

The European carbon balance. Part 3: forests

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Abstract

We present a new synthesis, based on a suite of complementary approaches, of the primary production and carbon sink in forests of the 25 member states of the European Union (EU-25) during 1990–2005. Upscaled terrestrial observations and model-based approaches agree within 25% on the mean net primary production (NPP) of forests, i.e. $520 \pm 75 \text{ g C m}^{-2} \text{ yr}^{-1}$ over a forest area of $1.32 \times 10^6 \text{ km}^2$ to $1.55 \times 10^6 \text{ km}^2$ (EU-25). New estimates of the mean long-term carbon forest sink (net biome production, NBP) of EU-25 forests amounts $75 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$. The ratio of NBP to NPP is 0.15 ± 0.05 . Estimates of the fate of the carbon inputs via NPP in wood harvests, forest fires, losses to lakes and rivers and heterotrophic respiration remain uncertain, which explains the considerable uncertainty of NBP. Inventory-based assessments and assumptions suggest that $29 \pm 15\%$ of the NBP (i.e., $22 \text{ g C m}^{-2} \text{ yr}^{-1}$) is sequestered in the forest soil, but large uncertainty remains concerning the drivers and future of the soil organic carbon. The remaining $71 \pm 15\%$ of the NBP (i.e., $53 \text{ g C m}^{-2} \text{ yr}^{-1}$) is realized as woody biomass increments. In the EU-25, the relatively large forest NBP is thought to be the result of a sustained difference between NPP, which increased during the past decades, and carbon losses primarily by harvest and heterotrophic respiration, which increased less over the same period.

Keywords: covariance, ecosystem models, eddy, EU-25, forest inventories, greenhouse gas balance

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Introduction

Forests have supplied energy, fodder, food and construction materials as well as a grazing opportunity for centuries and have been exploited as such throughout the history of Europe. In Europe, periods of large-scale deforestation and reforestation have followed each other since the Roman era, with different chronologies

in different parts of Europe. The latest reforestation period followed World War II (UN-ECE & FAO, 2000b). Despite the reforestation efforts, most European forests were heavily depleted in carbon both in the soil and in the aboveground biomass by 1950, because of the harvesting of wood and litter (i.e., Behre, 1988; Bradshaw, 2004; Bürgi & Gimmi, 2007).

Since the 1950s, forest management moved toward intensive multipurpose systems which optimize several services including wood production, soil and water protection, recreation and conservation. The tendency to move away from solely production forests can be seen for instance, in the area of forests with a primarily

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protective function (i.e., climate, coastal, avalanche, wind protection and erosion protection) which increased from $1.0 \times 10^6 \text{ km}^2$ in 1990 to $1.4 \times 10^6 \text{ km}^2$ in 2005 for the European continent including Russia, Belarus and Ukraine (FAO, 2007). The surface area of forests with a primary biodiversity conservation function increased from $0.10 \times 10^6 \text{ km}^2$ in 2000 to $0.12 \times 10^6 \text{ km}^2$ in 2005 for the European Union (EU) and EFTA countries (UN-ECE & FAO, 2007).

Today, forests cover, depending on the source and the definition of forest, 1.32 (EEA, 2007) to $1.55 \times 10^6 \text{ km}^2$ (UN-ECE & FAO, 2007) of the EU-25 (for a list of abbreviations see P. Ciais *et al.*) area and the improvement of silvicultural practices together with increased atmospheric CO_2 concentrations and nitrogen deposition has led to a substantial increase in growth across Europe (Nabuurs *et al.*, 2003). Despite the intensive management that resulted in an absolute increase of wood harvest, European forests have continued to accumulate carbon at a high rate in their biomass (Janssens *et al.*, 2003) and soils (Schulze, 2000). This carbon sequestration is thought to be the result of a sustained difference between net primary productivity (NPP), which increased during the past decades, and carbon losses by harvest and heterotrophic respiration (R_h), which increased less strongly over the same period.

- The goal of this paper is to contribute to a better level of understanding of the productivity and carbon balance of European forests in relation to other terrestrial ecosystems such as croplands (P. Ciais *et al.*) and grasslands (P. Ciais *et al.*). Here, from a large database of ecological sites, we analyze repeated extensive forest inventories, and the output of biogeochemical models in order to address the following questions:
- What is the net biome production (NBP), and NPP of forests in the EU-25, as estimated by each independent data stream?
- What is the fate of the carbon incorporated in biomass and soils, and its return to the atmosphere?
- How does the long-term carbon balance or NBP relate to NPP?

Components of the carbon balance

A general description of the carbon balance is given in P. Ciais *et al.* (this thematic issue, part 1). In forests, the bulk of NPP is allocated to the production of biomass in different plant components: foliage, wood (including branches and stems) and roots (including coarse and fine roots). However, because not all of the produced biomass remains on site, direct measurements of total

NPP are impossible and removed biomass needs to be corrected for. Examples of biomass removal processes include harvest, and natural herbivory by insects and mammals. In addition other components of NPP are rarely measured such as understory plant growth, reproductive organs, emission of volatile organic compounds (VOC), exudation from roots and carbon transfer to root symbionts. The sum of all these components is the total ecosystem NPP. However, depending on the ecosystem some of these components are difficult to measure and of minor importance. For example, biogenic emission of isoprene totaled $3.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the EU-15 plus Norway and Switzerland (Armeth *et al.*, 2008) and total VOC emission, for which isoprene emissions is responsible for about half totaled $6 \text{ g C m}^{-2} \text{ yr}^{-1}$ from forests in France (Simon *et al.*, 2001). In this paper, NPP of forest denotes the sum of $\text{NPP}_{\text{foliage}}$, NPP_{wood} and $\text{NPP}_{\text{roots}}$.

The net ecosystem carbon balance (NECB) is the term applied to the total rate of organic carbon accumulation (or loss) from ecosystems (Chapin *et al.*, 2005). When integrated over time and space the NECB equals the NBP (Schulze & Heimann, 1998; Buchmann & Schulze, 1999; Chapin *et al.*, 2005). In this study, NBP of forest is quantified as: $\text{NBP} = \text{NEP} - D - F - H$ and thus, did not account for VOC and methane (CH_4) losses and nitrous (N_2O) flux (Goldberg & Gebauer, 2009). Where NEP is the net ecosystem production, D are losses through rivers and lakes, F are losses through fires and H stands for harvest. As our NPP estimate did not include VOC production, the omission of VOC production from NBP does not affect our estimate of NBP. However, the omission of herbivory from NPP and CH_4 from the NBP estimate could result in small biases of the forest NBP depending on the method (i.e., contrary to ecological site studies, inventory-based NBP estimates account for herbivory).

Materials and methods

Study area

The biogenic sinks and sources, representing the photosynthetic carbon uptake, respiratory and nonrespiratory releases, are estimated for forests in Europe. Our definition of forest followed the land use classification of the underlying data sources: for ecological site studies, we followed the classification of the principal investigator of the site; for forest inventories, we followed the national classification and when data came from ecosystem models, we followed the CORINE land use classification (EEA, 2007). Further, Europe was defined as the 25 member states of the European Union i.e., Austria, Belgium, Cyprus, Czech Republic, Denmark, Estonia, Finland, France, Germany, Greece, Hungary,

Table 1 Spatial and temporal coverage of the different methods

Method	Spatial coverage/upscaled to	Temporal coverage
National inventories and removal statistics	EU-25 excluding Malta, Cyprus, Estonia, Latvia and Lithuania but including Albania, Bosnia, Herzegovina, Bulgaria, Croatia, Macedonia, Norway Romania, Switzerland, Turkey and Yugoslavia	1990–1999
River database	European watershed draining into the Arctic Sea, Baltic Sea, North Sea, Atlantic Ocean, Mediterranean sea and Black sea	1980–2000
Direct measurement, NPP	EU-25	1971–2006
Direct measurement, R_h	EU-25	1991–2005
Eddy covariance, NEP	EU-25	1996–2006
BIOME-BGC	EU-25	1980–2005
CASA	EU-25	1997–2006
LPJ-DGVM	EU-25	1980–2005
Modified LPJ	EU-15	1990–2000
ORCHIDEE	EU-25	1980–2005

EU-25, 25 member states of the European Union; NPP, net primary production; R_h , heterotrophic respiration; NEP, net ecosystem CO₂ production.

Ireland, Italy, Latvia, Lithuania, Luxembourg, Malta, Netherlands, Poland, Portugal, Slovakia, Slovenia, Spain, Sweden and United Kingdom.

In general, the numbers represent the mean values for the EU-25 for the last decade and a half (Table 1). However, with the need to understand better regional details in the carbon cycle's response to perturbations and gradual changes, boreal, temperate and Mediterranean forest biomes are discussed separately in sections. Despite the general nature of the results, estimates at the EU-25 level are derived from spatially explicit data sets and models. There are inevitable inconsistencies in the various input data set and methodologies that were used and presented.

Data sources

Most of the results presented here are data or model results, which were prepared between 2003 and 2008 (Fig. 1). References to these data or models are given in Table 2. When other data were needed to complete the analyses or discussion, in-text citations are given.

Inventories. We analyzed regionally aggregated statistics of 30 European countries, of which 20 countries are from the EU-25 over the period from 1990 to 1999. Data on growing stock, increment, harvest, species composition and forest area were collected from 400 000 plots through national inventories. In their most basic form, inventory surveys measure stand density and tree dimensions (diameter, height) at consecutive dates. These measurements were used to calculate whole tree biomass increments by means of species-specific allometric

relationships (Goodale *et al.*, 2002; Liski *et al.*, 2002, 2003; Nabuurs *et al.*, 2003). Subsequently, tree biomass increments and appropriate turnover rates for leaves and fine roots are used to estimate the litter fall. NPP was estimated by summing tree biomass increments and litter fall. Finally, NPP in combination with a heterotrophic respiration model (Liski *et al.*, 2002, 2003; Nabuurs *et al.*, 2003) are used to calculate carbon pool changes and the net carbon balance of individual forests. We used statistics in which national level averages per species group are provided for growing stock, increment, harvest and forest area. For Finland, Sweden, Ireland and Spain, uncertainties were estimated based on the allometric relationships, reported statistics and applied soil models (Meyer *et al.*, 2005). In this study, the coefficients of variations for these four countries were averaged and applied to the EU-25 estimates: 4.5% for the biomass carbon pool, 25% for the biomass carbon sink, 45% for the soil carbon pool and 30% for the soil carbon sink (Meyer *et al.*, 2005).

