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Modelling impacts of changes in carbon dioxide concentration, climate and nitrogen deposition on carbon sequestration by European forests and forest soils

G.W.W. Wamelink [a,*], H.J.J. Wieggers [a], G.J. Reinds [a], J. Kros [a], J.P. Mol-Dijkstra [a], M. van Oijen [b], W. de Vries [a]

[a] Alterra, Wageningen University and Research Centre, P.O. Box 47, Droevendaalse steeg 3, 6700 AA Wageningen, The Netherlands
[b] CEH, CEH-Edinburgh, Bush Estate, Penicuik EH26 0QB, UK

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ABSTRACT

Changes in the Earth's atmosphere are expected to influence the growth, and therefore, carbon accumulation of European forests. We identify three major changes: (1) a rise in carbon dioxide concentration, (2) climate change, resulting in higher temperatures and changes in precipitation and (3) a decrease in nitrogen deposition. We adjusted and applied the hydrological model Watbal, the soil model SMART2 and the vegetation model SUMO2 to asses the effect of expected changes in the period 1990 up to 2070 on the carbon accumulation in trees and soils of 166 European forest plots. The models were parameterized using measured soil and vegetation parameters and site-specific changes in temperature, precipitation and nitrogen deposition. The carbon dioxide concentration was assumed to rise uniformly across Europe. The results were compared to a reference scenario consisting of a constant CO_2 concentration and deposition scenario. The temperature and precipitation scenario was a repetition of the period between 1960 and 1990. All scenarios were compared to the reference scenario for biomass growth and carbon sequestration for both the soil and the trees.

The predicted effects of changes in climate, CO_2 concentration and nitrogen deposition on carbon sequestration by trees depend largely on tree species and location (latitude). The assumed decrease in nitrogen deposition causes a decrease of carbon accumulation all over Europe and for all modelled tree species. A rise in carbon dioxide concentration gives a rise in carbon accumulation all over Europe. Climate change gives a mixed result, with a decrease in carbon accumulation in the South of Europe and an increase in the North. When the scenarios are combined, an increase in biomass accumulation is predicted at most of the sites, with a rise in growth rate mostly between 0 and 100%. The predicted effects of a change in climate, CO_2 concentration and nitrogen deposition on soil carbon sequestration is generally lower than the effect on carbon sequestration by the trees. However, the magnitude is similar as is the location effect (latitude). A net carbon release was predicted at several sites in the south due to the effect of climate change. Overall, we conclude that where nitrogen deposition was a major driver for a change in forest growth in the past, it is climate change, and to a lesser extent CO_2 change, that will influence forest growth in the future.

1. Introduction

European forests play a major role in carbon sequestration (Kauppi et al., 1992; Nabuurs et al., 1997), thus affecting the speed of climate change. Forest growth has increased in recent decades, as shown by studies of temperate forests in North America (Reddy et al., 1995) and Europe (Spiecker et al., 1996; Hunter and Schuck, 2002). In Europe, the increases in net primary productivity (NPP), in past decades are associated with changes in forest management, influencing the standing growing stock (Nabuurs et al., 2001). Increased forest productivity has also been hypothesised to be due to increases in atmospheric CO_2 concentration (e.g. Friedlingstein et al., 1995), temperature, (e.g. Myneni et al., 1997) and nitrogen deposition (e.g. Nadelhoffer et al., 1999). Elevated CO_2 may favor NPP as well as increase water use efficiency of trees. However, trees may adapt to changing CO_2 concentrations and the effect may diminish soon (Magnani et al., 1998). Another factor influencing the carbon sequestration is the rise in the temperature. Higher

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* Corresponding author.
E-mail address: wieger.wamelink@wur.nl (G.W.W. Wamelink).

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temperature accelerates enzymatic processes and therefore biomass accumulation, unless other factors are limiting. Increasing temperature may also increase annual NPP by lengthening the growing season (Hasenauer and Monserud, 1997).

However, there is no consensus what the main environmental drivers are behind forest carbon sequestration, despite hundreds of papers on this topic (e.g. Ceulemans and Mousseau, 1994; Curtis, 1996; Curtis and Wang, 1998; Saxe et al., 1998; Long et al., 2004; Nowak et al., 2004; Ainsworth and Long, 2005). There is thus also no clarity as to the environmental drivers that have been dominant in temperate forests over the past decades. Some studies have suggested that in Europe the majority of forest growth increment can be accounted for by N deposition (Nellemann and Thomsen, 2001; Solberg et al., 2004; Van Oijen et al., 2004, 2008; Van Oijen and Jandl, 2004) and very little by elevated CO_2, but this does not seem to apply in all regions. First of all, the effects of enhanced N deposition are mostly growth enhancing (Schulze, 2000), they can be even detrimental at very high N loads (Magill et al., 2004). Furthermore, results of different free-air CO_2 enrichment (FACE) experiments in forest stands, suggest that elevated CO_2 has a significant impact on forest growth (e.g. Norby et al., 2005; McCarthy et al., 2006). However, other authors claim a much lower long-term stimulation of above-ground forest growth or productivity in a CO_2-richer future, except under high mineral nutrition (Korner et al., 2005; Körner, 2006). The differences are mainly related to the availability of nutrients (such as N or P). When these are – or become – limiting, CO_2 is assumed to have little influence, although there are indications that larger quantities of C entering the below-ground system under elevated CO_2 also result in greater N uptake, even in N-limited ecosystems (e.g. Finzi et al., 2007). The possible mechanism is that greater carbon availability will lead to an increase in fine root production, in soil organic matter decomposition and in adaptations in assimilate allocation and root morphology, that will increase access to nutrients sufficiently (Van Oijen et al., 2008).

By far the largest amount of C stored in forests in the northern hemisphere is stored in the soil due to the partial decomposition of litter. Soil processes probably account for the most significant unknowns in the C and N cycle. Apart from impacts of environmental drivers on the above-ground carbon sequestration, it also affects the soil carbon sequestration. Current hypotheses suggest that increased N deposition causes an increased rate of soil organic matter accumulation (e.g. Berg and Matzner, 1997; Harrison et al., 2000; Schulze et al., 2000; Hagedoorn et al., 2003). Understanding the N cycle in semi-natural ecosystems may be the key to understanding the long-term source or sink strength of soils for carbon. Using a meta-analysis Jastrow et al. (2005), of collective experimental studies, lasting at least 2 years, soil C increased by 5.6% in response to elevated CO_2, even though most experiments have been unable to document a response individually. Increasing temperature stimulates leaf litter decomposition, but the temperature response of litter at later stages of decomposition and of SOM is debatable (Hyvönen et al., 2007).

In this study we evaluate the combined effects of changes in the main drivers of carbon sequestration, i.e. carbon dioxide concentration, climatic variables (temperature and precipitation) and nitrogen deposition, on forest NPP and related carbon sequestration by trees and soils by applying a model chain. In this study, we used data from the largest current forest observation system in Europe, i.e. the Intensive Monitoring plots (De Vries et al., 2003) to parameterize the model chain and to evaluate the results on measured growth changes. Even though the effect of individual drivers cannot be validated on the growth data, the plausibilty of the effects can be evaluated on the basis of statistical relationships between different drivers and changes in forest growth at these plots, as presented in Solberg et al. (2009) and Laubhann et al. (2009).

