest Research*, **127**, 507-524.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.

Milne R, Van Oijen AR (2005) A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. *Annales of Forest Science*, **62**, 911-923.

Morales P, Hickler T, Rowell DP, Smith B, Sykes MT (2007) Changes in European ecosystems productivity and carbon balance driven by regional climate model output. *Global Change Biology*, **13**, 108-122.

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981-1991. *Nature*, **386**, 698-702.

Nalder IA, Wein RW (2006) A model for the investigation of long-carbon dynamics in boreal forests of western Canada I. Model development and validation. *Ecological Modelling*, **192**, 37-66.

Nave LE, Vogel CS, Gough CM, Curtis PS (2009a) Contribution of atmospheric nitrogen deposition to net primary production in a northern hardwood forest. *Canadian Journal of Forest Research*, **39**, 1108-1118.

Nave LE, Vance ED, Swanston CW, Curtis PS (2009b) Inpacts of elevated N inputs on north temperate forest soil C storage, C/N, and net N-mineralization. *Geoderma*, **153**, 231-240.

Nellemann C, Thomsen MG (2001) Long-term changes in forest growth: potential effects of nitrogen deposition and acidification. *Water, Air and Soil Pollution*, **128**, 197-205.

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Pipper Sc *et al.* (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, **300**, 1560-1563.

Norby RJ, De Lucia EH, Gielen B *et al.* (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. *PNAS*, **102(50)**, 18052-18056.

Oren R, Ellsworth DS, Johnsen KH *et al.* (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. *Nature*, **411**, 469-472.

Palmroth S, Oren R, McCarthy HR *et al.* (2006) Aboveground sink strength in forests controls the allocation of carbon below ground and its $[CO_2]$-induced enhancement. *Proceedings of the National Academy of Sciences of the United States of America*, **103(51)**, 19362-19367.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173-1179.

Parton W.J, Scurlock JMO, Ojima DS *et al.* (1993) Observations and modelling of biomass and soil organic matter dynamic for the grassland biome worldwide. *Global Biogeochemistry Cycles*, **7**, 785-809.

Peschel W (1938) Die mathematischen methoden zur herleitung der wachstumsgesetze von baum und bestand und die ergebnisse ihrer anwendung. *Tharandter Forstliches Jahrbuch* **89**,169-247.

Porté A, Loustau D (1998) Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. *Tree Physiology*, **18**, 223-232.

Porté A (1999) Modelisation des effets du bilan hydrique sur la production primaire et la croissance d'un couvert de pins maritimer (*Pinus pinaster* Aït.) en lande humide. Ph.D. Universite d'Orsay, Pris XI.

Porté A, Trichet P. Bert D, Loustau D (2002) Allometric relationships from branch and tree woody biomass of Marine pine (*Pinus pinaster* Aït.). *Forest Ecology and Management*, **158**, 71-83.

Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forest: biome patterns related to forest age. *Global Change Biology*, **10**, 2052-2077.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80(6)**, 1955-1969.

Rehfuess KE, Ágren GI, Andersson F *et al.* (1999) Relationships between recent changes of growth and nutrition of Norway spruce, Scots pine and European beech forests in Europe – RECOGNITION. Working Paper 19, European Forest Institute, Joensuu, Finland, 94 pp.

Rustad LE, Campell JL, Marion GM *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia, **126**, 543-562.

Ryan MG, Binkley D, Fownes JH, Giardina CP, Senock RS (2004) An experimental test of the causes of forest growth decline with stand age.. *Ecological Monographs*, **74**, 393-414.

Sands PJ (1995) Modelling canopy production II. From single-leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology*, **22**, 603-614.

Saxe H, Cannel MGR, Johnsen Ø, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369-400.

Schulze ED,Wirth C, Heimann M (2000) Managing forests after Kyoto. *Science*, **289**, 2058–2059.

Sievering H, Tomaszewski T, Torizzo J (2007) Canopy uptake of atmospheric N deposition at conifer forest: part I – canopy N budget, hotosynthetic efficiency and net ecosystem exchange. *Tellus B*, **59(3)**, 483-492.

Solberg S, Andreassen K, Clarke N, Torseth K, Tveito OE, Strand GH, Tomter S (2004) The possible influence of nitrogen and acid deposition on forest growth in Norway. *Forest Ecology and Management*, **192**, 241-249.

Solberg S, Dobbertin M, Reinds GJ *et al.* (2009) Analysis of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: A stand growth approach. *Forest Ecology and Management*, **258**, 1735-1750.

Sparks JP (2009) Ecological ramifications of the direct foliar uptake of nitrogen. *Oecologia* **159**, 1-13.

Spiecker H, Mielikäinen K, Kölh M, Skovsgaard JP (1996) Growth trends in European forests. Studies from 12 Countries. Research Report 5. Springer-Varlag, Berlin, Heidelberg, 372 pp.

Spiecker H (1999) Overview of recent growth trends in European forests. *Water, Air and Soil Pollution*, **116**, 33-46.

Spiecker H (2002) Tree rings and forest management in Europe. *Dentrochronologia*, **20/1-2**, 191-202.

Sitch S, Huntingford C, Gedney N *et al.* (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Changes Biology*, **14**, 2015-2039

Sutton MA, Simpson D, Levy PE, Smith RI, Reis S, van Oijen M, de Vries W (2008) Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, **14**, 1-7.

Thomas RQ, Canham CD, Weathers KC, Goodale CL (2010) Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience*, **3**, 13-17.

Thornley JHM (1991) A transport-resistance model forest growth and partitioning. *Annals of Botany*, **68**, 211-226.

Trichet P, Bakker MR, Augusto L, Alazar P, Merzeau D, Suar E (2009) Fifty year of fertilization experiments on *Pinus pinaster* in southwest France: the importance of phosphorus as a fertilizer. *Forest Science*, **55**, 390-402.

Van Oijen M, Jandl R (2004) Nitrogen fluxes in tow Norway spruce stands in Austria: an analysis by means of process-based modelling. *Austrian Journal of Forest Science*, **121**, 167-182.

Van Oijen M, Cannell MGR, Levy PE (2004) Modelling biogeochemical cycles in forests: state of art and perspectives. In: Andersson F, Birot Y, Päivinen R (Eds.), Towards the Sustainable Use of European's Forests-Forest Ecosystems and Landscape Research: Scientific Challenges and Opportunities. European Forest Institute, 157-169.

Van Oijen M, Agren GI, Chertov O, Kellomäki S, Komarov A, Mobbs DC, Murray MB (2008) Evaluation of past and future changes in European forests growth by means of four process-based models. In: Karjalainen T, Schuck A (Eds.). Causes and Consequences of Forest Growth in Europe – Results of RECOGNITION Project (Chapter 4.4), 183-199.

Wilson EJ, Tiley C (1998) Foliar uptake of wet-deposited nitrogen by Norway spruce: An experiment using N-15. *Atmospheric Environment*, **32,** 513-518.

Zaehle S, Bondeau A, Carter TR *et al.* (2007) Projected Changes in Terrestrial Carbon Storage in Europe under Climate and Land-use Change, 1990-200. *Ecosystems*, **10**, 380-401

CHAPTER 5

Discussion and conclusions

5.1 DISCUSSION AND CONCLUSIONS

Boreal and temperate forest ecosystems are currently an important carbon (C) sink. To be able to predict the future course of this sink, we need to identify the major driving factors. Potential drivers that have been identified include increasing atmospheric CO_2, temperature, N deposition and changes in management practices. Although several studies have investigated these effects of these factors individually on forest growth, there is still no consensus on their relative importance for forest NPP and C sequestration during recent decades, and how that might change in future.

The overall aim of this thesis project was to develop a simple ecosystem model which explicitly incorporates our best understanding of the impacts of N deposition, $[CO_2]$, temperature and forest management on forest functions, and to use it to investigate the sensitivity of the forest system to these factors and their interactions. Model code is presented in Appendix I.

To this end, a new version of the Generic Decomposition and Yield (G'DAY) model, originally developed by Comins & McMurtrie (1993), was developed. Unlike very process-specific models, such as MAESTRO (Wang & Jarvis, 1990), which provide very detailed simulations of canopy photosynthesis but not other processes, or very complex ecosystem models, such as the Edinburgh Forest Model (Thornley, 1991), which requires 261 parameters (Milne & Van Oijen, 2005), the G'DAY model represents a simple complete ecosystem model. It simulates tree and soil carbon and nitrogen dynamics over time using a limited number of equations and parameters. This simple model approach was appropriate for this study because it can adequately represent the aspect of ecosystem functions I was interested in and at the same time it is relatively simple to modifiedy, its behaviour is understandable and explicable in terms of the underlying assumptions. Moreover the model has been already tested against the daily version of CENTURY (Pepper *et al.,* 2005; Parton *et al.,* 1998) and validated against observation datasets (Corbeels *et al.,* 2005a, b, c).

In chapter 2 of this thesis, the model was applied to investigate the effects of N deposition on N limited forest C sequestration. The model was modified to take into account recent scientific advances in understanding of some key processes. In particular, it was used to examine the sensitivity of model predictions to assumptions about canopy nitrogen uptake, forest C allocation, canopy N uptake, leaf trait relationships, forest management, and leaching. Model simulations showed a strong relationship between net ecosystem production and N deposition, which was mediated by canopy N uptake, C allocation and forest management. In contrast, the model

predictions were not sensitive to assumptions about leaf trait relationships or leaching. Simulations with the model clearly show that assessment of forest ecosystem C sequestration must take into account effects of atmospheric N deposition, in particular for N-limited forests. For this purpose it is critical to know about forest management and N deposition history, since most of the northern temperate forests are, or have been, managed, and N is the most significant growth-limiting nutrient in many forests worldwide (LeBauer & Treseder, 2008). No comparisons with data are shown in the paper, since the model was here used as a tool to understand processes. However, comparing the values of leaf N concentration for low level of N deposition, under the assumption of canopy nitrogen uptake, I found a good correspondence with the vales observed by Calanni *et al.* (1999). The qualitative analysis undertaken identifies two key areas of uncertainty regarding forest ecophysiological processes considered by the model, namely canopy N uptake and C allocation. C allocation has long been identified as an important processes in forest response to N enrichment (Levy *et al.*, 2004; Milne & Van Oijen, 2005) requiring better information. The model formulation we chose for carbon allocation relates carbon allocated to root directly to NPP and already incorporate the CO_2 effect (Palmroth *et al.*, 2006), while the N deposition effect is directly related to NPP. We preferred this approach to that taken in other models (e.g. Thornley, 1991; Landsberg & Waring, 1997; Milne & van Oijen, 2005), in which root allocation is an explicit function of age and environmental factors, because of the advantage of its simplicity and of its empirical foundation. Canopy N uptake has been modelled previously using transport-resistance approaches to reproduce the instantaneous bi-directional exchange of N between leaves and atmosphere (Sutton *et al.*, 1998, 2009; Flechard *et al.*, 1999; Riedo *et al.*, 2002). However, the fine temporal scale and the level of detail of these models make them unsuitable for inclusion in a relatively simple forest ecosystem model. Despite the ability of these models to provide detailed hourly estimates of canopy N exchange, they are not complete ecosystem models, as they do not represent all the plant and soil feedbacks. I can therefore state that this is the first time that the canopy N uptake has been explicitly considered in a forest ecosystem model. Although the canopy N uptake formulation used in my thesis is relatively simple, the estimate assumed in the model of about 50% of total (wet+dry) deposition that could be absorbed through canopy N uptake is in line with results from the ICP-Forest monitoring network. Data from this network, which are based on the canopy budget approach, show that canopy exchange for both NO_3 and NH_4 is on average of the same order of magnitude of N throughfall, except for very high N deposition levels (De Vries *et al.,* 2001). More understanding of the potential relevant

processes identified by this model analysis, combined with a test of the assumptions presented in this chapter against more detailed models, is needed to reduce model uncertainty. In particular, research should focus on the formulation of canopy N uptake, replacing the the dependence on vegetation cover fraction c with the the dependence on LAI effect on wet and dry deposition, possible saturation effects and their relationship with canopy closure, meteorological conditions and plant internal N status on wet and dry deposition, and the inclusion of the N soil saturation effect on leaching and soil respiration.

In chapter 3, the G'DAY model was used to investigate the effect of elevated CO_2 and N interactions on forest productivity. The model was tested against data from the closed-canopy Sweetgum (*Liquidambar styraciflua* L.) plantation FACE experiment at Oak Ridge National Laboratory (ORNL). To achieve this comparison, the model was adapted to simulate deciduous forest processes, and a new sub-model (MATE) was introduced to simulate climate and CO_2 impacts on photosynthesis on short (experimental) timescales. Model results show that the model does not adequately represent the short-term transient response to a step increase in $[CO_2]$ at the ORNL site. While the model can reproduce the observed decline in NPP at ambient $[CO_2]$, which was caused by declining soil N availability as the stand aged, it failed to reproduce the observed short-term stimulation in productivity at elevated $[CO_2]$. Analysis of the mechanisms involved indicated a likely reason for the model failures was incorrect parameterization and/or formulation of the soil N uptake function. The observed short-term $[CO_2]$-induced increase in productivity was supported by enhanced N uptake at depth, which was not captured by the model. To correctly capture this response, an improved formulation for N availability and root N uptake as function of depth is needed. A possible alternative approach that can help to overcome the limitations of G'DAY to capture some of the ORNL responses is represented by the use of optimization models (Franklin, 2007; McMurtrie *et al.*, 2008) to investigate the optimum root depth and allocation patterns. Although the model failed to simulate the observed transient $[CO_2]$ response in this experimental system, the model is known to capture longer-term reduction in the $[CO_2]$ effect on productivity (Comins & McMurtrie, 1993; McMurtrie *et al.*, 2000, 2001; Medlyn *et al.*, 2000; Pepper *et al.*, 2005), indicating that it is still valid for simulating long-term responses to gradually increasing $[CO_2]$. It is debatable whether a relatively generic forest ecosystem, such as the G'DAY model, given its simplicity, is able to reproduce short-term response. However such relatively simple models represent very useful tools to explore and analyse model behaviour in

relation to new assumptions and different environmental factors, also when they fail to reproduce observed data trends.

