

Modelling changes in nitrogen cycling to sustain increases in forest productivity

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Modelling changes in nitrogen cycling to sustain increases in forest productivity under elevated atmospheric CO₂ and contrasting site conditions

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Abstract

If increases in net primary productivity (NPP) caused by rising concentrations of atmospheric CO₂ (C_a) are to be sustained, key N processes such as soil mineralization, biological fixation, root uptake and plant translocation must be hastened. Simulating the response of these processes to elevated C_a is therefore vital for models used to project the effects of rising C_a on NPP. In this modelling study, hypotheses are proposed for changes in soil mineralization, biological fixation, root uptake and plant translocation with changes in C_a . Algorithms developed from these hypotheses were tested in the ecosystem model *ecosys* against changes in N and C cycling measured over several years under ambient vs. elevated C_a in Free Air CO₂ Enrichment (FACE) experiments at the Duke Forest in North Carolina, the Oak Ridge National Laboratory forest in Tennessee, and the USDA research forest in Wisconsin, USA. Simulating more rapid soil N mineralization was found to be vital for modelling sustained increases in NPP measured under elevated vs. ambient C_a at all three FACE sites. This simulation was accomplished by priming decomposition of N-rich humus from increases in microbial biomass generated by increased litterfall modelled under elevated C_a . Simulating more rapid nonsymbiotic N₂ fixation, root N uptake and plant N translocation under elevated C_a was found to make much smaller contributions to modelled increases in NPP, although such contributions might be greater over longer periods and under more N-limited conditions than those simulated here. Greater increases in NPP with C_a were also modelled with increased temperature and water stress, and with coniferous vs. deciduous plant functional types. These increases were also associated with changes in N cycling.

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1 Introduction

The extent to which forest net primary productivity (NPP) increases under elevated atmospheric CO₂ concentration (C_a) has been found to vary greatly with site conditions. These increases are greater in warmer environments (Myers et al., 1999) because elevated C_a suppresses photorespiration (Long, 1991), in water-limited environments (Hättenschwiler et al., 1997) because elevated C_a reduces transpiration and raises water use efficiency (Rogers et al., 1983), and in nutrient-rich environments which enable more rapid nutrient uptake (Oren et al., 2001).

In temperate forests, increases in NPP with C_a have been found to be constrained by the availability of nitrogen (N). This constraint may be greater in deciduous than in coniferous forests because of their greater nutrient demands (Norby et al., 2010). Consequently studies of elevated C_a effects on forest NPP and growth have given variable results. Norby et al. (2005) found an increase in NPP of 23% after 1–3 yr under 560 vs. 360 $\mu\text{mol mol}^{-1}$ in a meta-analysis of Free Air CO₂ Enrichment (FACE) experiments with young, temperate-zone forests. However longer-term exposure of trees to elevated C_a has shown this increase to decline over time (Hättenschwiler et al., 1997; Idso, 1999; Medlyn et al., 1999; Norby et al., 2010) unless N uptake increases commensurately with NPP (Oren et al., 2001).

Several changes in N processes have been observed in experimental studies by which N uptake and accumulation may be hastened under elevated C_a , thereby moderating long-term N limitations to NPP:

1. more rapid mineralization of soil N primed by increased litterfall (Crow et al., 2009; Drake et al., 2011; Phillips et al., 2011),
2. more rapid symbiotic or nonsymbiotic N₂ fixation primed by increased root C allocation or litterfall (Hofmockel and Schlesinger, 2007; Norby, 1987),
3. more rapid N uptake from denser and deeper root growth (Iversen, 2010; Luxmore et al., 1986),

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4. greater translocation and recovery of N from senescing plant material (Drake et al., 2011).

Biogeochemical models used to forecast the response of forest productivity to rising C_a must therefore simulate changes in these processes that result in additional N uptake and retention (Crow et al., 2009; Finzi et al., 2007). These processes are either absent or poorly represented in current models used to study the effects of rising C_a on forest growth (Iversen, 2010), although they are represented in detail in the ecosystem model *ecosys* (Grant et al., 2007, 2009a, b, c, 2010, 2011a). The importance of these processes to simulating sustained increases in forest NPP and growth under elevated vs. ambient C_a was assessed by testing output from algorithms for these processes in *ecosys* against changes in forest N and C cycling under elevated vs. ambient C_a measured or calculated over several years from forest Free Air CO_2 Enrichment (FACE) experiments in the Duke Forest, Orange County NC, in the Oak Ridge National Laboratory (ORNL) forest at Oak Ridge TN, and the USDA Forest Service experimental farm in Rhinelander WI. Results from this testing were used to estimate the relative contribution from each of these four processes to sustaining increases in forest NPP with elevated C_a under contrasting climates (temperature and precipitation) and tree functional types (coniferous vs. deciduous).

2 Model description

The key algorithms governing the simulation of C and N transformations in *ecosys* are described in the Supplement to this article, in which equations and variables referenced in the Results below are described and listed in Appendices A through H. Algorithms representing biological processes in soil (Appendices A, G and H), physical processes driving soil – plant – atmosphere water transfer (Appendix B), biological processes in plants (Appendices C and F), and chemical processes governing soil solute transformations (Appendix E) were solved at an hourly time step from hourly changes

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in atmospheric boundary conditions. Algorithms representing physical processes driving soil water, heat, gas and solute transfers (Appendix D) were solved at a 5 min time step assuming constant boundary conditions during each hour. All parameters in these algorithms remained unchanged from those in earlier studies of forests, crops and grasslands cited in the Introduction. The key model hypotheses for the effects of elevated C_a on the four N processes given in the Introduction are described in further detail below with reference to equations in the Supplementary Material

2.1 Model hypotheses for changes in N cycling under elevated C_a

2.1.1 More rapid mineralization of soil N primed by increased litterfall

Decomposition

Organic transformations in *ecosys* occur in five organic matter–microbe complexes (coarse woody litter, leaf and fine non-woody litter, animal manure (if present), particulate organic matter (POM), and humus), each of which consists of five organic states (three decomposition substrates – solid organic C, N and P, sorbed organic C, N and P, and microbial residue C, N and P, their decomposition products – dissolved organic C, N and P (DOC, DON and DOP), and the decomposition agent, active microbial biomass (M)) in a surface residue layer and in each soil layer. The rates at which each of the three substrates decompose in each complex are first-order functions of M in diverse heterotrophic microbial functional types, including obligate aerobes (bacteria and fungi), facultative anaerobes (denitrifiers), obligate anaerobes (fermenters), heterotrophic (acetotrophic) and autotrophic (hydrogenotrophic) methanogens, and aerobic and anaerobic heterotrophic diazotrophs (non-symbiotic N_2 fixers) [A1, A2]. Decomposition rates are also Monod functions of substrate C concentrations in soil [A4], calculated from the fraction of substrate mass colonized by M [A5]. These decomposition rates drive transfers of C, N and P from the substrates to DOC, DON and DOP [A7].

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Mineralization

Growth of M by each microbial functional type in each organic matter–microbe complex [A25] is calculated from its uptake of DOC [A21], DON and DOP [A22]. Growth is driven by energy yields from growth respiration (R_g) [A20] remaining after subtracting maintenance respiration (R_m) [A18] from heterotrophic respiration (R_h) [A11] driven by DOC oxidation [A13]. The resulting contents of C, N and P in M drive rates of microbial decay [A23, A24], products of which are transferred to microbial residues and humus for further decomposition [A36]. Ratios of microbial C : N and C : P drive mineralization vs. immobilization of NH_4^+ [A26a, b] and H_2PO_4^- [A26d, e], soil concentrations of which control root and mycorrhizal uptake [C23].

Priming

Values of M used to drive decomposition [A1] are modelled by allowing M to transfer among the five organic matter-microbe complexes according to differences in the concentration of M with respect to that of its substrate in each complex [A3]. These transfers are indicated by changes in the relative sizes of the state variables for biomass vs. those of their substrates before and after redistribution in Fig. 1. The larger specific decomposition rates used in the fine litter and manure complexes [A4] cause concentrations of M vs. substrate in these complexes to be greater than those in the POM and humus complexes (Fig. 1). Consequently some M is transferred from the litter and manure to the POM and humus complexes, thereby priming decomposition of the substrates in these complexes. Similarly, some M may also be transferred from the POM to the humus complex. This transfer implements the hypothesis of Fontaine et al. (2004) that fast growing microbes specializing in utilization of fresh inputs produce extracellular enzymes that metabolize not only fresh material, but also existing SOC. The priming caused by this transfer in ecosys has been tested against changes in decomposition, CO_2 emission and N mineralization measured from litter-amended vs. non-amended soil in Grant et al. (1993). These transfers and consequent priming are greater with

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larger litter substrate and hence larger M generated by increased litterfall, as occurs under elevated C_a . Because POM and humus have lower C : N ratios than does litter, this priming favours mineralization over immobilization.

2.1.2 Greater biological N_2 fixation primed by increased litterfall

5 Nonsymbiotic diazotrophic M populations in each complex conduct N_2 fixation [A27] and associated respiration [A28] to remedy N deficits calculated from their biomass and C : N ratios. These deficits arise when biomass N from uptake of DON [A22] and immobilization of NH_4^+ and NO_3^- [A26b, c] is less than that needed to attain set C : N ratios with biomass C from uptake of DOC [A21]. These deficits increase with larger
10 litter substrate and hence larger diazotrophic M generated by increased litterfall, as occurs under elevated C_a , particularly when higher litterfall C : N ratios increase DOC vs. DON uptake. Under these conditions N_2 fixation rates increase, as observed experimentally by Jurgensen et al. (1992). The subsequent decay of diazotrophic M [A23] causes transfer of diazotrophic N [A24] to microbial residues and humus for decomposition and uptake by other M [A36], and to NH_4^+ through mineralization [A26a], from
15 which it can contribute to root and mycorrhizal uptake [C23]. These same algorithms are used to model symbiotic diazotrophic M populations in roots of leguminous host plants (Appendix F).

2.1.3 Greater N uptake from denser and deeper root growth

C allocation and root growth

20 Growth of branch, root and mycorrhizal organs is driven by growth respiration R_g [C17] and consequent assimilation of the nonstructural C product of CO_2 fixation (σ_C) [C20], coupled with assimilation of the nonstructural N and P products of root and mycorrhizal uptake (σ_N and σ_P). Amounts of σ_C , σ_N and σ_P in each organ are maintained by translocation
25 along branch-root-mycorrhizal concentration gradients [C50–C53] generated by

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production of σ_C from branch CO_2 fixation [C1–C12] and of σ_N and σ_P from root and mycorrhizal uptake [C23], vs. consumption of σ_C , σ_N and σ_P from R_g and phytomass growth [C20] (Grant, 1998).

Root growth and N uptake

5 Production and consumption in different plant organs are differently affected by environmental conditions such as water or nutrient stress, so that translocation of σ_C , σ_N and σ_P , and hence growth of different organs, change with environmental conditions. More rapid CO_2 fixation, as occurs under elevated C_a , raises $\sigma_C : \sigma_N$ and $\sigma_C : \sigma_P$ ratios in branches with respect to those in roots and mycorrhizae, and so increases branch-
10 root-mycorrhizal concentration gradients of σ_C [C50] while reducing those of σ_N and σ_P [C51]. These changes hasten transfer of σ_C from branches to roots and mycorrhizae [C50, C52], and slow transfer of σ_N and σ_P from roots and mycorrhizae to branches [C51, C53], thereby increasing root and mycorrhizal $\sigma_C : \sigma_N$ ratios and hence root and mycorrhizal growth at the expense of branch growth. Consequent increases in root and mycorrhizal surface areas and lengths hasten N and P uptake [C23a–f] with respect to
15 CO_2 fixation. Increases in root and mycorrhizal $\sigma_C : \sigma_N$ ratios may further hasten N and P uptake by reducing uptake product inhibition [C23g]. The model thus implements the shoot:root functional equilibrium hypothesis of Thornley (1995).