2. Materials and methods

2.1. Intensive Forest Monitoring plots

We used site-specific data from plots of the "Programme for Intensive and Continuous Monitoring of Forest Ecosystems" (De Vries et al., 2003). Only plots with two increment surveys, in the period 1995–2000, in combination with soil solution chemistry data (see also Mol-Dijkstra et al., 2009) were selected. We excluded plots that had been fertilized, had a growth period of less than 3 years, where tree diameter or tree height information was missing and plots with obvious severe data errors (see also Laubhann et al., 2009; Solberg et al., 2009). Plots that were thinned during the measurement period for increment were excluded as well. This led to a total number of 166 plots. Plot-specific meteorological data were available for 112 plots only. For the other plots, we used data from a meteorological database (New et al., 2000). Most selected plots are located in Northern Europe, Western Europe and Central Europe. Only a few plots are located in the Mediterranean countries (Fig. 1). Most common tree species in the plots are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Beech (*Fagus sylvatica)* and to a lesser extent Oak (*Quercus robur* and *Quercus petraea*).

2.2. Modelling approach

The applied model chain consists of process-based dynamic models simulating:

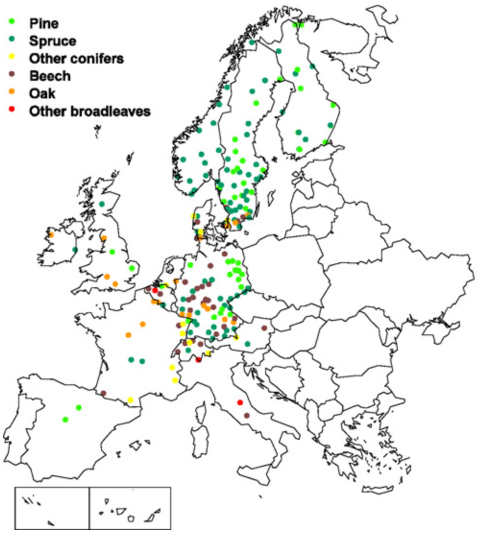
(i) actual NPP with nutrient fluxes (N, Ca, Mg and K) to and from the vegetation and carbon pool changes in the vegetation (SUMO2; Wamelink et al., 2000),
(ii) soil nutrient fluxes, soil acidity and soil carbon sequestration (SMART2; Kros et al., 1995) and
(iii) water fluxes (WATBAL; Starr, 1999, Fig. 2).

SUMO2 (Wamelink et al., 2000, 2009-a,b; Wamelink, 2007) is a dynamic growth and competition model. SUMO2 simulates the biomass, the biomass growth (NPP) and nutrient dynamics for five functional types: grasses/herbs, dwarf shrubs, shrubs, pioneer trees, and climax trees. In this study, SUMO2 is used exclusively to simulate forest growth. For each functional forest type, biomass is partitioned over three organs: root, stem and leaf. In each time step, of 1 year, biomass is computed from the biomass in the previous time step, NPP and death in the present time step and removal of biomass by management. In this study, forest management, consisted of the removal of biomass (and thus nutrients) from the system, by thinning according an enforced thinning cycle. Once every 10 years, an age and biomass dependent amount of biomass is removed from the system. The thinning cycle was only used for sites wherein field thinning is practiced. Inputs are initial vegetation type, soil data from SMART2 and management. Outputs include NPP and carbon pool changes in the vegetation and foliar nutrition.

Actual NPP is calculated in this study with the model SUMO2 using an assumed maximum NPP, which is a function of temperature and CO_2 concentration, that is reduced by nutrient availability (provided by SMART2), water availability (provided by WATBAL) and light interception, according to:

$$\mathrm{NPPact_t} = \mathrm{NPPmax}(T_{\mathrm{ref}}, \mathrm{CO_{2\,ref}})\,\mathrm{ST_t}\,\mathrm{SC_t}\,\mathrm{RI_t}\,\mathrm{RWa}\nu_{\mathrm{t}}\,\mathrm{RNa}\nu_{\mathrm{t}} \qquad (1)$$

where $\mathrm{NPPact_t}$ is the actual growth (kg $\mathrm{ha^{-1}\,yr^{-1}}$), NPPmax($T_{\mathrm{ref}}$, $\mathrm{CO_{2ref}}$) is the maximum growth at a given reference temperature and CO_2 concentration (for the Netherlands, in kg $\mathrm{ha^{-1}\,yr^{-1}}$), $\mathrm{SC_t}$ is a scaling factor for CO_2, $\mathrm{ST_t}$ is a scaling factor for the annual



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

Fig. 1. Locations of the Intensive Monitoring plots and the distribution over age classes used for calibration and model runs. The total number of plots is 166, including 41 for *Pinus sylvestris*, 65 for *Picea abies*, 3 for *Picea sitchensis*, 4 for *Abies alba*, 2 for *Pseudotsuga menziesii*, 1 for *Pinus nigra*, 28 for *Fagus sylvatica*, 8 for *Quercus petraea*, 11 for *Quercus robur*, 2 for *Quercus cerris* and 1 for *Fraxinus excelsior*.

temperature, RI_t, $RWav_t$ and $RNav_t$ are reduction factors for the availability of light, water and nutrients (nitrogen, calcium, magnesium potassium), respectively.

The original SUMO2 model only includes the effect of light, water and nitrogen limitations. The model was extended, incorporating the effects of CO_2, temperature, moisture availability and base cation (calcium, magnesium potassium) availability on the NPP. The way in which the various environmental factors were included is described in detail in Electronic appendix 1.

SMART2 (Kros et al., 1995) simulates soil chemistry as affected by atmospheric deposition. Inputs are deposition and seepage fluxes of S, N, base cations and water, plant nutrient uptake, weathering, climate parameters and soil properties. Outputs are soil chemistry (e.g. changes in N and C pools), soil solution chemistry and nutrient cycling fluxes. The model SMART2 was adjusted in this study, by accounting for the effect of N deposition on C decomposition, as described in detail in Electronic appendix 2.

WATBAL (Starr, 1999) is a water balance model for forest plots, simulating evapotranspiration, runoff and changes in soil moisture storage on a monthly basis. It uses both directly available input data (e.g. monthly precipitation and air temperature) and data which have been derived using transfer functions (Electronic appendix 3).

WATBAL provides SMART2 with information on water fluxes (precipitation excess) and SUMO2 with evapotranspiration (actual and potential) on a yearly basis. WATBAL needs the leaf area index (LAI) as input, which is provided by SUMO2 on a yearly basis. The yearly LAI is transformed into a monthly soil cover for the water flux modelling. There is no feedback from SMART2 to WATBAL.