Leaching of carbon from terrestrial ecosystems was calculated as the sum of CO₂ outgassing and the carbon load in inland waters. Organic and inorganic carbon concentrations in inland water and river discharge were compiled using the main European rivers database (Meybeck & Ragu, 2006) and extrapolated for the European sea's catchments (8.2×10^6 km²) on the basis of runoff, land cover and rock types similarities (Ciais *et al.*, 2008a). The additional carbon loss as CO₂ outgassing from rivers, lakes and estuaries was derived from a previous estimate at the European scale (Ciais *et al.*, 2008a) that considered the ecosystem's typical average water–air CO₂ fluxes and river, lakes and

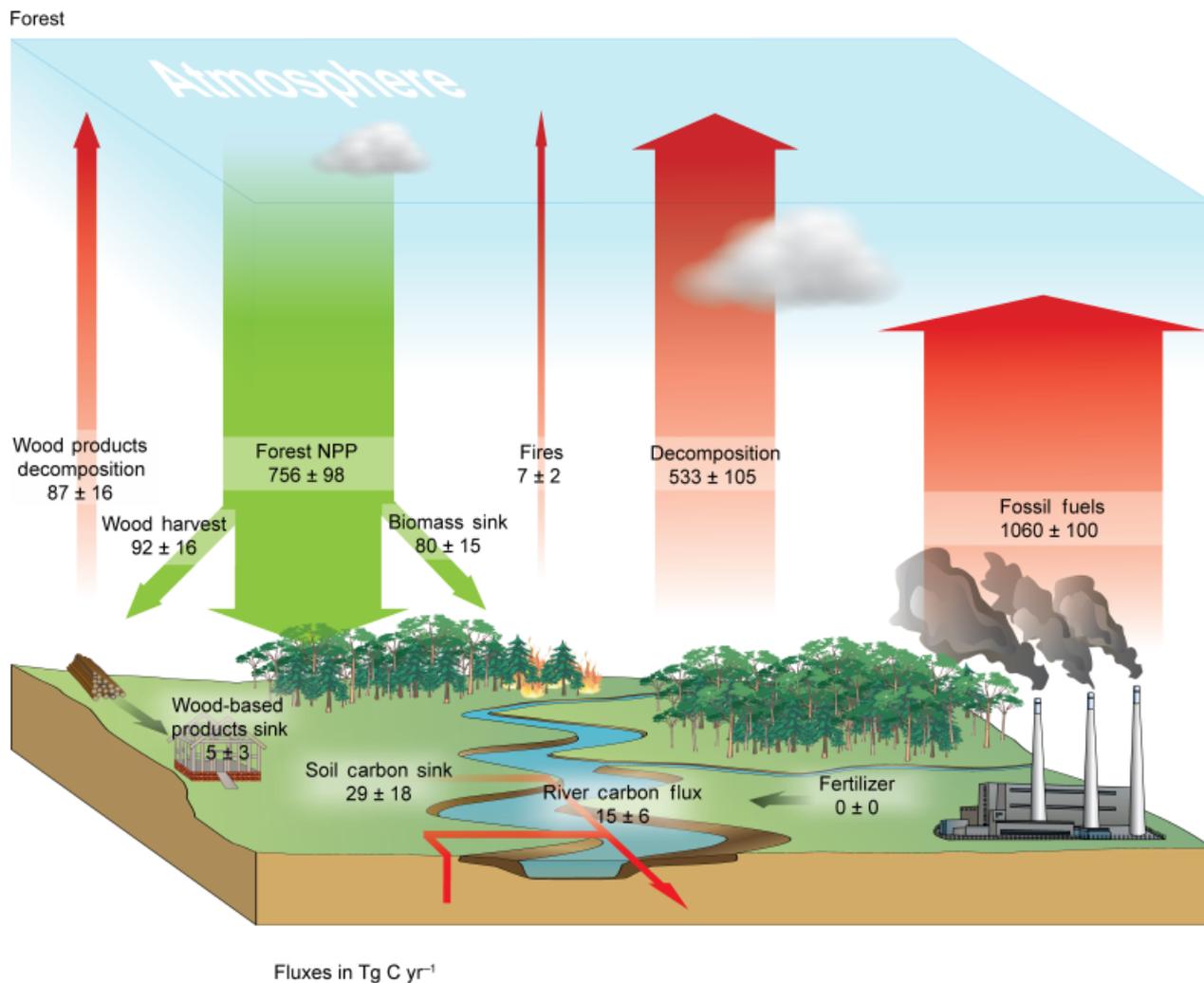


Fig. 1 Summary of the 25 member states of the European Union (EU-25) forest carbon cycle. Fluxes in TgCyr⁻¹ over a forest area of 1.46×10^6 km². Heterotrophic respiration was calculated as the residual term to make the balance close, the observed heterotrophic respiration is 600 ± 45 TgC yr⁻¹. 16 TgC yr⁻¹ out of 685 TgC yr⁻¹ (the sum of wood harvest, fires and R_h) is due to natural disturbances such as fires, storms and pests. The total sink of 109 ± 45 TgC yr⁻¹ was estimated to be for almost 40% (40 TgC yr⁻¹) due to land use change. The uncertainties show the standard deviation of the variability across approaches, hence, low uncertainties indicate convergence between methods.

estuaries surface areas (Lehner & Döll, 2004). This sum was then corrected by the ratio of organic over total carbon concentrations in inland water (Ciais *et al.*, 2007). The number represents the average estimate and the contributions of forests, grasslands and croplands cannot be separated. The uncertainty of the estimated leaching depends on the uncertainty in both terms and the ratio. The uncertainty of 30% was calculated as the spatio-temporal variability within the relevant databases.

Ecological site studies. Estimates of NPP, NEP and R_h were collected from peer-reviewed literature, established databases and personal communication with research groups involved in the regional networks of FLUXNET

(Baldocchi *et al.*, 2001). The NEP estimates that were included in our data set (Luyssaert *et al.*, 2007) were typically derived from eddy covariance measurements of net ecosystem exchange (NEE). NPP estimates were included in our data set when they were based on direct measurements of foliage, wood and root NPP. Only estimates based on *in situ* measurements of fine-root production were included. Estimates of R_h were included when based on subtracting upscaled chamber measurements of root respiration (Hanson *et al.*, 2000) from undisturbed soil respiration measurements or from chamber measurements after trenching or girdling. Also R_h estimates based on isotopes or soil C mineralization (Persson *et al.*, 2000) were included. In the following text,

Table 2 Data sources of the new analyses presented in this study

	Site observations	Models	Inventories
Net primary production (NPP)	Direct measurements of ecological studies (Luyssaert <i>et al.</i> , 2007)	BIOME-BGC (White <i>et al.</i> , 2000), LPJ-DGVM (Sitch <i>et al.</i> , 2003), ORCHIDEE (Krinner <i>et al.</i> , 2005) and CASA (Potter <i>et al.</i> , 2003)	National forest inventories, removal statistics and a simple soil model (Nabuurs <i>et al.</i> , 2003)
Harvest (<i>H</i>)	Difference in R_h between managed and unmanaged sites (Luyssaert <i>et al.</i> , 2007)	na	Removal statistics (Nabuurs <i>et al.</i> , 2003)
Fires (<i>F</i>)		Modified LPJ representing fires (Zaehle <i>et al.</i> , 2006) and MODIS products (Giglio <i>et al.</i> , 2006) coupled to the fire module of the CASA model (van der Werf <i>et al.</i> , 2006)	
Losses to rivers (<i>D</i>)			European rivers database (Meybeck & Ragu, 2006) upscaled on the basis of runoff, land cover and rock types similarities (Ciais <i>et al.</i> , 2008a)
Heterotrophic respiration (R_h)	Direct measurements of ecological studies (Luyssaert <i>et al.</i> , 2007)	BIOME-BGC (White <i>et al.</i> , 2000), LPJ-DGVM (Sitch <i>et al.</i> , 2003) and ORCHIDEE (Krinner <i>et al.</i> , 2005)	National forest inventories, removal statistics and a simple soil model (Nabuurs <i>et al.</i> , 2003)
N ₂ O and CH ₄	Literature study (Jungkunst & Fiedler, 2007)		
Net biome production (NBP)	Direct measurements of ecological studies (Luyssaert <i>et al.</i> , 2007) combined with F (models) and D (inventories)	Modified LPJ representing fires and generic forest management (Zaehle <i>et al.</i> , 2006)	National forest inventories, removal statistics and a simple soil model (Nabuurs <i>et al.</i> , 2003)

The data sources and model structures are described in detail in tabulated references. na, not applicable.

these types of studies were called ecological or intensive site studies.

Site-level NPP estimates were upscaled to the EU-25 by estimating the fluxes as the mean flux of the nearest three observations weighted by their inverse distance in climate space, where climate space was defined by radiation and precipitation during the growing season. The growing season was defined by the months with a mean temperature above 3 °C. Temperature was thus implicitly included in the analysis as it determined the length of the growing season. Climate data were extracted from harmonized data sets between 1990 and 2002 (Mitchell & Jones, 2005) and incoming radiation was calculated based on harmonized cloud cover data between 1990 and 2002 using the respective submodel from ORCHIDEE (Krinner *et al.*, 2005). Subsequently, the region-specific weighted mean was calculated by weighting the flux estimates by the appropriate forest area. Forest area and distribution were taken from Loveland *et al.* (2000).

The controls of NPP, NEP and R_h were quantified by means of a multiplicative regression model of two power functions quantifying the relationship of radiation and precipitation during the growing season with the carbon fluxes under study.

$$FLUX = a \times f(\text{radiation}) \times f(\text{precipitation}), \quad (1)$$

where $f(\text{radiation}) = (\text{radiation sum during growing season})^b$, $f(\text{precipitation}) = (\text{precipitation sum during growing season})^c$ and a , b and c are fitted to the data.

Further, linear relationships were fitted to NPP, NEP and R_h stratified according to management regime or N-deposition class. ANCOVA was used to test for statistical differences of the regressions statistic between management and deposition classes. N-deposition classes were based on ground observations (EMEP, NADP and NDDN) of several N species that are available for Western Europe and the conterminous USA (Holland *et al.*, 2005) and model simulations (Galloway *et al.*, 2004; Dentener, 2006) for the rest of the world.

In general, uncertainties in the flux estimates have not been reported in the literature. Therefore, we estimated the total uncertainty for every component flux contained in the data set using a consistent framework based on expert judgment (Taylor & Kuyatt, 1994). A prior uncertainty, depending on the latitude was determined by expert judgment. This prior can be seen as an estimate of NPP in the absence of any measurement. Because all our NPP estimates were based on measurements this prior uncertainty was reduced by a reduction factor which depends on the method and the length of the time series. For more details on this approach, see Luyssaert *et al.* (2007). Thus, the uncertainty framework in the database was designed to account for differences in data quality between sites owing to length of time series (e.g., inter-annual variability) and methodology (e.g., eddy covariance).

These uncertainties were fully accounted for in the statistical analyses by means of Monte Carlo simulations. Within each Monte Carlo simulation, normally distributed random errors, based on the uncertainty framework of the database, were added to the observed fluxes. The Monte Carlo-based uncertainties, however, do not account for representativeness of the site observations currently in the database. As a proxy for the latter uncertainty, we upscaled the fluxes to the EU-25 for 100 realizations, each realization using 90% of the available sites. The reported uncertainties combine the standard deviation of the Monte Carlo simulations and network representativeness. Uncertainty in the climate data used for upscaling are not accounted for.

