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CO\textsubscript{2} balance of boreal, temperate, and tropical forests derived from a global database


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Abstract

Terrestrial ecosystems sequester 2.1 Pg of atmospheric carbon annually. A large amount of the terrestrial sink is realized by forests. However, considerable uncertainties remain regarding the fate of this carbon over both short and long timescales. Relevant data to address these uncertainties are being collected at many sites around the world, but syntheses of these data are still sparse. To facilitate future synthesis activities, we have assembled a comprehensive global database for forest ecosystems, which includes carbon budget variables (fluxes and stocks), ecosystem traits (e.g. leaf area index, age), as well as ancillary site information such as management regime, climate, and soil characteristics. This publicly available database can be used to quantify global, regional or biome-specific carbon budgets; to re-examine established relationships; to test emerging hypotheses about ecosystem functioning [e.g. a constant net ecosystem production (NEP) to gross primary production (GPP) ratio]; and as benchmarks for model evaluations. In this paper, we present the first analysis of this database. We discuss the climatic influences on GPP, net primary production (NPP) and NEP and present the CO2 balances for boreal, temperate, and tropical forest biomes based on micrometeorological, ecophysiological, and biometric flux and inventory estimates. Globally, GPP of forests benefited from higher temperatures and precipitation whereas NPP saturated above either a threshold of 1500 mm precipitation or a mean annual temperature of 10 °C. The global pattern in NEP was insensitive to climate and is hypothesized to be mainly determined by nonclimatic conditions such as successional stage, management, site history, and site disturbance. In all biomes, closing the CO2 balance required the introduction of substantial biome-specific closure terms. Nonclosure was taken as an indication that respiratory processes, advection, and non-CO2 carbon fluxes are not presently being adequately accounted for.

Nomenclature:

\[
\begin{align*}
\text{DOC} & = \text{dissolved organic carbon;} \\
\text{fNPP} & = \text{foliage component of NPP;} \\
\text{GPP} & = \text{gross primary production (GPP > 0 denotes photosynthetic uptake);} \\
\text{mNPP} & = \text{missing component of NPP;} \\
\text{NBP} & = \text{net biome production (NBP > 0 denotes biome uptake);} \\
\text{NECB} & = \text{net ecosystem carbon balance (NECB > 0 denotes ecosystem uptake);} \\
\text{NEE} & = \text{net ecosystem exchange (NEE > 0 denotes ecosystem uptake);} \\
\text{NEP} & = \text{net ecosystem production (NEP > 0 denotes ecosystem uptake);} \\
\text{NPP} & = \text{net primary production (NPP > 0 denotes ecosystem uptake);} \\
\text{R_a} & = \text{autotrophic respiration (R_a > 0 denotes respiratory losses);} \\
\text{R_c} & = \text{ecosystem respiration (R_c > 0 denotes respiratory losses);} \\
\text{R_h} & = \text{heterotrophic respiration (R_h > 0 denotes respiratory losses);} \\
\text{rNPP} & = \text{root component of NPP;} \\
\text{R_s} & = \text{soil respiration (R_s > 0 denotes respiratory losses);} \\
\text{VOC} & = \text{volatile organic compounds;} \\
\text{wNPP} & = \text{wood component of NPP}
\end{align*}
\]

Keywords: carbon cycle, CO2, forest ecosystems, global database, gross primary productivity, net ecosystem productivity, net primary productivity

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Introduction

By sequestering large amounts of atmospheric carbon, forests play an important role in the global carbon cycle and are thought to offer a mitigation strategy to reduce global warming (Schimel et al., 2001). The awareness that fossil fuel burning has perturbed the carbon cycle, with feedbacks to global climate, has inspired researchers and funding agencies worldwide to invest in carbon cycle research. Hence, many more data on carbon cycling in forests have become available in recent decades. Knowledge of global patterns in net primary production (NPP) improved substantially during the 1970s thanks to the International Biological Program (IBP; Jager et al., 2000). More recently, additional insight in global NPP was gained by analyses of updated comprehensive data summaries (Scurlock & Olson, 2002; Ciais et al., 2005), as well as by modelling studies, such as the Potsdam NPP model intercomparison study (Cramer et al., 1999). Global patterns (both spatial and temporal) in gross primary production (GPP) and respiration (R_a) are mainly based on modelling exercises (i.e. Schimel et al., 2001). Exceptions include analyses of NEP and GPP measurements from eddy covariance flux networks (Valentini et al., 2000; Janssens et al., 2001; Law et al., 2002; Reichstein et al., 2003) and a synthesis of the CO2 balance of a boreal, temperate and tropical forest site (Malhi et al., 1999).

Because the wide spread application of the eddy covariance technique our understanding of the magnitude, temporal, and spatial variability of CO2 cycling in terrestrial ecosystems has evolved quickly (Baldocchi, 2003). However, considerable uncertainties remain regarding the current status of terrestrial sinks and the fate of the carbon sequestered by the terrestrial biosphere over both short and long timescales. The flow of carbon between the different components of forest ecosystems and its eventual allocation to long-term storage pools (wood and soil organic matter) is likely to vary across forests of different growth strategies (deciduous vs. evergreen), age, management regime, and climate. The relevant data are collected at many sites around the world, but need to be synthesized to address the remaining uncertainties. Therefore, we have assembled a comprehensive global database for forest ecosystems, which includes carbon budget variables (fluxes and stocks), ecosystem traits (e.g. leaf area index, age), as well as ancillary site information such as management regime, climate, and soil characteristics. This publicly available database is dedicated to quantifying the global and biome-specific carbon budget of the forests, re-examination of previously hypothesized global relationships, testing emerging hypotheses about ecosystem functioning, and providing benchmarks for ecosystem model evaluations. The database will be updated as additional data become available.