In chapter 4 the model was applied to investigate the combined effects of observed increases in N deposition, atmospheric [CO_2] and air temperature on productivity and C storage of a maritime pine forest during recent decades. The aim was to analyse the relative importance of these drivers for the C cycle in the past, giving a basis for predictions of how the sink is likely to change in future. Simulations results showed that enhanced N availability could explain the observed increase in forest growth rates. Model simulations allowed us also to discriminate between the different mechanisms responsible for such an increase in N availability, and their relative importance. In particular, increasing N deposition was found to greatly increase N availability both through direct canopy uptake, which produces a short term stimulation effect on forest growth, and through stimulation of net soil N mineralization, which produces a long term effect on forest growth. In addition, increased temperature was found to enhance N availability, but at a lower rate than N deposition. Finally, the observed increase in atmospheric [CO_2] was found to be important only when N was not limiting, as a result of either N deposition or higher temperatures and faster N mineralization rates.

I should stress here that the analysis undertaken in this thesis project is a qualitative analysis in which the model was mainly used as a tool to understand processes and explore their potential relevance for forest productivity, without attempting to quantitatively reproduce real data. In this context, simulating model responses to step changes are very useful because they allow straightforward analysis of model outputs. However, experimental data sets on the response of forest ecosystems to long-term N fertilization are indeed available (Hyvönen *et al.,* 2008), which are conceptually similar to the step increase in N deposition that we have simulated in the chapter 2, and they will be analyzed in future developments.

I should also stress that I have only shown the output variables that are most important for the purpose of the particular analysis. Therefore, for example, in chapter 2, where the analysis aim was to show the effect of the new assumptions on C-fluxes, fluxes are shown rather than state variables, as these represent the integral of fluxes over time and therefore are less sensitive to short-term changes in forcing conditions. On the other hand, in chapter 4, where the aim was to relate the increase in forest productivity and forest growth of different environmental drivers, also the values of total system carbon, wood carbon and mean annual increment are shown.

General conclusions

The large variety of forest ecosystem models in existence illustrates that the selection of a model should carefully be matched with analysis objectives. Models provide a versatile means to quantify how ecosystem processes may vary and affect forest growth and other properties. No single model, however, should be expected to apply to all situations.

The model developed for this thesis project appears to be an effective tool for analysis of the effects of a range of environmental drivers on carbon sequestration by forest ecosystems. Although the model failed to reproduce the specific transient $[CO_2]$ response at the ORNL site, it is nonetheless valuable for simulating long-term impacts on rising $[CO_2]$ on forest stands.

Model results show that N availability has a key role in determining forest ecosystem C sequestration. Moreover, the model demonstrates that atmospheric N deposition has an important role to play in enhancing N availability, in particular for N-limited forests. Although N deposition rates are predicted to decrease in near future, the fertilizing effect due to past N deposition is likely to continue for some decades. Therefore, assessments of the forest ecosystem C sink over the next century need to consider the role of atmospheric N deposition. Rising temperature also increases C storage by enhancing soil N availability but at a lower rate than N deposition, while increasing $[CO_2]$ significantly affects forest growth and C storage only when N availability is not limiting.

An important role of modelling is to identify key process uncertainties. In this thesis, model analysis demonstrated that there are several important uncertainties in our understanding of forest ecophysiological processes that require further investigation and improved model representations. In particular, the processes of C allocation, canopy N uptake and root N uptake at depth have a critical role in determining the C storage capacity of forest ecosystems. Better knowledge of these processes is needed if we are to improve our understanding of, and predictive capacity for, the forest carbon sink.

5.2 REFERENCES

Calanni J, Berg M, Wood M, Mangis D, Boyce R, Weathers W, Sievering H (1999) Atmospheric nitrogen deposition at a conifer forest: response of free amino acids in Engelmann spruce needles. *Environmental Pollution*, **105**, 79-89.

Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited forests to CO_2 enrichment; equilibrium behaviour of plant-soil models. *Ecological Application*, **3(4)**, 666-681.

Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005a) A processed-based model of nitrogen cycling in forest plantation Part I. Structure, calibration and analysis of the decomposition model. *Ecological Modelling*, **187**, 246-448.

Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005b) A processed-based model of nitrogen cycling in forest plantation Part II. Simulating growth and nitrogen mineralisation of *Eucalyptus globulus* plantations in south-western Australia. *Ecological Modelling*, **187**, 449-474.

Corbeels M, McMurtrie RE, Pepper DA, Mendham DS, Grove TS, O'Connell AM (2005c) Long-term changes in productivity under different harvest residue and nitrogen management practices: a model analysis. *Ecological Modelling*, **217**, 1-18.

De Vries W, Reinds GJ, van der Salm C, et al (2001) *Intensive Monitoring of Forest Ecosystems in Europe. Technical Report 2001*. EC, UN/ECE, Brussels, Geneva.

Flechard CR, Fowel D, Sutton MA, Cape JN (1999) A dynamic chemical model of bi-directional ammonia exchange between semi-natural vegetation and the atmosphere. *Quarterly Journal of the Royal Meteorological Society*, **125 (559)**, 2611-2641.

Franklin O (2007) Optimal nitrogen allocation controls tree responses to elevated CO2. *New Phytologist*, **174**, 811-822.

Hyvönen R, Persson T, Andrsson S, Olsson B, Ågren GI, Linder S (2008) Impact of long-term nitrogen addition on carbon stock in trees and soils in northern Europe. *Biogeochemistry*, **89(1)**, 121-137.

Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Landsberg JJ, Waring RH, Coops NC (2003) Performance orf the forest productivity model 3-PG applied to wide range of forest types. *Forest Ecology and Management*, **172**, 199-214.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**, 371-379

Levy PE, Wendler R., van Oijen M, Cannel MGR, Millard P (2004) The effect of nitrogen enrichment on the carbon sink in coniferous forests: uncertainty and sensitivity analyses of three ecosystem models. *Water, Air and Soil Pollution*, **4**, 67-74.

McMurtrie RE, Dewar RC, Medlyn BE, Jeffreys MP (2000) Effects of elevated [CO_2] on forest growth and carbon storage: a modeling analysis of the consequences of changes in litter quality/quantity and root exudation. *Plant and Soil*, **224**, 135-152.

McMurtrie RE, Medlyn BE, Dewar RC (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 Physiology*, **21**, 831-839.

McMurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM (2008) Why is plant-growth response to elevated CO_2 amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. *Functional Plant Biology*, **35**, 521-534.

Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys MP (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research*, **30(6)**, 873-888.

Milne R, Van Oijen AR (2005) A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. *Annales of Forest Science*, **62**, 911-923.

Palmroth S, Oren R, McCarthy HR *et al.* (2006) Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO_2]-induced enhancement.

Proceedings of the National Academy of Sciences of the United States of America, **103(51)**, 19362-19367.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal*, **51**, 1173-1179.

Pepper DA, Del Grosso SJ, McMurtrie RE, Parton WJ (2005) Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO_2], temperature and nitrogen input. *Global Biogeochemical Cycles*, **19**, GB1004, doi:10.1029/2004GB002226.

Riedo M, Milford C, Schmid M, Sutton MA (2002) Coupling soil-plant-atmosphere exchange of ammonia with ecosystem functioning in grasslands. *Ecological Modelling*, 158, 83-110.

Sutton MA, Burkhardt JK, Guerin D, Nemitz E, Foeler D (1998) Development of forest resistance models to describe measurements of bi-directional ammonia surface-atmosphere exchange. *Atmospheric Environmental*, **32(3)**, 473-480.

Sutton MA, Nemitz E, Milford C, Campbell C *et al.* (2009) Dynamics of ammonia exchange with cut grassland: synthesis of results and conclusions of the GRAMINAE Integrated Experiment. *Biogeosciences*, **6**, 2907-2934.

Thornley JHM (1991) A transport-resistance model of forest growth and partitioning. *Annals of Botany*, **68**, 211-226.

Wang YP, Javis PG (1990) Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: Application of a model (MAESTRO). *Tree Physiology*, **7**, 297-317.

Waring RH, Running SW (2007) Comparison of forest ecosystem model. In: Waring RH, Running SW (2007) (Eds), Forest ecosystems: analysis at multiple scales, third edition, Elsevier Academic Press, Oxford, UK, 96-98.