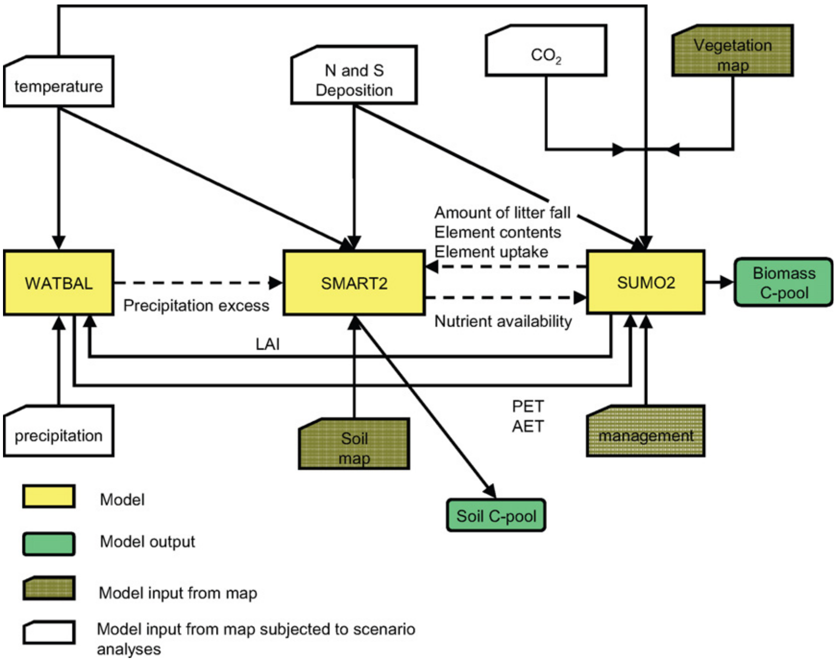


Fig. 2. The integrated model chain WATBAL–SMART2–SUMO2, including the most important exchanged variables between the models and the most important input maps.

2.3. Model application

2.3.1. Model parameterization

Here we summarize the parameterization of the models SUMO2, SMART2 and WATBAL. Detailed information on the parameterization is presented in Electronic appendix 4.

The SUMO2 model parameters are related to parameters describing impacts of CO_2 on NPP (β), the maximum NPP at a reference temperature of 10 °C and minimum and maximum foliar nutrient contents. β values were derived from literature data on experiments with information on growth rates at elevated and reference levels of carbon dioxide. Values of NPPmax at 10 °C were mainly derived from literature data on growth experiments of tree species (mostly pot-experiments), field experiments where biomass growth was measured by harvesting or estimated by indirect from measurements (published and unpublished data) and values from other models. A problem with field estimates is that it merely reflects the actual growth as a result of growth-limiting factors as nutrient availability, water availability, etc. That is why the NPPmax values were often adjusted in the calibration process. Minimum and maximum values for N, Ca, Mg and K, needed in SUMO2 to assess the foliar contents and derive the impact of nutrient limitation, are based on literature research. Data thus derived for β, NPPmax at 10 °C and foliar contents for the tree species included in this study, together with the literature information used, are given in Electronic appendix 4.

The derivation of the soil parameters in *SMART2* is described by De Vries et al. (2003). CEC and exchangeable cations were directly derived from field measurements. The exchange constants were calibrated and the weathering rates were estimated from the budget (as the average of the differences between deposition and leaching, corrected for base cation uptake) of Ca, Mg, K and Na. Furthermore, parameters that determine nitrogen immobilisation, denitrification and nitrification were estimated (De Vries et al., 2003). Immobilisation depends on the C/N ratio in the mineral soil. Denitrification is derived by a function of texture and gley class, the nitrification was computed from the measurements of N fluxes.

Apart from meteorological data, the main WATBAL input parameters are the available water capacity, the ratio between actual soil water content and water content at which transpiration is reduced (AWC ratio) and the soil cover over the year. Available water capacity for WATBAL was estimated as function of soil type and texture class according to Batjes (1996) who provides texture class dependent AWC values for all FAO soil types based on an extensive literature review. AWC ratios were computed as a function of soil texture according to the standard WATBAL procedure. The soil cover over the year was related to the seasonal trajectory of the LAI as compared to its maximum value, as described in Electronic appendix 4.

2.3.2. Model calibration

We calibrated the SUMO2 model for the sites using measured site-specific data for soil and vegetation and verified the WATBAL results. The SMART2 model was not calibrated, we used the values as described in the model parameterization.

2.3.2.1. SUMO2. SUMO2 was calibrated on the standing biomass and biomass increment at the sites. SMART2–SUMO2 was run from the planting date for each plot to simulate woody biomass of the trees. Out of the 166 sites, 153 plots with reliable biomass measurements were available for at least 1 year. Based on the field biomass the NPP was calculated (when two measurements were available). Four plots with a negative growth were omitted (most likely due to management), giving 120 plots for model calibration for biomass growth and 149 plots for the calibration of the simulated biomass.

The calibration was not done per site, but per species. This method is in line with the way SUMO2 is set up, and it gives the possibility to use the data set as a check on the performance of the model, though the data are not independent and the check can thus not be regarded as a validation. Consequently, the modelled tree biomass and tree biomass growth does not match exactly the growth at each site. Calibration took place by adjusting model parameters within the range of measured values reported in the literature for the maximum growth, light interception and minimum and maximum N-content to reasonably match the field data. The relation between measured and simulated biomass results includes the first measurement from a plot where two measurements were available (Fig. 3). Ideally, the regression line (in grey) would not differ significantly from the $y = x$ line (in black). The simulated biomass looks adequate, however the regression coefficient differs significantly from 1.0 and the intercept differs significantly from 0 ($y = 0.7825x + 71.011$; $R^2 = 0.60$). The simulations of the tree biomass growth over the measured period are less good (Fig. 4). Also here the regression coefficient differs significantly from 1 and the intercept differs significantly from 0 ($y = 0.4969x + 4.436$; $R^2 = 0.6482$). The consequences of especially the underestimation of the simulated tree growth above 15 ton/ha in the sampling period are discussed in Section 4.

2.3.2.2. WATBAL. The reliability of the water fluxes was checked by comparing the leaching of chloride (Cl) and sodium (Na) against

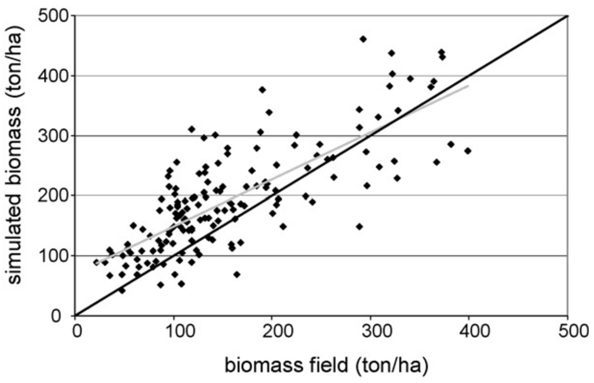


Fig. 3. Relation between field measurements and simulated biomass for 149 Intensive Monitoring forest plots in Europe. Most of the plots have two measurements of biomass, in that case only the first measurement was included. The black line shows the $y = x$ line, the grey line the regression line.