The objectives of this manuscript are to (1) present the database structure, explain data consistency and quality control mechanisms, (2) identify data gaps, (3) present global patterns in GPP, NPP and NEP, and (4) establish forest carbon budgets by biome.

Components of the C-balance

GPP of an ecosystem represents the gross uptake of CO2 that is used for photosynthesis. The synthesis of new plant tissue from CO2, water and nutrients and the maintenance of living tissues are energy demanding processes (Penning de Vries et al., 1974; Amthor, 2000). Hence, some photo-assimilated compounds are lost from the ecosystem as autotrophic respiration (R_a) due to the costs associated with growth and maintenance of foliage, wood, and roots. The amount of photosynthates that is not used for respiration and is available for other processes is defined as NPP and relates to GPP and R_a as

$$ GPP = NPP + R_a. \quad (1) $$

The bulk of NPP is allocated to the production of biomass in different ecosystem components: foliage (fNPP), wood (wNPP; including branches and stems), and root (rNPP; including coarse and fine roots) production. In addition to these measurable components, NPP also includes a variety of additional components and processes that are more difficult to measure and often ignored. In this manuscript, these components were called mNPP and include the carbon invested in understory plant growth and in reproductive organs (flowers, seeds, fruits), as well as carbon lost through herbivory, emitted as volatile organic compounds (VOC) and methane (CH4), and exuded from roots or transferred to mycorrhizae. The global average of production and losses contained in mNPP was estimated to be 11% (Randerson et al., 2002) but can easily amount to 20% of the sum of fNPP, wNPP, and rNPP in tropical forests (Clark et al., 2001). Thus,

$$ NPP = fNPP + wNPP + rNPP + mNPP. \quad (2) $$

The residence time of carbon, which is the time between fixation in photosynthates and the return to the atmosphere following respiration or chemical transformation into VOC, exudates or CH4, differs among NPP components. Carbon incorporated in wood, which is physiologically dead, has a residence time within the living tree of years to centuries, whereas the carbon deposited in foliage and fine roots has residence times of months to years. Each year part of the standing biomass is transferred to litter- and/or soil layer carbon
pools (each of which has different residence times). These carbon pools are subjected to decomposition by microbial activity, a process defined as heterotrophic respiration ($R_h$). The decomposition processes that contribute to $R_h$ include decomposition of current year biomass, but also contain decomposition of organic matter that accumulated in the ecosystem during the last decades, centuries or millennia. The imbalance between NPP and $R_h$ is the NEP

$$\text{NPP} = \text{NEP} + R_h.$$ (3)

The sum of $R_s$ and $R_h$ represents the total ecosystem respiration ($R_e$) and the sum of the belowground fraction of $R_s$ and $R_h$ is the soil respiration ($R_s$). NEP is determined by the difference between GPP and $R_e$ and differs from the net rate of organic carbon accumulation in ecosystems (Schulze et al., 2000).

$$\text{GPP} = \text{NEP} + R_e.$$ (4)

The carbon fluxes observed in experiments differ from the long-term carbon balance mainly because non-CO$_2$ losses and nonrespiratory CO$_2$ losses, which occur at a range of timescales, are typically ignored. Shortly (<1 year) after uptake, synthesized compounds are lost from the ecosystem as VOCs (Guenther et al., 1995) or as plant-produced CH$_4$ (Keppler et al., 2006). On longer timescales (>1 years), part of the annually accumulated NEP leaves the ecosystem as dissolved organic carbon (DOC) or microbially produced CH$_4$. In addition, all or part of the carbon that has been built up over the years by the accumulation of the annual NEP can leave the ecosystem and eventually return to the atmosphere as nonrespiratory CO$_2$ fluxes by forest fires, harvests and/or erosion (Randerson et al., 2001; Amiro et al., 2006). Therefore, non-CO$_2$ and nonrespiratory CO$_2$ losses should be accounted for in Eqn (4) to obtain the carbon balance. 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., 2006) and balances NEP as follows:

$$\text{NECB} = \text{NEP} - \text{nonrespiratory CO}_2 \text{ losses} - \text{non-CO}_2 \text{ losses} + \text{import from bordering ecosystems.}$$ (5)

GPP, NPP, NEP, and NECB may all represent carbon sinks or sources (except GPP which is always a sink) but the relevance of the sink or source depends on the temporal and spatial scale one wants to study. Where the carbon sink in GPP is only sustained for minutes, the sink or source quantified as the NECB equals the long-term carbon-sequestration by ecosystems. When integrated over time and space the NECB equals the net biome production (NBP; Schulze & Heimann, 1998; Buchmann & Schulze, 1999). It is the NBP that is reflected in the long-term atmospheric concentration of CO$_2$, CH$_4$ and other atmospheric carbon-compounds.

Materials and methods

Database

A comprehensive relational database structure was designed to store information on carbon fluxes, ecosystem properties, and site information of forest stands. Data entries originated from peer-reviewed literature, established databases (e.g. Olson et al., 2001; Papale et al., 2006) and personal communications with research groups involved in Fluxnet (Baldocchi et al., 2001). The high quality of the database is ensured by several features: (1) referential integrity is ensured by the structure of the database, (2) data selection is based on strict methodological criteria, (3) consistency of the NPP data is ensured by a hierarchical framework, (4) uncertainty of the fluxes are estimated in a consistent manner accounting for the methodological approach and the length of the time series, (5) the uncertainty of aggregated fluxes is estimated, and (6) a variety of observed and/or modelled meta-data is included in the database.