In parallel, an artificial neural network similar to the one described in Papale & Valentini (2003) was used to upscale the site-level eddy covariance measurements to the EU-25. Many of the eddy covariance sites used to train the neural network were also included in the upscaling approach described above. When being upscaled, there are three main sources of uncertainty in the eddy covariance data: uncertainty in the data used to train the neural network, uncertainty in the climate data used for upscaling and uncertainty in the representativeness of the network. Despite the recent progress in estimating the uncertainty and consistency of the eddy covariance data (Papale *et al.*, 2006; Richardson *et al.*, 2006; Moffat *et al.*, 2007; Lasslop *et al.*, 2008; Luyssaert *et al.*, 2009), the uncertainty of the neural network which is used to upscale these data has not been determined yet.

A proxy for the neural network uncertainty was calculated for 32 sites in Europe. The neural network was trained with one year of data for 31 sites, the trained network was then used to estimate the NEE at the site that had been removed from the training set. This approach mimics the uncertainty in the observations and representativeness of the network but does not deal with

uncertainty in the climate data used for upscaling. Also, this proxy for uncertainty is estimated at the site level. Compensation of site-level errors during upscaling may result in similar or lower uncertainties at the regional than that at the site level.

Ecosystem models. BIOME-BGC, LPJ-DGVM and ORCHIDEE (Table 2) were applied for the European continent at a spatial resolution of 25 km × 25 km using harmonized climate, land cover and soil input data (Vetter *et al.*, 2008), and their output was averaged over the EU-25. These models calculated NPP between 1980 and 2005 as a function of climate, soil properties and increasing atmospheric CO₂. None of these models account for disturbances, regrowth and management, although a modified version of LPJ including human-induced fires and generic forest management was run to simulate NBP of the EU-15 (Zaehle *et al.*, 2006, 2007). The modified version of LPJ evaluated the model estimates against yield tables and regional age-based forest statistics. Further, this version simulated the propagation of age-classed vegetation through time and accounted for changes in forest area, harvest derived from resource use statistics and process-based calculation of NPP, R_p , H and F that accounted for size-dependent growth. The modified version of LPJ also included a regional fire module that allowed to estimate carbon losses because of forest fires (Zaehle *et al.*, 2006).

A second version of BIOME-BGC, including a nitrogen cycle, was used to account for the effects of increases in atmospheric N deposition (Churkina *et al.*, 2007). In the BIOME-BGC model plant demand for nitrogen is calculated from potential gross primary productivity and carbon to nitrogen ratios of plant organs. Demand of soil microbial community for nitrogen is determined by potential litter and soil organic matter available for decomposition and carbon to nitrogen ratios of corresponding pools. Carbon to nitrogen ratios of plant organs and leaf litter are assumed to stay constant. The amount of nitrogen available to satisfy this demand is computed as the sum of nitrogen deposited from atmosphere, biological fixation and nitrogen mineralized from soil organic matter decomposition. Possible forest dieback subjected to high nitrogen inputs was not considered in this study, because the atmospheric nitrogen depositions were averaged over relatively coarse grid cells and did not reach the high values, which could cause nutritional imbalance of forests. Detailed description of nitrogen cycle in the BIOME-BGC model can be found elsewhere (Thornton, 1998 #2072).

Output from all three models comes with an uncertainty caused by driver (e.g., the climate data used to drive the model simulations), structural (e.g., equations

for soil respiration) parametric (e.g., setting for maximum stomatal conductance) and flux definition (e.g., excluding understory vegetation in NPP) uncertainties, which are all intermingled and cannot be easily teased apart. Complete uncertainty analysis are not available yet, therefore, we report the driver uncertainty which amounted 25% for GPP (Jung *et al.*, 2007a) and 40% for NPP (Zhao *et al.*, 2006). For both R_h and NEP, the parametric uncertainty of 30% (Zaehle *et al.*, 2005; Trusilova *et al.*, 2009) was used.

To estimate fire emissions (van der Werf *et al.*, 2006), we also compiled simulated NPP from CASA, a satellite-driven vegetation model. CASA was run at $1^\circ \times 1^\circ$ spatial resolution, forced by distinct climate and land cover data sets compared with the other three models. Carbon released through forest fire emissions (F) was estimated by coupling the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) data with the fire module of the CASA model (van der Werf *et al.*, 2006). Forest fire emissions were estimated monthly for the period 1997–2006. The burned fraction of each $1^\circ \times 1^\circ$ grid cell was estimated based on MODIS satellite data of burned area and fire hot spots (Giglio *et al.*, 2006). In the absence of a framework that accounts for uncertainties in CASA-derived NPP and MODIS classification, interannual variability was used as a proxy for the uncertainty in fire emissions and a driver uncertainty of 40% (Zhao *et al.*, 2006) as a proxy for the uncertainty of NPP.

Results and discussion

NPP

Estimates of NPP. The European (EU-25) forest NPP based on inventories was $447 \pm 112 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3). Upscaled stand-based NPP measurements from intensive ecological site studies (Luysaert *et al.*, 2007) estimated a mean NPP of $544 \pm 90 \text{ g C m}^{-2} \text{ yr}^{-1}$ for European forests (Table 3). The inventory-based and upscaled stand-level forest NPP values can be compared with the NPP simulated across the EU-25 by four process-based vegetation models (Table 2). Except for CASA which calculates NPP from satellite-derived NDVI, these models calculated NPP as a function of climate, soil properties and increasing atmospheric CO_2 . The mean NPP value from BIOME-BGC and CASA, respectively, 439 ± 176 and $461 \pm 184 \text{ g C m}^{-2} \text{ yr}^{-1}$ are comparable with the forest inventory estimate of $447 \pm 112 \text{ g C m}^{-2} \text{ yr}^{-1}$, while LPJ-DGVM and ORCHIDEE give somewhat higher values of 524 ± 210 and $574 \pm 230 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively, and are close to the upscaled stand-level NPP.

The NPP estimate for the modified version of LPJ-DGVM ($638 \pm 255 \text{ g C m}^{-2} \text{ yr}^{-1}$) exceeds all other estimates. Contrary to the other models, the modified LPJ-DGVM accounts for regrowth and age structure of the EU forests. This could explain why the estimate

Table 3 Forest component fluxes (values in $\text{g C m}^{-2} \text{ yr}^{-1}$) over EU-25 from different methods

Method	GPP	NPP	NEP	R_h	H	F	D	NEP/NPP	NBP*	NBP/NPP
<i>Inventories</i>										
National forest inventories	na	447 \pm 112	160 \pm 20	287 \pm 115	61 \pm 3	na	na	0.36 \pm 0.1	89 \pm 19	0.19 \pm 0.1
Soil losses to rivers	na	na	na	na	na	na	9.6 \pm 3.2	na	na	na
<i>Ecological sites</i>										
Sites studies	1199 \pm 77	544 \pm 90	200 \pm 52†	387 \pm 59	88 \pm 21	na	na	0.37 \pm 0.1	75 \pm 100†	0.14 \pm 0.3
Eddy covariance	1107 \pm 350	na	197 \pm 260	na	na	na	na	na	na	na
<i>Vegetation models</i>										
BIOME-BGC	985 \pm 246	439 \pm 176	42 \pm 13	397 \pm 119	na	na	na	0.09 \pm 0.3	na	na
LPJ-DGVM	899 \pm 225	524 \pm 210	19 \pm 6	505 \pm 151	na	na	na	0.04 \pm 0.3	na	na
Modified LPJ		638 \pm 255	125 \pm 38	511 \pm 153	64 \pm 4	7.0 \pm na			63 \pm 19	0.10 \pm 0.3
ORCHIDEE	1183 \pm 295	574 \pm 230	47 \pm 14	527 \pm 158	na	na	na	0.08 \pm 0.3	na	na
CASA	na	461 \pm 184	na	na	na	4.7 \pm 1.3	na	na	na	na

Forest component fluxes were updated with observation and model-based methods. The uncertainties show the standard deviation. Different methods report different uncertainties and method-specific definitions for uncertainty are provided in the section 'Materials and methods'. Consequently, low uncertainties do not necessarily indicate precise methods. Values in bold were used in Fig. 1.

*Inventory- and model-based NBP estimates account for C sink because of afforestation. The NBP estimate based on upscaling ecological site measurements likely underestimate the contribution of afforestation (see NBP estimates).

†Eddy covariance-based NEP and biometric-based NEP differ by $40 \text{ g C m}^{-2} \text{ yr}^{-1}$. Consequently, NBP is estimated as a range.

EU-25, 25 member states of the European Union; GPP, Gross primary productivity; NPP, net primary productivity; NEP, net ecosystem CO_2 production; R_h , heterotrophic respiration; H , harvest; F , losses through Fires; D , losses to rivers; NBP, net biome production; na, not applicable.

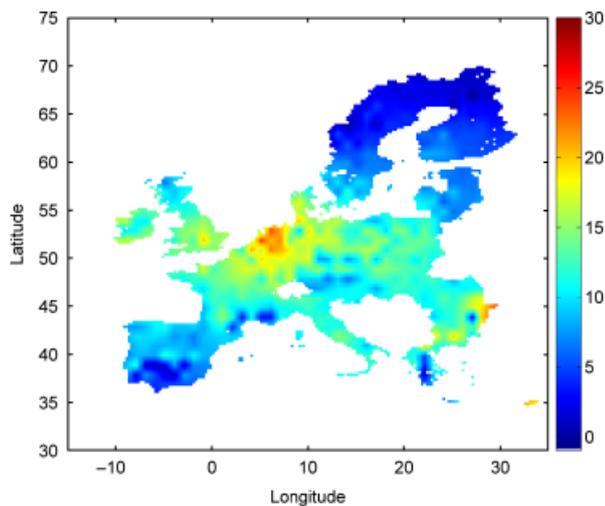


Fig. 2 Differences (%) in net primary productivity (NPP) between BIOME-BGC simulations with and without N deposition relative to NPP without N deposition. Not accounting for N deposition results in a mean underestimate of 11% of NPP across 25 member states of the European Union (EU-25).

is higher than the NPP of the other models and the ecological site estimate but does not explain why the estimate is higher than the inventory-based NPP which also account for regrowth and age structure.

BIOME-BGC, the only model that includes a nitrogen cycle and accounts for N deposition, estimated the lowest mean NPP (Table 3). Comparison of BIOME-BGC simulations with and without nitrogen cycle, all other drivers kept constant, shows that not accounting for N deposition results in an $11 \pm 30\%$ lower NPP for the EU-25 (Fig. 2). This result indicates that N limitation effects on NPP might not be ignored, and can lead to overestimation of NPP. However, the reduction in northern Europe and the southern Iberian Peninsula is negligible, whereas not accounting for N deposition could result in underestimating NPP by as much as 20% in high N-deposition regions in central Europe (Fig. 2). Because the model assumes a continuous vegetation cover, urban-island artifacts can be observed, i.e. an increase in NPP is predicted in areas that are currently urban and have no substantial NPP.