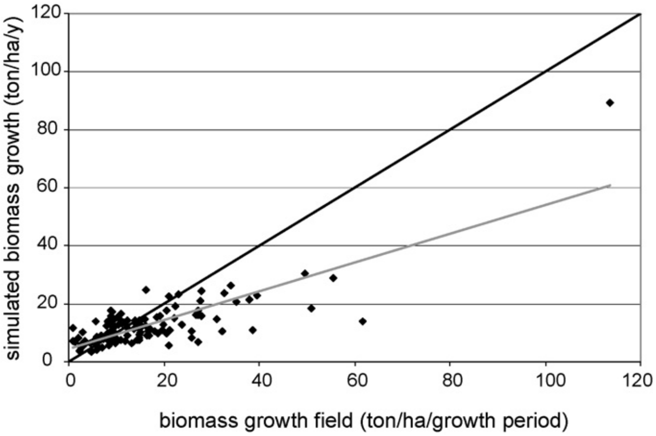


Fig. 4. Relation between field measurements and simulated biomass growth for 120 Intensive Monitoring forest plots in Europe. The black line shows the $y = x$ line, the grey line the regression line.

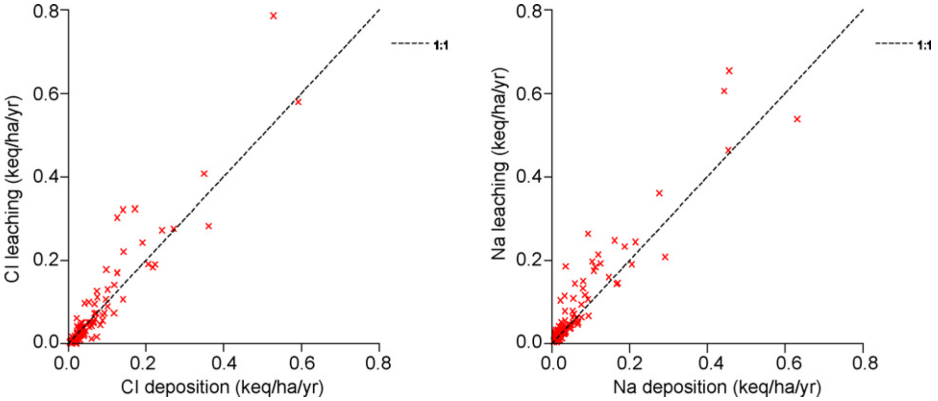


Fig. 5. Cl and Na input–output (deposition–leaching) relationships for SMART2.

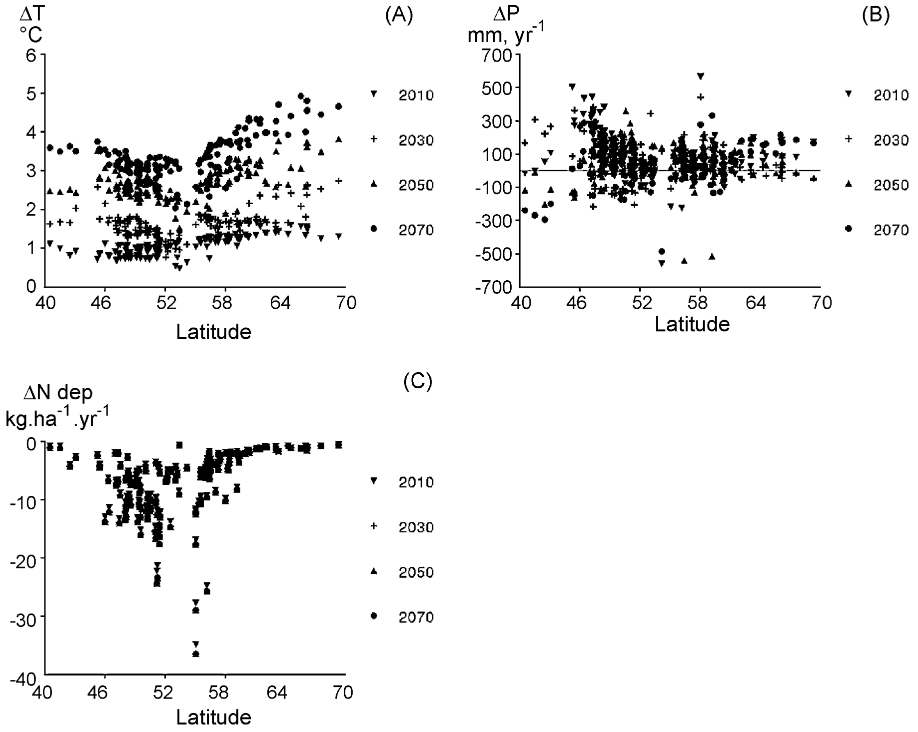


Fig. 6. Difference in temperature (A), and precipitation (B) and nitrogen deposition (C) between the reference run and the climate change scenario and N deposition scenario respectively in 2010, 2030, 2050 and 2070 as a function of latitude (see also Electronic appendix 5).

the deposition for the Intensive Monitoring plots. The (long-term average) leaching computed from the modelled downward water flux and the measured concentration should match the deposition. The average slope for Cl is close to 1, indicating that there is no overall bias in the hydrological model (Fig. 5). However, there are several plots with rather unbalanced inputs and outputs. In the case of Na, this could partly be explained by weathering. Part of the plots where chloride leaching is higher than chloride deposition is located close to the sea. This may cause imbalances in the budget due to salt spray that is not collected in the deposition samplers.

2.4. Scenarios

To assess the separate effects of an increase in carbon dioxide concentration, climate change and nitrogen deposition change and the combined effect of these three drivers on biomass accumulation in European forest, we applied the models the WATBAL–SMART2–SUMO2 model chain for the period 1990–2070 by comparing various scenarios with a reference run. The scenarios were applied using a common trajectory of increasing carbon dioxide concentration and site-specific estimates of the change in climatic parameters (precipitation and temperature) and nitrogen deposition. Four scenarios and a reference scenario were constructed, as summarized below (see also Table 1 and Fig. 6).

(1) CO_2 scenario. This scenario is identical for all the simulated plots and is based on an extrapolation of the time series of observed CO_2 concentrations from Mauna Loa Observatory (Keeling et al., 2005). The extrapolated CO_2 concentration for 2070 is 537 ppm CO_2. This scenario was compared to a constant CO_2 scenario of 339 ppm. This change is comparable to the predictions in response to the IPCC A2 scenario.
(2) Climate scenario. The temperature and precipitation for the period 2000–2100 is assumed to change according to the IPCC A2 scenario. Climate data were assigned to the plots by an

Table 1
Summary of the average effect of various scenarios on N deposition, temperature and precipitation in 2010 and 2070, as compared to 1990, per latitude class.

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

overlay with the meteo data grid. For temperature this follows the HADCM3 model (Mitchell & Jones, 2005). For precipitation, the measured site-specific precipitation was scaled with the changes in precipitation according to the HADCM3 model predictions. This scenario was compared with a scenario with a constant temperature and precipitation after 1990. To account for variations in meteorology, the "constant" scenario includes repetitions of the historic meteorology from the period 1960–1990.

(3) A nitrogen deposition scenario. Since the IPCC-SRES scenarios do not contain information on nitrogen deposition, we used the, standard, deposition scenario according the Gothenburg protocol (see Norby et al., 2005). In principal, this may lead to inconsistencies between the scenarios. However, we expect them to be of minor importance. The trends in SO_2, NO_x and NH_3 deposition were derived using RAINS country emissions based on historic data and emission projections from the Gothenburg protocol (Cofala and Syri, 1998a,b) and transfer matrices derived from the EMEP long-range transport model (Bartnicki et al., 2002) for 1960–2010. After 2010, the deposition was assumed to be constant. These trend curves, available on a 50 km × 50 km grid were scaled by the average computed total deposition (based on bulk and throughfall measurements) at the plot for the period 1996–2000. This scenario was compared with a scenario where the nitrogen deposition remains constant at the level of 1990.