Structure of the database. The database is structured by site. A site is a forest or a stand with a known geographical location, biome (US Department of Agriculture biome classification; Reich & Eswaran, 2002), tree species composition and management regime. Hence, different treatments within an experimental forest or different aged stands that form a chronosequence were recorded as different sites. Each site in the database is linked to at least one carbon balance component and each component is further linked to the methodology that was used to estimate it. Owing to its structure, the database can contain multiple estimates of the same flux for the same year (i.e. if these estimates were reported in different studies or estimated with different measurement techniques). Because data from different sources or references are stored as different entries, the structure of the database, thus ensures referential integrity.

Selection criteria. Flux estimates were included in the database when they were based on direct measurements (NPP, NEP, $R_e$, $R_h$, and $R_a$), derived from single or multiple direct measurements (GPP, NPP, NEP, $R_e$, $R_h$, and $R_a$) or modelled (GPP, NPP, NEP, $R_e$, $R_h$, $R_{\text{import}}$, and $R_a$).
NPP estimates were included in the database when they were based on direct measurements of the main components of NPP (Clark et al., 2001) if these were obtained as follows: the net annual production of leaves or needles was determined by collecting leaf/needle fall throughout the year; annual stem and branch increment were determined using species- and region-specific allometric equations relating aboveground woody biomass increment to the change in basal area of individual trees in the plot; and coarse-root production was determined through species- and region-specific allometric equations relating root mass to basal area and fine-root production was determined by repeated soil coring, isotopic estimates of fine-root turnover combined with biomass measurements, upscaled root-length production observed in minirhizotrons or the soil respiration and litterfall constraint formulated by Raich & Nadelhoffer (1989). Furthermore, to be included in the database, foliage, stem, branch, coarse and fine root biomass increment had to be corrected for the annual litterfall of these components. When available, we also included estimates of NPP which accounted for: the NPP of the understory vegetation through destructive harvests (available for 30% of the sites with NPP estimates); fruit and seed production (availability: <4%); herbivory (availability: <4%); emissions of volatile compounds (availability: 0%) and leaching of root exudates (availability: 0%). However, availability of these NPP components was not a necessary criterion for inclusion.

Direct measurements of annual and multiple-year NEP were included in the database when based on continuous measurements with a tower-based eddy covariance system. NEP estimates were accepted when data gaps due to system failure, stable atmospheric conditions or data rejection were filled by means of standardized methods (Falge et al., 2001; Reichstein et al., 2005) to provide complete data sets. These data, however, do not include corrections for possible effects of advection, which may lead to a systematic underestimation of night-time respiration even at high turbulence.

Biometric NEP estimates were included in our database when they were based on the difference between biomass production and heterotrophic respiration (e.g. Hanson et al., 2003) or repeated biomass inventories and soil respiration measurements (e.g. Law et al., 2004).

Estimates of \( R_s \) and its heterotrophic component \( R_h \) were included in the database when based on subtracting chamber measurements from undisturbed plots from measured and upscaled root respiration (Hanson et al., 2000) or chamber measurements after trenching or girdling. Directly measured estimates of \( R_s \) were included in the database when the estimate was based on up-scaled chamber measurements of foliage, stem and root respiration (e.g. Ryan et al., 1996).

Half-hourly eddy covariance measurements can be used to derive an estimate of \( R_s \) and GPP. At night there is no photosynthesis, so the site-specific relationship between the night-time NEE and soil temperature can be used to estimate the half-hourly respiration during the day given the daytime soil temperature. However, due to below-canopy CO2 storage and advection, nocturnal NEE measured on calm nights (\( u^* \) threshold) is not used to estimate \( R_s \). These rejected data were treated as gaps and filled by means of standardized methods (Falge et al., 2001). Only measured data were used to fit a relationship between night-time NEE and soil temperature, from which daytime respiration was estimated. The relationship can be fitted with constant parameter values (Falge et al., 2001) or with variable parameter values (Reichstein et al., 2005). Respiration estimates from either method of fitting were included in the database. Applying Eqn (4) results in half-hourly estimates of GPP that must be integrated over the course of a year to obtain an estimate of the annual GPP. On sites affected by advection, GPP and \( R_s \) are both likely to be underestimated.

When data are available for at least two flux components, the identities given by Eqs (1)–(4) can be used to estimate a missing flux (e.g. \( R_a \) can be calculated from the difference between \( R_h \) and \( R_s \)). Flux estimates obtained by applying these equations were also included in the database. However, modelled GPP, NPP, NEP, \( R_e \), \( R_a \), \( R_h \), and \( R_s \) estimates were only included when a mechanistic process model driven by daily or more detailed climatological input variables was used, and when the model was calibrated with site-specific parameters and/or validated against site-specific measurements such as biomass, NEP, etc.