Models also have systematic regional or biome-specific NPP differences with ecological sites and inventories. For example, ORCHIDEE and BIOME-BGC overestimated GPP in boreal forests by $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ (compared with eddy-covariance-based estimates) and hence NPP possibly by $50\text{--}100 \text{ g C m}^{-2} \text{ yr}^{-1}$, probably because of overestimated LAI (Jung *et al.*, 2007a). In Mediterranean forests, ORCHIDEE, LPJ-DGVM and BIOME-BGC underestimated GPP compared with eddy covariance sites. The tendency of all three models

to underestimate GPP in the water limited part of Europe indicates either issues of model structure regarding their soil hydrology, questionable meteorological input data over this region or biased evaluation sites (Jung *et al.*, 2007a).

Despite the large methodological differences, the mean forest NPP of the different approaches compare within 25% of each other. It is not possible to move one of these estimates forward as being the best estimate, since all are expected to have comparable uncertainties (Table 3) originating from different problems. The estimate based on the ecological sites probably represents the upper bound of the NPP. Ecological studies provide high-quality data at the site level but, their upscaling to the EU-25 level heavily depends on the representativeness of the available data. A lack of measurements in low productive sites, i.e., recently disturbed forests and shrublands, and not accounting for soil fertility in the upscaling procedure may have led to overestimation of NPP for the EU-25. On the other hand, the inventories which are based on 400 000 plots are representative at the EU-25 level but use general relationships to expand measured stem wood NPP to ecosystem NPP. Even small errors in the expansion factors for branches, foliage and root NPP could result in a substantially underestimated EU-25 NPP. As an example, the fraction of foliage and root NPP to the total NPP equals 0.35 in the inventory data, compared with values of 0.50 for conifers and 0.45 for broadleaved forests obtained from ecological site studies. Adding low productive sites to the network of ecological sites or applying regional expansion factors in the inventories would likely result in convergence of the inventory and ecological approach. Nonetheless, the robustness of NPP derived from independent methods is encouraging and shows that the ecosystem models and the inventory-based approaches are consistent with each other (see 'Controls of NPP').

Controls of NPP. Based on a global compilation of ecological site studies (Luyssaert *et al.*, 2007), we found that the amount of carbon that materializes as forest NPP depends to a large extent on the amount of carbon assimilated through photosynthesis (linear regression, $R^2 = 0.48$, $P < 0.01$, $n = 69$), N deposition (linear regression on the residuals of the NPP–GPP relationship, $R^2 = 0.13$, $P < 0.01$, $n = 69$) and marginally on LAI (linear regression on the residuals of the NPP–GPP relationship, $R^2 = 0.12$, $P < 0.14$, $n = 47$). At the global scale and for a given GPP, the allocation of assimilated compounds to NPP was insensitive to management (Fig. 3a; ANCOVA $P = 0.92$). We can also describe the global pattern in NPP as a function of climate (Lieth & Whittaker, 1975; Churkina & Running, 1998), however, climate explains less of the large-scale variability in NPP

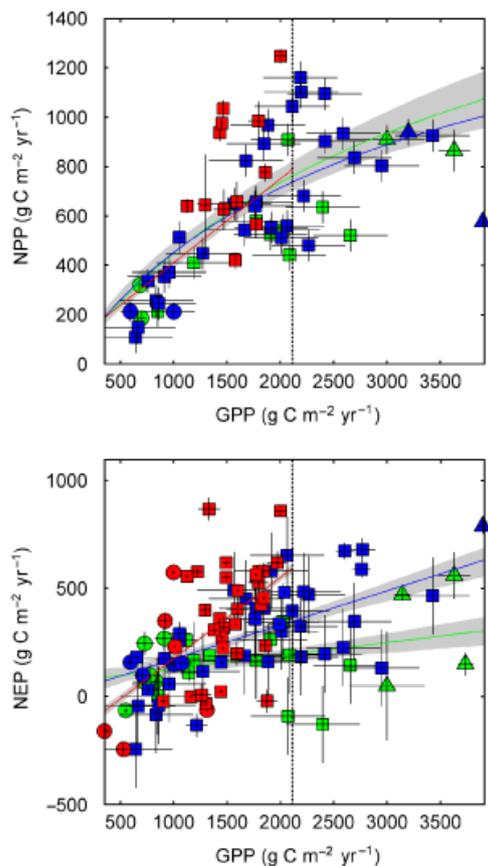


Fig. 3 Relationships between gross primary productivity (GPP) and the amount of carbon that is allocated to net primary production (NPP) and net ecosystem proportion (NEP). (a) Relationship between NPP and GPP, $n = 16$, $n = 40$, and $n = 13$ for unmanaged sites with background N deposition (green), managed sites with background N deposition (blue), and managed sites with elevated N deposition (red), respectively. (b) Relationship between NEP and GPP, $n = 25$, $n = 45$, and $n = 40$ for unmanaged sites with background N deposition (green), managed sites with background (blue), and managed sites with elevated N deposition (red), respectively. Circles, squares and triangles show boreal, temperate and tropical forests, respectively. The vertical lines mark the GPP range in which sites with elevated N deposition were observed. The error bars and gray zone around the curves show the standard deviation of the data and curve fitting, respectively.

than GPP (multiplicative regression model with two power functions, p : not defined for nonlinear regressions, $R^2 = 0.32$, $n = 254$). However, GPP is largely controlled by climate.

Subsequently, we described the observed GPP as a function of the precipitation and radiation sum during the growing season. Because radiation and temperature are strongly correlated at the site level (Pearson's correlation $\rho = 0.90$, $P < 0.01$, $n = 115$), temperature was included implicitly in this analysis, as it was used to

determine the length of the growing season and as such influences the precipitation and radiation sums. Globally, incident radiation and precipitation during the growing season, and temperature via its strong effect on the length of the growing season, exert the dominant control over large-scale patterns in GPP (multiplicative regression model with two power functions, p : not defined for nonlinear regressions, $R^2 = 0.67$, $n = 169$).

The observation-based controls on GPP and NPP indicate that GPP can be estimated when radiation, precipitation, temperature, LAI and N availability are known. Subsequently, NPP could be derived from GPP. Currently, ORCHIDEE, LPJ-DGVM and BIOME-BGC estimate photosynthesis (GPP) based upon climate factors and CO_2 concentrations, and further calculate NPP as the remaining carbon after the respiration needs of the plant have been fulfilled. Because these models are forced by (i.e., climate and CO_2) or calculate (i.e., LAI) most of the observed controls (except for nutrient availability) are accounted for, hence, a good agreement is to be expected and was indeed observed between the ecosystem models, the inventory and ecological site studies (Table 3).

Current ecosystem models seem to lack the controls of the regional differences in NPP (see NPP estimates). In general, regional representation of models could be improved by better representing (1) key processes such as seasonal water stress, crown development under nutrient and water constraints and nutrient constraints in general and (2) regional variability in plant traits. Currently, many important plant traits (e.g., leaf nitrogen concentration, specific leaf area, leaf longevity) that control biogeochemical cycling are represented as constant parameters within a plant functional type (PFT). However, these traits are known to vary within and between PFTs and systematically along environmental gradients (Wright *et al.*, 2004, 2006; Reich *et al.*, 2006).

Trends in NPP. During the past 50 years, NPP of forests in the EU-25 increased by a factor of 1.7 and the biomass stock per forest area of forest increased in parallel by a factor 1.8 (Ciais *et al.*, 2008b). Moreover, forest carbon stocks increased everywhere in Europe linearly with NPP (Fig. 4), both for conifer and broadleaved forest. The slope of the regression line between carbon stocks and NPP was reported to be similar between the different European countries, independently of differences in regional climate, soil conditions, initial stocks and NPP values, and management practices (Ciais *et al.*, 2008b).

Causes for the increase in NPP may be (no rank order given): (i) the juvenile age structure of the European forests, most of which are old coppices (broadleaves in Southern Europe) or post-war plantations (conifers in

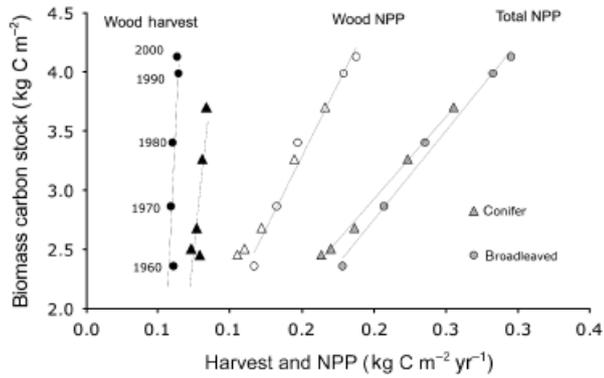


Fig. 4 Whole tree carbon stocks of European forests as a function of net primary productivity (NPP) inputs (filled symbols) and removals by harvest (open symbols). Data from sample-based inventories in selected countries are shown at 10-year intervals since 1960. The difference between harvest removals and NPP gains at a given stock value is the net carbon sink in trees (NBP in Table 3). Remarkable is the linear evolution of stocks vs. NPP showing a rather similar slope in each country, and the small harvest increments compared with the NPP increments indicating a strong increase in woody biomass. Each symbol represents a decadal mean.

Central and Northern Europe) that still show increasing increment rates, (ii) the increased fertility of forest soils following a reduction of nutrient removals by the cessation of practices such as grazing or litter raking and by the reductions of sulfur emissions, which induced nutrient leaching, (iii) forest area expansion resulting in an increasing share of young productive forests, (iv) changes in species composition toward more productive tree species (i.e., Sitka spruce in Ireland and the United Kingdom, poplar in France and Belgium and *Eucalyptus* in Portugal), (v) the fertilizing effects of increased nitrogen deposition and atmospheric CO_2 concentration and (vi) changes in management practices.

Future NPP is expected to further increase above current NPP levels owing to predicted increases in temperature (Meehl *et al.*, 2007) and CO_2 concentration (Norby *et al.*, 2005; Meehl *et al.*, 2007).

Expected increase in NPP (Cao & Woodward, 1998) could, however, be offset by progressive limitations of other nutrients (Gill *et al.*, 2006; Luo, 2007), water stress related to the predicted decreased growing season precipitation (Meehl *et al.*, 2007), climate change-induced changes in species composition (Cramer *et al.*, 2001; Parmesan & Yohe, 2003; Gamache & Payette, 2004; Jump *et al.*, 2006), increasing ozone concentrations (Sitch *et al.*, 2007), increasing frequency of insect outbreaks (Percy *et al.*, 2002; Logan *et al.*, 2003), increased frequency and intensity in forest fires owing to changes in species composition and climate (Westerling

et al., 2006; Bond-Lamberty *et al.*, 2007) or increasing storm damage because of increased storm intensity in the temperate zone (Meehl *et al.*, 2007) in combination to the increased cultivation of tree species outside their natural range (Schelhaas *et al.*, 2003). According to most emission scenarios, on the contrary, atmospheric N deposition over Europe is expected to decline over the next decades (Dentener *et al.*, 2006), resulting in a parallel decrease in forest NPP. The different dynamics of temperature, CO_2 and N deposition over the next century make it all the more important to partition the observed increase in forest growth among these driving variables.