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

Model results for carbon sequestration for 2070 in trees and soil were compared for the four different scenarios.

Runs were carried out for seven tree age classes (0–20, 20–39, 40–59, 60–79, 80–99, 100–160 and >160 years). The runs were started in the planting year of the class averages, i.e. in 1960 for the class 20–39 year for the 1990 results, or in 1940 for the class 100–160 year for the 2070 results.

3. Results

3.1. CO_2 scenario

A rise in CO_2 concentration leads to a higher carbon sequestration at all latitudes (Table 2). The effect CO_2 on the carbon sequestration is largest below the 57th latitude, which is mainly due to differences between tree species. We predict an increase in carbon sequestration by trees of approximately 1.0 kg C per ppm CO_2 at latitude >57 and a variation between 1 and 7 kg C per ppm CO_2 below this latitude. For soil, the increase in carbon sequestration is approximately 0.5 kg C per ppm CO_2 at latitude >57 and it varies between 1 and 3 kg C per ppm CO_2 below this latitude, leading to a total predicted increase of 1–10 kg C per ppm CO_2. Considering the predicted CO_2 increase of 197 ppm CO_2 between 1990 and 2070, this implies a predicted increase in CO_2 sequestration up to 1400 kg C for trees and up to 600 kg C for the soil. This implies a total sequestration up to 2000 kg C. Above latitude 57, the NPP rise is near 150–200 kg C, which implies an NPP rise of approximately 15% in 2070, below latitude 57, it is generally above 300–400 kg C implying an NPP rise above 30%.

3.2. Climate scenario

The temperature rise and precipitation changes also have a significant effect on the carbon sequestration but unlike the CO_2 scenario, the effect is not always positive (Table 3). The change in climate scenario may also lead to reduced carbon sequestration; also negative effects are present, especially in the soil. In both the North and the South, we simulated an average net release of carbon from the soil. For some Southern plots, the total carbon sequestration decreases. For the latitude groups, the carbon sequestration ranges from −5 till 206 kg C ha^{-1} yr^{-1} °C^{-1}, or from −1.5 till 16% (Table 3). For all plots in the North, the carbon sequestration increases. The three outliers are sites in mountainous areas where the NPP of the trees is almost zero without climate change. Higher temperatures give a NPP change and trees start to grow (approximately

Table 2
Average carbon sequestration per latitude class of European forest in 2070 compared to the reference run for the CO_2 scenario. The relative sequestration (in percentages) is given between brackets.

Latitude	ΔC_{seq} (kg C ha^{-1} yr^{-1})			$\Delta C_{seq}/\Delta CO_2$ (kg C ha^{-1} yr^{-1} ppm $CO_2{}^{-1}$)		
	Tree	Soil	Total	Tree	Soil	Total
40–50	425 (26)	165 (769)	590 (31)	2.2 (0.13)	0.84 (3.9)	3.0 (0.16)
50–60	397 (24)	186 (123)	583 (33)	2.0 (0.12)	0.95 (0.63)	3.0 (0.17)
60–70	158 (16)	85 (27)	242 (19)	0.81 (0.08)	0.43 (0.14)	1.2 (0.10)

Table 3
Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the temperature scenario, and between brackets the relative sequestration in percentages, solely per latitude class.

Latitude	ΔC_{seq} (kg C ha^{-1} yr^{-1})			$\Delta C_{seq}/\Delta T$ (kg C ha^{-1} yr^{-1} °C^{-1})		
	Tree	Soil	Total	Tree	Soil	Total
40–50	193 (13)	−214 (−23)	−21 (−4.8)	61 (3.8)	−67 (−7.4)	−5.1 (−1.5)
50–60	632 (48)	17 (77)	649 (52)	202 (15)	4.0 (23)	206 (16)
60–70	636 (67)	−30 (−8.8)	606 (48)	149 (15)	−7.6 (−2.2)	142 (11)

Table 4
Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the N-deposition scenario, and between brackets the relative sequestration in percentages, solely per latitude class.

Latitude	ΔC_{seq} (kg C ha^{-1} yr^{-1})			$\Delta C_{seq}/\Delta N$ (kg C ha^{-1} yr^{-1} kg N^{-1})		
	Tree	Soil	Total	Tree	Soil	Total
40–50	−32 (−1.4)	−35 (−43)	−67 (−2.5)	3.6 (0.15)	5.0 (4.6)	8.6 (0.30)
50–60	−25 (−1.3)	−31 (−18)	−56 (−2.6)	3.1 (0.18)	4.2 (2.7)	7.3 (0.38)
60–70	−13 (−1.5)	−13 (−3.7)	−26 (−2.0)	12 (1.4)	11 (3.3)	24 (1.9)

Table 5
Summary of the carbon sequestration of European forest in 2070 compared to the reference run for the combined scenario per latitude class.

Latitude	ΔC_{seq}, tree		ΔC_{seq}, soil		ΔC_{seq}, total	
	kg C ha^{-1} yr^{-1}	%	kg C ha^{-1} yr^{-1}	%	kg C ha^{-1} yr^{-1}	%
40–50	604	36	−120	466[a]	483	20
50–60	1072	75	167	188	1240	87
60–70	824	85	41	13	865	67

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

1 ton ha^{-1} yr^{-1}), resulting in a large NPP change and thus net carbon sequestration. On average, the simulated carbon sequestration change is larger in the North than in the South.

3.3. Nitrogen deposition scenario

The drop in N-deposition levels influences the biomass accumulation in a negative way. The effect is relatively small compared to the effects of the CO_2 and climate scenarios (Table 4). The predicted decrease, induced by the assumed decrease in N deposition compared to the reference run, ranges mostly between 0 and 50 kg C (giving a carbon sequestration decrease between 0 and 3%). The absolute effect is largest in the Southern countries and smallest in the Northern countries. However, when expressed per kg N change, the effect is largest in the Nordic countries. The C sequestration per kg N deposition ranges mostly between 1 and 15 kg C per kg N for trees, with maxima up to 25 kg C per kg N at latitude >60. In the soil, the variation is comparable. Here, the ratio in C sequestration per kg N deposition ranges mostly between 1 and 20 kg C per kg N with some values going up to 30 kg C/kg N. A few sites show an increase in NPP despite the lower N deposition implying a negative C sequestration per kg N deposition. The effect of N deposition on C sequestration is largest between the 45th and 55th latitude. Here, countries like the UK, the Netherlands, Belgium and Germany are situated, all with a high nitrogen deposition. In these areas, the decrease in nitrogen deposition is highest causing the largest decrease in carbon sequestration.