Consistency of the flux data. Despite the strict selection criteria there are still inconsistencies between methodological approaches (i.e. an eddy covariance-based estimate of GPP includes the understory, whereas most process models limit the GPP to the photosynthesis of the overstory vegetation). Depending on the methodological approach, respiration by mycorrhizae may be included either in \( R_a \) or in \( R_h \). These inconsistencies contribute to the observed variation among sites, but given the small contribution of understory and mycorrhizal fluxes are unlikely to have severely affected the results presented below. More problematic are the inconsistencies in NPP. Although NPP data are more widely available than other carbon-flux estimates, there are considerable...
problems of consistency among NPP studies. Reported NPP values can range from the NPP of a single component (e.g. foliage NPP) to the complete NPP of the ecosystem. The database accounted for these inconsistencies by combining 11 components and nine aggregation levels of NPP in a hierarchical framework (Fig. 1). At the lowest level, stem and foliage NPP were recorded. When both components were measured, the lowest possible level of aboveground NPP (ANPP_1; foliage + stem NPP) was calculated. The next level included branch NPP. If branch NPP was measured, wood NPP (stem + branch NPP) and ANPP_2 (foliage + stem + branch NPP or foliage + wood NPP) were calculated. Coarse and fine root NPP were recorded as separate components and summed to obtain the belowground NPP (BNPP_1; coarse + fine roots NPP). If all required low-level components were available, the total NPP (TNPP_1) was calculated as ANPP_2 + BNPP_1. If the understory NPP was measured, the next level of total NPP was calculated (TNPP_2). Adding estimates of the NPP of the reproductive parts, herbivory, root exudation and VOC’s and CH₄ resulted in TNPP_3, TNPP_4, TNPP_5, and TNPP_6, respectively. The framework was considered hierarchical because a certain level of NPP was calculated only when all underlying components were measured. For example, TNPP_4 was not calculated unless TNPP_3 was available and NPP consumed by herbivores was measured. There was, however, one exception: NPP calculated from the difference between GPP and Rₙ or the sum of NEP and Rₙ was set to TNPP_5 despite the absence of lower-level NPP estimates. The imbalance between GPP and Rₙ was assigned to TNPP level 5 instead of level 6 because most often GPP and NEP were estimated on the basis of eddy covariance measurements which do not capture VOC’s and CH₄ losses.

Given this careful processing and quality evaluation of data for each site, the NPP data are consistent when a single level of NPP data is used. For the majority of the sites, only a few components were reported such that TNPP_1 was the most common estimate for total NPP. It should be noted that minor inconsistencies remain within an individual component (i.e. the use of different cut-off diameters between coarse and fine roots). However, the variation due to these inconsistencies is expected to disappear when NPP estimates of a higher level are used [i.e. the variation due to different cut-off diameters are expected to disappear when total belowground NPP (BNPP_1) is used].

Uncertainty of the measured CO₂ fluxes. Although recently efforts have been made to quantify the uncertainties of eddy covariance measurements (Hollinger et al., 2004; Hollinger & Richardson, 2005; Richardson et al., 2006; Black et al., 2007), uncertainty of CO₂-flux estimates are only rarely reported in the literature and when reported it is often unclear whether the given value denotes instrumental, spatial, temporal and/or other sources of variability. Therefore, we ignored the reported uncertainty and instead estimated the total uncertainty for every component flux contained in the database. The uncertainty was estimated in a uniform way based on expert judgment. We could not identify prior information that could constrain the absolute range of the estimated NEP. Without measurements or prior information, experts agreed that the NEP of a forest most likely ranges from −100 to 600 g C m⁻² yr⁻¹. The absolute range of the NEP estimate is, thus, ±350 g C m⁻² yr⁻¹ (this manuscript). However, all methodological approaches contained in the database used site-specific observations and are therefore expected to reduce the uncertainty surrounding the NEP estimates. Consequently, the uncertainty was reduced with a method-specific factor (i.e. when NEP was determined by eddy covariance measurements), the precision was thought to be 30% of 350 or 105 g C m⁻² yr⁻¹. This estimate is similar to those presented by Griffis et al. (2003), Richardson & Hollinger (2005) and Oren et al. (2006). For tropical forest, where night-time measurements are often problematic the absolute range of the NEP estimate was set to ±700 g C m⁻² yr⁻¹. The applied method-specific reduction factors (i.e. 30% for eddy covariance, are given in Table 1). When a flux was a multiple-year mean value, its value is less prone to interannual variability and, therefore, its uncertainty

![Fig. 1 Hierarchical framework for net primary production (NPP) where 11 components of the NPP are hierarchically combined in nine aggregation levels of NPP.](Image)
was further reduced by accounting for the length of the time series. Thus,

\[ s_{ij} = \frac{p_i \times RF_j}{\sqrt{l_{ij}}} \]

where \( p_i \) is the initial uncertainty for site \( i \) in the absence of measurements according to Table 2 and \( RF_j \) is the reduction factor for method \( j \) according to Table 1 and \( l_{ij} \) is the length of the time series (in years) for site \( i \) for which the fluxes were estimated with method \( j \).

A similar approach was followed to estimate the uncertainty of GPP, NPP, NEP, \( R_e \), \( R_s \), \( R_h \), and \( R_a \). However, for these fluxes the latitude of the site contained prior information regarding their absolute range [i.e. GPP at a boreal site likely ranges from 0 to 1000 g C m\(^{-2} \) yr\(^{-1} \), whereas GPP at a tropical site likely ranges from 2000 to 4000 g C m\(^{-2} \) yr\(^{-1} \) (this manuscript)]. Consequently, the absolute range for GPP in the absence of measurements depends on the latitude (Table 2). For each site contained in the database the latitude was known and as such, the absolute range in the absence of measurements could be estimated. This initial uncertainty was then reduced by the method-specific factor (Table 1) and further adjusted for the length of the time series.

Aggregated fluxes and their uncertainty. According to the planned analysis, differently structured tables can be extracted from the database (e.g. for low-resolution model comparison, the data should be aggregated by latitudinal and longitudinal cells whereas for analyzing C balances of different forests the data should be aggregated by site). For a given site or cell \( i \), the flux component \( F_j \) was determined with \( k \) different methods \( j \). The average flux component determined by method \( j \) for site or cell \( i \) was then given as \( F_{ij} \). The average flux component across methods \( (\bar{F}_i) \) was calculated as the weighted mean:

\[ \bar{F}_i = \frac{\sum_{j=1}^{k} l_{ij} \times F_{ij}}{\sum_{j=1}^{k} l_{ij}}. \]

The uncertainty of the weighted mean was calculated by means of error propagation:

\[ s_i = \sqrt{\frac{\sum_{j=1}^{k} l_{ij} \times (s_{ij})^2}{\sum_{j=1}^{k} l_{ij}}} \]
where $n_i$ is the total number of observations for the flux component $F_i$ for site or cell $i$ and $l_{ij}$ is the number of observations determined with method $j$. Hence, the obtained uncertainty ($s_i$) is a proxy for the uncertainty surrounding the mean annual flux for the site or cell.