CHAPTER 6

Appendix 1: the model code

6.1 THE G'DAY MODEL CODE

```
C   MAIN PROGRAM GDAY
C   Author: Silvia Dezi
C   Date:    17.01.2007
C   Purpose: implementation of a new version of the G'DAY (Generic
C   Decomposition and Yield) model, a process-based model that simulates carbon
C   (C) and nitrogen (N) dynamics in a forest ecosystem (Comins & McMurtrie
C   1993). The new version explicitly incorporates our best understanding of
C   the impacts of N deposition, [CO2], temperature and forest management on
C   forest functions, and to use it to investigate the sensitivity of the
C   forest system to these factors and their interactions.
C   The G'DAY model links the plant production model of McMurtrie & Wolf (1983)
C   & McMurtrie (1985,1991),to CENTURY, the soil-carbon-nutrient model of
C   Parton et al. (1987,1993). The plant sub-model consists of three pools:
C   foliage, wood (stem, branches and coarse roots) and fine roots. The soil
C   sub-model consists of four litter pools (structural and metabolic, both
C   above and below ground), three soil organic matter pools with different
C   turnover time (active, slow and passive) of C and N content, and a pool for
C   available inorganic N. The model consists of a set of difference equations
C   describing the dynamics C  of tree and soil components. These components
C   are denoted by lower-case subscripts, as follows:
C   -Tree biomass components: foliage "f", wood "w" and fine roots "r"
C   -Four litter fractions: surface structural "u", soil structural "v",
C   surface metabolic "m", soil metabolic "n"
C   -Soil organic matter pools: active "a", slow "s", passive "p".
C   The rate of nitrogen uptake by trees depends on the rate at which soil
C   mineral nitrogen is made available and on the root carbon (Dewar and
C   McMurtrie,1996).
C   Allocation of carbon to the root pool is based on NPP (Palmroth et
C   al.2006).
C   Specific leaf area (SLA) and foliar mortality are based on foliar nitrogen
C   concentration (Reich et al.1999).
C   Canopy nitrogen uptake (CNU)is given by the mathematical product of canopy
C   nitrogen uptake efficiency, the fraction vegetation cover and the nitrogen
C   deposition.
C   Forest management is represented as thinning or/and clear cut. Thinning is
C   given by the exportation of dead woody stems from the system, while
C   branches and course roots of harvested trees enter litter pools. After the
C   clear cut no litter is left in the system.
C   Mineral nitrogen pool is divided in two different pools, an ammonium and a
C   nitrate pool,and the divided mineralization influx between these pools in
C   based on the soil C:N ratio (Aber et al.2003).
C   The increase in N deposition input is by step.
C   There are both the daily and yearly output.
C   This version is parameterized to simulate the equilibrium state and 200
C   years simulation for Bray (1801-2000)
C
C
C   ARGUMENTS
C
C   A           soil activity coefficient (-)
C   APAR        fraction of PAR intercepted (-)
C   B           exponential coefficient in etar equation (m2 y kgC-1)
C   c           fractional vegetation cover (-)
C   Ca          C content of active soil pool (kgC m-2)
C   Cf          C content of foliage (kgC m-2)
C   Cm          C content of surface metabolic litter (kgC m-2)
C   Cn          C content of soil metabolic litter (kgC m-2)
C   CNU         canopy nitrogen uptake efficency (kgN m-2 d-1)
C   CNU_e       canopy nitrogen uptake efficency (-)
C   CN_soil     average N:C ratio in mineral+organis soil (kg N / kg C)
C   CO2         atmospheric CO2 concentration (umol mol-1)
C   Cp          C content of passive soil pool (kgC m-2)
C   Cr          C content of roots (kgC m-2)
C   Cs          C content of slow soil pool (kgC m-2)
```

```
C  Cu         C content of surface structural litter (kgC m-2)
C  Cv         C content of soil structural litter (kgC m-2)
C  Cw         C content of wood (kgC m-2)
C  d          etaw/etaf (-)
C  daylen     daylength (h d-1)
C  DeltaES    slope of sat vapour pressure vs temperatue at mean daily
C             temperature (kPa K-1)
C  di         decay rates of litter and soil pools (d-1)
C  Ef         segmented function for dependence of LUE on foliage N/C (-)
C  e0         potential PAR utilisation efficiency (dry mass basis; kg MJ-1)
C  eps        ratio of the increase of latent heat content to increase of
C             sensible heat content of saturated air (DeltaES/gamma)(-)
C  etaf       allocation coefficient to foliage (-)
C  etar       allocation coefficient to roots (-)
C  etaw       allocation coefficient to wood (-)
C  Ev         daily evaporation (from equilibrium ev) (kg m-2 d-1 = mm d-1)
C  f          NPP/GPP ratio (-)
C  FC         filed capacity (m3/m3)
C  f_BR       fraction of wood carbon in branches (-)
C  f_CR       fraction of wood carbon in coarse roots (-)
C  FLAG2      CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1 Ur+CNU; FLAG2=2 CNU=0.)
C  fnit       fraction of nitrification (-)
C  Fwev       reduction factor of Ev due to soil moisture (-, between 0 and
C             1)
C  Fwev_min   effect of soil water on grass LUE & ground evap - Relative PAW
C             in top-soil layer for min(-)
C  Fwev_max   effect of soil water on grass LUE & ground evap - Relative PAW
C             in top-soil layer for max(-)
C  Fwr        moisture factor in belowground and SOM decomposition factors
C             (-)
C  Fwrmax     relative water content in rooting zone above which
C             decomposition is not limited by
C             moisture (-)(Corbeels et al/a 2005)
C  Fwrmin     relative water content in rooting zone below which there is no
C             decomposer activity (-)(Corbeels et al/a 2005)
C  Fwts       moisture factor in top soil layer decomposition factors for (-)
C  Fwtsmax    relative water content in top soil layer above which
C             decomposition is not limited by moisture (-)(Corbeels et al
C             2005a)
C  Fwtsmin    relative water content in top soil layer below which there is
C             no decomposer activity (-)(Corbeels et al/a 2005)
C  g          albedo (used in calculating Radnet)(-)
C  gamaw      fixed mortality/thinning coefficient for wood (y-1)
C  gamma      psychrometric constant (Pa K-1)
C  gammaf     fixed mortality coefficient for foliage (d-1)
C  gammar     fixed mortality coefficient for roots (d-1)
C  gammaw     fixed mortality/thinning coefficient for wood (d-1)
C  GPP        gross primary production (kgC m-2 d-1)
C  Iamm       flux of N entering ammonia nitrogen pool (kgN m-2 d-1)
C  Ijc        flux of C entering pool j (kgC m-2 d-1)
C  Ijn        flux of N entering pool j (kgN m-2 d-1)
C  Igmin      gross mineralisation flux (kgN m-2 d-1)
C  Il         rainfall interception per unit LAI (mm d-1)
C  Imm        N immobilization flux (kgN m-2 d-1)
C  Init       flux of N entering nitrate nitrogen pool (kgN m-2 d-1)
C  Inmin      net mineralisation flux (kgN m-2 d-1)
C  Jamm       flux of N leaving ammonia N pool (kgN m-2 d-1)
C  Jinon      flux of N leaving N inorganic (kgN m-2 d-1)
C  Jjc        flux of C leaving pool j (kgC m-2 d-1)
C  Jjn        flux of N leaving pool j (kgN m-2 d-1)
C  Jnit       flux of N leaving nitrate N pool (kgN m-2 d-1)
C  k          light extinction coefficient (-)
C  Kn         reducing decay rate coefficient of slow and passive soil polls
C             deposition (d-1)
C  Kr         value of root carbon at which 50% of the available N is taken
C             up (kgC m-2)
C  LAI        leaf aere index (m2 m-2)
```

```
C  lambda      latent heat of vapourisation (J kg-1)
C  lambdaf     ratio of litter N/C to live N/C for foliage (-)
C  lambdar     ratio of litter N/C to live N/C for roots (-)
C  lambdaloss  constant rate for N loss (d-1)
C  lambdau     constant rate for N uptake (d-1)
C  lambdawm    1-N re-translocated from wood (-)
C  Lfl         lignin to biomass ratio in leaf litter (-)
C  livesr      fixed life span coefficient for fine roots (y)
C  lmbdaloss   constant rate for N loss (Y-1)
C  lmbdau      constant rate for N uptake (y-1)
C  Lrl         lignin to biomass ratio in root litter (-)
C  Mng         forest management (yes=1;no=0) (-)
C  Na          N content of active soil pool (kgN m-2)
C  Namm        N content of ammonia nitrogen pool (kgN m-2)
C  NC_a0max    maximum N/C of newly SOM for active soil pool (kgN kg-1C)
C  NC_s0max    maximum N/C of newly SOM for slow soil pool (kgN kg-1C)
C  NC_p0max    maximum N/C of newly SOM for passive soil pool (kgN kg-1C)
C  NC_a0min    minimum N/C of newly SOM for active soil pool (kgN kg-1C)
C  NC_s0min    minimum N/C of newly SOM for slow soil pool (kgN kg-1C)
C  NC_p0min    minimum N/C of newly SOM for passive soil pool (kgN kg-1C)
C  NC_a0       N/C of newly SOM for active soil pool (kgN kg-1C)
C  NC_s0       N/C of newly SOM for slow soil pool (kgN kg-1C)
C  NC_p0       N/C of newly SOM for passive soil pool (kgN kg-1C)
C  NC_f        N/C for foliage (kgN kg-1C)
C  NC_fmax     maximum N/C for foliage, above which N content is not limiting
C              (kgN kg-1C)
C  NC_fmin     minimum N/C for foliage (kgN kg-1C)
C  NC_m        N/C for surface metabolic litter pool (kgN kg-1C)
C  NC_m0max    maximum N/C for surface metabolic litter pool (kgN kg-1C)
C  NC_m0min    minimum N/C for surface metabolic litter pool (kgN kg-1C)
C  NC_n        N/C for soil metabolic litter pool (kgN kg-1C)
C  NC_n0max    maximum N/C for soil metabolic litter pool (kgN kg-1C)
C  NC_n0min    minimum N/C for soil metabolic litter pool (kgN kg-1C)
C  NC_r        N/C for roots (kgN kg-1C)
C  NC_u        N/C for surface structural litter pool(kgN kg-1C)
C  NC_v        N/C for soil structural litter pool(kgN kg-1C)
C  NC_wnew     N/C for new wood as function of N/C for foliage (-)
C  NC_wnewa    intercept of relationship between N/C for new wood and N/C for
C              foliage
C  NC_wnewb    slop of relationship between N/C for new wood and N/C for
C              foliage
C  NC_ws       N/C for stuctural wood as function of N/C for foliage
C  NC_wsa      intercept of relationship between N/C for stuctural wood and
C              N/C for foliage
C  NC_wsb      slop of relationship between N/C for structural wood and N/C
C              for foliage
C  Ncrit       critical value for inorganic N (kgN m-2)
C  NEEP        net ecosystem production (kgC m-2 y-1)
C  NEP         net ecosystem production (kgC m-2 d-1)
C  Nf          N content of foliage (kgN m-2)
C  Nin         N input into the system for deposition or fixation (kgN m-2
C              d-1)
C  Nino        inorganic N (kgN m-2)
C  Nloss       loss of N for leaching or denitrification (kgN m-2 d-1)
C  Nlooss      loss of N for leaching or denitrification (kgN m-2 y-1)
C  Nm          N content of surface metabolic pool (kgN m-2)
C  Nn          N content of soil metabolic pool (kgN m-2)
C  Nnit        N content of nitrate nitrogen pool (kgN m-2)
C  Np          N content of passive soil pool (kgN m-2)
C  Nr          N content of roots (kgN m-2)
C  Ns          N content of slow soil pool (kgN m-2)
C  Nu          N content of surface structural pool (kgN m-2)
C  Nv          N content of soil structural pool (kgN m-2)
C  Nw          N content of wood (kgN m-2)
C  NPP         net primary production (kgC m-2 d-1)
C  Ntree       total N content of the tree (KgN m-2)
C  PAR         incident photosyntetically active radiation (MJ m-2 d-1)
c  PAWr        plant available water in root zone (mm)
```

```
C  PAWrmax      maximum plant available water in rooting zone (mm)
c  PAWts        plant available water in top soil layer (mm)
c  PAWtsmax     maximum plant available water in top soil layer (mm)
C  pij          fraction of C flow from C pool j into C pool i (-)
C  PN           annual net primary production (kgC m-2 y-1)
C  PG           annual gross primary production (kgC m-2 yr-1)
C  Q            coefficient in etar equation
C  qe           fraction of tree water uptake from top-soil layer (-)
C  R            nitrogen re-translocation rate (kgN m-2 d1)
C  Ra           autotrophic respiration (kgC m-2 d-1)
C  RAA          autotrophic respiration (kgC m-2 y-1)
C  Radlong      net long-wave radiation (MJ m-2 d-1)(for daylen h)
C  Radnet       net radiation (MJ m-2 d-1)
C  rain         daily precipitation (mm d-1)
C  raineff      daily effective rainfall (mm d-1)
C  Rg           ideal gas constant (J mol-1 °K-1)
C  Rh           heterotrophic respiration (kgC m-2 d-1)
C  RHH          heterotrophic respiration (kgC m-2 y-1)
C  ro           ratio of N/C of roots to that of foliage (-)
C  rotation     rotation length applied during initialization (y)
C  Rv           ideal gas constant for water vapour (J kg-1 °K-1)
C  rw           retranslocation rate of mobile wood N (y-1)
C  rwm          retranslocation rate of mobile wood N (d-1)
C  sd           soil depth (m), containing at least 75% of the root system
C  SLA          spacific keaf area (m2 kgC-1)
C  T            soil texture parameter (-)
C  Ta           air temperature for AM period (°C)
C  Tair         average air temperature equal to (Ta+Tp)/2 (°C)
C  Tk           average air temperature equal to (Ta+Tp)/2 (°K)
C  Tp           air temperature for PM period (°C)
C  Tr           plant transpiration (mm d-1)
C  Tsoil        average soil temperature (°C)
C  T0           0°C express in °K (°K)
C  Ur           total root nitrogen uptake (kgN m-2 d-1)
C  Uramm        root ammonia nitrogen uptake from (kgN m-2 d-1)
C  Urnit        root nitrate nitrogen uptake from (kgN m-2 d-1)
C  U            uptake rate of plant available nitrogen (kgN m-2 d-1)
C  UU           uptake rate of plant available nitrogen (kgN m-2 y-1)
C  VPDa         vapour pressure deficit for AM period (kPa)
C  VPDp         vapour pressure deficit for PM period (kPa)
C  w            C content of biomass (kgC kg-1DM)+
C  WCr          soil water content in root zone (m3/m3)
C  WP           wilting point (m3/m3)
C  WUE          mean water use efficiency(kgC m-2 mm-1)
C  years        number of 200 years cycles for computation (y)
C  Y0           costant in etar equation
C

       PROGRAM GDAY

C     ----------------------------------------------------------------------
C     Declare variables and parameters
C     ----------------------------------------------------------------------
C      REAL PAR(18262),Tsoil(18262),Ninn(18262),meteo(11,18262),year(50) !For
C      equilibrium state
C      REAL Nina(18262),Ta(18262),Tp(18262),VPDa(18262),VPDp(18262) !For
C      equilibrium state
C      REAL CO2a(18262),CO2e(18262),Nine(18262),CO2(18262),rain(18262) !For
C      equilibrium state
       REAL PAR(73050),Tsoil(73050),Ninn(73050),meteo(18,73050),year(200) !For
       200 years simulation
       REAL Nina(73050),Ta(73050),Tp(73050),VPDa(73050),VPDp(73050) !For 200
       years simulation
       REAL CO2a(73050),CO2e(73050),Nine(73050),CO2(73050),rain(73050) !For 200
       years simulation
       REAL PARa(73050),PARe(73050),Tsoila(73050),Tsoile(73050) !For 200 years
       simulation
```

```
         REAL raina(73050),raine(73050),Taa(73050),Tae(73050),Tpa(73050) !For 200
         years simulation
         REAL Tpe(73050),VPDaa(73050),VPDae(73050),VPDpa(73050) !For 200 years
         simulation
         REAL VPDpe(73050)
         REAL e0,APAR,Ef,k,SLA,Cf,w,NC_f,GPP,NPP,f,Ifc,etaf
         REAL Jfc,Cw,Lfl,Cm,Lrl,pau,pam,psu,psv,Nf,Nr,R
         REAL gammaf,Irc,etar,Jrc,gammar,Cr,Iwc,etaw,Jwc,gammaw
         REAL lambdaf,puf,A,du,Cu,Iuc,Juc,pmf,dm,Imc,Jmc
         REAL lambdar,pvr,NC_r,dv,Cv,Ivc,Jvc,pnr,dn,Cn,inc,Jnc
         REAL pav,pan,T,pas,pap,da,Ca,Iac,Jac,ds,dp,Cs,Cp,psa
         REAL Isc,Jsc,ppa,pps,Ipc,Jpc,Rh,NEP,ro,Iwn,Jwn,Nw
         REAL U,Ifn,Jfn,Irn,Jrn,Ntree,NC_u,NC_v,Iun,Jun
         REAL Nu,Ivn,Jvn,Nv,Imn,Jmn,Nm,NC_m,Nn,Jnn,NC_n
         REAL NC_a0max,NC_s0max,NC_p0max,NC_a0min,NC_s0min
         REAL NC_p0min,Jsn,Ipn,Jpn,FC,WP,sd,PAWtsmax
         REAL NC_a0,NC_s0,NC_p0,Ncrit,Nino,Na,Ns,Np,Ian,Jan,Isn