Moreover, recently the role of climate variability and extreme weather conditions such as the 2003 heat wave has been identified as a factor that may strongly alter responses of productivity to mean climate change (Ciais *et al.*, 2005; Reichstein *et al.*, 2007a). The effect of a single heat wave on site productivity carried over to the next year(s) because of lowered soil water availability and increased tree mortality (Granier *et al.*, 2007). Hence, it remains uncertain whether NPP will increase or decrease in the next decades.

Carbon losses

Estimates of carbon losses. The NPP is the amount of carbon that is available for the production of organic molecules after the respiratory needs for growth and cell maintenance have been met. Part of the NPP is lost from the ecosystem via processes such as herbivory and VOC emission. The remainder accumulates as biomass or is deposited as soil organic carbon (SOC). Part of the accumulated carbon is being consumed (Fig. 1) by heterotrophic respiration (R_h), harvest (H), forest fires (F) and losses to rivers (D). In the following paragraphs, we estimate these components of the EU-25 carbon balance.

Between 1990 and 1999 harvested wood (H) is estimated at $61 \pm 3 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3) (Nabuurs *et al.*, 2003). Despite a mean life-time of about 17–20 years for wood products excluding paper and cardboard (Profft *et al.*, 2008), the difference between the production of new wood products and decomposition and burning of disposed products ($62 \pm 3 \text{ g C m}^{-2} \text{ yr}^{-1}$) resulted only in a very small carbon sink in wood products of $1.5 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Nabuurs *et al.*, 2003). About half of the harvested wood is directly or indirectly used for energy production (as firewood in Mediterranean countries, and wood by-products in Northern countries) avoiding the use of 40 Mt of diesel annually (EEA, 2006). Comparison of the relationship between R_h and NPP in managed and unmanaged forests indicated an average H flux of $88 \pm 3 \text{ g C m}^{-2} \text{ yr}^{-1}$ for ecological site studies (Luyssaert *et al.*, 2007). The ecological site study and inventory approach both indicate that harvest (H) is only a small

fraction of NPP (causes for the high NPP are given in 'Trends in NPP'), which, in the absence of other large losses because of fires, die back and storm damage, implies a large potential carbon sink in the biomass of European forests (Ciais *et al.*, 2008b).

Estimates of the burnt area differ because of differences in methodology and its limitations. According to the MODIS estimates, 1 700 000–1 900 000 ha of land across EU-25 was burned annually. Forests covered 300 000–700 000 ha of that area (van der Werf *et al.*, 2006). Despite being spatially explicit, MODIS has difficulties in distinguishing forests from shrublands and other wooded lands. Official statistics report over the period 1990–2005 a yearly average of 520 000 ha of fires on forest and other wooded land (Schulte *et al.*, 2002), of which 270 000 ha was on forest land (Schelhaas *et al.*, 2001). In the 1990s, the annually burnt forest area represented 0.2% of the total forest area (Schelhaas *et al.*, 2003). The ratio of burned land is in reasonable agreement with the MODIS estimate of 0.4% of Europe including forests, shrubland, grassland and agricultural land (Giglio *et al.*, 2006; van der Werf *et al.*, 2006), most of the burned area in EU-25 being in Portugal and Spain (Fig. 5). In total, the Mediterranean countries account for 93% of the fires; in Portugal and Spain, 0.6% of the forest burns annually (Schelhaas *et al.*, 2003). Forest fires are a regional flux mainly confined to the Mediterranean. For comparison, each year 2500 forest fires destroy in total 1000 ha in Germany and Finland together (Schulte *et al.*, 2002).

Forest fire emissions (F) are estimated from satellite data of burned area and fire hot spots (Giglio *et al.*, 2006) and were coupled to the fire module of the CASA model (van der Werf *et al.*, 2006). The total annual loss due to forest fires is $5.1 \pm 1.4 \text{ TgC yr}^{-1}$ for the EU-25 or $4.7 \pm 1.3 \text{ g C m}^{-2} \text{ yr}^{-1}$, the uncertainty was estimated as the inter-annual variation between 1997 and 2006. A modified version of LPJ-DGVM estimated $6.8 \pm \text{na} \text{ g C m}^{-2} \text{ yr}^{-1}$ losses due to fire (Zaehle *et al.*, 2006).

The F flux is much larger for Mediterranean forests and shrublands that are mainly composed of broadleaved species (i.e., 15% needle evergreen, 20% broadleaved evergreen and 65% broadleaved summergreen; Loveland *et al.*, 2000), than for boreal and temperate forests that contain the bulk of the coniferous trees in the EU-25. At the EU-25 level, F equals $6.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ for broadleaved and $3.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ for conifer forest. At first, this seems counter intuitive because if both traits occur in the same region, the conifer trees are usually more prone to fires than the broadleaves (Meyer, 2005). However, young and dense stands favor fire spread, and forest floors with a high amount of flammable material are more vulnerable than others. In addition, climatic conditions in the Mediterranean area are more likely to support fires. Hence, in the EU-25, the dominance of the F flux in broadleaved species

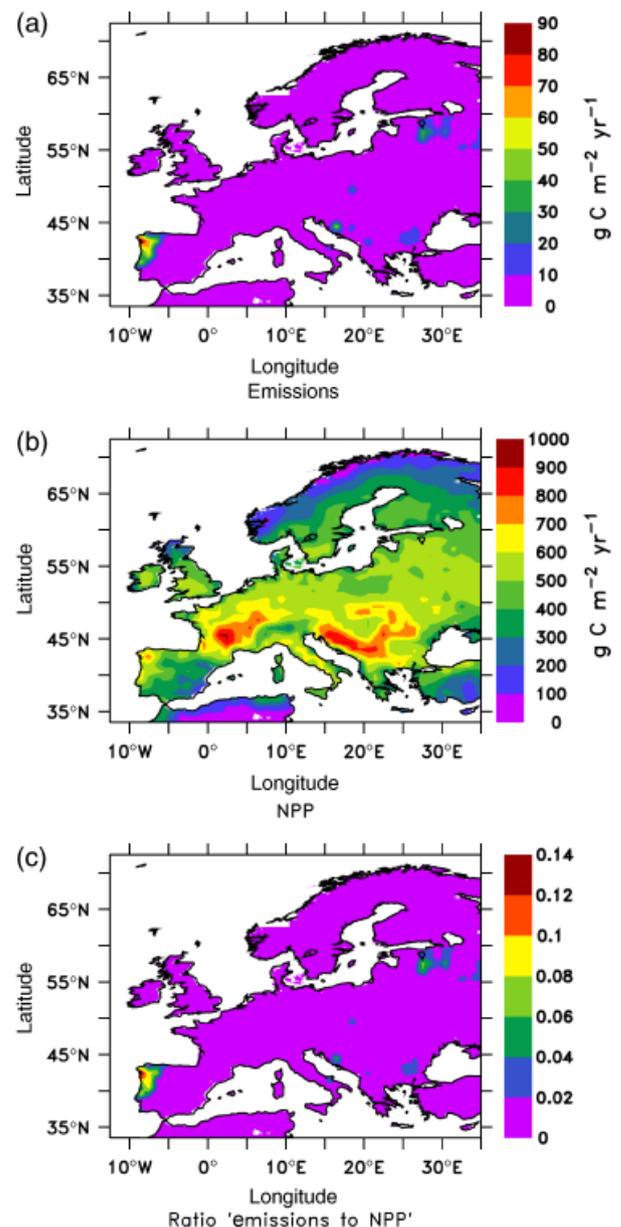


Fig. 5 Fire-related total carbon emissions from European ecosystems over 1997–2006 from the CASA model with input data from remote-sensing EOS-Terra-MODIS burned area. (a) Spatial distribution of fire emissions, summing up to a total source of $5.1 \pm 1.4 \text{ TgC yr}^{-1}$ over the 25 member states of the European Union (EU-25). (b) Annual net primary productivity (NPP) estimated by the CASA model, using a light-use efficiency parameterization and remotely sensed light absorption by canopy. (c) Ratio of fire emission to NPP over 1997–2006.

seems to be a management and climate, rather than a vegetation trait effect.

During 1990–2005, fire emissions represented on average 1% of forest NPP (Table 3). The spatial distribution of NPP (Fig. 5a) and fire emissions (Fig. 5b)

across Europe was derived from CASA. The ratio F/NPP , however, has large regional differences (Fig. 5c), ranging from <0.05 in humid temperate forests, up to 0.15 over northern Portugal, where exceptionally large fires occurred in 2003.

Disturbances through storm (Lindroth *et al.*, 2009) and pests are either salvaged or left on-site to decompose and therefore end up in the H or R_h flux. The joined contribution to the carbon sink of the main disturbances, i.e. fire, storm and pests is discussed in 'Controls of NBP'.

Leaching of carbon from forest soils into rivers (D) is estimated by upscaling the chemical composition of surface water and river flow measurements across Europe (Meybeck & Ragu, 2006). Only carbon of photosynthetic origin was accounted (Ciais *et al.*, 2007) by considering that up to 60% of the organic and inorganic carbon lateral flux transported by rivers to estuaries is of atmospheric origin, according to lithology and weathering intensity (Meybeck, 1987; Dürr *et al.*, 2005). The amount of carbon in inland water, that represented $40 \pm 10\%$ of the total carbon flux, is based on a very large data set of carbon concentrations in river waters (Ciais *et al.*, 2008a). The second term of CO_2 outgassing is much more uncertain owing to the general lack of CO_2 data in rivers and lakes, as well as the uncertainties on water surface areas (Lehner & Döll, 2004), which result in an uncertainty of 50% (Ciais *et al.*, 2008a). Our approach resulted in a flux of photosynthetic carbon exported from ecosystems to rivers of $9.6 \pm 3.2 \text{ g C m}^{-2} \text{ yr}^{-1}$. This estimate is close to the mean estimate of $11 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$ for Europe (Siemens, 2003) and the global mean estimate of $10 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Randerson *et al.*, 2002) carbon leaching to rivers and lakes. However, at the European scale it is impossible to determine whether D is an almost fixed fraction of NPP being channeled to the rivers or owing to disturbance of old soil organic matter pools.