Site description data. Additional site information related to stand characteristics, standing biomass, leaf area index and growing environment were added to the database as separate tables (see Appendix A). Stand characteristics such as basal area, mean tree diameter, mean tree height, mean tree density and mean stand age are available for many sites. Also, the observed standing biomass and its major components, the maximal observed leaf area index, and some methodological details of the leaf area measurement technique were available and stored in the database for many sites. A description of stand management was also included in the database. Among sites, information on management was of variable quality and detail. Therefore, a coarse classification, distinguishing managed (when the description contained a reference to planting, thinning or harvesting), unmanaged (when no management had occurred during the last 50 years), recently burned (when burned in the last 25 years), recently clear cut (when clear cut in the last 25 years) and fertilized and irrigated sites (when the site was fertilized or irrigated often as part of an experimental set-up). Finally, the growing environment was characterized by the observed mean annual temperature and annual precipitation.

For almost all sites, soil texture expressed as the volumetric percentage of sand, silt and clay was extracted from Global Soil Data Products (Global Soil Data Task, 2000). The spatial resolution is 5 min. Mass percentages were converted to volumetric percentages by dividing the mass percentage by the bulk density (i.e. 1.19 g cm$^{-3}$ for sand and 0.94 g cm$^{-3}$ for clay). The percentage silt was calculated as the difference of the volumetric percentage sand and clay from 100%. The normalized different vegetation index (NDVI) at a spatial resolution of 8 × 8 km$^2$ and 15-day interval were acquired from the Global Inventory Monitoring and Modelling Studies (GIMMS) group derived from the NOAA/AVHRR series satellites (NOAA 7, 9, 11 and 14) for the period January 1982 to December 2003 (Tucker et al., 2005). In addition to the direct measurements, monthly precipitation, air humidity and temperature were extracted from the CRU data set (Mitchell & Jones, 2005). The observed temperature and precipitation were strongly correlated to the CRU-derived temperature and precipitation ($r^2 = 0.93$ and 0.70, respectively). However, the CRU data were added to the database and used in the present analysis because these data was more complete and consistent (all from 1990 to 2003) than the observed data. Monthly net solar radiation, absorbed downward longwave radiation, net surface longwave radiation, soil moisture, dry nitrogen deposition, wet nitrogen deposition and ammonia deposition were simulated with the model ORCHIDEE (Krinner et al., 2005).

Biome-specific CO$_2$ balances

The different biomes were characterized by means of a stand and climate description. The stand description was based on observed values, the climate description was based on the CRU data set (Mitchell & Jones, 2005) and ORCHIDEE model output (Krinner et al., 2005). All data were extracted from the database and mean values with their SD were presented for the different biomes.

For the selected biomes, site-specific GPP, NPP, NEP, $R_a$, $R_h$, $R_i$ values and their uncertainty were extracted from the database and aggregated as explained above. Evergreen and deciduous sites were analyzed separately. Flux estimates affected by climatic anomalies such as El Niño events or the 2003 summer drought were included, however, recently cut, burned, fertilized or irrigated sites were excluded from the present analysis (although these are included in the database). Whenever an estimate was available for two of the three respiration components ($R_a$, $R_h$, and $R_i$), the missing component was calculated based on the relationship between the respiration components. A similar procedure was used to calculate $R_i$ when GPP and NEP were measured. The uncertainty of the calculated component was calculated by error propagation. In theory $R_a$ and/or $R_i$ can also be calculated when estimates of GPP and NPP and/or NPP and NEP are available. However, the NPP values that were extracted from the database were not the total NPP but just the sum of foliage, wood and root NPP (TNPP$_1$). Using Eqns (1)–(4) with only part of the NPP (TNPP$_1$) instead of the total NPP ($R_a = GPP-TNPP_5$ or $R_i = TNPP_5-NEP$) violates the underlying assumptions of the equations.

Subsequently, the biome-specific weighted mean was calculated for each flux, using the inverse of the uncertainty as the weight. Hence, the mean values are strongly determined by flux estimates from long-term experimental sites and by estimates obtained with more precise measurement techniques (see Table 1). The flux values in the CO$_2$ balances should be interpreted as the most reliable mean estimates currently available but it should be noted that the balances are only representative for a larger region as far as the sites with the long time series and more precise flux estimates are representative for that region. As with most general patterns, these mean fluxes, which are the result of both spatial
and temporal averaging may not apply to specific sites or specific years (Gower et al., 1996).

Robustness of the CO₂ balances was tested by removing the lowest and highest observed flux for each component and re-calculating the weighted mean. The weighted mean for the trimmed data set was compared with the weighted mean of the original data set. When, for all flux components, the difference between the original and truncated weighted means was less than ±10%, the CO₂ balance was considered robust. CO₂ balances for which none of the weighted means of the trimmed components deviated more than 25% from the weighted means of the original components were considered acceptable. If one of the weighted means deviated more than 25% from its original value, the CO₂ balance was considered sensitive to the available data.