         REAL Iinon,Jinon,Nin,Nloss,lambdaloss,lambdau
         REAL PG,PN,x,RAA,RHH,NEEP,UU,Nlooss,NC_fmax,NC_fmin
         REAL d,Kr,rotation,f_BR,f_CR,c,CNU_e,CNU,g,PAWrmax
         REAL Ur,B,Q,Y0,Kn,Igmin,Inmin,Iamm,Init,PPN
         REAL Uramm,Urnit,Nnit,Namm,fnit,Jamm,Jnit,CN_soil
         REAL Nws,Nwm,NC_wnew,NC_ws,NC_wnewb,NC_wsb,rwm
         REAL Jwns,Jwnm,Iwns,Iwnm,lambdawm,gammaww,fixu,fixv,fix_relm
         REAL daay,dd,vv(730),zz(730),SUM,lmbdaloss,lmbdau,livesr
         REAL NC_m0max,NC_m0min,NC_n0max,NC_n0min,fix_reln,gamaw
         REAL Fwrmax,Fwrmin,Fwtsmax,Fwtsmin,PAWr,PAWts,WUE,Tair,Tk
         REAL lambda,gamma,Tr,LAI,raineff,Il,daylen,Radlong,Radnet
         REAL DeltaES,eps,Fwev,Fwev_max,Fwev_min,ev,Fwr,Fwts,qe,WCr
         INTEGER h,n,years,FLAG,Mng,coppice,FLAG2,m,day,daayy
         CHARACTER*84 IPARMS,SOILTYPE,IVALUES,IVALUESS
         PARAMETER (PI=3.1415926536,Rg=8.3144472,T0=273.15,Rv=461.5)

C        ---------------------
C        Open files for output
C        ---------------------
         OPEN(10,file='Output_C_ag_y.txt',status='unknown')
         OPEN(20,file='Output_C_bg_y.txt',status='unknown')
         OPEN(30,file='Output_N_ag_y.txt',status='unknown')
         OPEN(40,file='Output_N_bg_y.txt',status='unknown')
         OPEN(35,file='Output_C_ag_d.txt',status='unknown')
         OPEN(45,file='Output_C_bg_d.txt',status='unknown')
         OPEN(55,file='Output_N_ag_d.txt',status='unknown')
         OPEN(75,file='Output_N_bg_d.txt',status='unknown')

C        --------------------------------------------------------------------
C        Print to file headings of output variables and corresponding units
C        --------------------------------------------------------------------
         WRITE(10,*)'GPP ','NPP ','Ra ','Rh ','NEP ','Cf ','Cr ','Cw ','gammar ',
     *        'LUE ','PAWr ','PAWts '
         WRITE(10,*)'kgC/m2yr ','kgC/m2yr ','kgC/m2yr ','kgC/m2yr ', ,'kgC/m2yr '
     *        , 'kgC/m2   ','kgC/m2   ','kgC/m2   ','d-1 ','kgC/MJPAR ','mm
     *        ','mm '
         WRITE(20,*)'Cu ','Cm ','Cv ','Cn ','Ca ','Cs ','Cp ','etaf ','etar '
         WRITE(20,*)'kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2
     *        ','kgC/m2 ','- ','- '
         WRITE(30,*)'Nf ','Nr ','Nw ','Ntree ','NC_f ','U ','etaw ','SLA ',
     *        'gammaf ','Nws ','Nwm ','Namm ','Nnit '
         WRITE(30,*)'kgN/m2 ','kgN/m2 ','kgN/kgC ','kgN/m2yr ','- ','m2/kgC ','d-
     *        1 ','kgN/m2yr ','kgN/m2yr '
         WRITE(40,*)'Nu ','Nm ','Nv ','Nn ','Na ','Ns ','Np ','Nino ','Nloss ',
     *        'CNU ','kgN/m2 ','kgN/m2 '
         WRITE(40,*)'kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ',
     *        'kgN/m2 ','kgN/m2 ','kgN/m2yr ','kgN/m2d ','kgN/m2 ','kgN/m2 '
         WRITE(35,*)'GPP ','NPP ','Ra ','Rh ','NEP ','Cf ','Cr ','Cw ','gammar ',
     *        'LUE ','J25 ','Vc25 ','PAWr ','PAWts '
         WRITE(35,*)'kgC/m2d ','kgC/m2d ','kgC/m2d ','kgC/m2d ','kgC/m2d ', *
     *        'kgC/m2 ','kgC/m2 ','kgC/m2 ','d-1 ','kgC/MJPAR ','mm ','mm '
```

```
         WRITE(45,*)'Cu ','Cm ','Cv ','Cn ','Ca ','Cs ','Cp ','etaf ','etar ', *
               'alfam ','alfapm '
         WRITE(45,*)'kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2 ','kgC/m2
         *       ','kgC/m2 ','- ','- ','molCO2/molPAR ','molCO2/molPAR '
         WRITE(55,*)'Nf ','Nr ','Nw ','Ntree ','NC_f ','U ','etaw ','SLA ', *
               'gammaf ','GrossMin ','NetMin ','kgN/kgC '
         WRITE(55,*)'kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2d ','- ', *
               'm2/kgC ','d-1 ','kgN/m2d ','kgN/m2d '
         WRITE(75,*)'Nu ','Nm ','Nv ','Nn ','Na ','Ns ','Np ','Nino ','Nloss ', *
               'CNU ','Namm ','Nnit '
         WRITE(75,*)'kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ','kgN/m2 ',
         *       'kgN/m2 ','kgN/m2 ','kgN/m2d ','kgN/m2d ','kgN/m2 ','kgN/m2 '

C        ------------------------
C        Input parms and variables
C        ------------------------
C        OPEN(15,file='years50.txt',status='old') !For equilibrium state
         OPEN(15,file='years1801-2000.txt',status='old') !For 200 years
          simulation
         READ(15,*)year
C        OPEN(25,file='meteodata50.txt',status='old') !For equilibrium state
         OPEN(25,file='meteodata1801-2000.txt',status='old') !For 200 years
          simulation
         READ(25,*) meteo
C        DO 10 i=1,18262        !For equilibrium state
         DO 10 i=1,73050        !For 200 years simulation
          PARa(i)= meteo(1,i)/1000000./2. !incident photosyntetically active
           radiation for model initialization(MJ m-2 d-1)
          PARe(i)= meteo(2,i)/1000000./2. !incident photosyntetically active
           radiation historical trend(MJ m-2 d-1)
C        PAR(i)= meteo(1,i)*0.217  !incident photosyntetically active radiation
          (MJ m-2 d-1) if the input is in mol m-2 d-1
          Tsoila(i)= meteo(3,i)       !average soil temperature for model
           initialization(°C)
          Tsoile(i)= meteo(4,i)       !average soil temperature historical
           trand(°C)
          raina(i)= meteo(5,i)        !daily precipitation for model
           initialization(mm d-1)
          raine(i)= meteo(6,i)        !daily precipitation historical trend(mm d-1)
          Taa(i)= meteo(7,i)          !air temperature for AM period for model
           initialization(°C)
          Tae(i)= meteo(8,i)          !air temperature for AM period historical
           trend(°C)
          Tpa(i)= meteo(9,i)          !air temperature for PM period for model
           initialization(°C)
          Tpe(i)= meteo(10,i)         !air temperature for PM periods historical
           trend(°C)
          VPDaa(i)= meteo(11,i)/1000.  !vapour pressure deficit for AM period for
           model initialization(kPa)
          VPDae(i)= meteo(12,i)/1000.  !vapour pressure deficit for AM period
           historical trend(kPa)
          VPDpa(i)= meteo(13,i)/1000.  !vapour pressure deficit for PM period for
           model initialization(kPa)
          VPDpe(i)= meteo(14,i)/1000.  !vapour pressure deficit for PM period
           historical trend(kPa)
          CO2a(i)= meteo(15,i)         !atmospheric CO2 concentration for model
           initialization(umol mol-1)
          CO2e(i)= meteo(16,i)         !atmospheric CO2 historical trend (umol
           mol-1)
          Nina(i)= meteo(17,i)/1000.  !N input for deposition or fixation for
           model initialization (kgN m-2 y-1)
          Nine(i)= meteo(18,i)/1000.  !N input for deposition or fixation
           historical trend (kgN m-2 y-1)
10       CONTINUE
         PAR= PARe
         Tsoil= Tsoile
         rain= raine
```

```
        Ta= Tae
        Tp= Tpe
        VPDa= VPDae
        VPDp= VPDpe
        CO2= CO2e
        Ninn= Nine


C       -----------------
C       Define parameters
C       -----------------
        IPARMS='C:\My Projects\gDAY\BRAYf\parms Bray.txt'
        CALL RDINIT (1 ,0 ,IPARMS)
        CALL RDSREA('k'        , k          ) !light extinction coefficient (-)
        CALL RDSREA('w'        , w          ) !C content of biomass (kgC kg-1DM)
        CALL RDSREA('f'        , f          ) !NPP/GPP ratio (-)
        CALL RDSREA('d'        , d          ) !etaw/etaf (-)
        CALL RDSREA('ro'       , ro         ) !ratio of N/C of roots to that of
        foliage (-)
        CALL RDSREA('NCfmax'   , NC_fmax    ) !maximum N/C for foliage, above
        which N content is not limiting(kgN kg-1C)
        CALL RDSREA('NCfmin'   , NC_fmin    ) !minimum N/C for foliage (kgN kg-
        1C)
        CALL RDSREA('Lfl'      , Lfl        ) !lignin to biomass ratio in leaf
        litter (-)
        CALL RDSREA('lambf'    , lambdaf    ) !ratio of litter N/C to live N/C
        for foliage (-)
        CALL RDSREA('lambr'    , lambdar    ) !ratio of litter N/C to live N/C
        for roots (-)
        CALL RDSREA('fBR'      , f_BR       ) !fraction of wood carbon in
        branches (-)
        CALL RDSREA('fCR'      , f_CR       ) !fraction of wood carbon in coarse
        roots (-)
        CALL RDSREA('T'        , T          ) !soil texture parameter (silt +
        clay fraction)(-)
        CALL RDSREA('c'        , c          ) !fractional vegetation cover (-)
        CALL RDSREA('CNUe'     , CNU_e      ) !canopy nitrogen uptake efficiency
        (-)
        CALL RDSREA('sd'       , sd         ) !soil depth (m), containing at
        least 75% of the root system
        CALL RDSREA('lloss'    , lmbdaloss  ) !constant rate for N loss (y-1)
        CALL RDSREA('lambu'    , lmbdau     ) !constant rate for N uptake (y-1)
        CALL RDSREA('livesr'   , livesr     ) !fixed life span coefficient for
        fine roots (y)
        CALL RDSREA('Ncrit'    , Ncrit      ) !fixed life span coefficient for
        fine roots (y)
        CALL RDSREA('Kr'       , Kr         ) !fixed life span coefficient for
        fine roots (y)
        CALL RDSREA('NCwnwa'   , NC_wnewa   ) !intercept of relationship between
        N/C for new wood and N/C for foliage
        CALL RDSREA('NCwnwb'   , NC_wnewb   ) !slop of relationship between N/C
        for new wood and N/C for foliage
        CALL RDSREA('NCwsa'    , NC_wsa     ) !intercept of relationship between
        N/C for structural wood and N/C for foliage (-)
        CALL RDSREA('NCwsb'    , NC_wsb     ) !slop of relationship between N/C
        for structural wood and N/C for foliage (-)
        CALL RDSREA('rwm'      , rw         ) !retranslocation rate of mobile
        wood N (y-1)
        CALL RDSREA('FC   '    , FC         ) !field capacity (m3 m-3)
        CALL RDSREA('WP'       , WP         ) !wilting point (m3 m-3)
        CALL RDSREA('Il'       , Il         ) !rainfall interception per unit LAI
        (mm d-1)
        CALL RDSREA('g'        , g          ) !albedo (used in calculating
        Radnet)(-)
        CALL RDSREA('qe'       , qe         ) !fraction of tree water uptake from
        top-soil layer (-)
        CALL RDSREA('FevM'     , Fwev_max   ) !effect of soil water on grass LUE
        & ground evap - Relative PAW in top-soil layer for max(-)
        CALL RDSREA('Fevmi'    , Fwev_min   ) !effect of soil water on grass LUE
```

```
      & ground evap - Relative PAW in top-soil layer for min(-)
      CLOSE (1)
      days= 365.

      PAWrmax= (FC-WP)*sd*1000.  !maximum plant available water in rooting
      zone (mm)
      PAWtsmax= PAWrmax/2.        !maximum plant available water in top soil
      layer (mm)
      Fwrmax= 0.7    !relative water content in rooting zone above which
      decomposition is not limited by moisture (-)(Corbeels et al/a 2005)
      Fwrmin= 0.1    !relative water content in rooting zone below which there
      is no decomposer activity (-)(Corbeels et al/a 2005)
      Fwtsmax= 0.5   !relative water content in top soil layer above which
      decomposition is not limited by moisture (-)(Corbeels et al/a 2005)
      Fwtsmin= 0.    !relative water content inj top soil layer below which
      there is no decomposer activity (-)(Corbeels et al/a 2005)
      B= 2.309        !exponential coefficient in etar equation (m2 yr kgC-1)
      (Palmroth et al.2006)
      Q= 9.499        !coefficient in etar equation (Palmroth et al.2006)
      Y0= 0.138       !costant in etar equation (Palmroth et al.2006)
      NC_u= 1./150. !N/C for surface structural litter pool(kgN kg-1C) (Comins
      & McMurtrie,1993)
      NC_v= 1./150. !N/C for soil structural litter pool (kgN kg-1C) (Comins &
      McMurtrie,1993)
      NC_m0max= 1./10.   !maximum N/C metabolic surface litter pool(kgN kg-1C)
      NC_m0min= 1./25.   !minimum N/C metabolic surface litter pool(kgN kg-1C)
      NC_n0max= 1./10.     !maximum N/C metabolic soil litter pool(kgN kg-1C)
      NC_n0min= 1./25.     !minimum N/C metabolic soil litter pool (kgN kg-1C)
C     New ranges of soil N:C ratios as a function of soil mineral N, valid for
C     forest ecosystems (see CENTURY slides)
      NC_a0max= 1./8.       !maximum N/C of newly SOM for active soil pool (kgN
      kg-1C) (Nalder & Wein 2006)
      NC_a0min= 1./16.      !minimum N/C of newly SOM for active soil pool (kgN
      kg-1C) (Nalder & Wein 2006)
      NC_s0max= 1./12.       !maximum N/C of newly SOM for slow soil pool
      (kgN kg-1C) (Nalder & Wein 2006)
      NC_s0min= 1./40.      !minimum N/C of newly SOM for slow soil pool (kgN
      kg-1C) (Nalder & Wein 2006)
      NC_p0max= 1./6.       !maximum N/C of newly SOM for passive soil pool
      (kgN kg-1C) (Nalder & Wein 2006)
      NC_p0min= 1./20.      !minimum N/C of newly SOM for passive soil pool
      (kgN kg-1C) (Nalder & Wein 2006)
      Lrl= 0.127+ 0.393*Lfl  !lignin to biomass ratio in root litter (-) (as a
      function of leaf lignin; Newman & Hart,2006)
      gamaw=0.

C     ----------------------------------------------------
C     Initial variables and parameters for initialization
C     ----------------------------------------------------
C     IVALUES='C:\My Projects\gDAY\BRAYf\Invalueseql.txt' !For equilibrium
C     state
      IVALUES='C:\My Projects\gDAY\BRAYf\Invalues.txt'    !For 200 years
      Simulation
      CALL RDINIT (1 ,0 ,IVALUES)
      CALL RDSREA('Namm'    , Namm      ) !N content of ammonia nitrogen pool
      (kgN m-2)
      CALL RDSREA('Nnit'    , Nnit      ) !N content of nitrate nitrogen pool
      (kgN m-2)
      CALL RDSREA('Cf'      , Cf        ) !plant C pools (kgC m-2)
      CALL RDSREA('Cr'      , Cr        )
      CALL RDSREA('Cw'      , Cw        )
      CALL RDSREA('Cu'      , Cu        ) !litter C pools (kgC m-2)(High value
      for initialization)=10*(Flakaliden, Eliasson et al.2005,fig.7)
      CALL RDSREA('Cm'      , Cm        )
      CALL RDSREA('Cv'      , Cv        )
      CALL RDSREA('Cn'      , Cn        )
      CALL RDSREA('Ca'      , Ca        ) !soil C pools (kgC m-2) (High value
```

```
        for initialization)
        CALL RDSREA('Cs'       , Cs        )
        CALL RDSREA('Cp'       , Cp        )
        CALL RDSREA('NCf'      , NC_f      ) !N/C for foliage (kgN kg-1C)
        CALL RDSREA('Nf'       , Nf        ) !N content of foliage (kgN m-2)
        CALL RDSREA('Nr'       , Nr        ) !N content of roots (kgN m-2)
        CALL RDSREA('Nm'       , Nm        ) !N content of surface metabolic
        litter pool (kgN m-2)
        CALL RDSREA('Nn'       , Nn        ) !N content of soil metabolic litter
        pool (kgN m-2)
        CALL RDSREA('Nu'       , Nu        ) !N content of surface structural
        litter pool (kgN m-2)
        CALL RDSREA('Nv'       , Nv        ) !N content of soil structural litter
        pool (kgN m-2)
        CALL RDSREA('Na'       , Na        ) !N content of active soil pool (kgN
        m-2)
        CALL RDSREA('Ns'       , Ns        ) !N content of slow soil pool (kgN
        m-2)
        CALL RDSREA('Np'       , Np        ) !N content of passive soil pool (kgN
        m-2)
        CALL RDSREA('NPP'      , PPN       ) !net primary production of the
        previous year (for allocation Palmroth et al.2006) (kgC m-2 d-1)
        CLOSE (1)

C       --------------------
C       Initialize variables
C       --------------------
        Nino= Namm+Nnit     !inorganic N (kgN m-2)
        IF (Nino.LE.0.) THEN
         NC_a0= NC_a0min  !N/C of new SOM entering active soil pool (kgN kg-1C)
         NC_s0= NC_s0min  !N/C of new SOM entering slow soil pool (kgN kg-1C)
         NC_p0= NC_p0min  !N/C of new SOM entering passive soil pool (kgN kg-1C)
        ELSE IF (Nino.GT.Ncrit) THEN
         NC_a0= NC_a0max
         NC_s0= NC_s0max
         NC_p0= NC_p0max
        ELSE
         NC_a0= 1./(1./NC_a0min+(1./NC_a0max-1./NC_a0min)*(Nino/Ncrit))
         NC_s0= 1./(1./NC_s0min+(1./NC_s0max-1./NC_s0min)*(Nino/Ncrit))
         NC_p0= 1./(1./NC_p0min+(1./NC_p0max-1./NC_p0min)*(Nino/Ncrit))
        END IF
        NC_r= ro*NC_f                    !N/C for roots (kgN kg-1C)
        NC_wnew= NC_wnewa+NC_wnewb*NC_f  !N/C for new wood as function of N/C