2.1.4 Greater translocation of N from senescing plant material

20 First-order respiration of σ_C [R_c in C14] drives autotrophic respiration (R_a) by all branches, roots and mycorrhizae [C13]. R_c is first used to meet maintenance respiration requirements (R_m), calculated independently of R_c from the N content in each organ [C16]. Any excess of R_c over R_m is expended as growth respiration R_g , which drives organ growth [C20]. When R_m exceeds R_c , the shortfall is met by the respiration of remobilizable C (R_s) in leaves, roots and mycorrhizae [C15]. This R_s drives the
25 translocation of remobilizable N and P associated with the C respired as R_s into σ_N

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and σ_P . Translocation of remobilizable N or P can also occur when ratios of $\sigma_N : \sigma_C$ or $\sigma_P : \sigma_C$ become smaller than those of structural N : C or P : C required for growth of new phytomass, from the assumption that productivity is improved if new phytomass has priority for limiting nutrient reserves. This translocation increases retention of σ_N or σ_P , and hence availability of σ_N or σ_P for new growth.

Non-remobilizable C associated with translocated C is lost as litterfall C [C18], so that litterfall is not prescribed from assumed turnover rates, but arises from fixation vs. respiration of C and uptake vs. assimilation of N and P as determined by soil and weather. Elevated C_a could therefore hasten litterfall and increase translocation by increasing R_m with respect to R_C , or by reducing $\sigma_N : \sigma_C$ with respect to structural N : C required for growth. Amounts of litterfall N and P are reduced with respect to that of litterfall C by additional translocation of remobilizable N and P to σ_N and σ_P . This additional translocation increases as ratios of $\sigma_N : \sigma_C$ or $\sigma_P : \sigma_C$ decline [C19], so that N : C and P : C ratios in litterfall decline from those in the living phytomass from which it originates. This decline in litterfall nutrient ratios therefore increases with declining nutrient status as frequently, although not always, observed in field studies (Barnes et al., 1998; Kimmins, 2004). Elevated C_a could therefore increase this additional translocation by lowering ratios of $\sigma_N : \sigma_C$.

In branches, translocation and hence litterfall start at the lowest node at which leaves are present, and proceeds upward until the requirement for R_s , σ_N or σ_P by the branch is met. In roots or mycorrhizae, translocation and hence litterfall start with secondary axes and proceeds to primary axes in each soil layer until the requirement for R_s , σ_N or σ_P by roots or mycorrhizae in the soil layer is met. For deciduous plant functional types, litterfall is hastened by phenologically-driven withdrawal of σ_C , σ_N and σ_P into storage pools under shortening photoperiods and declining temperatures during autumn. These storage pools then replenish σ_C , σ_N and σ_P under lengthening photoperiods and rising temperatures to drive leafout during the following spring (e.g. Grant et al., 2009c).

2.2 Effects of changes in N cycling on CO₂ fixation modelled under elevated C_a

Each of the four changes in N processes described above contributes to maintaining foliar σ_N vs. σ_C under elevated C_a, the first three through increased N uptake, and the fourth through increased N retention. In so doing, these changes help to maintain σ_C and σ_N assimilation and hence leaf N concentrations [C12] and to reduce σ_C product inhibition (downregulation) of CO₂ fixation [C11] under elevated C_a. These changes therefore help to maintain elevated rates of CO₂ fixation under elevated C_a.

3 Model testing

Ecosys was tested against measurements of NPP, phytomass growth and N concentrations in leaves and litterfall under ambient vs. elevated C_a in FACE experiments at the Duke Forest in Orange County NC (35.98° N, 79.91° W), at the Oak Ridge National Lab (ORNL) in Oak Ridge TN, (35.90° N, 84.33° W) and at the USDA Forest Service experimental farm in Rhinelander WI (45.61° N, 89.51° W). A summary of site characteristics and methodology for these experiments is given in Finzi et al. (2007), Norby et al. (2005), and in other references cited below. Modelling methodology at each site followed a common approach described below:

3.1 The Duke Forest FACE Experiment

Productivity of a loblolly pine (*Pinus taeda*) stand planted in 1983 was measured from 1997 to 2005 under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 571 \mu\text{mol mol}^{-1}$) C_a (Drake et al., 2011; McCarthy et al. 2010). The history of this site was simulated by planting a temperate coniferous functional type (e.g. Grant et al., 2007; 2009a) in 1958 on a soil with properties given in Oh and Richter (2005), and growing it until 1983 under historical C_a and repeating sequences of ½-hourly weather data recorded from 1997 to 2005 at the Duke Forest. Ammonium and nitrate concentrations in precipitation

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were set to give wet N deposition rates reported in Drake et al. (2011), and atmospheric ammonia concentrations used to calculate ammonia deposition [D15] were set to 5 nmol mol^{-1} . This spinup allowed the model to achieve stable changes in C stocks during successive weather sequences. The modelled stand was then clearcut (Grant et al., 2007) and a second stand was planted in 1983 with the same plant density as that at which the field site was planted in the same year. This stand was grown until 2006 under $371 \text{ } \mu\text{mol mol}^{-1} C_a$ and repeating sequences of $\frac{1}{2}$ -hourly weather data recorded from 1997 to 2005 at the Duke Forest. This run was then repeated from 1997 to 2005 under $571 \text{ } \mu\text{mol mol}^{-1} C_a$. To simulate the response to N fertilizer measured at the site, both runs were repeated with annual fertilizer applications of 11.2 g N m^{-2} as urea from 1998 to 2005 as described in McCarthy et al. (2010). Model output for NPP, phytomass and key N transfers were compared with those measured over the same period under the same changes in C_a and N. Seasonal changes in forest productivity modelled under ambient C_a were also tested against daily net CO_2 exchange measured by eddy covariance in the Duke Forest under contrasting weather conditions (Katul and Oren, 2012).

3.2 The ORNL FACE Experiment

Productivity and N relations of a sweetgum (*L. styraciflua* L.) stand planted in 1988 was measured from 1998 to 2008 under ambient ($\sim 370 \text{ } \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \text{ } \mu\text{mol mol}^{-1}$) C_a (Norby et al., 2010). The history of this site was simulated by planting a temperate deciduous functional type (e.g. Grant et al., 2009a) in 1954 on a soil with properties given in Johnson et al. (2004), and growing it until 1988 under historical C_a and repeating sequences of $\frac{1}{2}$ -hourly weather data recorded from 1990 to 1998 at the ORNL Walker Branch site, and from 1999 to 2008 at the ORNL FACE site (Riggs et al., 2010). Ammonium and nitrate concentrations in precipitation were set to give wet N deposition rates reported in Norby et al. (2010), and atmospheric ammonia concentrations were set to 5 nmol mol^{-1} . This spinup allowed the model to achieve stable changes in C stocks during successive weather sequences.

The modelled stand was then clearcut and a second stand was planted in 1988 with the same plant density as that at which the field site was planted in the same year. This stand was grown until 2008 under $370\ \mu\text{mol mol}^{-1} C_a$ and repeating sequences of 1/2-hourly weather data recorded from 1990 to 1998 at the ORNL Walker Branch site and from 1999 to 2008 at the ORNL FACE site. This run was then repeated from 1998 to 2008 under $550\ \mu\text{mol mol}^{-1} C_a$. To simulate the response to N fertilizer measured at the site (Norby et al., 2010), the run under $370\ \mu\text{mol mol}^{-1} C_a$ was repeated with annual fertilizer applications of $20\ \text{g N m}^{-2}$ as urea from 2004 to 2008. Model results for NPP, wood increment, leaf N concentrations and root mass were compared with those measured over the same period under the same changes in C_a and N.

3.3 The Rhinelander FACE Experiment

Productivity and N relations of an aspen (*Populus tremuloides* Michx.) stand planted in 1998 was measured from 1998 to 2006 under ambient ($\sim 374\ \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 541\ \mu\text{mol mol}^{-1}$) C_a (King et al., 2005, Kubiske et al., 2010; Talhelm et al., 2012). The history of this site was simulated by planting an annual cereal functional type (e.g. Grant et al., 2011b) each year from 1956 to 1971 on a soil with properties given in Dickson et al. (2000), under historical C_a and repeating sequences of 1/2-hourly weather data recorded from 1999 to 2006 at the Rhinelander FACE site. Ammonium and nitrate concentrations in precipitation were set to give wet N deposition rates reported in NADP maps for Wisconsin, and atmospheric ammonia concentrations were set to $5\ \text{nmol mol}^{-1}$. A boreal deciduous functional type (e.g. Grant et al., 2009a) was then planted in 1972 and grown under 1999–2006 hourly weather data until 1996. This spinup allowed the model to achieve stable changes in C stocks during successive weather sequences. The stand was then clearcut and a second boreal deciduous stand was planted in 1996 with the same plant density as that at which the field site was planted in the same year. This stand was grown until 2006 under $374\ \mu\text{mol mol}^{-1} C_a$ and repeating sequences of 1/2-hourly weather data recorded from

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1999 to 2006 at the Rhinelander FACE site. This run was then repeated from 1998 to 2006 under $541 \mu\text{mol mol}^{-1} C_a$. Model results for NPP, wood increment and litter N concentration were compared with those measured over the same period under the same changes in C_a .

3.4 Sensitivity of modelled NPP to changes in N cycling under ambient vs. elevated C_a

To examine sensitivity of NPP modelled under elevated vs. ambient C_a to the N processes described above, the model runs at the Duke FACE site were repeated with selected processes disabled. The extent to which priming of soil N mineralization (hypothesis 1) raised NPP under elevated vs. ambient C_a was examined by setting the transfer rate constant in [A3a] to zero and offsetting the consequent slowing of POM and humus decomposition by increasing the specific rate constants for POM and humus decomposition in [A4a]. In this way POM and humus decomposition was made independent of changes in litterfall caused by changes in C_a . The extent to which more rapid nonsymbiotic N_2 fixation (hypothesis 2) raised NPP under elevated vs. ambient C_a was examined by disabling diazotrophic fixation in [A27]. The extent to which greater translocation and recovery of N (hypothesis 4) raised NPP under elevated vs. ambient C_a was examined by setting the translocation fractions for N and P in [C19c,d] to a common value that was independent of changes in nonstructural N:C ratios caused by changes in C_a . The extent to which increased root growth (hypothesis 3) raised NPP under elevated vs. ambient C_a was not directly tested because a simple intervention to make root growth independent of C_a in the model was not available. Results for NPP with each disabled process were then compared with those from the model runs with all processes enabled.

To examine whether sensitivity of NPP modelled under elevated vs. ambient C_a differed with plant functional type, the ORNL FACE runs were re-executed with the temperate deciduous functional type replaced by the temperate coniferous functional type

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used in the Duke FACE runs. NPP modelled under elevated vs. ambient C_a at ORNL was then compared for the deciduous vs. coniferous types.

4 Results

4.1 The Duke Forest FACE Experiment

5 Net primary productivity measured and modelled without fertilizer at the Duke Forest rose by 23–30 % from 1997 through 2001 after C_a was increased from 371 to 571 $\mu\text{mol mol}^{-1}$ (Fig. 2a). Both rises were greater than 30 % in 2002 when drought reduced modelled NPP less under elevated vs. ambient C_a . However measured rises in NPP remained near 30 % during 2003 and 2004, while modelled rises declined to near 20 %. Almost 80 % of the measured and modelled rises in NPP were allocated to leaves (Fig. 3a) and wood (Fig. 3b), and only about 20 % to roots (Fig. 3c).