It is conceivable that GPP could be estimated for many years on a site where $R_h$ was not measured or that GPP at a given site was measured with a precise method whereas $R_h$ was measured with a less precise technique. Consequently, the biome-specific CO₂ balances were not necessarily closed. Closure of the balances was enforced by introducing terms that closed the budget. Six closure terms, one for each flux, were introduced to Eqs (1), (3) and (4) introduced. The equations can be rewritten as follows:

$$
\begin{align*}
\text{GPP} + \delta \text{GPP} &= \text{NPP} + \delta \text{NPP} + R_a + \delta R_a, \\
\text{NPP} + \delta \text{NPP} &= \text{NEP} + \delta \text{NEP} + R_h + \delta R_h, \\
\text{GPP} + \delta \text{GPP} &= \text{NEP} + \delta \text{NEP} + R_e + \delta R_e.
\end{align*}
$$

The CO₂ balance was further constrained by introducing the soil respiration ($R_s$). Following the definitions of the respiration components the following inequalities apply:

$$
\begin{align*}
R_a + \delta R_a &> R_e + \delta R_e - R_s, \\
R_a &> R_h + \delta R_h, \\
R_e + \delta R_e &> R_s, \\
R_a + \delta R_a + R_h + \delta R_h &> R_s.
\end{align*}
$$

For the selected biomes, mean biome-specific estimates were available for GPP, NPP, NEP, $R_e$, $R_a$, $R_h$, and $R_s$. The closure terms were optimized by means of quadratic programming such that the objective function $(\|\delta \text{GPP}\| + \|\delta \text{NPP}\| + \|\delta \text{NEP}\| + \|\delta R_h\| + \|\delta R_a\| + \|\delta R_s\|)^2$ was minimal and the CO₂-balance closed.

The closure terms are a numerical way to approach data quality and flux uncertainty on the biome level. Ideally each individual closure term should be zero; deviations from zero indicate a closure problem. Small deviations indicate a good agreement between the fluxes unless the fluxes were not measured independently. Large closure terms (i.e. beyond uncertainties in measured fluxes) could indicate problems with the accuracy of the measurement technique or missing components in the CO₂ balance but could also be due to a high natural variability within the biome because a different set of sites may have been used to calculate the different carbon fluxes. An underestimation of one flux (i.e. NPP can be accounted for by adding a closure term to NPP but also by decreasing $R_a$ or GPP). Therefore, the sum of the absolute values of the closure terms were discussed instead of individual closure terms.

Mean biome-specific fluxes (weighted by the inverse uncertainty), closure terms and NPP components were calculated for 1000 bootstrap data sets for GPP, NPP, fNPP, wNPP, rNPP, NEP, $R_e$, $R_a$, and $R_h$. Consequently, the SD of the mean fluxes, closure terms and NPP components could be estimated for each biome.

Results and discussion

Available data

In total, 513 forest sites are included in the database: 309 needle-leaved, 181 broadleaved and 23 mixed sites or 345 evergreen, 146 deciduous and 22 mixed sites. The database contains 519 GPP estimates for 133 sites, 298 NPP (TNPP_1) estimates for 244 sites, 714 NEP estimates for 164 sites, 504 $R_e$ estimates for 112 sites, 40 $R_a$ estimates for 21 sites and, 186 $R_h$ estimates for 138 sites. Irrespective of the classification, southern hemisphere ecosystems were highly underrepresented with just 21 sites (Fig. 2). Many common tree species from the southern hemisphere are, therefore, not represented in the database and coverage would greatly benefit from additional southern hemisphere data. However, only part of the data that is collected within the frame of Fluxnet was made available for use at this moment. Therefore, we expect that more GPP, NEP, and $R_e$ data will become available in the near future, especially for South America.

The applied biome classification (Reich & Eswaran, 2002) distinguished eight forest biomes; the database contained 96 boreal humid (13% of the forested biomes vs. 19% of the sites), 38 boreal semiarid (5% area vs. 19% sites), 299 temperate humid (17% area vs. 58% sites), 17 temperate semiarid (10% area vs. 3% sites), 18 meditarian warm (5% area vs. 4% sites), 0 mediterranean cold (1% area vs. 0% sites), 29 tropical humid (20% area vs. 3% sites) and 16 tropical semiarid sites (28% area vs. 6% sites). Although the temperate humid forest are overrepresented compared with their areal extent, all main climatic regions that support forest growth are present in the database. The lack of data for mediterranean cold forests is considered less essential because these ecosystems account for <1% of the global biomes.
that support forest growth. Their extent is limited to the Sierra Nevada and Cascade mountain ranges in the western US, the western half of the Russian-Kazakh border and the Caucasian mountain range between eastern Turkey and northwestern Iran (Reich & Eswaran, 2002). Semi-arid forests, particularly tropical semi-arid forests (covering almost 30% of the global forested biomes) appear understudied. It is not clear whether the data gaps are the result of a lack of data or whether the data exists but the ecosystems were not classified as forest. The difference between forests, shrublands and savannas is not always clear, and this is especially a problem in semi-arid regions where forests are less dense and individual trees are smaller than in more mesic regions.

Beside climatic conditions, growth strategy (i.e. evergreen vs. deciduous) is also expected to influence the CO₂ balance. Therefore, evergreen and deciduous sites were analyzed separately. Highly disturbed sites such as recently cut, burned, fertilized or irrigated sites are included in the database but were excluded from the current analysis. Separation by growth strategy highlighted several data gaps. Subdividing the data according to climate and growth strategy revealed that only the CO₂ balances of temperate humid evergreen, temperate humid deciduous and tropical humid evergreen forests were robust. Our robustness measure quantifies the leverage of individual observations on the overall mean but contains no information concerning the representativeness or the quality of the observations. The robustness of the CO₂ balance for boreal humid evergreen and temperate semi-arid evergreen was acceptable and for the other biomes (i.e. boreal semi-arid evergreen, boreal semi-arid deciduous and mediterranean warm evergreen forests), CO₂ balances were only indicative because the current estimates were highly sensitive to the available data due to smaller sample sizes and greater variability among sites.