The only source of *in situ* heterotrophic respiration estimates is ecological site studies. When these estimates are upscaled, R_h was on average $387 \pm 59 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the EU-25. The highest field observation of R_h is almost twice as large as the lowest estimate, and the upscaled observations are close to mid-range. Heterotrophic respiration of EU-25 forests is modeled at $283 \pm 115 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the period 1990–1999 by the forest inventory methods (Table 1). The ecosystem models estimated R_h as a function of soil carbon stock, available nitrogen (only in BIOME-BGC) and soil temperature and moisture at $397 \pm 119 \text{ g C m}^{-2} \text{ yr}^{-1}$ (BIOME-BGC), $505 \pm 151 \text{ g C m}^{-2} \text{ yr}^{-1}$ (LPJ-DGVM) and $527 \pm 158 \text{ g C m}^{-2} \text{ yr}^{-1}$ (ORCHIDEE). Ecosystem models calculate R_h as a function of soil carbon stock, which in turn is a function of NPP (Krinner *et al.*, 2005). Consequently, high NPP estimates are propagated in the soil carbon stock estimates and are likely to produce high

R_h estimates. The relationship between soil temperature and soil moisture is often formalized as an exponential function known as the Q_{10} function. Owing to the mathematical properties of this function, small differences in temperature sensitivity or Q_{10} values could result in large differences in R_h (Davidson & Janssens, 2006; Davidson *et al.*, 2006). The lack of convergence in R_h estimates across methods will be reflected in a wide range of NEP and ultimately NBP estimates (see 'NBP').

Controls of carbon losses. Strictly speaking, harvest has no natural drivers and the mean harvest rate largely depends on the physical characteristics and socio-economic status of the regions within Europe (i.e., urban vs. rural regions). Global demand and wood supply of distant regions such as Siberia, Canada and the tropics, policy decisions as well as technological innovations are likely reflected in the EU-25 harvest intensity. In the past, industrial changes (i.e., the raise and fall of the coal mining industry) resulted in changes in harvest intensity and characteristics (Johann, 2007). At the regional level, mean harvest rates may be disrupted by salvage logging following fires, insect outbreaks and windfall which is the most important cause of forest damage in the EU-25 (Nabuurs *et al.*, 2003).

To be started and propagated, forest fires need fuel, favorable weather conditions and an ignition source. Overly dense stands where management (or the absence of management) and fire suppression has led to increased fuel stocks (Miller & Urban, 2000; Mason *et al.*, 2006) combined with prolonged periods of drought (Mollicone *et al.*, 2006; Achard *et al.*, 2007) favor forest fires. Typically, lightning is the natural source of ignition, however, even in rather remote regions like Russia most of the forest fires are of human origin (Mollicone *et al.*, 2006; Achard *et al.*, 2007). Consequently, in densely populated regions such as the Mediterranean the majority of the fires are expected to be started by arson.

A review of dissolved organic carbon (DOC) fluxes and concentrations in temperate forests (Michalzik *et al.*, 2001) indicated no general difference between coniferous and hardwood sites, increasing fluxes of DOC in forest floor leachates with increasing annual precipitation, increasing fluxes of DOC in forest floor leachates with increasing fluxes of DOC in throughfall and higher concentrations of DOC in forest floor leachates were observed for higher pH of the forest floor, within a pH range of 3.3–4.4. Further, increasing DOC leaching was observed in response to NO_3^- deposition (Smemo *et al.*, 2006), increased primary production (Froberg *et al.*, 2006; Harrison *et al.*, 2008) and increased temperature (Harrison *et al.*, 2008). Sorption dynamics and depletion of DOC explains, respectively, peaks in DOC after periods of droughts (Froberg *et al.*, 2006) and low DOC

fluxes after periods of intense precipitation (Harrison *et al.*, 2008). Forest management practices such as liming are reported to increase the carbon losses through DOC and DIC (Nilsson *et al.*, 2001).

However, not all of the DOC and DIC reach the rivers and lakes. The positive water balance in boreal Europe and the local importance of peatlands with anaerobic conditions favors high DOC and DIC concentrations in rivers and lakes. In the temperate region, the water balance is only positive in winter and soil conditions are dominantly aerobic resulting in low DOC fluxes. The DOC flux in forest floor leachates of temperate forests ranged between 10 and 40 g C m⁻² yr⁻¹ (Michalzik *et al.*, 2001). Whereas the mean average DOC fluxes from forests (both boreal and temperate) to rivers and lakes is 4 g C m⁻² yr⁻¹ (Siemens, 2003). Consequently, DOC and DIC from forest floor leachates never enter rivers and lakes because they are decomposed or retained in deeper soil layers.

Heterotrophic respiration or microbial decomposition depends on soil temperature, soil moisture, NPP of the vegetation and substrate quality (Raich & Nadelhoffer, 1989; Janssens *et al.*, 2001; Davidson & Janssens, 2006). Higher temperature, soil moisture, NPP and substrate quality all result in an increase of microbial activity. Also, heterotrophic respiration is sensitive to the N availability. Decomposition of fresh, recently fallen litter is N limited (C/N litter ~ 50) and as such its early-stage decomposition is accelerated by high internal N concentration (Parton *et al.*, 2007) and by elevated N deposition (Knorr *et al.*, 2005). In later phases of the decomposition process, lignin concentration regulates decay of the remaining biomass, both the ligneous and the more easily palatable tissues protected by lignin fibres. N deposition has been found to reduce activity of peroxidases, enzymes responsible for degrading lignin among other molecules, which explains why N deposition retards the decay of litter during later stages of the decomposition process (Fog, 1988; Berg & Matzner, 1997; DeForest *et al.*, 2004; Knorr *et al.*, 2005; Pregitzer *et al.*, 2008). Moreover, the deposition-derived ammonium could stimulate the formation of recalcitrant humic compounds and thus further reduce the heterotrophic CO₂ losses (Fog, 1988).

Hence, nitrogen deposition could exert an overall stimulating effect on decomposition where sufficient high-quality litter occurs and the stimulatory N effect dominates litter decay (Knorr *et al.*, 2005). At the site-level, decreases in R_h because of N additions have often been reported (Persson *et al.*, 2000; Bowden *et al.*, 2004; Burton *et al.*, 2004; Olsson *et al.*, 2005; Phillips & Fahey, 2007; Mo *et al.*, 2008). Observations in forests do, however, contradict the increase in R_h that was observed following fertilization of alpine and arctic tundra ecosystems (Neff *et al.*, 2002; Mack *et al.*, 2004),

suggesting that decomposition of the soil organic matter in these ecosystems is much more N limited as compared with boreal and temperate forests.

Trends in carbon losses. Since 1960, the fast increasing wood demand in Europe was met only to a small extent by an increase in harvest (i.e., the harvest increased by 20% between 1960 and 2000 to a total of ~ 450 million m³ in 1999) (UN-ECE & FAO, 2005; Eurostat, 2008). To a large extent, the increase in demand was met by increased processing efficiency (i.e., sawing losses that are used by the pulp industry and a highly efficient recycling of paper). Since 1960, demand and supply are almost in balance but the gap (i.e., 22 million m³ in 1999) needs to be closed by an increasing net import of wood products (FAO, 2008). The ecological site study and inventory approaches both indicate that current harvest (H) is only a small fraction of NPP, which, in the absence of large-scale mortality, implies a large potential sink in the biomass of European forests. This has not always been true; in the 1950s the H to NPP ratio was 1.5 times higher than today (UN-ECE & FAO, 2005). Consequently, over the past 50 years, relative harvest intensity has decreased throughout the EU-25 resulting in a real increase of standing biomass (Fig. 4).

Wood demand is expected to further increase but could be met by the increasing productivity of EU-25 forests without affecting the harvest intensity (UN-ECE & FAO, 2005). However, the decision to increase the share of renewable energy to 20% of the total energy consumption by 2020 within Europe (COM, 2008), is expected to almost double the wood demand for bioenergy in EU-25. Such demand can only be met by increasing the harvest rate of 55% of annual volume increase in 2001 to 100% in 2020 (Ragwitz *et al.*, 2005) unless 11.5 × 10⁶ ha of short rotation forests are established (Kuiper *et al.*, 1998).

Not only the quantity but also the quality of the harvested wood products may affect the carbon sequestration potential of the EU-25 forests. Today, for example, trees with smaller dimensions than before are harvested, because of a shift toward wood-based panels such as laminated, particle, fiber and oriented strand boards (UN-ECE & FAO, 2005). The same technological innovations also resulted in a more common use of hardwood fibers than before. The industry thus demands smaller dimension which are produced in young forests with short rotations and smaller carbon pools compared with older forests managed with longer rotations. In Mediterranean countries, on the contrary, the reduced demand for fuelwood and increase in rotation length has resulted in an increase in harvested tree dimensions and standing carbon pools.

In the last two decades, several major storms, i.e., Viviane in 1990, Wiebke in 1990, Martin in 1999, Lothar in 1999, Kyrill in 2007 and Emma in 2008 resulted in increased salvage logging. The exceptional storms in 1990 and 1999 alone damaged 120 million and 180 million m³ of wood, respectively, or the equivalent of 30–50% of the annual fellings (Eurostat, 2008). Such storms were often followed by bark beetle outbreaks (Wermelinger, 2004) which further increased the volume of salvage logging. As long as the salvaged volume is lower than the wood demand, storms and pest does not affect the total volume of wood harvest, however, forest owners are likely to shorten rotation periods to minimize storm damage. Although the mean annual effect of storm on forest NBP is quite small, i.e. a reduction of 2%, large storms such as Lothar in 1999 were estimated to reduce the NBP by as much as 30% (Lindroth *et al.*, 2009). Consequently, a future increase in storm frequency and intensity could lower the NBP for the EU-25.

Between 1980 and 2000, the fire frequency in the Mediterranean area increased from 35 000 to 60 000 per year (Schulte *et al.*, 2002). However, within the same time frame, fire forecasting (i.e., European Forest Fire Risk Forecasting System, EFFRFS) combined with rapid intervention reduced the area of burnt forest and shrubland from 550 000 to 450 000 ha yr⁻¹ (Schulte *et al.*, 2002). Decreases in harvest intensity (Ciais *et al.*, 2008b), afforestation of abandoned lands (Schelhaas *et al.*, 2003) and probably also cessation of the removal of small logs because of lower market value than the cost for hauling and harvest (Mason *et al.*, 2006) contributed to increased fuel stocks and retention of fuel ladders. Over the last decades or so, summer drought has become more frequent and intense in the EU (Luterbacher *et al.*, 2004). Temperature and precipitation anomalies further increase flammability of forests with an already increased fuel stock (Westerling *et al.*, 2006). Probably the interplay of management, climate anomalies and arson, especially in areas of unsettled property rights, increased the fire risk and frequency in the Mediterranean. Depending on the fire severity only part of the ecosystem carbon pool is oxidized and released in the atmosphere.