3.4. Combined scenario

A comparison per latitude class for the combined scenario shows that a negative carbon sequestration mainly occurs at the latitudes from 40 to 50 in the soil, induced mainly by the effects of climate change (Table 5). On average, the carbon sequestration is

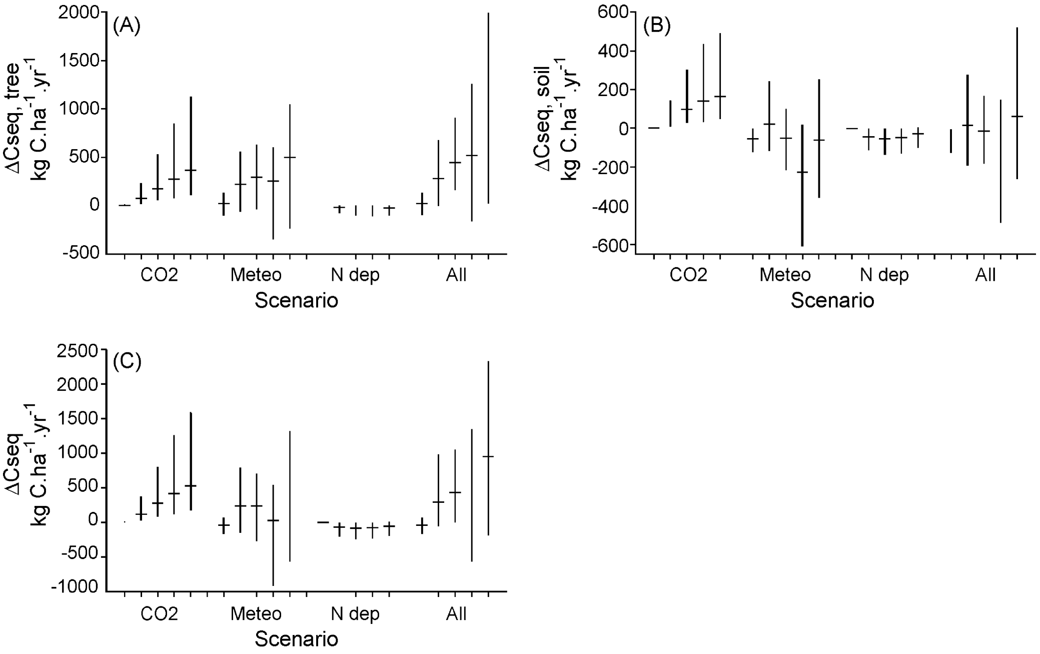


Fig. 7. The average carbon sequestration for the four scenarios (CO_2, Climate; Meteo, N deposition; N dep and the combined scenario; all) compared to the carbon sequestration in 1990. Given are the average (horizontal line) and the standard error (vertical line) for the years 1990, 2010, 2030, 2050 and 2070 for the trees (A), the soil (B) and the total of trees and soil (C).

Table 6
Changes in carbon sequestration simulated by SMART2–SUMO2–WATBAL for 2070 for four scenarios (averages of 2065–2074) per tree species as compared to the reference run.

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

positive for all latitude groups. The amount of carbon sequestrated is highest from the latitude 50–60. The total yearly sequestration ranges from 483 till 1240 kg C ha^{-1} yr^{-1}. Most sites show an increase of carbon sequestration between 0 and 100%, however large differences are present between the sites. Some sites have almost no growth in 1990; therefore, a small absolute growth increase gives already a strong relative effect on the carbon sequestration.

The carbon sequestration by the trees increases in time for all the scenarios except for N deposition (Fig. 7). The variation in carbon sequestration in the trees is quite large over the examined plots. Both in the combined scenario and in the climate scenario, there are plots where the carbon sequestration decreases. Where the carbon sequestration for the trees generally increases in response to the scenarios (Fig. 7A), the carbon sequestration in the soil gives a negative effect for many plots, except for CO_2 (Fig. 7B). However, the climate scenario gives in general a negative effect on the carbon sequestration; the average sequestration is lower for all years except in 2010. As for the trees, there is a negative effect of the N deposition scenario on the carbon sequestration in the soil; a lower N deposition causes a lower carbon sequestration. The strong negative effect of the climate scenario also strongly influences the carbon sequestration of the combined scenario, causing negative average carbon sequestrations for some years. This implies that at least in some years, the relative dry years, a net release of carbon from the soil can be expected. When the effects of the scenarios on carbon sequestration of trees and soil are viewed together then there is, on average, a positive effect of the carbon sequestration present, except for the N deposition scenario (Fig. 7C). The strong negative effect of the climate scenario on the carbon sequestration in the soil is dimmed by the effect of the trees, which is in most cases stronger than the effect on the soil. We conclude that, in general, the expected changes in climate, CO_2 concentration and nitrogen deposition will give a higher carbon sequestration in large parts of the European forest, despite the lower N deposition and the periodic lower water availability.

3.5. Species response

The effect of the various scenarios on the predicted carbon sequestration varies strongly with tree species (Table 6). A higher CO_2 concentration increases the carbon sequestration of all species, but huge differences are present, varying from approximately 2% for *Pseudotsuga menziesii* till over 80% for *Quercus cerris*. The average climate response is for most species positive. *Quercus petrea* shows a clear negative response on climate change; *Abies alba* shows a minor negative response. The drop in nitrogen deposition gives for all species a relative small decrease in biomass accumulation. From this, we conclude that in general all species will show a positive growth response for the examined plots.

4. Discussion and conclusion

4.1. Importance of different atmospheric drivers on changes in carbon sequestration

In general, our model simulations indicate a significant increase in carbon sequestration by European forests in response to expected changes in CO_2 concentration and climate, whereas the expected decrease in nitrogen deposition only leads to a relative small decrease in carbon sequestration. To investigate the effect of the changes in CO_2 concentration, climate and N deposition on carbon sequestration in the combined scenario, we carried out a multiple regression of the NPP response for the combined scenario with the NPP responses of the individual scenarios as explanatory variables. Results showed a highly significant relation between the NPP response of the CO_2 scenario and the climate scenario and the NPP response for the combined scenario (Table 7). There is no significant relation between NPP changes of the combined scenario and the deposition scenario, indicating that the influence of N deposition on the result of the combined scenario is minimal. The interactions between the CO_2 scenario and the climate scenario and between the deposition and climate scenario are highly significant, as is the three-way interaction. Together the three scenarios (including the interaction terms) explain almost all variance (98.9%). To complete the analyses, each combination of scenarios and each single scenario were used to explain the results of the combined scenario. Results show that by far the largest portion of variance is explained by the climate scenario, followed by the rise in the CO_2 concentration. Though some interactions are significant, they do not contribute much to the explanation of the variance. From this very simple sensitivity analyses, it can be concluded that the model results for the combined scenario seem to be mainly determined by climate change and in a lesser way by the change in CO_2 concentration. The interactions play a minor role and the sensitivity for N deposition scenario is negligible.

The dominating influence of climate and to a lesser extent of CO_2 on the expected change in carbon sequestration is opposite to the results of historic studies on the relative impact of these drivers, with nitrogen being the major driver, while changes in climate and CO_2 concentration are of less importance (e.g. Van Oijen and Jandl, 2004; Van Oijen et al., 2008). This is mainly because future changes in N deposition compared to the reference run (1990 deposition) are small compared to the expected changes in CO_2 and climate, whereas historic changes in N deposition between 1960 and 2000 have been large compared to changes in CO_2 and climate. It is important to realize that we choose 1990 as the starting year of the scenarios against which the simulations were compared. Since nitrogen deposition has slightly decreased since 2000 (Kelly et al., 2002; Tarasón et al., 2003) and is expected

Table 7
Regression analyses of the carbon sequestration changes of the combined scenario with the NPP changes of the individual scenarios as explanatory variables. The accumulated analysis of variance is shown, with degrees of freedom (d.f.), sum of squares (s.s.), mean of squares (m.s.), variance ratio (v.r.), F probability (F pr.) and the parameter estimates, standard error (s.e.) and t probability (t pr.). The Capitals preceding 2070 indicate the scenarios (C: carbon dioxide, D: nitrogen deposition and M: meteo).