Annual fertilizer applications caused modelled and measured NPP and phytomasses to rise above unfertilized values over time (Fig. 2a, b), indicating a slight N limitation to forest productivity at the Duke site. However rises in NPP modelled under 571 vs. 371 $\mu\text{mol mol}^{-1}$ C_a with fertilizer were similar to those without fertilizer (20–30 %), while measured rises were smaller (10–20 %) (Fig. 2a). Consequently gains in phytomass modelled under elevated C_a with fertilizer were larger than those measured (Fig. 2b).

The presence of an eddy covariance flux tower in the Duke Forest enabled testing of net CO_2 exchange modelled under ambient C_a and seasonal changes in air temperature (T_a) and precipitation during two years, 2001 and 2002, with lower than average annual precipitation. In 2001 with well-distributed precipitation during summer (Fig. 4a), daily-aggregated net CO_2 uptake rose with T_a until late June, but declined slightly with further warming during July and August, so that the Duke forest remained a net sink of CO_2 during most of the year (Fig. 4b). In 2002 with more variable precipitation (Fig. 4d), daily-aggregated net CO_2 uptake rose with T_a until late May, after which it declined sharply with soil drying caused by low precipitation in June and August (Fig. 4d),

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so that the Duke forest became a net source of CO₂ during late summer (Fig. 4e). Consequently annual NPP was lower in 2002 than in 2001 (Fig. 2a).

Increases in net CO₂ exchange modelled under elevated vs. ambient C_a were then examined under the same seasonal changes in T_a and precipitation in 2001 and 2002.

Increases in net CO₂ uptake modelled in 2001 rose with T_a from near zero while T_a was less than 15 °C during winter (Fig. 4a, d) to as much as 50 % when T_a rose above 25 °C during summer (Fig. 4c). Increases modelled in 2002 rose with soil drying during August because net CO₂ uptake declined more slowly under elevated vs. ambient C_a (Fig. 4f). This slower decline was caused by higher soil water contents (θ) modelled under elevated C_a before the drought (about 0.03 m³ m⁻³) which allowed greater water uptake, transpiration and hence CO₂ fixation under elevated C_a as the drought progressed. This higher θ was caused by transpiration which had been reduced from that under ambient C_a [B1c] since the start of the experiment in 1997 by increased canopy stomatal resistance (r_c) modelled from the different responses of carboxylation and diffusion to elevated C_a [B2a] (Grant et al., 1999, 2004). During the drought, increased r_c modelled under elevated C_a caused higher canopy water potential (ψ_c) [B14] and hence slower rises in r_c [B2b] while ψ_c declined, further enabling CO₂ fixation to be sustained during periods of low precipitation [C6a, C7a, C9] (Fig. 4f). These slower declines in net CO₂ fixation during drought caused greater increases in annual NPP to be modelled under elevated vs. ambient C_a in 2002 than in 2001, although such increases were not as apparent in the measured NPP (Fig. 2a).

These increases in NPP were driven by ones in gross primary productivity (GPP in [C1]) modelled under 571 vs. 371 $\mu\text{mol mol}^{-1} C_a$ (Table 1) caused by increases in mesophyll aqueous CO₂ concentrations [C6a], calculated from intercellular gaseous CO₂ concentrations assumed to rise proportionally with C_a. These increases in GPP were partially offset by increases in autotrophic respiration (R_a in [C13]) driven by increased biomass R_m [C16] and R_g [C17] (Fig. 2b) when calculating increases in NPP. These increases drove a cumulative gain in NPP of 2032 g C m⁻² (2317 g C m⁻² including root exudation) from 1997 to 2004 that was similar to one of 2216 g C m⁻² derived from

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biometric measurements by McCarthy et al. (2010) (Table 1). This gain was partially offset by a cumulative increase in R_h of 685 g C m^{-2} that was consistent with one of 800 g C m^{-2} estimated by Drake et al. (2011). This gain was further offset by small increases in C losses from CH_4 emission, leaching and runoff, when calculating net biome productivity (NBP) (= Flux Gains – Flux Losses in Table 1).

Almost 70 % of the cumulative gain in NPP modelled from 1997 to 2004 appeared in plant foliage, wood, root and nonstructural C stocks, giving a total gain in plant biomass of 1593 g C m^{-2} (Fig. 2b) which was similar to one of 1735 g C m^{-2} derived from biometric measurements by McCarthy et al. (2010). The remaining 724 g C m^{-2} of this gain in NPP were returned to the soil as litterfall, consistent with an increase of $79 \text{ g C m}^{-2} \text{ yr}^{-1}$ measured in 1998 by Finzi et al. (2001). Of this increase in litterfall, 316 g C m^{-2} was above-ground, corresponding to increased inputs of $48 \pm 14 \text{ g C m}^{-2} \text{ yr}^{-1}$ measured in the forest floor by Lichter et al. (2008), which included some root litterfall. The remaining 408 g C m^{-2} of the increase in modelled litterfall was below-ground, which was greater than an increase of $15 \text{ g C m}^{-2} \text{ yr}^{-1}$ in root litterfall averaged from measurements over this period by Pritchard et al. (2008a).

This increase in modelled litterfall generated a rise in midseason M of 21 % under elevated C_a [A25], similar to one of 15 % in microbial C estimated by Drake et al. (2011), which drove the modelled increase in R_h [A11] (Table 1). Differences between increases in litterfall and R_h caused changes in soil C stocks, including a gain in litter, but a loss in POC and humus, the decomposition of which was primed by the increase in M from litterfall [A3] (Fig. 1). These gains in soil C were slightly smaller than those estimated by Drake et al. (2011) (Table 1).

Additional N required to sustain the increase in GPP modelled under elevated vs. ambient C_a was partially provided by a small cumulative increase in nonsymbiotic N_2 fixation [A27] driven by that in R_h (Table 1). This increase arose from modelled rates of N_2 fixation averaging 0.180 vs. $0.175 \text{ g N m}^{-2} \text{ yr}^{-1}$ under elevated vs. ambient C_a , close to potential rates measured in the forest floor plus mineral soil by Hofmockel and Schlesinger (2007). However the modelled increase in N_2 fixation was mostly offset by

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a decrease in atmospheric NH_3 deposition to the canopy [D15], and by an increase in N leaching, both caused by reduced stomatal conductance (g_c) and transpiration modelled under elevated C_a [B2a], except during drought as described earlier. Wet N deposition was the same under both ambient and elevated C_a and so was not included in Table 1.

The cumulative difference in N inputs modelled under elevated vs. ambient C_a did not account for the gains in plant structural N stocks needed to sustain the increases in plant structural C stocks (Table 1). Most of these gains were consequently drawn from plant nonstructural N stocks in seasonal reserves used in the model to buffer differences between plant N requirements and root N uptake under variable growth conditions. The remainder of these gains was drawn from soil N stocks through increased mineralization of POM and humus N [A26a], driven by the more rapid decomposition of POM and humus C described earlier (Table 1). The consequent decline in POM and humus N stocks (Table 1) was partially offset by a gain in litter N stocks from immobilization of some of the additional NH_4^+ and NO_3^- [A26b, c] mineralized from POM and humus. This loss in POM and humus N stocks, and gain in litter N stocks, were consistent with the loss in mineral-associated C and gain in organic horizon C estimated by Drake et al. (2011) (Table 1).

The gain of plant N and loss of soil N modelled under elevated vs. ambient C_a (Table 1) was achieved by increased root and mycorrhizal uptake [C23] of the N mineralized from POM and humus and not immobilized in litter, and by increased translocation of N from senescing plant material [C19] (Fig. 5). This increase in translocation caused litterfall N modelled under elevated C_a to remain similar to that modelled under ambient C_a , in spite of the increase in litterfall C (Table 1), and so enabled the increase in N uptake modelled under elevated C_a to be almost fully retained in the forest canopy. These modelled increases in uptake and translocation were corroborated by experimental findings (Drake et al., 2011) (Fig. 5).

The modelled increases in N_2 fixation, uptake and translocation (Table 1; Fig. 5) maintained σ_N vs. σ_C and hence increases in GPP [C6, C11, C12] and NPP under

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elevated C_a as the experiment progressed (Fig. 2). The contribution of each of these processes to increases in NPP was then examined by modelling changes in these increases when each process was disabled. When the algorithm for priming POM and humus decomposition by litterfall was disabled [A3] (Fig. 1), the model was unable to simulate rises in NPP consistent with those modelled and measured after the first 2 yr under elevated C_a (Fig. 6a). When the algorithm for the effect of $\sigma_N : \sigma_C$ ratios on translocation was disabled [C19], the model simulated rises in NPP under elevated C_a that were only slightly smaller than those with the algorithm enabled (Fig. 6b). When nonsymbiotic N_2 fixation was disabled [A27], NPP modelled under both ambient and elevated C_a was only marginally reduced (Fig. 6c). The algorithm for priming was apparently essential for modelling NPP response to elevated C_a , while those for translocation and N_2 fixation were much less so.

However modelled gains in plant N through increased root N uptake and translocation under elevated C_a (Fig. 5) were not commensurate with those in plant C through increased NPP (Fig. 2a). Consequently the model simulated a rise in the NPP:N uptake ratio from 162 to 173 g C g N⁻¹ under 371 vs. 571 $\mu\text{mol mol}^{-1} C_a$. The increase in this ratio was consistent with one from 158 to 170 g C g N⁻¹ (assuming 0.5 g C g DM⁻¹) measured at the Duke FACE site by Finzi et al. (2007). Consequently foliar N concentrations modelled in 1998 declined from 24.0 to 22.6 mg N g C⁻¹ while those measured in the same year by Finzi et al. (2001) declined from 21.0 to 18.8 mg N g C⁻¹, although this measured decline was considered to be nonsignificant. These rises in NPP:N uptake ratios and consequent declines in foliar N concentrations suggest a gradually increasing N limitation that will eventually reduce future increases in NPP.

4.2 The ORNL FACE Experiment

Net primary productivity modelled at ORNL was generally larger than that derived from measurements (Fig. 7a), although wood growth increments were similar (Fig. 7b). NPP modelled under 550 $\mu\text{mol mol}^{-1} C_a$ rose sharply above that under 370 $\mu\text{mol mol}^{-1} C_a$ during the first two years of the experiment (Fig. 7a), but declined relatively more

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thereafter so that gains in NPP modelled under elevated C_a became smaller as the experiment progressed. Almost 80 % of the modelled rise in NPP was allocated to leaves (Fig. 8a) and wood (Fig. 8b), and only *ca.* 20 % to roots (Fig. 8c) as was modelled at Duke (Fig. 3). Gains in leaf NPP modelled under elevated C_a in the model were larger, while those in root NPP were smaller, than gains derived from biometric measurements by Norby et al. (2010) who attributed most of the total gain in NPP at ORNL to root production, particularly in 2000–2002 (Fig. 8c). The greater modelled vs. measured NPP (Fig. 7a) was mostly attributed to greater modelled vs. measured root NPP (Fig. 8c).

Norby et al. (2010) attributed these declining gains in NPP to more rapid declines in tree N status, apparent in lower foliar N concentrations measured under elevated C_a (Fig. 9). Lower foliar N concentrations were also modelled [C6, C12] through changes in σ_N vs. σ_C [C11], although values were consistently 15 mg N g C⁻¹ larger than those measured (Fig. 9). Strong N limitations to NPP were also indicated by the sharp rise in wood increment measured and modelled under ambient C_a after fertilizer application started in 2004 (Fig. 7b). In the model, declining N status caused greater allocation of σ_C , σ_N and σ_P to roots vs. leaves and wood [C50–C53], so that root NPP was maintained (Fig. 8c) while leaf and wood NPP declined (Fig. 8a, b) as the experiment progressed.