Future climate, with more frequent and intense summer droughts (Beniston, 2004; Luterbacher *et al.*, 2004), is expected to increase the fire risk of forests in the EU. Whether these favorable climatic condition will result in more and larger fires, ultimately depends on the evolution of fuel stocks (and thus harvest), successful fire prevention (given that most of the fires are ignited by humans), rapid intervention and the ability of forest managers to adapt fuel structure and composition to the predicted longer and more severe fire seasons (Hirsch *et al.*, 2001; Palma *et al.*, 2007).

Across northern Europe including the UK, a widespread increase in concentrations of DOC in surface waters has been reported (Worrall *et al.*, 2004; Monteith *et al.*, 2007). The rising trends in DOC between 1990 and 2004 can be precisely explained by changes in atmospheric sulfur deposition and catchment acid-sensitivity (Monteith *et al.*, 2007). The large-scale increase was unrelated to climatic factors and N deposition. However, DOC concentrations have increased in proportion to the rates at which atmospherically deposited anthropogenic sulfur and sea salt have declined (Monteith *et al.*, 2007). Owing to the unfavorable conditions for DOC production in central and southern Europe compared with northern Europe (see section 5.2), it is no surprise that we could not identify studies that presented long-term trends in DOC concentrations in rivers and lakes in central and southern Europe.

Given the large-scale drivers of DOC production, future DOC fluxes are expected to follow NPP and DOC fluxes in throughfall. However, DOC production could be further enhanced or suppressed by changes in deposition chemistry, i.e. reductions in S-deposition and increases in N deposition, respectively.

To our knowledge there are no direct observations, spanning several decades, which could be used to establish the magnitude and direction of past and current trends in R_h , if any. During the past decades, increasing temperature and NPP possibly stimulated R_h . This increase, however, could be overridden by decreasing R_h because of substrate limitations owing to lower slash inputs as a result from decreasing harvests and reduction of R_h because of widespread N deposition especially in central Europe (Persson *et al.*, 2000; Smemo *et al.*, 2006). Whether there really is a widespread reduction of R_h because of N deposition remains an open question which needs to be resolved by further study (Janssens & Luyssaert, 2009). However, R_h could have increased in, for example, deciduous forest because of the expected litter stock following ageing of the forests. Hence, the current and future trends in R_h are among the key unknowns to predict the direction (i.e., sink or source) of the future terrestrial carbon balance (Davidson *et al.*, 2003).

NBP

Estimates of NBP. NBP is the carbon that remains in the long term in the ecosystem (Chapin *et al.*, 2005) and is sequestered in wood and soil carbon. Thus, NBP is the amount of atmospheric CO₂ sequestered in forest ecosystems and represents the direct contribution of ecosystems to climate change mitigation. In this study, NBP was formalized as $NPP - H - F - D - R_h$. Over long periods of time and in a constant environment, global

forest NBP is expected to be near-zero, but in today's changing environment the net carbon balance is believed to be substantial.

In a first assessment, the NBP of the European forests was estimated between 70 and 160 g C m⁻² yr⁻¹ (Janssens *et al.*, 2003). More recent estimates indicate that the NBP is likely to be lower than these initial estimates. In the inventory method, NBP is inferred with models based on sample plots data of annual stem volume increment and felling volume statistics (Kauppi *et al.*, 1992; Liski *et al.*, 2002, 2005; Nabuurs *et al.*, 2002, 2003). After correction for heterotrophic respiration, harvest, fire and losses to rivers, the inventory approach suggests an increase in tree biomass of 69 ± 17 g C m⁻² yr⁻¹ and in soil carbon content of 20 ± 10 g C m⁻² yr⁻¹, leading to a total NBP of 89 ± 19 g C m⁻² yr⁻¹ (Table 3). However, the increase in soil carbon content is estimated from model simulations and therefore the current (incomplete) uncertainty estimate, i.e. a coefficient of variation of 45%, appears optimistic.

Different inventory-based NBP estimates have been reported (Nabuurs *et al.*, 2003), using data from the 1980s and mid-1990s, mainly from UN-ECE/FAO (UN-ECE & FAO, 1985, 1992, 2000a). The studies covered different areas, i.e., 15 western-European countries (Nabuurs *et al.*, 1997), 30 European countries (Nabuurs *et al.*, 2003), or the entire European continent (Goodale *et al.*, 2002; Liski *et al.*, 2003). These estimates differed by the methods used to convert the timber stocks and growth into carbon pools or fluxes. The reported NBP in living wood largely differs between studies, i.e. 25–35 g C m⁻² yr⁻¹ between 1971 and 1990 (Kauppi *et al.*, 1992), 46 ± na g C m⁻² yr⁻¹ between 1990 and 1999 (Goodale *et al.*, 2002) or 69 ± 17 g C m⁻² yr⁻¹ in the late 1990s (Nabuurs *et al.*, 2003). These values include afforestation but do not account for woody encroachment of abandoned lands, nor for Mediterranean shrublands and woodland ecosystems which are not sampled by national inventories.

When using the EU-25 estimates for *F* and *D* and the upscaled ecological measurements for NPP, *H* and *R_p*, the NBP ranges between 53 and 98 g C m⁻² yr⁻¹ in wood and soils based on ecological measurements, however, the uncertainty is high because of the limited number of sites available for upscaling to the EU-25. Few ecological sites monitor the carbon fluxes following afforestation and the upscaling procedure does not explicitly address afforestation, therefore it is impossible to estimate to which extent the NBP estimate accounts for the effects of afforestation. Eddy covariance measurements of NEP at European forest sites were combined with maps of climate and NDVI in a neural network to give a forest NEP of 197 g C m⁻² yr⁻¹ (Table 3). Combining the eddy covariance-based NEP with losses because of *H*, *D* and *F* results in an NBP of 121 ± 260 g C m⁻² yr⁻¹. The

between-approach difference in NBP remains unresolved but suggests that the EC network is biased toward young productive forests. Although these new estimates of NBP confirm the magnitude of the previous assessment, the uncertainty warrants further research.

Inventories and ecological studies estimate a forest carbon sink of about 10–20% of the NPP (Table 3), probably caused by reforestation, restocking soil carbon after over-use in the past and a build-up in the stem wood because of incomplete harvesting of annual wood increment (Liski *et al.*, 2002; Ciais *et al.*, 2008b). Harvest is estimated at 15% of NPP (Table 3), leaving around 65–75% of the NPP for respiratory and other losses. The partitioning of NBP between live biomass, and SOC and litter pools is relatively similar among the inventory studies (Nabuurs *et al.*, 1997; Goodale *et al.*, 2002): 29 ± 14% of NBP goes into the soil and 71 ± 15% into live biomass. Apparent convergence does not necessarily reflect biological processes because all inventory studies use similar models to estimate the belowground carbon sequestration.

A modified version of LPJ constrained by regional forest statistics estimated an NBP of 63 g C m⁻² yr⁻¹ after accounting for *D* and afforestation (Zaehle *et al.*, 2006). As BIOME-BGC, LPJ-DGVM and ORCHIDEE do not include harvests and disturbances, these models are not able to predict a proxy of NBP. Instead, these models predict only NEP.

For forests on mineral soils, emissions of other greenhouse gases are usually very low and around 1 g C m⁻² yr⁻¹ (Jungkunst & Fiedler, 2007). Consequently, their effect on radiative forcing does not substantially diminish the carbon-based estimate of the sink-strength. Moreover, in drought conditions, forest soils can serve as a small but persistent sink for nitrous oxide (Goldberg & Gebauer, 2009).

Controls of NBP. Since the development of the eddy covariance technique, NEP is among the most common ecosystem fluxes available. The difference between the photosynthetic and respiratory CO₂ flux is the net ecosystem CO₂ production (NEP). At the ecological site studies, <5% of the observed variability in NEP (multiplicative regression model with two power functions, *p*: not defined for nonlinear regressions, R² = 0.04, *n* = 164) could be explained by precipitation and radiation during the growing season. However, NEP is not a physiological process in itself, but the combined result of several ecosystem processes with different time scales and drivers (Piao *et al.*, 2008). In particular, time since disturbance has been found to explain 92% of the total variability in NEP (Magnani *et al.*, 2007). This explains the lack of correlation between annual NEP and environmental variables

Table 4 Overview of expected effects of CO₂, temperature, precipitation, N-deposition and management on NBP and its component fluxes

	NPP	R _h	H	F	D	NBP
[CO ₂]	+	+	0	0	?	?
Temperature	+	+	0	+	+	?
Precipitation	+	+	0	-	+	?
N-deposition	+	?	0	0	+	+
Management	+	-	+	-	?	-

A positive relationship is shown by '+' (i.e., higher temperature result high R_h), a negative relationship by '-' (i.e., more precipitation results less fires), controls for which no relationship was reported or for which a relationship is thought to be irrelevant are shown by '0', and when the relationship is unknown a '?' is shown.

NPP, net primary productivity; R_h, heterotrophic respiration; H, harvest; F, losses through Fires; D, losses to rivers; NBP, net biome production.

such as temperature, radiation or precipitation (Law *et al.*, 2002; Reichstein *et al.*, 2007b).

Similar to NEP, NBP is not a physiological process in itself, but the combined result of several ecosystem processes with different time scales and drivers. Therefore, NBP is controlled by the balance of its component fluxes and thus the controls of these components fluxes (Table 4). Consequently, for a given driver the magnitude and direction (i.e., sink or source) of NBP are often ambiguous. Complex analyses or ecosystem models such as the modified version of LPJ are needed to account for the interactions between the potential drivers of NBP. As appear with NEP, there does not appear to be an important direct climatic control over NBP in European forests, however, indirect climatic controls on NBP exists through forests fires, wind storms die-back and pests.

Forest area has been increasing in the EU-25 territory with a 5% increase for conifer forests and an 8% increase for broadleaved since 1950 (UN-ECE & FAO, 2000b). In their sampling scheme, forest inventories measure the biomass of newly established forests, and over a sampling cycle, the NBP in biomass. Soil carbon changes following reforestation are more difficult to assess because they are a legacy of former land use. Therefore, we have to rely on model results to quantify the impact of reforestation on EU-25 NBP which is only in the order of 3 g C m⁻² yr⁻¹ in the soil and 21 g C m⁻² yr⁻¹ in the biomass (Zaehle *et al.*, 2006) or 27 g C m⁻² yr⁻¹ in total (S.L. Piao, unpublished results). Current uncertainty estimates for model output are around 30% (Zhao *et al.*, 2006; Jung *et al.*, 2007b), however, these estimates quantified uncertainties in

parameter values and input data. In the case of land-use change, the main source of uncertainty is expected to be the representation of the legacy effect of land-use change which largely depends on past agricultural management practices, which are poorly quantified at the European scale. Nevertheless, the changes in area alone cannot explain the observed NBP deduced by the inventory method over the last decade (see 'Estimates of NBP'). Model simulations indicated that changes in age-structure and harvest intensity probably contributed to about a half of the present-day forest C uptake in EU-25, with the remainder attributed to changes in growth rates based on climate and increased atmospheric CO₂ levels (Zaehle *et al.*, 2006).