Although robustness is not solely a function of the number of sites, we observed a relationship between the number of sites included in the budget calculation and the robustness of individual flux estimates (not shown). Across biomes and fluxes, weighted means calculated from at least 18 sites consistently produced robust flux estimates. In addition, 16% of the \( R_a \) and 33% of the \( R_h \) were estimated with process models (compared with 10% of the GPP, 3% of NEP, 5% of \( R_e \), and 1% of the NPP). The low number of real observations and the correspondingly high share of modelled values, tend to suggest that more effort should be put into measuring the components of \( R_e \) (i.e. \( R_a \) and \( R_h \) independently). More direct (and thus less uncertain) observations would increase the robustness of the flux estimates and would also be valuable for testing or improving models of heterotrophic and autotrophic respiration. Even up-scaled measurements of aboveground autotrophic respiration and soil respiration from chamber measurements would be valuable data with which constraints on \( R_a \) and \( R_h \) could be improved. For all biomes, data of non-CO₂ and nonrespiratory CO₂ losses are rare. Consequently, more data are needed before these carbon fluxes can be included in biome-specific balances.

How do climate, stand characteristics and CO₂ fluxes differ among biomes?

Climate and stand characteristics across biomes. Mean climate, stand characteristics and CO₂ fluxes of the biomes are based on the observations contained in the

Fig. 2 Geographical distribution of the sites contained in the database.
database. Hence, the values given in Tables 3–5 are representative for the sites contained in the database and not necessarily representative for the entire biome. Nevertheless, the well-known climatological contrasts between biomes were obvious across the investigated sites. Going from boreal towards tropical forests, the mean annual temperature at sites in the database increases from −3 to 23 °C and the difference in mean temperature between winter (December, January and February for the northern hemisphere and June, July, and August for the southern hemisphere) and summer (June, July, and August for the northern hemisphere increases from −3 to 23 °C and the difference in mean temperature between winter (December, January and February for the northern hemisphere and June, July, and August for the southern hemisphere) and summer (June, July, and August for the northern hemisphere

Table 3  Mean carbon fluxes, NPP components, sum of closure terms [Σ(δFlux) = |ΔGPP| + |ΔNPP| + |ΔR_a| + |ΔR_h|] and their standard deviation for the different biomes. The SD refer to the variability surrounding the mean values

<table>
<thead>
<tr>
<th></th>
<th>Boreal humid</th>
<th>Boreal semi-arid</th>
<th>Temperate humid</th>
<th>Temperate semi-arid</th>
<th>Mediterranean</th>
<th>Tropical humid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Evergreen</td>
<td>Evergreen</td>
<td>Evergreen</td>
<td>Deciduous</td>
<td>Evergreen</td>
<td>Evergreen</td>
</tr>
<tr>
<td>GPP</td>
<td>973 ± 83</td>
<td>773 ± 35</td>
<td>1201 ± 23</td>
<td>1762 ± 56</td>
<td>1375 ± 56</td>
<td>1228 ± 286</td>
</tr>
<tr>
<td>NPP</td>
<td>271 ± 17</td>
<td>334 ± 55</td>
<td>539 ± 73</td>
<td>783 ± 45</td>
<td>738 ± 55</td>
<td>354 ± 33</td>
</tr>
<tr>
<td>fNPP</td>
<td>73 ± 9</td>
<td>47 ± 5</td>
<td>109 ± 11</td>
<td>159 ± 19</td>
<td>235 ± 13</td>
<td>56 ± 11</td>
</tr>
<tr>
<td>wNPP</td>
<td>205 ± 28</td>
<td>110 ± 20</td>
<td>304 ± 36</td>
<td>280 ± 29</td>
<td>329 ± 47</td>
<td>117 ± 20</td>
</tr>
<tr>
<td>rNPP</td>
<td>69 ± 9</td>
<td>157 ± 31</td>
<td>112 ± 22</td>
<td>235 ± 14</td>
<td>207 ± 20</td>
<td>172 ± 19</td>
</tr>
<tr>
<td>NEP</td>
<td>131 ± 79</td>
<td>40 ± 30</td>
<td>178 ± NA</td>
<td>398 ± 42</td>
<td>311 ± 38</td>
<td>133 ± 47</td>
</tr>
<tr>
<td>R_a</td>
<td>824 ± 112</td>
<td>734 ± 37</td>
<td>1029 ± NA</td>
<td>1336 ± 57</td>
<td>1048 ± 64</td>
<td>1104 ± 260</td>
</tr>
<tr>
<td>R_h</td>
<td>489 ± 83</td>
<td>541 ± 35</td>
<td>755 ± 31</td>
<td>951 ± 114</td>
<td>673 ± 87</td>
<td>498 ± 58</td>
</tr>
<tr>
<td>R_a/NEP</td>
<td>0.88 ± 0.09</td>
<td>0.97 ± 0.04</td>
<td>0.86 ± 0.01</td>
<td>0.77 ± 0.03</td>
<td>0.77 ± 0.04</td>
<td>0.87 ± 0.22</td>
</tr>
<tr>
<td>R_h/NEP</td>
<td>0.85 ± 0.14</td>
<td>0.95 ± 0.06</td>
<td>0.86 ± 0.02</td>
<td>0.76 ± 0.04</td>
<td>0.76 ± 0.06</td>
<td>0.96 ± 0.38</td>
</tr>
</tbody>
</table>

The R_h/NEP ratio was calculated for each bootstrap before and after balance closure.
NPP, net primary production; NEP, net ecosystem production; GPP, gross primary production.