The modelled trend towards smaller gains in NPP as the experiment progressed was reversed in 2002, 2006 and 2007 (Fig. 7a). During these years soil drying following lower than average precipitation in 2001 and in 2005–2007 caused smaller declines in NPP to be modelled under elevated vs. ambient C_a (Fig. 7a), as at the Duke Forest in 2002 (Fig. 2a). Smaller declines under elevated C_a were also apparent in NPP derived from measurements in 2002, but not in 2006 and 2007. The greater decline in NPP measured under elevated vs. ambient C_a in 2007 was attributed by Warren et al. (2011) to greater declines in transpiration, g_c and hence C gain under elevated C_a during the 2007 drought. In the model, however, soil water conserved before droughts by reductions in transpiration under elevated vs. ambient C_a , as was observed by Warren

et al. (2011), allowed smaller declines in transpiration, g_c and hence in net C uptake to be modelled under elevated C_a as droughts progressed.

Increases in GPP [C1] modelled under 550 vs. 370 $\mu\text{mol mol}^{-1}$ C_a drove a cumulative gain in NPP from 1998 to 2008 of 1858 g C m^{-2} (1971 g C m^{-2} including root exudation), slightly greater than one of 1542 g C m^{-2} derived from biometric measurements by Norby et al. (2010) (Table 2). This gain was partially offset by an increase of 680 g C m^{-2} in R_h , and by a small increase in C losses from leaching and runoff, when calculating NBP (Table 2).

About two-thirds of the gain in NPP modelled from 1998 to 2008 appeared in plant wood, root and nonstructural C stocks (Table 2). Gains in foliar stocks were not modelled because values were calculated at the end of each year after leafoff. The remaining 640 g C m^{-2} of this gain in NPP were returned to the soil as litterfall, of which 302 g C m^{-2} was above-ground, consistent with an annual increase of 40 $\text{g C m}^{-2} \text{yr}^{-1}$ in surface litterfall measured in 2000 by Johnson et al. (2004). The remaining 338 g C m^{-2} of the increase in modelled litterfall was below-ground, which was less than the $675 \pm 500 \text{ g C m}^{-2}$ increase in total root litterfall estimated to 2006 by Iversen et al. (2008).

This increase in modelled litterfall generated a rise in midseason M of 9% [A25], similar to one of 13% in microbial C measured in July 2000 by Johnson et al. (2004), which drove the modelled increase in R_h [A11] (Table 2). This increase slightly exceeded that in litterfall, causing small declines in litter, POM and humus C stocks primed by the increase in M from litterfall [A3] (Fig. 1). These declines contrasted with a substantial increase in soil C measured by Iversen et al. (2012) under elevated vs. ambient C_a in 2009, but this increase was also apparent in pretreatment measurements of soil C by Johnson et al. (2004) and so may have been caused by natural soil variability.

Additional N required to sustain the increase in GPP modelled under elevated vs. ambient C_a was partially provided by a small cumulative increase in nonsymbiotic N_2 fixation [A27], and in atmospheric NH_3 deposition due to greater N immobilization at the soil surface [D15] (Table 2). Additional N was provided by reductions in N

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losses from emissions and leaching caused by greater N immobilization [A26] in the soil profile at this N-limited site (Table 2). The reduction in N loss from leaching in the model was consistent with one of $0.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ measured experimentally in 1999 by Johnson et al. (2004).

The cumulative net gains in N inputs partly accounted for the substantial increase in plant structural N stocks needed to sustain increases in plant structural C stocks (Table 2). Some of this increase in plant structural N stocks was drawn from plant non-structural N stocks, and the remainder was drawn from soil N stocks through increased mineralization of POM and humus N [A26a], driven by the more rapid decomposition of POM and humus C described earlier.

As for the Duke Forest, the gain of plant N and loss of soil N modelled under elevated vs. ambient C_a at ORNL (Table 2) was achieved by increased root and mycorrhizal uptake [C23], some of which might be attributed to increased root and mycorrhizal growth as well as to priming of humus decomposition. Detailed measurements of root productivity by Iversen et al. (2008) enabled testing of changes in root growth and function modelled under ambient vs. elevated C_a (Fig. 10a). Modelled root and mycorrhizal mass densities increased under 550 vs. $370 \mu\text{mol mol}^{-1} C_a$ (Fig. 9), but less than did measured values during 2001 (Fig. 10a), the year of greatest root productivity reported in Iversen et al. (2008) (Fig. 8c).

In the model, greater root and mycorrhizal growth [C20b] under elevated C_a was driven by greater shoot- root and root-mycorrhizal transfers of σ_C [C50, C52] from greater concentration gradients generated by greater CO_2 fixation [C1] (Grant, 1998) (Fig. 10a). Greater growth drove greater root and mycorrhizal elongation [C21b, c] (Fig. 10b) used to calculate path lengths and surface areas for mineral N uptake [C23a–d]. Greater σ_C concentrations drove an increase in C exudation [C19e–i] of 53 vs. $42 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Grant, 1993) (Fig. 10c), while more rapid root and mycorrhizal respiration [C15] and lower σ_N vs. σ_C drove an increase in root and mycorrhizal litterfall [C18] of 234 vs. $208 \text{ g C m}^{-2} \text{ yr}^{-1}$. This increase in litterfall was smaller, but not significantly different, than one of 255 ± 148 vs. 161 ± 87 measured in 2001 by Iversen et

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al. (2008). These increases in exudation and litterfall provided more substrate for litter M growth [A1] and hence priming of POM and humus decomposition [A3] (Fig. 1) under elevated C_a . However greater root and mycorrhizal elongation generated only slightly more rapid mineral N uptake [C23a–d], in which increases in mycorrhizal uptake offset reductions in root uptake below 0.5 m (Fig. 10d).

Gains in NPP modelled and measured at ORNL were smaller than those at the Duke Forest after the third year under elevated C_a (Fig. 7a vs. Fig. 2a) in spite of similar soil attributes and climate, suggesting that deciduous forests may respond less to elevated C_a than do coniferous. When the deciduous functional type used in the ORNL simulations was replaced with the coniferous one used at Duke, values of NPP modelled under ambient and elevated C_a remained similar to those modelled earlier from 1998 to 2004 (Fig. 11a). However NPP modelled for the coniferous functional type under ambient C_a did not decline thereafter while that under elevated C_a rose (Fig. 11a). The smaller gains in NPP modelled for the deciduous functional type under elevated C_a from 2005 through 2008 were attributed to larger declines in leaf N concentrations than those for the coniferous functional type (Fig. 11b). These greater declines were caused by greater N loss from above-ground litterfall relative to N gain from root uptake, and hence less retention of N in the deciduous canopy than in the coniferous. This lesser retention was caused by phenology-driven withdrawal of branch σ_C , σ_N and σ_P and consequent additional litterfall modelled during autumn in deciduous functional types. Less retention of N was apparent in smaller ratios of NPP:N uptake modelled at ORNL (90 vs. 108 g C g N⁻¹ under 370 vs. 550 $\mu\text{mol mol}^{-1} C_a$) than at Duke (162 vs. 173 g C g N⁻¹). These smaller ratios were consistent with ones of 120 vs. 112 g C g N⁻¹ (assuming 0.5 g C g DM⁻¹) measured at ORNL by Finzi et al. (2007). Consequently ratios of NPP modelled under elevated vs. ambient C_a remained smaller for the deciduous vs. coniferous functional type at ORNL (Fig. 11c), explaining the smaller response of NPP to elevated C_a modelled at ORNL vs. Duke (Fig. 2a vs. Fig. 7a).

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4.3 The Rhinelander FACE Experiment

The forest stands at Rhinelander were exposed to elevated vs. ambient C_a within a year of planting, so that elevated C_a raised GPP [C1] and hence NPP during early growth by increasing both CO_2 fixation rates per unit leaf area [C6a] and leaf area growth [C21a]. Consequently gains in NPP modelled under elevated C_a were relatively large during 1998 and 1999 when elevated C_a increased leaf area growth at low values of LAI limiting to CO_2 fixation (Fig. 12a). These gains declined from 2000 to 2004 when LAI attained values less limiting to CO_2 fixation. Only ~60% of these gains in NPP were allocated to foliar and wood production in the model (Fig. 13a, b), with the remainder allocated to root production (Fig. 13c). However measured gains were allocated more to foliar and wood production and less to root production than were modelled gains, so that root and hence total NPP in the model rose above that measured as the experiment progressed.

Declining gains in NPP modelled from 2001 to 2004 (Fig. 12a) were not attributed to increasing N limitation, because litterfall N concentrations measured and modelled under ambient and elevated C_a did not decline as the experiment progressed, in contrast to ORNL where foliar N concentrations declined (Fig. 9). Some N limitation to gains in NPP was apparent in lower litterfall N concentrations measured and modelled under elevated C_a (Fig. 14), due in the model to lower foliar N concentrations and greater N translocation as modelled at the other sites (Figs. 5 and 9). Kubiske et al. (2010) attributed declining gains in tree growth measured from 2001 to 2004 under elevated vs. ambient C_a (Fig. 12b) to declining July radiation recorded at Rhinelander. This decline was accompanied by one in temperature, causing modelled and measured rises in NPP and wood increment to slow under ambient C_a , and more so under elevated C_a , during 2001–2004 (Fig. 12a, b). Conversely, radiation and T_a recorded at Rhinelander were higher in 2005 than in 2001–2004, causing modelled rises in NPP and wood increment to increase under ambient C_a , and more so under elevated C_a .

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These responses of modelled NPP to radiation and T_a suggested that some of the interannual variation in gains of NPP under elevated vs. ambient C_a could be attributed to responses of CO_2 fixation to seasonal variation in weather. Because 2004 and 2005 were the coolest and warmest years respectively during the experimental period (May–September 2004 vs. 2005: average radiation 18.4 vs. $19.7 \text{ MJ m}^{-2} \text{ d}^{-1}$, average T_a 15.1 vs. 17.1°C), days with contrasting radiation and T_a in these two years were selected to examine modelled response of diurnal CO_2 exchange to 541 vs. $374 \mu\text{mol mol}^{-1} C_a$ (Fig. 15). Radiation recorded during DOY 202–203 was higher in 2005 than in 2004 (Fig. 15a) while daytime T_a was similar (Fig. 15b). Rises in CO_2 influxes modelled under elevated vs. ambient C_a were greater during DOY 202–203 in 2005 vs. 2004, particularly with lower radiation during DOY 203 in 2004 (Fig. 15c). Greater rises in CO_2 influxes with higher C_a were modelled under higher radiation because CO_2 -limited carboxylation [C6a] responded more to C_a than did radiation-limited carboxylation [C7a, b].

Values of T_a recorded during DOY 218–219 were higher in 2005 than in 2004 (Fig. 15a) while radiation was similar (Fig. 15b). Rises in CO_2 influxes modelled under elevated vs. ambient C_a were greater during DOY 218–219 in 2005 vs. 2004, particularly with lower T_a during DOY 218 in 2004 (Fig. 15c). Greater rises in CO_2 influxes with elevated C_a were modelled under higher T_a because elevated C_a offset adverse effects of higher T_a on carboxylation through increased CO_2 compensation points [C6c, d] and Michaelis-Menten constants [C6e], and through decreased solubility of CO_2 vs. O_2 [C6a], thereby reducing photorespiration vs. carboxylation. These greater rises in CO_2 influxes modelled with higher C_a under higher radiation and T_a contributed to the greater gains in NPP and wood increment modelled in 2005 vs. 2004 (Fig. 12).