        for foliage (-)(Medlyn et al 2000)
        NC_ws= NC_wsba+NC_wsb*NC_f       !N/C for structural wood as function of
        N/C for foliage (-)(Medlyn et al 2000)
        gammaw= (gamaw/days)      !fixed mortality coefficient for wood (d-1)
        rwm= (rw/days)            !re-translocation rate of mobile wood N (d-1)
        (McMurtrie et al 2000)
        lambdawm= gammaw/(gammaw+rwm)  !1-N re-translocated from wood (-)
        Nw= Nwm+Nws                    !N content of wood (kgN m-2)
        NPP= 0.                        !net primary production (kgC m-2 d-1)
        Kn= 1.                         !reducing decay rate coefficient of slow
        and passive soil (-)
        PAWr= PAWrmax          !plant available water in root zone (mm)
        PAWts= PAWtsmax        !plant available water in top soil layer (mm)
        WCr= PAWr/sd/1000.+wp  !soil water content in root zone (m3/m3)

C       -------------------------------------
C       Runtime parameters for initialization
C       -------------------------------------
C       FLAG=0.          !control marker (FLAG=0 equilibrium; FLAG=1 simulation)
        years= 1500      !number of 50 years cycles for equilibrium state
        years= 1.        !number of 200 years cycles for 200 years simulation
C       Nin= (0.0004/days) !N input into the system for deposition or fixation
        during model initialization (kgN m-2 d-1)
        rotation= 50     !rotation length applied during initialization (y)
        coppice= 0.
```

```
           Mng= 0.          !forest management (yes=1;no=0) (-)
           FLAG2= 1.   !CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1 Ur+CNU; FLAG2=2
           CNU=0.)
           vv= 0.         !variable using in computing C allocation
           SUM= 0.        !variable using in computing C allocation

           lmbdaloss=0.05*lmbdau/0.95

C          --------------------
C          Start of simulations
C          --------------------
50         CONTINUE
           m= 1                !simulating years count
           DO 100,h=1,years
            day= 1             !simulating days count (1 to 365/6*years) and starting
            day for daily simulations
C           DO 90,i=1,50       !For equilibrium state
            DO 90,i=1,200      !For 200 years simulation
             daay= year(i)/4.   !computing number of days per years
             daayy= year(i)/4.
             dd= daay/daayy
             IF (dd.eq.1.) THEN
              days= 366
             ELSE
              days= 365
             END IF
             mng=0             !forest management (yes=1;no=0) (-)
             gamaw=0.          !fixed mortality coefficient for wood (y-1)
C           --------------------------
C           Imposing periodic thinning
C           --------------------------
             IF ((i.EQ.24).OR.(i.EQ.74).OR.(i.EQ.124).OR.(i.EQ.174)) THEN
              mng= 1           !forest management (yes=1;no=0) (-)
              gamaw= 0.15      !fixed mortality/thinning coefficient for wood (y-1)
             END IF
             IF ((i.EQ.30).OR.(i.EQ.80).OR.(i.EQ.130).OR.(i.EQ.180)) THEN
              mng= 1           !forest management (yes=1;no=0) (-)
              gamaw= 0.14      !fixed mortality/thinning coefficient for wood (y-1)
             END IF
             IF ((i.EQ.35).OR.(i.EQ.85).OR.(i.EQ.135).OR.(i.EQ.185)) THEN
              mng= 1           !forest management (yes=1;no=0) (-)
              gamaw= 0.12      !fixed mortality/thinning coefficient for wood (y-1)
             END IF
             IF ((i.EQ.40).OR.(i.EQ.90).OR.(i.EQ.140).OR.(i.EQ.190)) THEN
              mng= 1           !forest management (yes=1;no=0) (-)
              gamaw= 0.05      !fixed mortality/thinning coefficient for wood (y-1)
             END IF
             IF ((i.EQ.45).OR.(i.EQ.95).OR.(i.EQ.145).OR.(i.EQ.195)) THEN
              mng= 1           !forest management (yes=1;no=0) (-)
              gamaw= 0.05      !fixed mortality/thinning coefficient for wood (y-1)
             END IF
             lambdaloss= (lmbdaloss/days    !constant rate for N loss (d-1)
             gammar= 1./(livesr*days)  !fixed mortality coefficient for roots (d-1)
             lambdau= (lmbdau/days)     !constant rate for N uptake (d-1)
             gammaw= (gamaw/days)       !fixed mortality/thinning coefficient for
             wood (d-1)
             rwm= (rw/days)             !re-translocation rate of mobile wood N (d-
             1) (McMurtrie et al 2000)
             lambdawm= gammaw/(gammaw+rwm)  !1-N re-translocated from wood (-)
             Nin=(Ninn(day)/days)                  !N input into the system for
             deposition or fixation (kgN m-2 d-1)
             gammaf= 1./2./days        !fixed mortality coefficient for foliage (d-1)
             IF (FLAG2.EQ.2.) THEN     !CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1
              Ur+CNU; FLAG2=2 CNU=0.)
              CNU= 0.
             ELSE
              CNU= Nin*c*CNU_e         !CNU efficiency (kgN m-2 d-1)
```

```
          END IF
C         Reset to zero all annual fluxes
          PG= 0.            !annual gross primary production (kgC m-2 yr-1)
          PN= 0.            !annual net primary production (kgC m-2 y-1)
          RAA= 0.           !autotrophic respiration (kgC m-2 y-1)
          RHH= 0.           !heterotrophic respiration (kgC m-2 y-1)
          NEEP= 0.          !net ecosystem production (kgC m-2 y-1)
          UU= 0.            !uptake rate of plant available nitrogen (kgN m-2 y-1)
          Nlooss= 0.     !loss of N for leaching or denitrification (kgN m-2 y-1)
          DO 70,n=1,days
           IF (NC_f.GT.NC_fmax) THEN    !segmented function for dependence of LUE
             on foliage N/C (-)
            Ef= 1.
           ELSE IF (NC_f.LE.0.) THEN
            Ef= 1.E-6
           ELSE
            Ef= NC_f/NC_fmax
           END IF
           Ef= 1.

           etar= 1./(1.+1./(f*(Y0+Q*exp(-B*PPN))))  !allocation coefficient to
           root (-)(Palmroth et al.2006)
C          etaf= (1-etar)/(1.+d)          !allocation coefficient to foliage (-)
C          etaw= d*etaf                   !allocation coefficient to wood (-)
           etaf= 0.26                     !allocation coefficient to foliage (-)
           IF ((etar+etaf).GT.1.) THEN
            etar= 1.-etaf                      !allocation coefficient to root (-)
           END IF
           etaw= 1.-etar-etaf                  !allocation coefficient to wood (-)
C          SLA= 767.6565*NC_f**1.0889 !specific leaf area (m2 kg-1C)(from Reich
C           et al 1999) Fitting on data
           SLA= 11.2/w            !specific leaf area (m2 total leaf area  kg-1C)
C          gammaf= (1./(0.0108*NC_f**(-1.424)))/days        !variable mortality
C           coefficient for foliage(d-1)(from Reich et al 1999)Fitting on data
           LAI= SLA*Cf/2.57             !leaf aere index (m2 m-2)


           CALL MATE(k,e0,NC_f,days,day,Ta(day),Tp(day),VPDa(day),VPDp(day),
      *       CO2(day),PAR(day),SLA,WUE,WCr,FC,WP,daylen,J25,VC25,alfam,alfpm)

C          ------------------------------------
C          Compute transpiration & evaporation
C          ------------------------------------
           (Ta+Tp)/2(°C)
           Tk= Tair+T0           !average air temperature equal to (Ta+Tp)/2 (°K)
           lambda= 2513000.-2367.*Tair    !latent heat of vapourisation (J kg-1)
           gamma= 66.+0.05*Tair                 !psychrometric constant (Pa K-1)
           raineff= MAX(0.,rain(day)-LAI*Il) !daily effective rainfall (mm d-1)
           Radlong= (107.-0.3*Tair)*daylen*3.6/1000.    !net long-wave radiation
           (MJ m-2 d-1)(for 12 h)(Priciples of environmental physics)
           Radnet=MAX(0.,((1.-g)*PAR(day)*2.-Radlong))   !net radiation (MJ m-2
           d-1)
           DeltaES= 0.611*(lambda/Rv)*(1/(Tk**2))*exp((lambda/Rv)*
      *       ((Tk-T0)/(T0*Tk)))    !slope of sat vapour pressure vs
               temperature at mean daily temperature (kPa K-1)
           eps= DeltaES*1000./gamma !ratio of the increase of latent heat
            content to increase of sensible heat content of saturated
            air(DeltaES/gamma)(-)
           Fwev= MIN(1.,MAX(0.,(PAWts/PAWtsmax-Fwev_min)/ (Fwev_max-Fwev_min)))
            !reduction factor of Ev due to soil moisture (-, between 0 and 1)
           Ev= eps*Radnet/(eps+1.)/lambda*1000000.     !daily evaporation (from
           equilibrium ev) (kg m-2 d-1 = mm d-1)
           Ev= Ev*EXP(-0.398*LAI)*Fwev            !daily evaporation corrected for
            canopy shading and for soil moisture(kg m-2 d-1 = mm d-1)
           Ev= min(Ev,PAWts+raineff)

C          --------------------------
C          Fluxes in plant C dynamics
C          --------------------------
```

```
            APAR= 1.-exp(-k*SLA*Cf/2.57)   !fraction of PAR intercepted (-)
            GPP= PAR(day)*e0*APAR*Ef        !gross primary production (kgC m-2 d-1)
            NPP= GPP*f                      !net primary production (kgC m-2 d-1)
            Ra= GPP*(1-f)                   !autotrophic respiration (kgC m-2 d-1)
            Ifc= NPP*etaf        !flux of C entering pool foliage (kgC m-2 d-1)
            Irc= NPP*etar        !flux of C entering pool roots (kgC m-2 d-1)
            Iwc= NPP*etaw        !flux of C entering pool wood (kgC m-2 d-1)
            Jfc= Cf*gammaf       !flux of C leaving pool foliage (kgC m-2 d-1)
            Jrc= Cr*gammar       !flux of C leaving pool roots (kgC m-2 d-1)
            Jwc= Cw*gammaw       !flux of C leaving pool wood (kgC m-2 d-1)
            Tr= GPP/WUE          !plant transpiration (mm d-1)

C           -------------------------------------------------------------
C           Fluxes in soil and litter C dynamics  (Comins & McMurtrie,1993)
C           -------------------------------------------------------------
            IF (Tsoil(day).LT.0.) THEN
             A= 0.
            ELSE
             A=0.0326+0.00351*(Tsoil(day)**1.652)-((Tsoil(day)/41.748)**7.19)
             !soil activity coefficient (-)
            END IF

            Fwts= MIN(1.,MAX(0.,(PAWts/PAWtsmax-Fwtsmin)/(Fwtsmax-Fwtsmin)))
             !moisture factor in top soil layer decomposition factors for (-)
C           -------------------------------------------
C           Flux partitioning to litter and soil pools
C           -------------------------------------------
            puf= 0.15+0.018*Lfl/(w*lambdaf*NC_f)  !fraction of C flow from C
             foliage pool into C surface structural pool (-)
            IF(puf.GT.1.) puf= 1.                 !constrain its value between 0-1
            IF(puf.LT.0.) puf= 0.
            pmf= 1.-puf    !fraction of C flow from C foliage pool into C surface
             metabolic pool (-)
            pvr= 0.15+0.018*Lrl/(w*lambdar*NC_r)  !fraction of C flow from C root
             pool into C soil structural pool (-)
            IF (pvr.GT.1.) pvr= 1.                !constrain its value between 0-1
            IF (pvr.LT.0.) pvr= 0.
            pnr= 1.-pvr         !fraction of C flow from C root pool into C soil
             metabolic pool (-)
            pau= 0.55*(1-Lfl)       !fraction of C flow from C surface structural
             pool into C active soil pool (-)
            pam= 0.45              !fraction of C flow from C surface metabolic pool
             into C active soil pool (-)
            pav= 0.45*(1-Lrl)    !fraction of C flow from C soil structural pool
             into C active soil pool (-)
            pan= 0.45              !fraction of C flow from C soil metabolic pool
             into C active soil pool (-)
            pas= 0.42              !fraction of C flow from C slow soil pool into C
             active soil pool (-)
            pap= 0.45              !fraction of C flow from C passive soil pool into
             C active soil pool (-)
            psa= 0.996-(0.85-0.68*T) !fraction of C flow from C active soil pool
             into C slow soil pool (-)
            psu= 0.7*Lfl               !fraction of C flow from C surface structural
             pool into C slow soil pool (-)
            psv= 0.7*Lrl         !fraction of C flow from C soil structural pool
             into C slow soil pool  (-)
            ppa= 0.004          !fraction of C flow from C active soil pool into C
             passive soil pool (-)
            pps= 0.03              !fraction of C flow from C slow soil pool into C
             passive soil pool (-)

C           ------------
C           Decay rates
C           ------------
            du= 0.076*A*exp(-3*Lfl)/7.    !decay rates of surface structural pool
             (d-1)
```

```
           dm= 0.28*A/7.             !decay rates of surface metabolic pool (d-1)
           dv= 0.094*A*exp(-3*Lrl)/7.*Fwts   !decay rates of soil structural
            pool (d-1)
           dn= 0.35*A/7.*Fwts             !decay rates of soil metabolic pool (d-1)
           da= 0.14*A*(1-0.75*T)/7.*Fwts !decay rates of active soil pool (d-1)
           ds= 0.0038*A*kn/7.*Fwts       !decay rates of slow soil pool (d-1)
           dp= 0.00013*A*Kn/7.*Fwts      !decay rates of passive soil pool (d-1)


C          -----------------
C          Flux computation
C          -----------------
           Juc= du*Cu    !flux of C leaving surface structural pool (kgC m-2 d-1)
           Jmc= dm*Cm    !flux of C leaving surface metabolic pool (kgC m-2 d-1)
           Jvc= dv*Cv    !flux of C leaving soil structural pool (kgC m-2 d-1)
           Jnc= dn*Cn    !flux of C leaving soil metabolic pool (kgC m-2 d-1)
           Jac= da*Ca    !flux of C leaving soil active pool (kgC m-2 d-1)
           Jsc= ds*Cs    !flux of C leaving soil slow pool (kgC m-2 d-1)
           Jpc= dp*Cp    !flux of C leaving soil passive pool (kgC m-2 d-1)
           IF (Mng.EQ.1) THEN
            Iuc= puf*Jfc+f_BR*Jwc    !flux of C entering surface structural pool
             (kgC m-2 d-1)
           ELSE
            Iuc= puf*Jfc+Jwc*(1-f_CR)
           END IF
           Imc= pmf*Jfc    !flux of C entering surface metabolic pool (kgC m-2
            d-1)
           Ivc= pvr*Jrc + f_CR*Jwc  !flux of C entering soil structural pool
            (kgC m-2 d-1)
           Inc= pnr*Jrc    !flux of C entering soil metabolic pool (kgC m-2 d-1)
           Iac= pau*Juc+pam*Jmc+pav*Jvc+pan*Jnc+pas*Jsc+pap*Jpc        !flux of C
            entering soil active pool (kgC m-2 d-1)
           Isc= psa*Jac+psu*Juc+psv*Jvc   !flux of C entering soil slow pool
            (kgC m-2 d-1)
           Ipc= ppa*Jac+pps*Jsc   !flux of C entering soil passive pool (kgC m-2
            d-1)

           Rh= (Juc+Jmc+Jvc+Jnc+Jac+Jsc+Jpc)-(Iac+Isc+Ipc)  !heterotrophic
            respiration (kgC m-2 d-1)
           NEP= GPP-Ra-Rh               !net ecosystem production (kgC m-2 d-1)


C          --------------------------
C          Fluxes in plant N dynamics
C          --------------------------
           Jfn= MIN((Nf*gammaf),(Nf+Ifn))         !flux of N leaving pool foliage
            (kgN m-2 d-1)
           Jrn= MIN((Nr*gammar),(Nr+Irn))         !flux of N leaving pool root
            (kgN m-2 d-1)
           Jwns= MIN((Nws*gammaw),(Nws+Iwns))     !flux of N leaving pool
            structural wood (kgN m-2 d-1)
           Jwnm= MIN((Nwm*gammaw+Rwm*Nwm),(Nwm+Iwnm))   !flux of N leaving pool
            mobile wood (kgN m-2 d-1)
C          R= (1-lambdaf)*Jfn+(1-lambdar)*Jrn+(Rwm*Nwm) !N re-translocation rate
            (kgN m-2 d-1)
           R= (1.-lambdaf)*Jfn+(1.-lambdar)*Jrn+(1.-lambdawm)*Jwnm       !N re-
            translocation rate (kgN m-2 d-1)
           Uramm= MAX(lambdau*Namm*Cr/(Cr+Kr),0.)        !root ammonia N uptake
            from (kgN m-2 d-1)
           Urnit= MAX(lambdau*Nnit*Cr/(Cr+Kr),0.)        !root nitrate N uptake
            from (kgN m-2 d-1)
           Ur= Uramm+Urnit              !total root N uptake (kgN m-2 d-1)
           Iwns= Iwc*NC_ws              !flux of N entering pool structural wood