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

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

Percentage variance accounted for 98.9.

to decrease further a negative carbon sequestration response is found as a result. However, this ignores the effect of the rise in the nitrogen deposition since 1960. If the nitrogen deposition effects would have been compared with 1960, a positive effect would have been visible (cf. Wamelink et al., 2009-b) and the impacts of CO_2, N deposition and climate might have been more comparable.

4.2. Relevance of including nutrient limitation in simulating carbon sequestration

Our results show that an elevated carbon sequestration due to CO_2 increase is partly levelled off by an increased nutrient limitation. This is illustrated in Table 8, showing that the nutrient reduction factor for the scenario with an increase in CO_2 concentration is slightly lower than the scenario with the constant 1990 inputs. However, the impact is small, and the assumed much lower long-term stimulation of aboveground forest growth or our simulations do not confirm productivity in a CO_2-richer future, except under high mineral nutrition (Korner et al., 2005; Körner, 2006). The reduction in growth due to nutrient limitation is mainly due to nitrogen deficiency (in approximately 80% of the plots in 2070 for both the constant and CO_2 scenario) and for 20% by base cation deficiency. The impact of P availability is not included in the simulations but this will most likely not lead to a different conclusion. Our simulations thus suggest that even though nutrient limitation has an effect, it does not imply that the effect of an increased C sequestration due to elevated CO_2 levels is only temporary. This is in line with model results presented by Van Oijen et al. (2008). The simulations, however, also show that neglecting nutrient limitation, as done in many Earth System Models, leads to a strong overestimation of the impacts of CO_2 increase and climate change on carbon sequestration. This has been shown earlier by Hungate et al. (2003) and recently, Zaehle and Friend (personal communication) showed that including N deposition in Earth System Model O–CN reduces the impact of CO_2 and climate change by approximately 65% at a global scale. This is an even much larger reduction that simulated at the Forest Monitoring plots where nutrient availability is relatively high compared to other parts of the world. It, however, illustrates the need of including nutrient availability and preferably not nitrogen alone.

Table 8
Ranges in calculated nutrient reduction factor for the scenario with the constant 1990 inputs and the scenario with an increase in CO_2 concentration alone.

Scenario	Nutrient reduction factor				
	Minimum	5%	50%	95%	Maximum
Constant	0.457	0.594	0.752	0.902	1.000
CO_2 increase	0.380	0.551	0.727	0.882	1.000

4.3. Geographic variation in impacts of atmospheric drivers on carbon sequestration

The impact of the various drivers on the carbon sequestration in forest ecosystems (both trees and soil) is largely dependent on the latitude, as illustrated in Fig. 8. From the simulations, it appears that at all latitudes, the NPP is increasing with an increase in CO_2 concentration but above a latitude of 58 the carbon sequestration is always below 500 kg/ha/yr, whereas it varies from approximately 100 to 2000 kg/ha/yr below a latitude of 58 (Fig. 8A). This variation is mainly due to the difference in tree species with latitude. The simulated effect of climate change in 2070 as compared to the reference run is always positive above latitude 52, but below this latitude, in the Mediterranean areas, the effect can also be negative (Fig. 8B). Temperature rise itself raises the carbon sequestration, but the rise in evapotranspiration because of the higher temperature may hamper it. Changes in precipitation however, can both increase tree growth by an increased water availability or reduce tree growth in response to drought stress. Yearly changes in both temperature and precipitation thus lead to year-to-year changes in carbon sequestration. The positive effect of temperature increase on tree growth is dominating in the higher latitudes, while the negative effect of a change in precipitation leading to reduced tree growth in response to drought stress often occurs in southern Europe. Apart from reduced growth induced by precipitation changes, carbon loss may occur due to increased soil mineralisation induced by elevated temperature. Due to the variation in temperature and precipitation, the carbon sequestration also differs largely between the years (not shown). The simulated negative effect of the climate (precipitation) scenario on carbon sequestration in Southern Europe is much higher in the soil than in the forest trees.

With respect to N deposition, the impact is lowest in Northern Europe (above latitude 58), where N deposition changes are smallest (compare Figs. 8C and 6C), using 1990 N deposition as the reference. Ultimately, we simulated that the combined scenario of CO_2 increase, climate change and a decreasing N deposition will

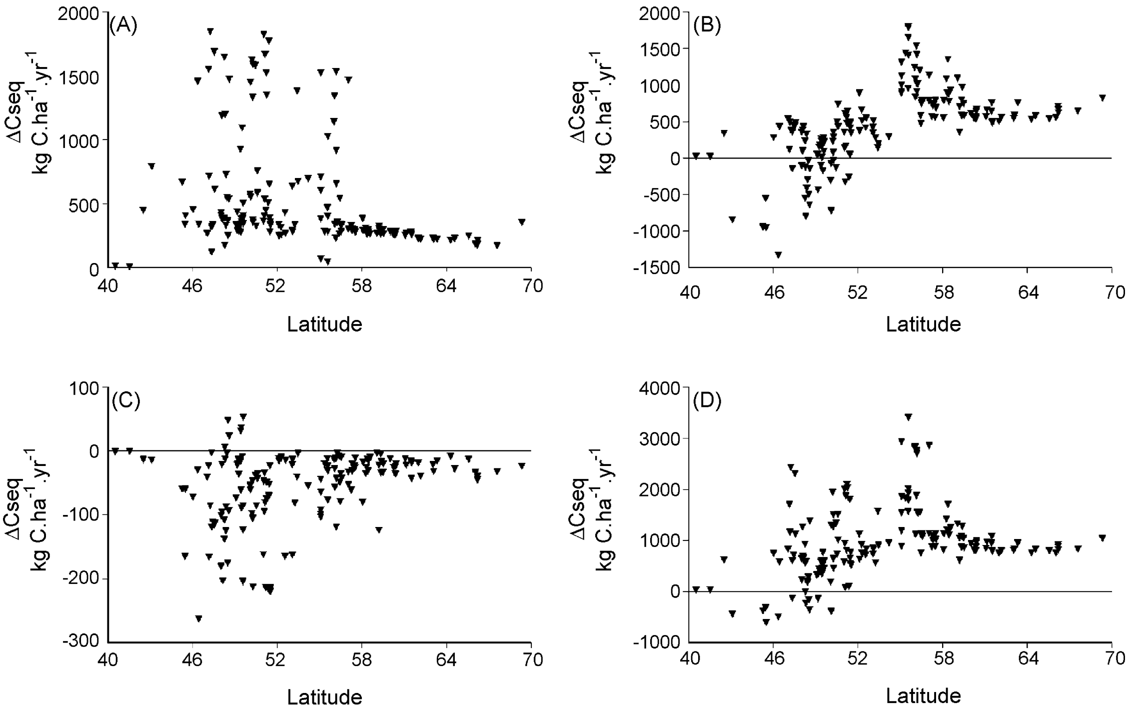


Fig. 8. Changes in carbon sequestration of European forests in 2070 compared to the reference run as a result of an increasing CO_2 concentration (A), climate change (B), a changing (reduced) nitrogen deposition (C) and the combined scenario (D) as a function of latitude.

generally lead to an increase in carbon sequestration except for parts of Southern Europe. In this region, we often simulate that the carbon storage in the soil will decrease at least up to 2070 due to the expected climate change and change in nitrogen deposition. This may also affect the occurrence of species direct or indirect dependent on the soil circumstances, and thereby influence the biodiversity in the forests.