Increases in GPP [C1] modelled under 541 vs. $374 \mu\text{mol mol}^{-1} C_a$ [C1] (Fig. 15) drove a cumulative gain in NPP from 1998 to 2006 of 860 g C m^{-2} (Table 3) which on an annual basis was smaller than one of 807 g C m^{-2} from 1998 to 2003 derived from biometric measurements by King et al. (2005) (Fig. 11a). However the modelled gain rose to 929 g C m^{-2} if exudation was included. This gain was partially offset by

an increase in R_h of 387 g C m^{-2} and by small increases in C losses from emission, leaching and runoff (Table 3).

About 55% of modelled gains in NPP appeared in plant wood, root and nonstructural C stocks (Table 3). Gains in foliar stocks were not modelled because values were calculated at the end of each year after leafoff. The remaining 415 g C m^{-2} of this gain in NPP were returned to the soil as litterfall, of which 149 g C m^{-2} was above-ground, consistent with an increase in annual surface litterfall of $32 \text{ g C m}^{-2} \text{ yr}^{-1}$ measured in 2003 by Liu et al. (2005) and an average of $30 \text{ g C m}^{-2} \text{ yr}^{-1}$ measured from 2002 to 2008 by Talhelm et al. (2012). The remaining 266 g C m^{-2} of the increase in modelled litterfall was below-ground.

This increase in modelled litterfall drove the modelled increase in R_h (Table 3) which almost entirely offset that in litterfall, causing a small rise in litter C stocks and a small decline in POM and humus C stocks primed by an increase in M from litterfall [A3] (Fig. 1). These changes in soil C stocks in the model were consistent with a small increase in coarse POM stocks and concurrent small decrease in mineral-associated organic matter observed by Hofmockel et al. (2011b) under elevated vs. ambient C_a at Rhineland.

Additional N required to sustain the increase in GPP modelled under elevated vs. ambient C_a was partially provided by a small cumulative increase in nonsymbiotic N_2 fixation [A27], partially offset by a small decrease in atmospheric NH_3 deposition (Table 3). Additional N was provided by reductions in N losses from emissions and leaching caused by greater N immobilization in the soil profile [A26].

The cumulative net gain in soil N inputs partly accounted for the increase in plant structural N stocks needed to sustain the increase in plant structural C stocks (Table 3). The remainder of this increase was drawn from soil N stocks through increased mineralization of POM and humus N [A26a], driven by the more rapid decomposition of POM and humus C described earlier. This contribution of this increased mineralization to plant N stocks was partially offset by increased immobilization of N in litter [A26b, c] and consequent gain in litter N stocks (Table 3).

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5 Discussion

5.1 Effects of changes in N cycling on NPP under elevated C_a

5.1.1 More rapid mineralization of soil N primed by increased litterfall

More rapid litterfall [C18, C19a–d] and root exudation [C19e–i] (Grant, 1993) modelled under elevated vs. ambient C_a (Tables 1, 2 and 3; Fig. 10d) increased litter stocks and hence litter M [A25]. Consequent increases in litter M concentrations drove greater transfer of litter M to POM and humus [A3] (Fig. 1), thereby hastening (priming) POM and humus decomposition as demonstrated in Grant et al. (1993). Because C : N ratios in humus were lower than those in litter, priming also hastened net N mineralization [A26a] and uptake [C23] (Tables 1, 2 and 3; Figs. 4, 9c).

This model representation of priming was consistent with the experimental findings of increased root exudation, microbial biomass and exoenzyme activity (Phillips et al., 2011) from greater litterfall (Lichter, 2008) that hastened soil respiration and hence N mineralization and uptake from older SON fractions under elevated vs. ambient C_a (Drake et al., 2011; Hofmockel et al., 2011a, b). However gains in root N uptake modelled with priming under elevated C_a were partially offset by increased N immobilization [A26b,c] apparent in greater litter N stocks (Tables 1, 2 and 3) generated by greater litterfall with higher C : N ratios (Fig. 14). These model results were consistent with experimental findings that increased litterfall under elevated C_a induced concurrent increases in immobilization of plant-derived SOM and in mineralization of mineral-associated SOM (Hofmockel et al., 2011b; Holmes et al., 2006).

When priming was disabled, the model was unable to simulate sustained increases in NPP under elevated C_a (Fig. 6a), indicating that simulation of priming was vital to modelling the response of NPP to C_a in an ecosystem model with fully coupled C-N cycles. Models in which decomposition and mineralization of humus are independent of litterfall are unlikely to be able accurately to simulate long-term changes in forest productivity under elevated vs. ambient C_a .

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5.1.2 Greater biological N₂ fixation primed by increased litterfall

Greater litterfall under elevated C_a in the model increased growth of diazotrophic M [A25] and hence increased nonsymbiotic N₂ fixation [A27] (Grant et al., 2007). However these increases were small with respect to those in plant N stocks (Tables 1, 2 and 3), contributed little to increases in NPP (Fig. 6c), and so were unlikely to be the main source for increased N uptake. Hofmockel and Schlesinger (2007) did not detect increases in nonsymbiotic N₂ fixation from incubated samples of forest floor and mineral soil taken from plots under elevated vs. ambient C_a in the Duke FACE experiment. However they did measure substantial increases from these samples with additions of labile C representing litterfall, as has been modelled by *ecosys* in other studies (e.g. Fig. 1 in Grant et al., 2007). Hofmockel and Schlesinger (2007) concluded that increases in nonsymbiotic N₂ fixation would not enable the more rapid N uptake required to sustain increases in NPP under elevated C_a . This conclusion was consistent with the relatively minor contribution of these increases to those in plant N stocks in the model, although this contribution may become more important in longer-term responses to elevated C_a under more N-limited conditions than those at the FACE sites modelled here.

5.1.3 Greater N uptake from increased root growth

Root growth has consistently been found to increase under elevated C_a (reviewed in Iversen, 2010), as modelled here (Fig. 10a). Mycorrhizal growth has been found to increase relatively more than root growth under elevated C_a , particularly below 0.15 m (Pritchard et al., 2008b), as also modelled here (Fig. 10a). These increases in growth, and hence elongation (Fig. 10b), reduced path lengths for N diffusion [C23a, c] and increased surface areas for active N uptake [C23b, d]. However N uptake (Fig. 10d) was also determined by aqueous concentrations of NH₄⁺ [C23a, b] and NO₃⁻ [C23c, d] which were governed by exchange with M through mineralization [A26a] and immobilization [A26b, c], and also by adsorption [E10], nitrification [H11], denitrification [H7-9] and leaching [D19]. Consequently increases in N uptake modelled under elevated C_a

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(Fig. 5; Tables 1, 2 and 3) could not be unambiguously attributed to increases in root and mycorrhizal growth since the effects on N uptake of this growth could not be separated from those of soil N transformations.

5.1.4 Greater translocation of N from senescing plant material

5 Greater translocation was modelled under elevated C_a [C19] (Fig. 5), but made only a limited contribution to increases in NPP (Fig. 6b). Both modelled and measured leaf N concentrations consistently declined under elevated C_a (Fig. 9). Such declines frequently induce greater translocation of N from senescing plant material (Barnes et al., 1998), further reducing N concentrations in litter (Fig. 14) from those in leaves. Greater
10 translocation modelled under elevated C_a caused leaf litterfall N to remain similar to that under ambient in spite of greater litterfall C, as observed experimentally by Johnson et al. (2004). However evidence for greater translocation under elevated C_a has been inconsistent, being found in some experiments (Drake et al., 2011), but not in others (Johnson et al., 2004). Greater translocation of N from senescing plant material
15 is therefore likely to be a less important process in maintaining increases in NPP under elevated C_a than is soil priming.

5.2 Effects of other changes in site conditions on NPP under elevated C_a

5.2.1 Temperature

20 Changes in N cycling under elevated C_a interacted with changes in other site conditions such as T_a , radiation, precipitation and plant functional type to determine increases in NPP. The greater increase in NPP with C_a under higher vs. lower T_a and radiation (Fig. 15) was an inherent response of the biochemical model of CO_2 fixation [C1–C8] (Farquhar et al., 1980) widely used to simulate CO_2 fixation in ecosystem models. The model response to T_a occurred because higher C_a reduced ratios of photorespiration
25 to carboxylation more when these ratios were larger under higher T_a (Long, 1991). This

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response caused greater increases in net CO₂ uptake with higher C_a to be modelled under higher T_a at seasonal (Fig. 4c, f) and diurnal (Fig. 15c) time scales. This model behaviour was consistent with results from a meta-analysis by Wang et al. (2012) in which elevated C_a raised net photosynthetic rates more at elevated vs. ambient T_a, particularly in woody species. This model behaviour would also explain the large response of pine growth to elevated C_a at the Duke FACE site (MAT = 15.5 °C) and the lack of response of pine growth to similarly elevated C_a found by Dawes et al. (2011) at a FACE site in an alpine climate (MAT = 1.8 °C). However greater rises in net CO₂ exchange and growth with elevated C_a under higher T_a have not always been found in controlled experiments (e.g. Tjoelker et al., 1998; Wertin et al., 2012).

It should be noted that greater increases in net CO₂ uptake with C_a under higher T_a can only be sustained through commensurate increases in the uptake of limiting soil nutrients. In the model, soil warming under higher T_a hastened decomposition [A1, A6], R_h [A6, A13], hence N mineralization [A26a] and root and mycorrhizal N uptake [C22, C23]. These soil processes may explain the greater rise in *Larix* growth under elevated vs. ambient C_a found by Dawes et al. (2011) in years following earlier snowmelt and warmer soil in an alpine climate. Greater rises in both CO₂ and N uptake caused larger gains in NPP to be modelled for deciduous trees in a warmer climate at ORNL (MAT = 14.2 °C) (Fig. 7a, Table 2) than in a cooler climate at Rhinelander (MAT = 4.9 °C) once LAI was no longer limiting to CO₂ fixation (Fig. 12a, Table 3). However gains in NPP modelled at Rhinelander may have been underestimated.

5.2.2 Precipitation

Reduced transpiration modelled under elevated C_a [B1c] from increased r_c [B2a] during periods with higher precipitation conserved soil water, enabling greater water uptake and hence slower declines in ψ_c [B14], g_c, transpiration and CO₂ fixation [C6a, C7a, C9] during subsequent periods of low precipitation, as at Duke in 2002 (Figs. 2a, 4f) and ORNL in 2002, 2006 and particularly in 2007 (Fig. 7a). The slower decline in CO₂ fixation caused a smaller decline in annual NPP modelled under elevated C_a

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and consequently a greater gain from that under ambient C_a , particularly at Duke in 2002 (Fig. 2a). The water conservation modelled under elevated C_a was consistent with that observed in deciduous trees during droughts under elevated C_a by Leuzinger and Körner (2007), and with observations by Wertin et al. (2010) that increases in C_a may mitigate declines in net photosynthesis of loblolly pine during periods of drought. However these slower declines were not consistent with more rapid declines in transpiration measured at ORNL during drought under elevated vs. ambient C_a by Warren et al. (2011).

As noted earlier with respect to higher T_a , greater increases in net CO_2 uptake with C_a under lower precipitation can only be sustained through commensurate increases in the uptake of limiting soil nutrients. Declines in NPP during droughts reduced the assimilation of σ_N , increasing its concentration with respect to σ_C and thereby reducing its mycorrhizal-root-shoot concentration gradients [C51] and uptake [C23g] (Fig. 5). Reduced assimilation of σ_N during soil drying partially alleviated N limitations, allowing the greater gains in NPP modelled under elevated C_a to be achieved.