            (kgN m-2 d-1)
           Iwnm= Iwc*(NC_wnew-NC_ws)    !flux of N entering pool mobile wood
            (kgN m-2 d-1)
           IF(FLAG2.EQ.0.) THEN   !CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1 Ur+CNU;
            FLAG2=2 CNU=0.)
            U= Ur               !uptake rate of plant available N (kgN m-2 d-1)
           ELSE
```

```
              U= Ur+CNU
            END IF
            IF((Iwns+Iwnm).GT.(U+R)) THEN   !If R+Ur is not enough, put it all in
             N stem pools
             Iwns= Iwns*(U+R)/(Iwns+Iwnm)
             Iwnm= Iwnm*(U+R)/(Iwns+Iwnm)
            END If
            IF(FLAG2.EQ.0.) THEN   !CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1 Ur+CNU;
             FLAG2=2 CNU=0.)
             Irn= (U+R-Iwns-Iwnm)*((ro*etar)/(etaf+ro*etar))  !flux of N entering
             pool root (kgN m-2 d-1)
             Ifn= (U+R-Iwns-Iwnm-Irn) + CNU      !flux of N entering pool foliage
             (kgN m-2 d-1)
            ELSE
             Ifn= (U+R-Iwns-Iwnm-Irn)              !flux of N entering pool foliage
             (kgN m-2 d-1)
            END IF

C         --------------------------------------------------------------
C         Fluxes in soil and litter N dynamics  (Comins & McMurtrie,1993)
C         --------------------------------------------------------------
            IF (Mng.EQ.1) THEN                   !forest management (yes=1;no=0)
             Iun= MIN((NC_u*Iuc),(Jfn*lambdaf+f_BR*(Jwns+Jwnm-Rwm*Nwm)))  !flux
             of N entering surface structural pool (kgN m-2 d-1)Mass balance
             guaranteed
             Imn= (Jfn*lambdaf+f_BR*(Jwns+Jwnm-Rwm*Nwm))-Iun    !flux of N
             entering surface metabolic pool (kgN m-2 d-1)
            ELSE
             Iun= MIN((NC_u*Iuc),(Jfn*lambdaf+(Jwns+Jwnm-Rwm*Nwm)*(1-f_CR)))
             Imn= (Jfn*lambdaf+(Jwns+Jwnm-Rwm*Nwm)*(1-f_CR)) - Iun
            END IF
            Ivn= MIN((NC_v*Ivc),(Jrn*lambdar+f_CR*(Jwns+Jwnm-Rwm*Nwm))) !flux of
            N entering soil structural pool (kgN m-2 d-1)Mass balance guaranteed
            Inn= Jrn*lambdar+f_CR*(Jwns+Jwnm-Rwm*Nwm)-Ivn      !flux of N entering
            soil metabolic pool (kgN m-2 d-1)

            IF (Iun.LT.(NC_u*Iuc)) THEN    !Fix N from Inorganic pool to keep N:C
             of structural pools equals to 1/150
             fixu= NC_u*Iuc-Iun
             Iun= Iun+fixu
            ELSE
             fixu= 0.
            END IF
            IF (Ivn.LT.(NC_v*Ivc)) THEN    !Fix N from Inorganic pool to keep N:C
             of structural pools equals to 1/150
             fixv= NC_v*Ivc-Ivn
             Ivn= Ivn+fixv
            ELSE
             fixv= 0.
            END IF
            IF (Imn.LT.(NC_m0min*Imc)) THEN  !Fix or release N from/to Inorganic
             pool to keep N:C of metabolic pools between N:Cmin and N:Cmax
             fix_relm= NC_m0min*Imc-Imn
            ELSE IF (Imn.GT.(NC_m0max*Imc)) THEN
             fix_relm= NC_m0max*Imc-Imn
            ELSE
             fix_relm= 0.
            END IF
            Imn= Imn+fix_relm
            IF (Inn.LT.(NC_n0min*Inc)) THEN
             fix_reln= NC_n0min*Inc-Inn
            ELSE IF (Inn.GT.(NC_n0max*Inc)) THEN
             fix_reln= NC_n0max*Inc-Inn
            ELSE
             fix_reln= 0.
            END IF
            Inn= Inn+fix_reln
```

```
      IF (Nino.LT.0.) THEN
       NC_a0= NC_a0min     !N/C of new SOM entering active soil pool (kgN
        kg-1C)
       NC_s0= NC_s0min !N/C of new SOM entering slow soil pool (kgN kg-1C)
       NC_p0= NC_p0min     !N/C of new SOM entering passive soil pool (kgN
        kg-1C)
      ELSE IF (Nino.GT.Ncrit) THEN
       NC_a0= NC_a0max
       NC_s0= NC_s0max
       NC_p0= NC_p0max
      ELSE
       NC_a0= 1./(1./NC_a0min+(1./NC_a0max-1./NC_a0min)*(Nino/Ncrit))
       NC_s0= 1./(1./NC_s0min+(1./NC_s0max-1./NC_s0min)*(Nino/Ncrit))
       NC_p0= 1./(1./NC_p0min+(1./NC_p0max-1./NC_p0min)*(Nino/Ncrit))
      END IF
      Ian= NC_a0*Iac     !flux of N entering active soil pool (kgN m-2 d-1)
      Isn= NC_s0*Isc     !flux of N entering slow soil pool (kgN m-2 d-1)
      Ipn= NC_p0*Ipc     !flux of N entering passive soil pool (kgN m-2 d-1)
      Jun= MIN((du*Nu),(Nu+Iun))  !flux of N leaving surface structural
       pool (kgN m-2 d-1)
      Jvn= MIN((dv*Nv),(Nv+Ivn))  !flux of N leaving soil structural pool
       (kgN m-2 d-1)
      Jmn= MIN((dm*Nm),(Nm+Imn))  !flux of N leaving surface metabolic pool
       (kgN m-2 d-1)
      Jnn= MIN((dn*Nn),(Nn+Inn))  !flux of N leaving soil metabolic pool
       (kgN m-2 d-1)
      Jan= MIN((da*Na),(Na+Ian))  !flux of N leaving active soil pool (kgN
       m-2 d-1)
      Jsn= MIN((ds*Ns),(Ns+Isn))  !flux of N leaving slow soil pool (kgN m-
       2 d-1)
      Jpn= MIN((dp*Np),(Np+Ipn))  !flux of N leaving passive soil pool (kgN
       m-2 d-1)
      Nloss= MAX(0.,(lambdaloss*Nnit))            !loss of N for leaching or
       denitrification (kgN m-2 d-1)

      CN_soil= (Ca+Cs+Cp)/(Na+Ns+Np)  !average N:C ratio in mineral+organis
       soil (kgN kg-1C)
      IF (CN_soil.GT.22.5) THEN
       fnit= 0.
      ELSE IF (CN_soil.LT.17.5) THEN
       fnit= 1.
      ELSE
       fnit=4.5-0.2*CN_soil            !fraction of nitrification (-)
      END IF

      Igmin= Jfn*lambdaf+Jrn*lambdar+(Jwns+Jwnm-Rwm*Nwm)+Jun+Jmn+Jvn+Jnn+
     *    Jan+Jsn+Jpn               !gross mineralisation flux (kgN m-2 d-1)
      Imm= (Iun+Imn+Ivn+Inn)+(Ian+Isn+Ipn)     !N immobilization flux (kgN
       m-2 d-1)

      IF((Nino+Igmin+(Nin-CNU)-Imm-Uramm-Urnit-Nloss).LE.0.) THEN  !ensure
        that Nino does not fall below zero, reduce all outgoing fluxes in
        parallel
       Imm= Imm * (Nino+Igmin+(Nin-CNU))/(Imm-Uramm-Urnit-Nloss)
       Uramm= Uramm * (Nino+Igmin+(Nin-CNU))/(Imm-Uramm-Urnit-Nloss)
       Urnit= Urnit * (Nino+Igmin+(Nin-CNU))/(Imm-Uramm-Urnit-Nloss)
       Nloss= Nloss * (Nino+Igmin+(Nin-CNU))/(Imm-Uramm-Urnit-Nloss)
       Ur= Uramm+Urnit
       U=Ur
      END IF

      Inmin= Igmin-Imm            !net mineralisation flux (kgN m-2 d-1)
      Iamm= 0.33*(Nin-CNU)+Inmin*(1.-fnit)   !flux of N entering ammonia
       N pool (kgN m-2 d-1)
      Init= 0.67*(Nin-CNU)+Inmin*fnit        !flux of N entering nitrate N
       pool (kgN m-2 d-1)
      Jamm= Uramm    !flux of N entering ammonia nitrogen pool (kgN m-2 d-1)
```

```
              Jnit= Urnit+Nloss


C             ----------------
C             Update C pools
C             ----------------
              Cf= Cf+Ifc-Jfc                    !update C content of foliage (kgC m-2)
              Cr= Cr+Irc-Jrc                    !update C content of roots (kgC m-2)
              Cw= Cw+Iwc-Jwc                    !update C content of wood (kgC m-2)
              Cu= Cu+Iuc-Juc       !update C content of surface structural pool (kgC
              m-2)
              Cm= Cm+Imc-Jmc       !update C content of surface metabolic pool (kgC
              m-2)
              Cv= Cv+Ivc-Jvc    !update C content of soil structural pool (kgC m-2)
              Cn= Cn+Inc-Jnc    !update C content of soil metabolic pool (kgC m-2)
              Ca= Ca+Iac-Jac    !update C content of soil active pool (kgC m-2)
              Cs= Cs+Isc-Jsc    !update C content of soil slow pool (kgC m-2)
              Cp= Cp+Ipc-Jpc    !update C content of soil passive pool (kgC m-2)


C             ----------------
C             Update N pools
C             ----------------
              Nf= Nf+Ifn-Jfn         !update N content of foliage (kgN m-2)
              Nws= Nws+Iwns-Jwns     !update N content of structural wood (kgN m-2)
              Nwm= Nwm+Iwnm-Jwnm     !update N content of mobile wood (kgN m-2)
              Nw= Nws+Nwm            !update N content of total wood (kgN m-2)
              Nr= Nr+Irn-Jrn         !update N content of root (kgN m-2)
              Ntree= Nf+Nr+Nw        !total N content of trees (kgN m-2)

              NC_f= MAX(Nf/Cf,NC_fmin)      !N/C for foliage (kgN kg-1C)
              IF (FLAG2.EQ.0) THEN  !CNU strategy (FLAG2=0 Nf+CNU; FLAG2=1 Ur+CNU;
               FLAG2=2 CNU=0.)
               NC_r=ro*(NC_f-CNU/Ifc)     !N/C for roots (kgN kg-1C)
              ELSE
               NC_r=ro*NC_F
              END IF
              NC_ws= NC_wsa+NC_wsb*NC_f       !N/C ratio of structural wood as a
              function of foliage N:C ratio (kgN kg-1C)
              NC_wnew= NC_wnewa+NC_wnewb*NC_f  !N/C ratio of new wood as a function
              of foliage N:C ratio (kgN kg-1C)

              Nu= Nu+Iun-Jun     !update N content of litter surface structural pool
              (kgN m-2)
              Nv= Nv+Ivn-Jvn     !update N content of litter soil structural pool
              (kgN m-2)
              Nm= Nm+Imn-Jmn     !update N content of litter surface metabolic pool
              (kgN m-2)
              Nn= Nn+Inn-Jnn     !update N content of litter soil metabolic pool
              (kgN m-2)
              NC_m= Nm/Cm       !N/C for litter surface metabolic pool (kgN kg-1C)
              (1/10:1/25)
              NC_n= Nn/Cn       !N/C for litter soil metabolic pool (kgN kg-1C)
              (1/10:1/25)
              Na= Na+Ian-Jan    !update N content of active soil pool (kgN m-2)
              Ns= Ns+Isn-Jsn    !update N content of slow soil pool (kgN m-2)
              Np= Np+Ipn-Jpn    !update N content of passive soil pool (kgN m-2)
              Namm=Namm+Iamm-Jamm     !update N content of ammonia N pool (kgN m-2)
              Nnit=Nnit+Init-Jnit     !update N content of nitrate N pool (kgN m-2)
              Nino=Namm+Nnit          !update N inorganic pool (kgN m-2)

C             ----------------------
C             Update annual fluxes
C             ----------------------
              PG= PG+GPP             !annual gross primary production (kgC m-2 y-1)
              PN= PN+NPP             !annual net primary production (kgC m-2 y-1)
              RAA= RAA+Ra            !annual autotrophic respiration (kgC m-2 y-1)
              RHH= RHH+Rh            !annual heterotrophic respiration (kgC m-2 y-1)
              NEEP= NEEP+NEP         !annual net ecosystem exchange (kgC m-2 y-1)
```

```
          UU= UU+U                !annual plant N uptake (kgN m-2 year-1)
          Nlooss=Nlooss+Nloss     !annual N losses (kgN m-2 year-1)


C         --------------------
C         Update water balance
C         --------------------
          PAWr= MAX(0.,MIN(PAWrmax,PAWr+raineff-Tr-Ev)) !plant available water
           in root zone (mm)
          PAWts= MAX(0.,MIN(PAWtsmax,PAWts+raineff-Tr*qe-Ev,PAWr))        !plant
           available water in top soil layer (mm)
          WCr= PAWr/sd/1000.+WP        !soil water content in root zone (m3/m3)

          DO 60 j=1,729
           zz(j)= vv(j+1)
           SUM= SUM+zz(j)
60        CONTINUE
          zz(730)= npp
          SUM= SUM+npp
          vv= zz
          PPN= SUM/2.
          SUM= 0.

C         IF ((FLAG.EQ.0).AND.(m.LE.(years*50-50))) THEN !For equilibrium state
          IF ((FLAG.EQ.0).AND.(m.LE.(150.))) THEN      !For 200 years simulation
           GOTO 65
          END IF
          WRITE(35,1000)gpp,npp,RA,RH,NEP,Cf,Cr,Cw,gammar,e0,J25,VC25,PAWr,
     *        PAWts
          WRITE(45,1000)Cu,Cm,Cv,Cn,Ca,Cs,Cp,etaf,etar,alfam,alfpm
          WRITE(55,1000)Nf,Nr,Nw,Ntree,NC_f,U,etaw,SLA,gammaf,Igmin,Inmin
          WRITE(75,1000)Nu,Nm,Nv,Nn,Na,Ns,Np,Nino,Nloss,CNU,Namm,Nnit

65        day=day+1
70        CONTINUE

C         -----------------------------------------------
C         Impose harvesting at the end of the rotation
C         -----------------------------------------------
C         IF (((i)/rotation).EQ.INT((i)/rotation)) THEN   !update pools for
           management and slash release
           CONTINUE
           IF (coppice.EQ.0) THEN
            CONTINUE
           Jfc= Cf - 0.001   !C flux leaving the foliage pool at harvest (kgC
            m-2)
           Jrc= Cr - 0.001    !C flux leaving the fine root pool at harvest
           (kgC m-2)
           Jwc= Cw            !C flux leaving the wood pool at harvest (kgC m-2)
           Jfn= Jfc*NC_f      !N flux leaving the foliage pool at harvest (kgN
            m-2)
           Jrn= Jrc*NC_r      !N flux leaving the fine root pool at harvest
           (kgN m-2)
           Jwns= Jwc*NC_ws    !flux of N leaving pool strustural wood (kgN m-2
            d-1)
           Jwnm= Jwc*(NC_wnew-NC_ws)    !flux of N leaving pool mobile wood
           (kgN m-2 d-1)

           Iuc= 0.    !flux of C entering surface structural pool at harvest
           (kgC m-2)
           Imc= 0.    !flux of C entering surface metabolic pool at harvest
           (kgC m-2)
           Ivc= 0.    !flux of C entering soil structural pool at harvest (kgC
            m-2)
           Inc= 0.    !flux of C entering soil metabolic pool at harvest (kgC
            m-2)
           Iun= 0.    !flux of N entering surface structural pool at harvest (kgN
            m-2)
           Imn= 0.    !flux of N entering surface metabolic pool at harvest (kgN
```

```
                  m-2)
                  Ivn= 0.    !flux of N entering soil structural pool at harvest (kgN
                  m-2)
                  Inn= 0.     !flux of N entering soil metabolic pool at harvest (kgN
                  m-2)
              END IF

                  Cf= Cf - Jfc              !foliage C (kgC m-2)
                  Cr= Cr - Jrc              !fine root C (kgC m-2)
                  Cw= Cw - Jwc              !wood C (kgC m-2)
                  Nf= Cf*NC_f               !foliage N (kgN m-2)
                  Nr= Cr*NC_r               !fine root N (kgN m-2)
                  Nws= Cw*NC_ws             !update N content of structural wood (kgN m-2)
                  Nwm= Cw*(NC_wnew-NC_ws) !update N content of mobile wood (kgN m-2)
                  Nw=Nws+Nwm
                  Cu= Cu + Iuc   !C content of litter surface structural pool (kgC m-2)
                  Cm= Cm + Imc   !C content of litter surface metabolic pool (kgC m-2)
                  Cv= Cv + Ivc   !C content of litter soil structural pool (kgC m-2)
                  Cn= Cn + Inc   !C content of litter soil metabolic pool (kgC m-2)
                  Nu= Nu + Iun   !N content of litter surface structural pool (kgN m-2)
                  Nm= Nm + Imn   !N content of litter surface metabolic pool (kgN m-2)
                  Nv= Nv + Ivn   !N content of litter soil structural pool (kgN m-2)
                  Nn= Nn + Inn   !N content of litter soil metabolic pool (kgN m-2)
                  vv=0.
                  PPN=0.
              END IF

C         -------------------------------------------------
C         Print results to file at the end of each year
C         -------------------------------------------------
C         IF ((FLAG.EQ.0).AND.(m.LE.(years*50-200))) THEN
              IF ((FLAG.EQ.0).AND.(m.LE.(years*200-200))) THEN
               GOTO 80
              END IF

              WRITE(10,1000)PG,PN,RAA,RHH,NEEP,Cf,Cr,Cw,gammar,E0,PAWr,PAWts
              WRITE(20,1000)Cu,Cm,Cv,Cn,Ca,Cs,Cp,etaf,etar
              WRITE(30,1000)Nf,Nr,Nw,Ntree,NC_f,UU,etaw,SLA ,gammaf,Nws,Nwm
              WRITE(40,1000)Nu,Nm,Nv,Nn,Na,Ns,Np,Nino,Nlooss,CNU,Namm,Nnit

80        m=m+1
90         CONTINUE
100      CONTINUE

C       --------
C       Formats
C       --------
1000    FORMAT(20(1x,f30.11))

        STOP
        END

C ------------
C References
C ------------
C
C Aber JD, Goodale CL, Ollonger SV et al. (2003) Is nitrogen deposition
C altering the nitrogen status of north eastern forests? Biosciences 53,
C 375-389.
C
C Comins HN, McMurtrie RE (1993) Long-term response of nutrient-limited
C forests to CO2 enrichment; equilibrium behavior of plant-soil models.
C Ecological Applications 3(4),666-681.
C
C Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005a) A processed-based
C model of nitrogen cycling in forest plantation Part I. Structure,
C calibration and analysis of the decomposition model. Ecological Modelling
```