4.4. Changes in carbon sequestration per unit change in CO_2 concentration, temperature and N deposition

4.4.1. Impacts of CO_2

Results show an increase in carbon sequestration by trees up to 1400 kg/ha/yr C for trees and up to 600 kg/ha/yr C for soil. This implies a total sequestration up to 2000 kg/ha/yr C for a predicted CO_2 increase of 197 ppm CO_2 between 1990 and 2070, leading to a maximum response of 10 kg C ha^{-1} yr^{-1} ppm $CO_2{}^{-1}$. The amount of C sequestration varies largely between the tree species (between 1 and 7 kg C ha^{-1} yr^{-1} ppm $CO_2{}^{-1}$) and this mainly explains the variation in CO_2 response. When trees are planted for C-sequestration purposes *Pinus nigra* and *Quercus cerris* are the most appropriate species, also because the combined effect with climate change gives the highest increase in carbon sequestration. For soils, it varies mostly between 1 and 3 kg C ha^{-1} yr^{-1} ppm $CO_2{}^{-1}$. On average, the total response is near 3 kg C ha^{-1} yr^{-1} ppm $CO_2{}^{-1}$ with the tree response being three times as high as the soil response (see also Table 2).

4.4.2. Impacts of climate change

The impact of climate change on carbon sequestration is determined by both the increase in temperature, leading to an increase in carbon sequestration and a change in precipitation. Taking both aspects into account and relating the change in carbon sequestration to temperature change alone, shows a range of −200 to 500 kg C ha^{-1} yr^{-1} °C^{-1} with respect to the trees (being comparable to a growth rate change between −20 and 50%) and a range of −200 to 200 kg C ha^{-1} yr^{-1} °C^{-1} for the soil, largely dependent on latitude as discussed above (Fig. 9). On average, the response of the trees is near 200 kg C ha^{-1} yr^{-1}, where the soil response is on average negative. The predicted change in net primary productivity (NPP) of approximately −20 to 50% for an increase in temperature of 1 °C is consistent with the response that was found for the monitoring plots by Solberg et al. (2009) for combined growth data for the period 1995–2000 and changes in temperature, precipitation

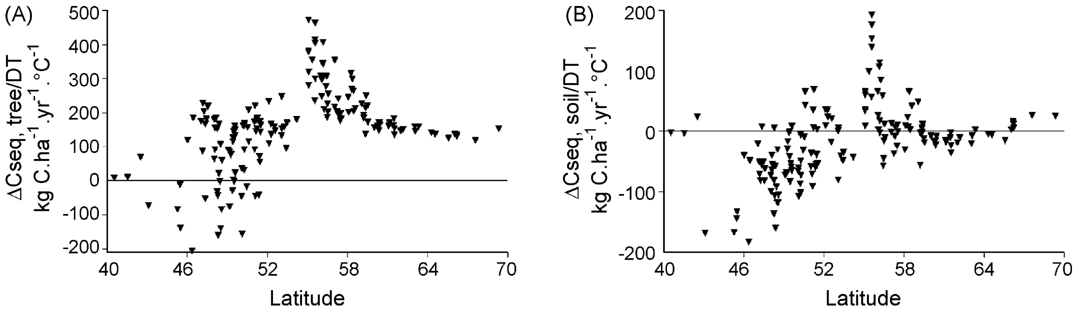


Fig. 9. Changes in carbon sequestration of European forests in 2070 per unit temperature change compared to the reference run for the forests (A) and soil (B) as a function of latitude.

and N deposition. These authors found a response that ranged mostly between 20 and 40% increase in growth for 1 °C temperature increase, which is in line with the predicted NPP change in the North, above a latitude of 52 (see Fig. 9A). As mentioned above, the negative values in the model simulations occurring in the southern part of Europe (below latitude 52) are due to the interaction between temperature and drought stress affected by a change in both temperature and precipitation.

4.4.3. Impacts of N deposition

Interesting is the relative small reaction of the carbon sequestration on the decrease in nitrogen deposition. It ranges mostly between 1 and 15 kg C/kg N with values going up till 25 for trees and 20 for soil. This is comparable to Currie et al. (2004) who found a carbon sequestration of 5 kg C/kg N. Compared to earlier results by Wamelink et al. (2009-b) for the Netherlands this is a relatively low range. They found an average simulated increase was 20–30 kg carbon per kg nitrogen deposition. Solberg et al. (2009) and Laubhann et al. (2009) found a comparable response for the monitoring plots using combined growth data for the period 1995–2000 and changes in N deposition and temperature. Results from N fertilization experiments, ^{15}N experiments and other model simulations give similar results (see De Vries et al., 2009). Our results indicate that a decrease in nitrogen deposition will not result in a similar decrease in carbon sequestration as was found for the increase in carbon sequestration by increasing nitrogen deposition. We argue that a decrease in nitrogen deposition not automatically leads to a decrease in nitrogen availability for the vegetation and thus a lower NPP and carbon sequestration. The build up N-pool is not decreasing as rapidly as it was built up due to the nitrogen deposition. A decrease in N-pool can only be expected because of either the harvest of trees or by leaching to the groundwater. Moreover, the present nitrogen pool may also be diluted over the newly formed biomass, thus giving a relative high NPP and carbon sequestration at a lower N-content.

4.5. Limitations of the modelling study

In simulating the impacts of environmental change on forest NPP and carbon sequestration, it has to be realized that several influencing aspects have not been accounted for. First, the impact of temperature change on the length of the growing season, mainly by an earlier start of the growing season is not included in SUMO2, as this models simulates the various processes at an annual time step. In principle the assessed impacts of temperature on NPP, simulated by SUMO2 (see also Electronic appendices 1 and 4), includes both a direct effect of temperature and an indirect effect of lengthening of the growing season on NPP. Second, the impact of nutrient availability was limited to N and base cations not including possible P limitation. Even though P fluxes can be simulated by SMART2 and SUMO2, we did not apply this module due to problems in parameterising P adsorption constants on a European scale. The effect is most likely small, since at most sites the growth is limited by nitrogen (Tamm et al., 1999). Third, we did not include the impact of moisture on the decomposition of organic matter. Most likely, this impact is small. Very wet or dry circumstances, that may cause a strong reduction of decomposition rates, do not occur at the examined plots.

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

Despite these limitations, we believe that the major results of this study are plausible in view of field data on the impacts of atmospheric drivers on tree and soil carbon sequestration and illustrate the potential of future changes in these drivers on the carbon sequestration potential of forests in Europe.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.05.018.

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