5.2.3 Plant functional type

Smaller increases in NPP under elevated C_a modelled for deciduous vs. coniferous functional types (Fig. 11c) were attributed to more rapid leaf turnover which reduced retention of canopy N, apparent in smaller ratios of NPP:N uptake modelled and measured at ORNL vs. Duke. Franklin et al. (2009) attributed these smaller increases to more rapid fine root turnover at ORNL vs. Duke because a greater fraction of the increase in NPP measured under elevated C_a at ORNL was allocated to roots (Fig. 8c) (Norby et al., 2010). However in the model, increases in NPP were allocated to roots similarly at ORNL and Duke (Fig. 8c vs. Fig. 3c) because parameters in the algorithms for shoot-root-mycorrhizal transfers of σ_C , σ_N and σ_P did not change with functional type [C50–C53]. Both attributions indicate that NPP of functional types with more rapid turnover of plant material will experience greater N limitation and hence will increase less over time under elevated C_a .

Supplementary material related to this article is available online at:
[http://www.biogeosciences-discuss.net/10/6783/2013/
bgd-10-6783-2013-supplement.pdf](http://www.biogeosciences-discuss.net/10/6783/2013/bgd-10-6783-2013-supplement.pdf).

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Table 1. Differences in cumulative fluxes and stocks of C and N estimated from biometric measurements (E) or modelled (M) at the Duke Forest FACE experiment after 8 yr (1997–2004) under 571 vs. 371 $\mu\text{mol mol}^{-1}$ CO_2 .

	C		N	
	E	M	E	M
	$\text{g C m}^{-2} \text{ 8 yr}^{-1}$		$\text{g N m}^{-2} \text{ 8 yr}^{-1}$	
Fluxes: Gains				
Δ Fixation (CO_2 , N_2)		+3459		+0.4
Δ Deposition (NH_3)				-0.3
Δ NPP: biometric	+2216 ^c	+2032		
Δ NPP: total		+2317 ^a		
Fluxes: Losses				
ΔR_h	+800 ^b	+685		
Δ Emission (CH_4 , N_2 + N_2O)		+10		-0.1
Δ Leaching + runoff		+12	0 ^b	+0.3
Δ NBP		+1610		-0.1
Stocks: Plants				
Δ Biomass: foliage		+92	+1.8 ^d	+1.0
Δ Biomass: wood		+1420	+11.5 ^d	+6.0
Δ Biomass: root	+473 ^b	+33		+0.3
Δ Biomass: non-structural		+48		-5.5
Δ Biomass: total	+1735 ^c	+1593	+3.3 ^e , +15.4 ^d	+1.8
Stocks: Soil				
Δ Litter	+165 ^b	+78	+6.4 ^b	+2.5
Δ POM, humus	+16 ^b	-79	-4.0 ^b	-4.9
Δ Dissolved (DIC, DIN)		+18		+0.5
Δ Total		+1610		-0.1

^a Includes root exudation, ^b Drake et al. (2011), ^c McCarthy et al. (2010), ^d Hofmockel et al. (2011), ^e Finzi et al. (2007).

Table 2. Differences in cumulative fluxes and stocks of C and N estimated from biometric measurements (E) or modelled (M) at the ORNL FACE experiment after 11 yr (1998–2008) under 550 vs. 370 $\mu\text{mol mol}^{-1}$ CO_2 .

	C		N	
	E	M	E	M
	$\text{g C m}^{-2} \text{ 11 yr}^{-1}$		$\text{g N m}^{-2} \text{ 11 yr}^{-1}$	
Fluxes: Gains				
Δ Fixation (CO_2 , N_2)		+2829		+0.2
Δ Deposition (NH_3)				+0.4
Δ NPP: biometric	+1542 ^b	+1858		
Δ NPP: total		+1971 ^a		
Fluxes: Losses				
ΔR_h		+680		
Δ Emission (CH_4 , N_2 , N_2O)		0		-0.1
Δ Leaching + runoff		+26		-0.7
Δ NBP		+1265		+1.4
Stocks: Plants				
Δ Biomass: foliage		0		0
Δ Biomass: wood	+487 ^b	+1228		+4.9
Δ Biomass: root	+40 ^c	+64	+0.6 ^c	+0.7
Δ Biomass: non-structural		+39		-0.6
Δ Biomass: total		+1331		+5.0
Stocks: Soil				
Δ Litter		-39		-0.4
Δ POM, humus		-32		-3.4
Δ Dissolved (DIC, DIN)		+5		+0.2
Δ Total		+1265		+1.4

^a Includes root exudation, ^b Norby et al. (2010), ^c Iversen et al. (2012).

Table 3. Differences in cumulative fluxes and stocks of C and N estimated from biometric measurements (E) or modelled (M) at the Rhinelander FACE experiment after 9 yr (1998–2006) under 541 vs. 374 $\mu\text{mol mol}^{-1}$ CO_2 .

	C		N	
	E	M	E	M
	$\text{g C m}^{-2} \text{ 9 yr}^{-1}$		$\text{g N m}^{-2} \text{ 9 yr}^{-1}$	
Fluxes: Gains				
Δ Fixation (CO_2 , N_2)		+1606		+0.2
Δ Deposition (NH_3)				-0.1
Δ NPP: biometric	+807 ^d	+860		
Δ NPP: total		+929		
Fluxes: Losses				
ΔR_h		+387		
Δ Emission (CH_4 , N_2 , N_2O)		+2		-1.1
Δ Leaching + runoff		+11		-0.2
Δ NBP		+529		+1.4
Stocks - Plants				
Δ Biomass: foliage		0		0
Δ Biomass: wood		+409		+1.6
Δ Biomass: root	+50 ^b , +11 ^c	+90		+1.3
Δ Biomass: non-structural		+15		+0.1
Δ Biomass: total		+514		+3.0
Stocks: Soil				
Δ Litter		+41		+1.5
Δ POM, humus	-220 ^a	-29		-3.2
Δ Dissolved (DIC, DIN)		+3		+0.1
Δ Total		+529		+1.4

^a Talhelm et al. (2012), ^b Pregitzer et al. (2008), ^c Rhea and King (2012) to 1 m depth (nonsignificant), ^d King et al. (2005) from 1998 to 2003.

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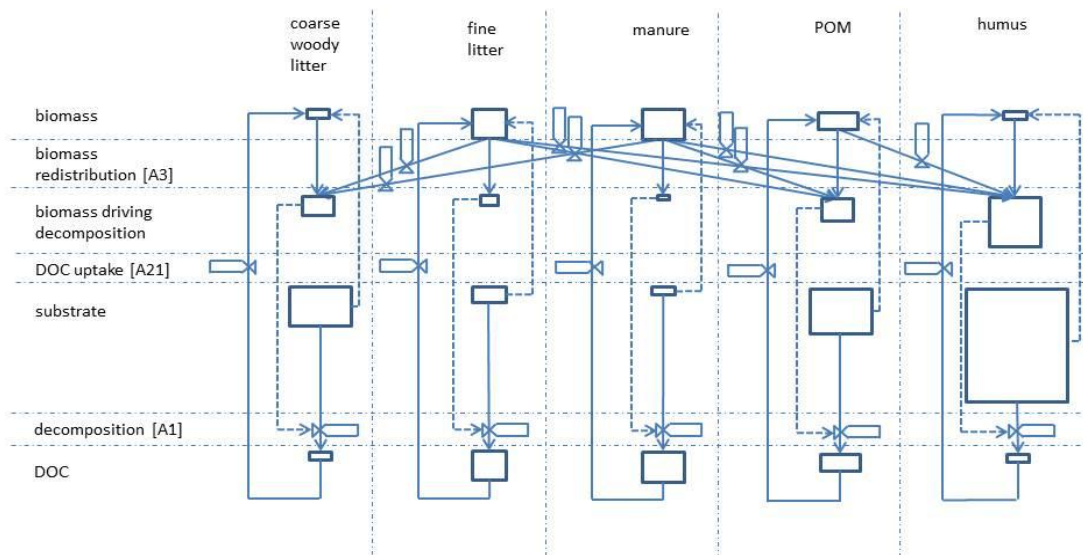


Fig. 1. Conceptual model for priming implemented in ecosys. Biomass in each of five substrate-microbe complexes (coarse woody litter, fine litter, manure, particulate organic matter (POC) and humus) is driven by uptake of DOC from decomposition. This biomass is then redistributed across these complexes according to biomass: substrate ratios in each complex. The redistributed biomass then drives decomposition. Expressions in brackets refer to equations in the Supplement. Boxes represent state variables, sizes of which indicate relative sizes of biomass or substrate in each complex. Solid lines with valves represent rates of transfer among states, dashed lines represent drivers of these transfers.

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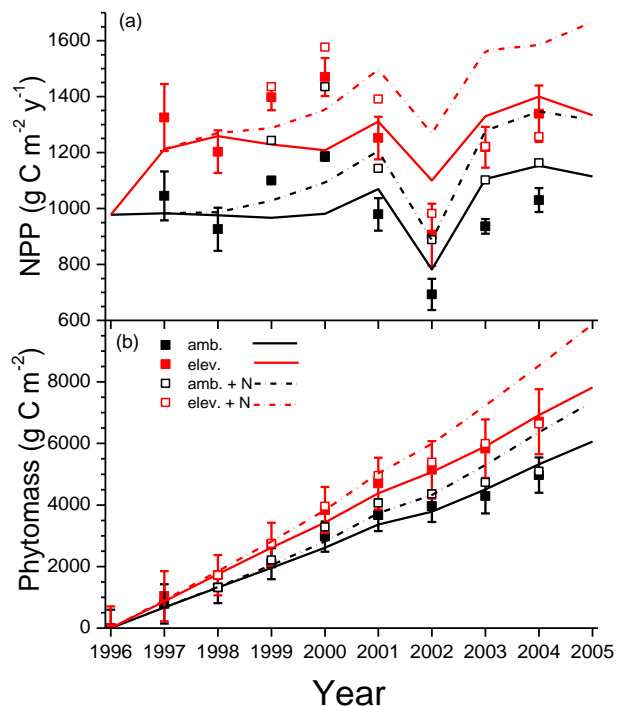


Fig. 2. (a) Annual net primary productivity (NPP) and (b) gain in total phytomass measured (symbols) and modelled (lines) from 1997 to 2004 under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 571 \mu\text{mol mol}^{-1}$) atmospheric CO_2 concentration (C_a) with or without N fertilizer at the Duke FACE experiment. Measured data from McCarthy et al. (2010). Root exudation (Grant, 1993) was excluded from modelled NPP to simulate biometric measurements.

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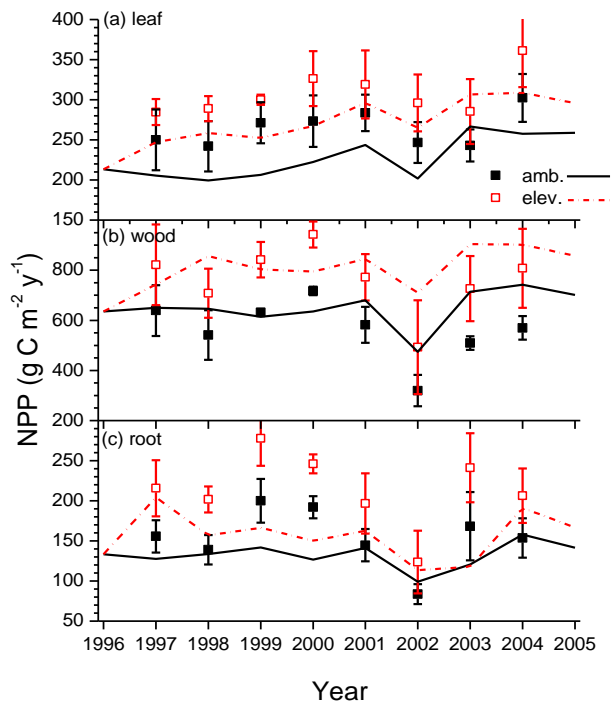


Fig. 3. (a) Annual net primary productivity (NPP) measured (symbols) and modelled (lines) in (a) leaves, (b) wood and (c) roots from 1997 to 2004 under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 571 \mu\text{mol mol}^{-1}$) C_a at the Duke FACE experiment. Measured data from McCarthy et al. (2010). Root exudation (Grant, 1993) was excluded from modelled NPP to simulate biometric measurements.