C 187,246-448.
C
C Corbeels M, McMurtrie RE, Pepper DA, O'Connell AM (2005b) A processed-based
C model of nitrogen cycling in forest plantation Part II. Simulating growth
C and nitrogen mineralisation of Eucalyptus globulus plantations in south-
C western Australia. Ecological Modelling 187,449-474.
C
C Dewar RC, McMurtrie RE (1996) Analytical model of stemwood growth in
C relation to nitrogen supply. Tree Physiology 16, 161-171.
C
C Medlyn BE, McMurtrie RE, Dewar RC, Jeffreys MP (2000) Soil processes
C dominate the long-term response of forest net primary productivity to
C increased temperature and atmospheric CO2 concentration. Can. J. For. Res.
C 30,873-888.
C
C McMurtrie RE, Wolf JL (1983) Above and belowground growth of forest stands:
C a carbon budget model. Annals of Botany 52,437-448.
C
C McMurtrie RE (1985) Forest productivity in relation to carbon partitioning
C and nutrient cycling: a mathematical model. Pages 194-207 in M. G. R.
C Cannell and J. E. Jackson, editors. Attributes of trees as crop plant.
C Institute of Terrestrial Ecology, Abbots Ripton, Huntingdon, England. 199
C 1. Relationship of forest productivity to nutrient and carbon supply-a
C modelling analysis. Tree Physiology 9,87-99.
C
C McMurtrie RE (1991) Relationship of forest productivity to nutrient and
C carbon supply - a modelling analysis. Tree Physiol 9,87-99.
C
C Nalder IA, Wein RW (2006) A model for the investigation of long-term carbon
C dynamics in boreal forests of western Canada I. Model development and
C validation. Ecological Modelling 192,37-66.
C
C Palmroth S, Oren R, McCarthy HR et al. (2006) Aboveground sink strength in
C forests controls the allocation of carbon below ground and its [CO$_2$]-induced
C enhancement. Proceedings of the National Academy of Sciences of the United
C States of America 103(51),19362-19367.
C
C Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors
C controlling soil organic matter levels in Great Plains grasslands. Soil
C Science Society of America Journal 51,1173-1179.
C
C Parton WJ, Scurlock JMO, Ojima DS et al. (1993) Observations and modeling
C of biomass and soil organic matter dynamics for the grassland biome
C worldwide. Global Biogeochemical Cycles 7,785-809.
C
C Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD
C (1999) Generality of leaf trait relationships: a test across six biomes.
C Ecology 80(6),1955-1969.