Natural disturbances also impact NBP, affecting on average 0.15% per year of the standing wood volume, which amounts to 35 million m³ of damaged wood and thus roughly 8.5 Tg C yr⁻¹ with large interannual variability (Schelhaas *et al.*, 2003). The impact of disturbance on NBP depends on the nature of disturbance and on the fate of the damaged wood. Storm-broken stems of trees can be collected and transformed into wood products, while burned forests release CO₂ to atmosphere. There is a dominance of storms among the natural disturbances, causing 53% of total wood damage, followed by fires (16%), biotic disturbances (16%, half of it bark beetle infestation) and snow (3%) (Schelhaas *et al.*, 2003). Based on the estimates of Schelhaas *et al.* (2003) the losses because of fire would be closer to 1.2 ± na g C m⁻² yr⁻¹ than to 4.7 ± 1.3 g C m⁻² yr⁻¹ as estimated by remote sensing (van der Werf *et al.*, 2006). However, scaling wood damage does not account for the carbon losses from burning the forest litter. Optical remote sensing, on the other hand, cannot readily distinguish between forests and other wooded lands which are in general more prone to fires. The inventory and remote sensing approach provide the brackets that limit our estimates for carbon losses because of fires. Despite the importance of natural disturbances on the economy of the forest sector, their immediate impact on NBP appears to be small, i.e. 11 g C m⁻² yr⁻¹ (6.5–1.2 + 4.7 g C m⁻² yr⁻¹), but their long-term effects, especially on the soil carbon balance, remain to be assessed.

Evidence is becoming available that in between major disturbance, old-growth forests are not carbon neutral as previously thought (Odum, 1969) but continue to sequester atmospheric carbon (Pregitzer & Euskirchen, 2004; Luyssaert *et al.*, 2008). In managed forests, practices such as thinning reduce R_h by the frequent removal of woody biomass and, thus, C substrates for R_h. However, thinning products are usually used in wood products with a short life-span and with burning, CO₂ is released back to the atmosphere. Although management strongly

enhances NEP of forests, its effect on NBP is still controversial as management is likely to add CO₂ to the atmospheric because the reduced life-span of wood products, even of lumber, is shorter than the life-span of on-site carbon storage (Harmon *et al.*, 1990). Although old growth forests are uncommon in the EU-25, extensifying or giving up management may be considered as a strategy to increase the terrestrial carbon pool in Europe. Ageing of the currently young European forests is expected to have a strong positive, albeit transient, effect on the European carbon sink strength (Vetter *et al.*, 2005; Ciais *et al.*, 2008b).

Two climate change mitigation strategies each on an extreme end of the forest management spectrum are developing. Short rotation forests with high productivities could be established and its wood products (pulp and energy) would partly substitute the need of fossil fuels and thus would slow down the emission of CO₂. However, frequent disturbance would result in small carbon pools and a negligible NBP. On the other hand, management could be extensified. Large carbon pools and substantial NBP would come at the cost of lower productivities than in short rotation systems. Its high-quality wood products should be put to a chain of cascading demands, i.e. after an initial use as lumber the wood could be used as pulp and the pulp burned to produce energy. The application of these systems should depend on soil quality, site accessibility and stock price for CO₂ (A. Freibauer, unpublished result).

The NPP of foliage and fine roots, short-lived tissues that are rapidly transferred to the soil, is between 50% and 60% of the total NPP for the inventory and ecological studies, respectively (Ciais *et al.*, 2008b). This leads to a soil carbon sequestration ratio ($NBP_{\text{soil}}/NPP_{\text{foliage + roots}}$) of 0.14 ± 0.09 , and to a live biomass sequestration ratio ($NBP_{\text{biomass}}/NPP_{\text{wood}}$) of 0.35 ± 0.08 . Therefore, an increasing harvest, which is likely because of the promotion of biomass energy (Ragwitz *et al.*, 2005) would immediately decrease the forest sector NBP.

Although BIOME-BGC, LPJ-DGVM and ORCHIDEE do not include harvests and disturbances which is a prerequisite to predict NBP, comparison of model outputs with observations are indicative for the importance of the processes currently absent in the models. Because a model spin-up guarantees steady-state conditions at the start of the simulations and these versions of the models do not account for carbon losses through harvesting all the carbon remains on-site and is decomposed by R_h with a time lag. Consequently, almost all of the NPP (>90%) is converted to R_h in the models, and there is only a very small sink (NEP/NPP) in the range of 4–10% of the NPP, compared with 36% observed by inventory and ecological measurements (Table 3). The discrepancy between modeled and measured NEP

confirms that management practices (Kowalski *et al.*, 2004), age structure (Kowalski *et al.*, 2004; Magnani *et al.*, 2007) (i.e., with many young forests accumulating carbon in the measured NEP estimate) and in some regions nitrogen deposition (Magnani *et al.*, 2007), rather than changes in CO₂ and climate, control the carbon sequestration ratio (NBP/NPP) in EU-25 forests.

These models simulate NEP only as affected by climatic variability, long-term changes in climate, N deposition (only for BIOME-BGC) and rising CO₂ trends. The models include the effects of CO₂ fertilization, and of the longer growing seasons as a result of global warming, as a result NPP increases in excess of R_h . The resulting NEP is, however, a transient effect because in the long term any increase in NPP will result in an increase in modeled litter production, which feeds the soil carbon pool which in turn will result in an increased modeled R_h . Hence, the modeled NEP ranged from 19 to $47 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3). At best, the NEP of these models can be seen as the fraction of NEP that is caused by climate change and rising CO₂, in the absence of harvest and disturbances. The ratio of NEP_{models} over NBP_{inventory} thus, suggests that 20–50% of NBP can be attributed to changes in climate and CO₂ (and nitrogen in the case of BIOME-BGC), and that the rest of the NBP were because of aging, management, leaching and fires. The modified version of LPJ, accounting for forest fires, management, age-structure and reforestation estimated a forest NEP of $125 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3) of which also about 50% was caused by non-climatic factors.

Trends in NBP. In forest ecosystems, NBP is mainly realized in the woody biomass, with smaller contributions of coarse woody debris and soil organic matter. During the past 50 years, NPP increased by a factor of 1.7 (Ciais *et al.*, 2008b). Meanwhile, harvest and fires did not keep pace with the NPP increase, which resulted in an increasing woody biomass. The carbon sequestration ratio (NBP/NPP) between 1950 and 2000 was in general higher for broadleaved than for conifer species (Fig. 6). The interannual variability could be owing to changes in harvest intensity and natural disturbances. NBP is also realized in coarse woody debris and litter. No long-term EU-wide observations are available to quantify changes in litter production.

Last a fraction of NBP is realized through carbon sequestration in soil organic matter. Despite the evidence in support of carbon accumulation in forest soils in Belgium (Lettens *et al.*, 2005), repeated sampling indicated losses of SOC across England and Wales (Bellamy *et al.*, 2005) although its drivers are not necessarily climate related (Fontaine *et al.*, 2007; Smith *et al.*, 2007) as suggested by the authors. The difference in sign of the above estimates shows that the

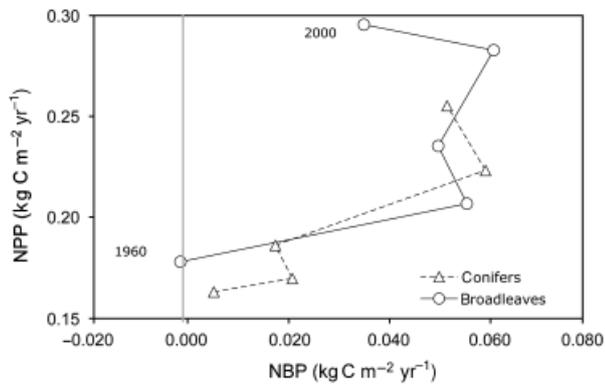


Fig. 6 Standing biomass C stocks as a function of net biome production (NBP) since 1950. One can see that for a given net primary productivity (NPP), the NBP is higher for broadleaved than for conifer forests, most likely because harvest removals is a lower fraction of wood NPP in broadleaved than in conifer forests (see Fig. 4). Each point corresponds to the average value for one decade since 1950.

current and future drivers and subsequent trends in carbon sequestration rates in forest soils warrant future research.

Conclusions and recommendations

The mean forest NPP of EU-25 derived from three independent approaches, i.e. ecosystem modeling, forest inventories, and upscaling of ecological data, was found to agree within 25%. The overall mean NPP was $520 \pm 75 \text{ g C m}^{-2} \text{ yr}^{-1}$. New estimates of the mean forest NBP of EU-25, were somewhat lower than previous estimates, and ranged between 50 and $100 \text{ g C m}^{-2} \text{ yr}^{-1}$. In the EU-25, forest is thus a carbon sink resulting from changes in forested area (i.e., 5–10%), the juvenile age structure and the increasing NPP because of CO_2 -fertilization, elevated atmospheric nitrogen deposition and climate change (i.e., 20–50%). The carbon sequestration ratio (NBP/NPP) is 0.10–0.20 for the EU-25 forests.

Although all fluxes were presented with their uncertainty, at present, uncertainties across methods are inconsistent and reflect only part of the total uncertainty. Consequently, methods that report a low uncertainty are not necessarily more reliable than methods with a high uncertainty as it is possible that the latter simply report a more complete uncertainty estimate. Despite our error analysis being incomplete and uncertain, it gives a sense of the level of uncertainty that we are dealing with to estimate carbon sinks/sources at the regional level. Currently, any individual method is prone to so much uncertainty that several, preferably independent, methods need to be used to estimate a regional C budget. Confidence concerning the accuracy

of such a budget is given by convergence across methods of the different flux estimates rather than low uncertainty within methods. Ideally, several precise estimates obtained from independent methods should converge.

Convergence of the NPP estimates obtained from different methods could be further improved by separately analyzing wood, leaf and root NPP between models and data, and between forest inventories and ecological sites. Performance of the models could be enhanced by accounting for processes that control regional variation in growth (i.e., nutrient availability, drought tolerance, crown development) and an enhanced representation of vegetation diversity in the PFT. This will allow for a more direct NPP comparison with inventory data. All observation-based estimates would benefit from further harmonizing ecological measurements and national inventory data (e.g., roots and leaves expansion factors). Extension of all the ecosystem models with management rules (i.e., Thornton *et al.*, 2002; Zaehle *et al.*, 2007) should be a priority as this will enable a more direct comparison between modeled and observed NBP estimates. Moreover, the depletion of soil C because of past management practices should be taken into account, as the assumption of steady-state conditions is likely to overestimate R_h and underestimate NBP. Currently all large-scale SOC estimates and carbon losses from soils to rivers are modeled based on sparse observations. Consequently, improving process understanding and extending direct observations through repeated sampling is likely to reduce the uncertainty in the SOC, DOC and thus the NBP estimates.

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