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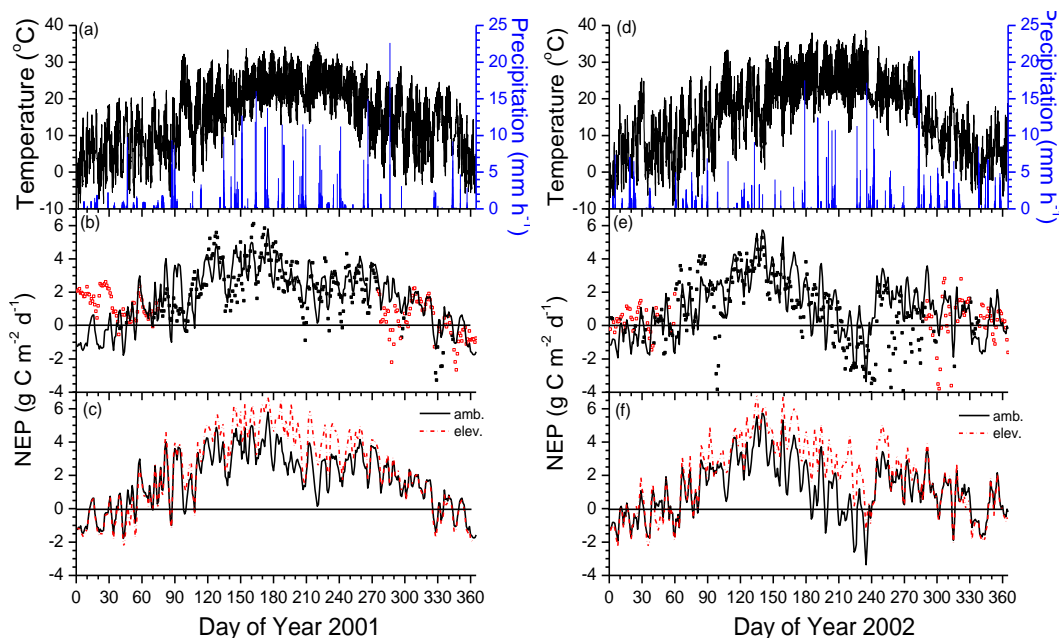


Fig. 4. (a), (d) Air temperature and precipitation, (b), (e) net ecosystem productivity (NEP) modelled (lines) and derived from eddy covariance (EC) measurements (symbols) under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) C_a , (c), (f) NEP modelled under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 571 \mu\text{mol mol}^{-1}$) C_a at the Duke FACE experiment during 2001 and 2002. Positive or negative NEP represent net uptake or emission of CO_2 . Open or closed symbols represent NEP derived from less or more than 24 $\frac{1}{2}$ -hourly EC measurements.

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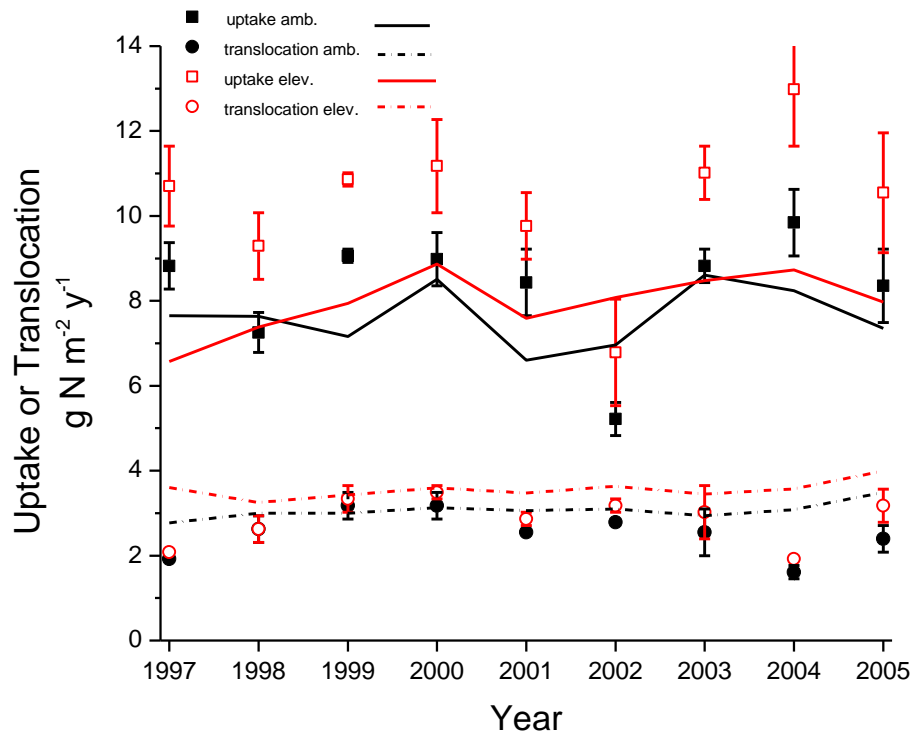


Fig. 5. Rates of N uptake and translocation estimated from measurements (symbols) and modelled (lines) from 1997 to 2004 under ambient ($\sim 371 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 571 \mu\text{mol mol}^{-1}$) C_a at the Duke FACE experiment. Estimated values from Drake et al. (2011).

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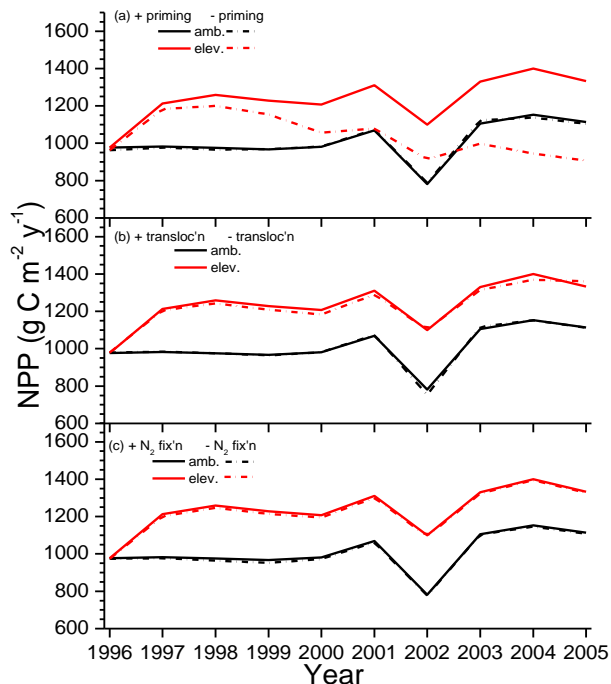


Fig. 6. Annual net primary productivity (NPP) modelled from 1997 to 2004 under ambient ($371 \mu\text{mol mol}^{-1}$) vs. elevated ($571 \mu\text{mol mol}^{-1}$) C_a without N fertilizer at the Duke FACE experiment with the model algorithms for **(a)** priming by litterfall [A3], **(b)** translocation driven by plant N status [C19], and **(c)** nonsymbiotic N_2 fixation enabled (+) or disabled (-). NPP modelled with the algorithms enabled are the same as those in Fig. 2a. Agreement between enabled and disabled algorithms for NPP modelled under ambient ($371 \mu\text{mol mol}^{-1}$) C_a was achieved by offsetting changes in model parameters affected by disabling as described in the Methods.

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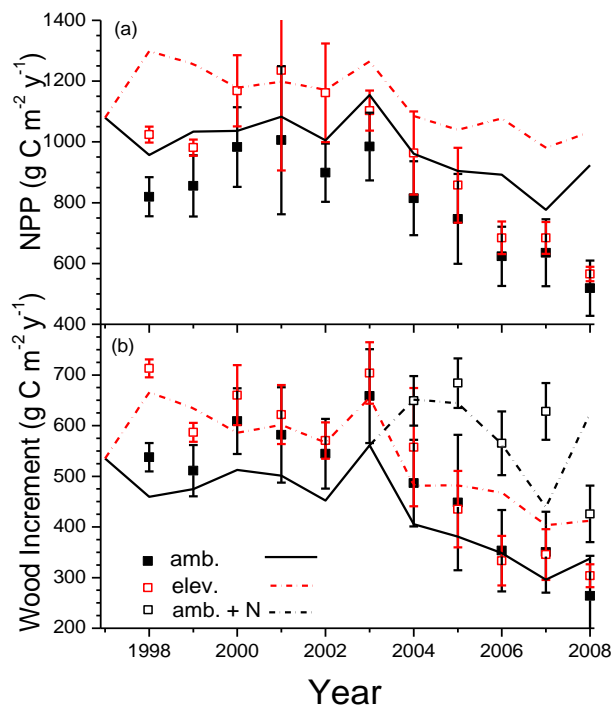


Fig. 7. (a) Annual net primary productivity (NPP) and **(b)** gain in biomass measured (symbols) and modelled (lines) from 1998 to 2008 under ambient ($\sim 370 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \mu\text{mol mol}^{-1}$) C_a with or without N fertilizer at the ORNL FACE experiment. Measured data from Norby et al. (2010). Root exudation (Grant, 1993) was excluded from modelled NPP to simulate biometric measurements.

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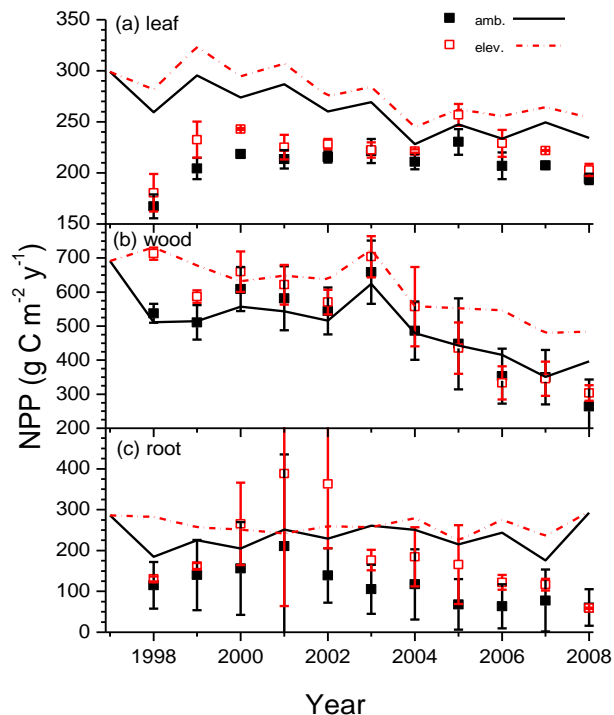


Fig. 8. (a) Annual net primary productivity (NPP) and (b) gain in biomass measured (symbols) and modelled (lines) in (a) leaves, (b) wood and (c) fine + coarse roots from 1998 to 2008 under ambient ($\sim 370 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \mu\text{mol mol}^{-1}$) C_a at the ORNL FACE experiment. Measured data from Norby et al. (2010) and Iversen et al. (2008). Root exudation (Grant, 1993) was excluded from modelled root NPP to simulate biometric measurements.