6.2 THE MATE MODEL CODE

```
C  MAIN PROGRAM MATE
C  Author: Silvia Dezi
C  Date:   11.08.2008
C  Pourpose: implementation of the RMATE model (Model Any Terrestrial
C  Ecosystems) (McMurtrien et al, in preparation), that incorporates the
C  effect of atmospheric [CO$_2$] and meteorological data (T, PAR, RH, rain) on
C  light use efficiency (LUE)
C
C
C  ARGUMENTS
C
C  Aam,Apm          rate of leaf photosynthesis for AM, PM periods (umol CO2
C                   m-2 s-1)
C  Acam,Acpm        rate of leaf photosynthesis when Rubisco activity is
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C                   limiting for AM, PM periods (umol CO2 m-2 s-1)
C  Ajam,Ajpm        rate of leaf photosynthesis when RUBP regeneration is
C                   limiting for AM, PM periods (umol CO2 m-2 s-1)
C  alfam,alfpm      quantum efficiency for AM, PM periods (mol CO2 mol-1 PAR)
C  Ca               atmospheric CO2 concentration (umol mol-1)
C  CiCa_am,CiCa_pm  ratio intercellular to atmospheric CO2 concentration for
C                   AM, PM periods(-)
C  d                factor for identify hemisphere (1 north, -1 south) (-)
C  daylen           daylength (h d-1)
c  declination      declination of the sun to the the Equator (rad)
C  delSJ            (J mol-1 k-1)
C  DeltaES          slope of sat vapour pressure vs temperatue at mean daily
C                   temperature (kPa K-1)
C  doy              day of year (-)
C  eam,epm          light-use efficency for AM, PM periods (mol CO2 mol-1 PAR)
C  EaV              activation energy for Rubisco(J mol-1)
C  EaJ              activation energy for electron transport(J mol-1)
C  EdJ              deactivation energy for electron transport(J mol-1)
C  e                mean light-use efficency (mol CO2 mol-1 PAR)
C  FC               field capacity (m3 m-3)
c  g                albedo (-)
C  gamma            convertion factor for PAR (from mol PAR to umol PAR)
C  gammap           psychrometric constant (Pa K-1)
C  GamStaram,       light compensation point for AM periods(umol umol-1)
C  GamStarpm        light compensation point for PM periods(umol umol-1)
C  gi               slope parameter for B-B model(-)
C  gw               reduction factor in B-B model due to soil moisture (-,
C                   between 0 and 1)
C  Il               rainfall interception per unit LAI (mm d-1)
C  Jmam,Jmpm        maximum rate of electron transport for AM, PM periods(umol
C                   CO2 m-2 s-1)
C  J25              maximum rate of electron transport at 25°C(umol CO2 m-2 s-1)
C  ke               light extinction coefficient (-)
C  kmam,kmpm        Michaelis constant for CO2 fixation for AM, PM periods(umol
C                   umol-1)
C  LAI              leaf area index (m2 m-2)
C  lambda           latent heat of vapourisation (J kg-1)
C  Lat              Latitude (° + '/60 + ''/3600) (-)
C  Pa               air vapor pressure (kPa)
C  PARR             incident photosyntetically active radiation (molPAR m-2 d-1)
C  pi               value of pi greco ???
C  PS               saturation vapor pressure (kPa)
C  qam,qpm          mormalised daily irradiance for AM, PM periods (-)
C  Radlong          net long-wave radiation (MJ m-2 d-1)
C  Radnet           net radiation (MJ m-2 d-1)
C  rain             daily precipitation (mm d-1)
C  raineff          daily effective rainfall (mm d-1)
C  Rg               ideal gas constant (J °K-1 mol-1)
C  RH               atmosheric relative humidy(-)
C  RHam,RHpm        atmosheric relative humidy for AM, PM periods(-)
C  RHav             mean atmosheric relative humidy(-)
C  Rv               gas constant for water vapour (J K-1 kg-1)
C  SLAA             spacific keaf area (m2 kgC-1)
C  SWP              soil water potential in rooting zone (MPa=kJ kg-1)
C  Tam,Tpm          atmospheric temperature for AM, PM periods(°C)
C  Tav              mean atmospheric temperature (°C)
C  Tmax             maximum atmospheric temperature (°C)
C  Tmin             minum atmospheric temperature (°C)
C  teta             shape of light-response curve (-)
C  Tkam,Tkpm        atmospheric temperature for AM, PM periods in Kelvin(K)
C  Tavk             mean atmospheric temperature in Kelvin(K)
C  Tr               plant transpiration (mm d-1)
C  Tref             reference temperature in Kelvin (K)
C  T0               °C in Kelvin (K)
C  Vmam,Vmpm        maximum rate of Rubisco activity for AM, PM periods(umol CO2
C                   m-2 s-1)
C  VPDam,VPDpm      vapour pressure deficit for AM, PM periods(kPa)
```

```
C  Vc25           maximum rate of Rubisco activity at 25°C(umol CO2 m-2 s-1)
C  WC             water content in root zone (m3m-3)
C  WP             wilting point (m3 m-3)
C  WUE            mean water use efficiency(kgC m-2 mm-1)
C  WUEam,WUEpm    water use efficiency for AM, PM periods(kgC m-2 mm-1)
C
       SUBROUTINE MATE(ke,e,NCf,doys,doy,Tam,Tpm,VPDam,VPDpm,Ca,PARR,SLAA
     *      ,WUE,WC,FC,WP,daylen,J25,VC25,alfam,alfpm)

C       --------------------------------
C       Declare variables and parameters
C       --------------------------------
       REAL sen(6),gam(6),gpm(6),PARR,Ca,RHpm,Tam,Tpm,RHam,SLAA
       REAL qq,ke,alfam,alfpm,PAR,daylen,Amax,PI,Lat,Decl,Acam,Acpm
       REAL Aam,Apm,qam,qpm,ggam,ggpm,teta,Rg,Jmam,NCf
       REAL CiCa_pm,RHaam,RHppm,gi,GamStaram,GamStarpm,T0,Tmax
       REAL Tkam,Tkpm,J25,EaV,EaJ,EdJ,delSJ,Tav,HR,Vc25,Vmam
       REAL  kmpm,RHav,Jmpm,CiCa_am,Tmin,Tref,Vmpm,kmam
       REAL e,Ajam,Ajpm,k,ee(3287),Tavk,Tr,rainn,raineff,LAI,Il
       REAL Radlong,Radnet,g,lambda,gammap,DeltaES,Rv,SWP,gw
       REAL VPDam,VPDpm,WUEam,WUEpm,WUE,FC,WP,doys
       INTEGER gamma,doy,d,j,days,years,day
       CHARACTER*40 IPARMS
       PARAMETER (PI=3.1415926536,Rg=8.3144472,T0=273.15,Rv=461.5)

C       ------------------
C       Define parameters
C       ------------------
       teta= 0.95    !shape of light-response curve (-)(Medlyn et al. 2005)
       Vcmax= 80     !maximum rate of Rubisco activity at 25°C  (umol CO2 m-2
       s-1)(Medlyn et al. 2005)
       EaV= 58520.   !activation energy for Rubisco(J mol-1)(Medlyn et al.
        2005)
       Jmax= 120     !maximum rate of electron transport at 25°C (umol CO2 m-2
       s-1)(Medlyn et al. 2005)
       EaJ= 38670.   !activation energy for electron transport(J mol-1)
        (Medlyn et al. 2005)
       EdJ= 200000.  !deactivation energy for electron transport(J mol-1)
        (Medlyn et al. 2005)
       delSJ= 624.4  !(J mol-1 K-1)(Medlyn et al. 2002,Medlyn et al. 2005)
       gi= 8.63      !slope parameter for Leuning model(-)(Medlyn et al. 2005)
       Lat= 44.7     !Latitude 44° 42'(° + '/60 + ''/3600)(Medlyn et al. 2005)
       Il= 0.5       !rainfall interception per unit LAI (mm d-1)
       (19991.2000R1_THWaterBal20080710RM_Ring1.xls & McMurtrie et al 1990)
       g= 0.2        !albedo (used in calculating Radnet)(-)
       (19991.2000R1_THWaterBal20080710RM_Ring1.xls)
       Tref= 25.+T0  !reference temperature in Kelvin (K)

C       ---------------------
C       Start of simulations
C       ---------------------
       DO 10 i=1,6
        sen(i)=SIN((i*2-1)*PI/24)
10      CONTINUE
       J25= (48.7*NCf/SLAA*1000.-2.5)*2.*0.8     !maximum rate of Rubisco
        activity at 25°C(umol CO2 m-2 s-1)(Medlyn et al 2002)
       VC25= (25.8*NCf/SLAA*1000.+11.7)*2.*0.8   !maximum rate of electron
        transport at 25°C(umol CO2 m-2 s-1)(Medlyn et al 2002)

C       ---------------------------------------
C       Computation rate of leaf photosynthesis
C       ---------------------------------------
       gw= 1.-MIN(1.,0.0156*EXP(4.269*(FC-WC)/(FC-WP)))   !reduction factor in
       gs model due to soil moisture (-, between 0 and 1)(BRAY,Granier &
       Loustau 1994)
       Tkam= Tam+T0     !atmospheric temperature for AM period in Kelvin(K)
       Tkpm= Tpm+T0     !atmospheric temperature for PM period in Kelvin(K)
       CiCa_am= MAX((1.-1.6/(gi*gw)*(1.+VPDam/1.39)),0.2)  !ratio intercellular
```

```
            to atmospheric CO2 concentration for AM period(-)(BRAY,Medlyn et al
            2005)
            CiCa_pm= MAX((1.-1.6/(gi*gw)*(1.+VPDpm/1.39)),0.2)  !ratio intercellular
            to atmospheric CO2 concentration for PM period(-)(BRAY,Medlyn et al
            2005)
            GamStaram = 42.75*EXP(37830*(Tam-25.)/(Rg*Tkam*Tref))         !light
            compensation point for AM period(umol umol-1)
            GamStarpm = 42.75*EXP(37830*(Tpm-25.)/(Rg*Tkpm*Tref))         !light
            compensation point for PM period(umol umol-1)
            kmam= 404.9*EXP(79430*(Tam-25.)/(Rg*Tkam*Tref))*(1.+ 205000./ 278400.
        *      /EXP(36830*(Tam-25.)/(Rg*Tkam*Tref)))   !Michaelis constant for
            CO2 fixation for AM period(umol umol-1)
            kmpm= 404.9*EXP(79430*(Tpm-25.)/(Rg*Tkpm*Tref))*(1.+ 205000./278400.
        *      /EXP(36830*(Tpm-25.)/(Rg*Tkpm*Tref)))      !Michaelis constant for
            CO2 fixation for PM period(umol umol-1)
            Jmam= J25*EXP(EaJ*(Tam-25.)/(Rg*Tkam*Tref))*(1.+ EXP((delSJ*Tref-EdJ)/
        *      Rg/Tref))/(1.+EXP((delSJ*Tkam-EdJ)/Rg/Tkam))    !maximum rate of
            electron transport for AM period(umol CO2 m-2 s-1)
            Jmpm= J25*EXP(EaJ*(Tpm-25.)/(Rg*Tkpm*Tref))*(1.+ EXP((delSJ*Tref-EdJ)/
        *      Rg/Tref))/(1.+EXP((delSJ*Tkpm-EdJ)/Rg/Tkpm))    !maximum rate of
            electron transport for PM period(umol CO2 m-2 s-1)
            Vmam= Vc25*EXP(EaV*(Tam-25.)/(Rg*Tkam*Tref))    !maximum rate of Rubisco
            activity for AM period(umol CO2 m-2 s-1)
            Vmpm= Vc25*EXP(EaV*(Tpm-25.)/(Rg*Tkpm*Tref))    !maximum rate of Rubisco
            activity for PM period(umol CO2 m-2 s-1)
            Acam= MAX(0.,(Ca*CiCa_am-GamStaram))*Vmam/(Ca*CiCa_am+kmam)  !rate of
            leaf photosynthesis when Rubisco activity is limiting for AM period
            (umol CO2 m-2 s-1)
            Acpm= MAX(0.,(Ca*CiCa_pm-GamStarpm))*Vmpm/(Ca*CiCa_pm+kmpm)  !rate of
            leaf photosynthesis when Rubisco activity is limiting for PM period
            (umol CO2 m-2 s-1)
            Ajam= (Jmam/4.)*((Ca*CiCa_am-GamStaram)/(Ca*CiCa_am+2.*GamStaram))
            !rate of leaf photosynthesis when RUBP regeneration is limiting for AM
            period (umol CO2 m-2 s-1)
            Ajpm= (Jmpm/4.)*((Ca*CiCa_pm-GamStarpm)/(Ca*CiCa_pm+2.*GamStarpm))
            !rate of leaf photosynthesis when RUBP regeneration is limiting for PM
            period (umol CO2 m-2 s-1)
            Aam= MIN(Acam,Ajam)    !rate of leaf photosynthesis for AM period (umol
            CO2 m-2 s-1)
            Apm= MIN(Acpm,Ajpm)    !rate of leaf photosynthesis for PM period (umol
            CO2 m-2 s-1)
            alfam=(0.2+0.15)/2./4.*MAX(0.,(Ca-GamStaram))/(Ca+2.*GamStaram) !quantum
            efficiency for AM periods (mol CO2 mol-1 PAR)
            alfpm=(0.2+0.15)/2./4.*MAX(0.,(Ca-GamStarpm))/(Ca+2.*GamStarpm) !quantum
            efficiency for PM periods (mol CO2 mol-1 PAR)

C       -------------------------------
C       Computation light-use efficency
C       -------------------------------
            Decl= -23.45*pi/180.*COS(2.*PI*(doy+10.)/doys)    !declination of the
            sun to the the Equator (rad)
            daylen= ACOS(-TAN(Lat*PI/180.)*TAN(Decl))*24./PI   !daylength (h d-1)
            IF (Aam.LE.0.) THEN    !computation light-use efficency for AM period
             (mol CO2 mol-1 PAR)
             eam= 0.
            ELSE
             qam= (PI*ke*alfam*PARR*2*2000000.)/(2.*daylen*3600*Aam)    !mormalised
             daily irradiance for AM period (-)
             ggam= 0.
             DO 20 j=1,6
              gam(j)= sen(j)/(1.+qam*sen(j)+SQRT(((1.+qam*sen(j))**2)-
        *      4.*teta*qam*sen(j)))
              ggam=ggam+gam(j)
20          CONTINUE
             eam= alfam*PI*ggam/6.        !light-use efficency for AM period (mol CO2
             mol-1 PAR)
            END IF
```

```
        IF (Apm.LE.0.) THEN     !computation light-use effecency for PM period
         (mol CO2 mol-1 PAR)
         epm= 0.
        ELSE
         qpm= (PI*ke*alfpm*PARR*2*2000000.)/(2*daylen*3600*Apm)     !mormalised
         daily irradiance for PM period (-)
         ggpm= 0.
         DO 30 j=1,6
          gpm(j)= sen(j)/(1.+qpm*sen(j)+SQRT(((1.+qpm*sen(j))**2)-
     *       4*teta*qpm*sen(j)))
          ggpm=ggpm+gpm(j)
30       CONTINUE
         epm= alfpm*PI*ggpm/6.          !light-use effecency for PM period (mol CO2
         mol-1 PAR)
        END IF
        e= (eam+epm)/2.        !mean light-use effecency (mol CO2 mol-1 PAR)
        e= e*12/1000/0.217     !mean light-use effecency (kgC MJ-1 PAR)

C       --------------------------------
C       Computation water use efficiency
C       --------------------------------
        WUEam= Ca*(1-CiCa_am)/1.6/VPDam/10./1.5/1000.   !water use efficiency
         for AM periods(kgC m-2 mm-1)
        WUEpm= Ca*(1-CiCa_pm)/1.6/VPDpm/10./1.5/1000.   !water use efficiency
         for PM periods(kgC m-2 mm-1)
        WUE= (WUEam+WUEpm)/2.            !mean water use efficiency (kgC m-2 mm-1)

        RETURN
        END

C  -----------
C  References
C  -----------
C
C  Granier A, Loustau D (1994) Measuring and modelling the transpiration of
C  maritime pine canopu from sapflow data. Agricultural and Forest Meteorology
C  71, 61-81.
C
C  McMurtrie RE, Rook DA, Kelliher FM (1990) Modelling the yield of Pinus
C  radiata on a site limited by water and nitrogen. Forest Ecology and
C  Management, 30, 381-413.
C
C  Medlyn BE, Loustau D, Delzon S (2002) Temperature response of parameters of
C  a biochemically based model of photosynthesis. I. Seasonal changes in
C  mature maritime pine (Pinus pinaster Aït.). Plant, Cell and Environment,25,
C  1155-1165.
C
C  Medlyn BE, Berbigier P, Clement R et al. (2005) Carbon balance of
C  coniferous forests growing in contrasting climates: Model-based analysis.
C  Agricultural and Forest Meteorology 131,97-124C
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« Com'ero buffo, quand'ero un burattino!... e come ora son contento di essere diventato un ragazzino perbene!.... »
("How ridiculous I was as a Marionette!... And how happy I am, now that I have become a real boy!...")

(Carlo Collodi, incipit de "Le avventure di Pinocchio")