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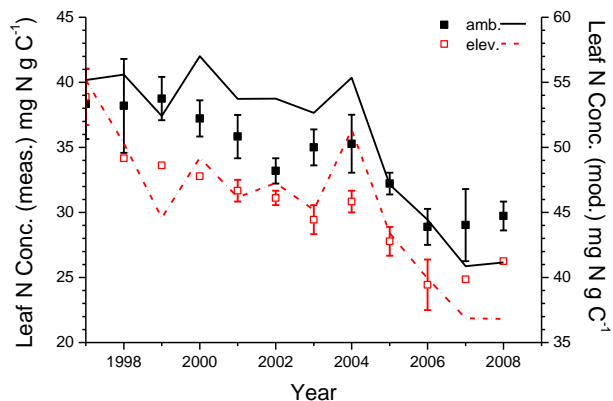


Fig. 9. Leaf N concentrations measured (symbols) and modelled (lines) from 1998 to 2008 under ambient ($\sim 370 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \mu\text{mol mol}^{-1}$) C_a without N fertilizer at the ORNL FACE experiment. Measured data from Norby et al. (2010).

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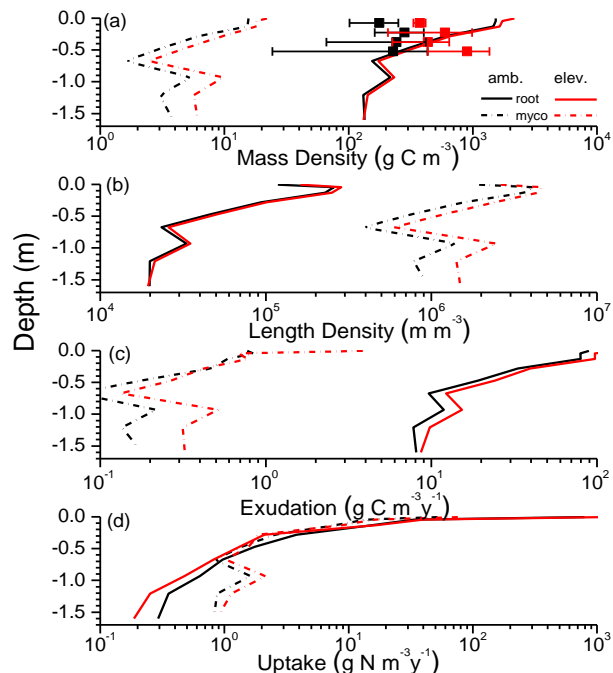


Fig. 10. Root and mycorrhizal **(a)** mass and **(b)** length density, **(c)** $\text{NH}_4^+ + \text{NO}_3^-$ uptake and **(d)** C exudation measured (symbols) and modelled (lines) vs. depth during 2001 under ambient ($\sim 370 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \mu\text{mol mol}^{-1}$) C_a without N fertilizer at the ORNL FACE experiment. Measured data from Iversen et al. (2008).

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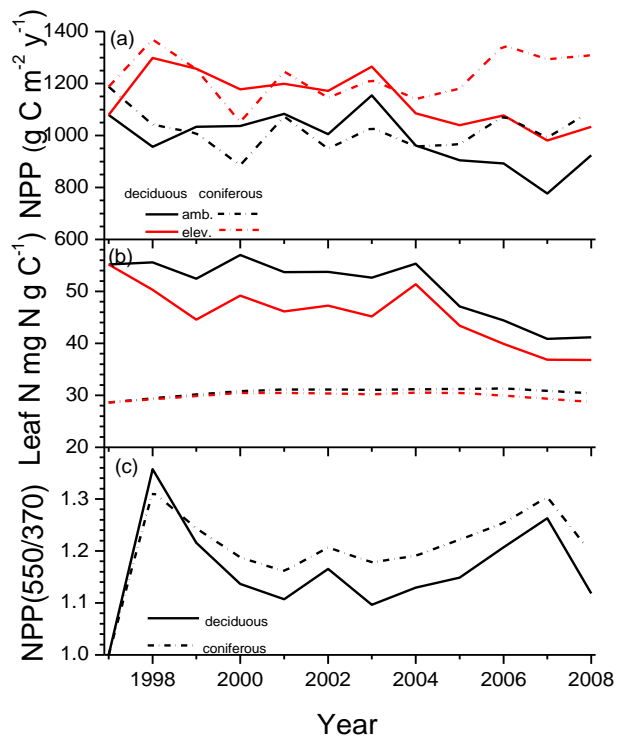


Fig. 11. (a) Annual net primary productivity (NPP), (b) leaf N concentrations and (c) ratios of NPP modelled from 1998 to 2008 under ambient ($\sim 370 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 550 \mu\text{mol mol}^{-1}$) C_a with deciduous vs. coniferous plant functional types at the ORNL FACE experiment. Values of NPP and leaf N concentrations modelled with the deciduous plant functional type are the same as those in Figs. 7a and 9.

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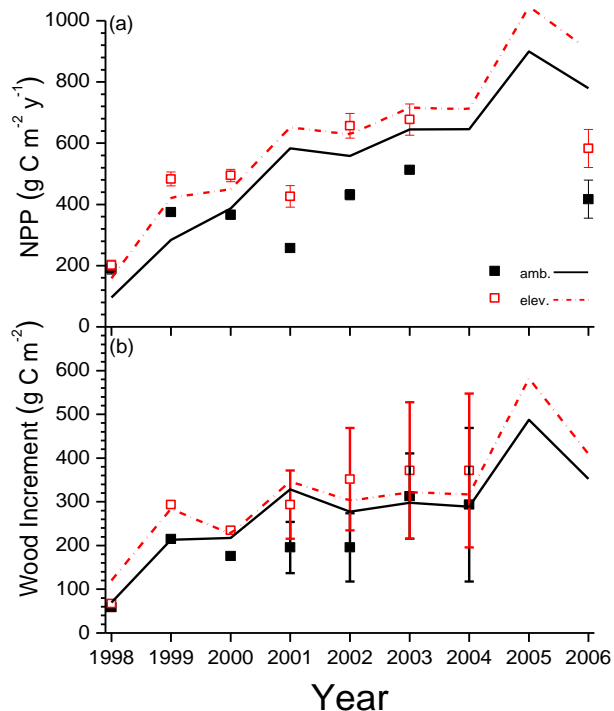


Fig. 12. (a) Annual net primary productivity (NPP) and (b) gain in biomass measured (symbols) and modelled (lines) from 1998 to 2006 under ambient ($\sim 374 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 541 \mu\text{mol mol}^{-1}$) C_a at the Rhineland FACE experiment. Measured NPP from King et al. (2005) to 2003, and from Zak et al. (2011) in 2006, measured wood increments from Kurbiske et al. (2010). Root exudation (Grant, 1993) was excluded from modelled NPP to simulate biometric measurements.

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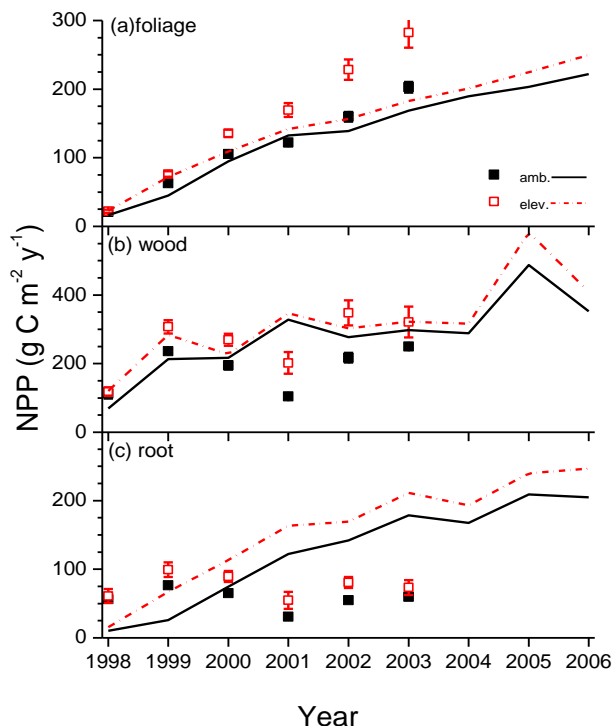


Fig. 13. (a) Annual net primary productivity (NPP) measured (symbols) and modelled (lines) in (a) leaves, (b) wood and (c) roots 1998 to 2006 under ambient ($\sim 374 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 541 \mu\text{mol mol}^{-1}$) C_a at the Rhinelander FACE experiment. Measured data from King et al. (2005). Root exudation (Grant, 1993) was excluded from modelled NPP to simulate biometric measurements.

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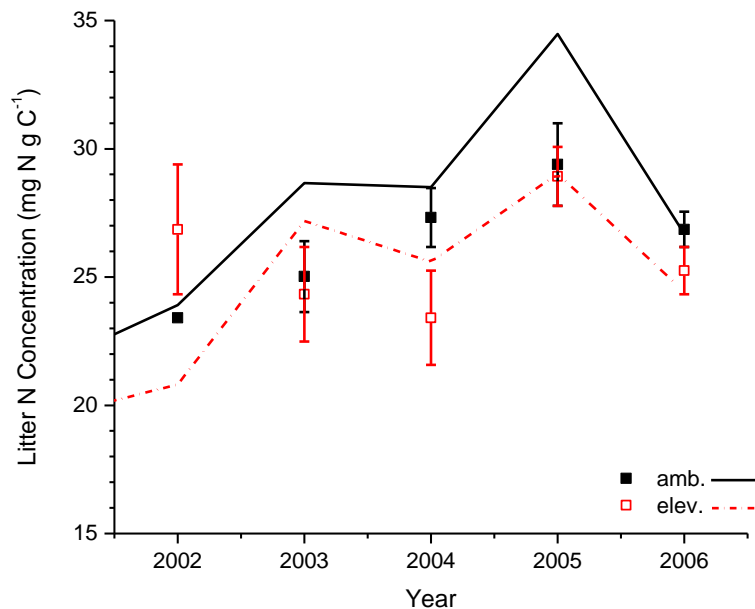


Fig. 14. Litter N concentrations measured (symbols) and modelled (lines) under ambient ($\sim 374 \mu\text{mol mol}^{-1}$) vs. elevated ($\sim 541 \mu\text{mol mol}^{-1}$) C_a at the Rhineland FACE experiment. Measured data from Talhelm et al. (2012).

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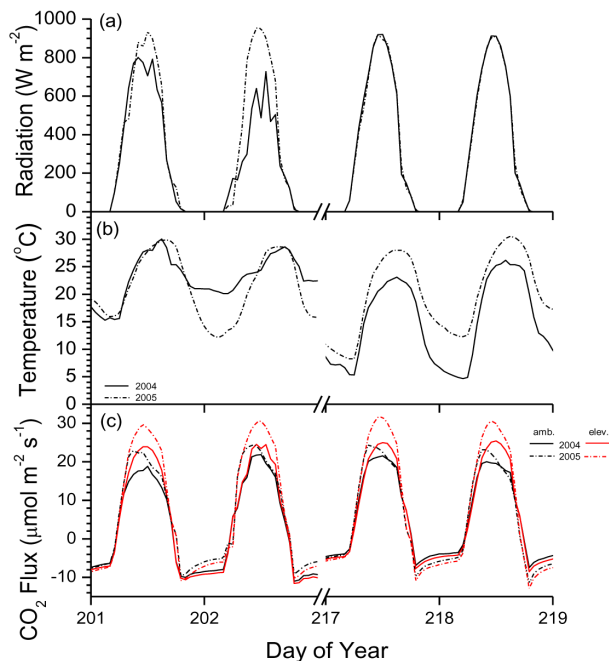


Fig. 15. (a) Radiation, (b) temperature and (c) CO_2 fluxes modelled under ambient ($374 \mu\text{mol mol}^{-1}$) vs. elevated ($541 \mu\text{mol mol}^{-1}$) C_a during periods with different radiation and similar temperatures (DOY 202–203) and with similar radiation and different temperatures (DOY 218–219) in 2004 and 2005.

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