Table 4  Stand climate characterized by the mean ± SD in winter (December, January and February in the northern hemisphere and June, July and August in the southern hemisphere) and summer (June, July and August in the northern hemisphere and December, January and February in the southern hemisphere) for the different biomes

<table>
<thead>
<tr>
<th></th>
<th>Boreal humid</th>
<th>Boreal semi-arid</th>
<th>Temperate humid</th>
<th>Temperate semi-arid</th>
<th>Mediterranean</th>
<th>Tropical humid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Evergreen</td>
<td>Evergreen</td>
<td>Evergreen</td>
<td>Deciduous</td>
<td>Evergreen</td>
<td>Evergreen</td>
</tr>
<tr>
<td>Mean winter temperature (°C)</td>
<td>−9 ± 7</td>
<td>−18 ± 6</td>
<td>−20 ± 8</td>
<td>4 ± 5</td>
<td>2 ± 9</td>
<td>0 ± 5</td>
</tr>
<tr>
<td>Mean summer temperature (°C)</td>
<td>13 ± 4</td>
<td>13 ± 4</td>
<td>13 ± 4</td>
<td>17 ± 4</td>
<td>20 ± 5</td>
<td>14 ± 3</td>
</tr>
<tr>
<td>Precipitation sum winter (mm)</td>
<td>205 ± 110</td>
<td>52 ± 33</td>
<td>47 ± 31</td>
<td>449 ± 337</td>
<td>183 ± 164</td>
<td>356 ± 182</td>
</tr>
<tr>
<td>Precipitation sum summer (mm)</td>
<td>144 ± 88</td>
<td>183 ± 105</td>
<td>156 ± 86</td>
<td>194 ± 234</td>
<td>356 ± 259</td>
<td>81 ± 99</td>
</tr>
<tr>
<td>Net radiation sum winter (W m⁻²)</td>
<td>46 ± 48</td>
<td>46 ± 31</td>
<td>33 ± 29</td>
<td>147 ± 92</td>
<td>150 ± 100</td>
<td>152 ± 141</td>
</tr>
<tr>
<td>Net radiation sum summer (W m⁻²)</td>
<td>216 ± 35</td>
<td>359 ± 102</td>
<td>348 ± 108</td>
<td>473 ± 104</td>
<td>425 ± 78</td>
<td>502 ± 95</td>
</tr>
<tr>
<td>Mean winter air humidity (%)</td>
<td>86 ± 16</td>
<td>83 ± 19</td>
<td>79 ± 22</td>
<td>84 ± 11</td>
<td>79 ± 11</td>
<td>85 ± 18</td>
</tr>
<tr>
<td>Mean summer air humidity (%)</td>
<td>72 ± 12</td>
<td>71 ± 6</td>
<td>70 ± 6</td>
<td>67 ± 12</td>
<td>77 ± 5</td>
<td>50 ± 6</td>
</tr>
</tbody>
</table>

The temperature, precipitation and air humidity values are based on the CRU data set. Net radiation are model outputs from ORCHIDEE.

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Table 5 Stand characteristics for the different biomes

<table>
<thead>
<tr>
<th></th>
<th>Boreal semiarid</th>
<th>Temperate humid</th>
<th>Mediterranean warm</th>
<th>Tropical humid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Evergreen</td>
<td>Deciduous</td>
<td>Evergreen</td>
<td>Deciduous</td>
</tr>
<tr>
<td>Latitude (°)</td>
<td>58 ± 7</td>
<td>59 ± 5</td>
<td>61 ± 5</td>
<td>44 ± 8</td>
</tr>
<tr>
<td>Max LAI (m² m⁻²)</td>
<td>4.1 ± 3.0</td>
<td>3.4 ± 1.8</td>
<td>3.5 ± 1.5</td>
<td>7 ± 2.9</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>14 ± 7</td>
<td>8 ± 2</td>
<td>19 ± 5</td>
<td>20 ± 12</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹)</td>
<td>28 ± 12</td>
<td>26 ± 10</td>
<td>28 ± 2</td>
<td>42 ± 24</td>
</tr>
<tr>
<td>Tree density (number ha⁻¹)</td>
<td>3767 ± 5652</td>
<td>4230 ± 3018</td>
<td>1451 ± 720</td>
<td>1399 ± 1985</td>
</tr>
<tr>
<td>Stand age (years)</td>
<td>72 ± 52</td>
<td>121 ± 67</td>
<td>78 ± 31</td>
<td>91 ± 141</td>
</tr>
<tr>
<td>Aboveground biomass</td>
<td>5761 ± 3708</td>
<td>4766 ± 2498</td>
<td>7609 ± 2438</td>
<td>14934 ± 13562</td>
</tr>
<tr>
<td>(g C m⁻²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belowground biomass</td>
<td>1388 ± 836</td>
<td>1604 ± 925</td>
<td>1352 ± 645</td>
<td>4626 ± 4673</td>
</tr>
<tr>
<td>(g C m⁻²)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The values are the mean ± the standard deviation of the observed values for the sites included in the CO₂-balances.

and December, January, and February for the southern hemisphere) decreased from 31 to 1 °C (Table 4). Along the same gradient, the difference in net radiation sum between winter and summer decreased from 315 to 76 W m⁻². The annual precipitation sum in boreal semiarid forests was <400 mm and exceeded 2200 mm in tropical humid forests. In the semiarid forests, the difference in precipitation between winter and summer was more pronounced than in the humid biomes (Table 4). Pronounced differences between winter and summer relative air humidity were only present in the temperate semiarid and mediterranean warm forests.

The distribution of plant species and, thus, forest ecosystems depends on historical events (i.e. ice ages), migrational ability and ability to adapt to present environmental conditions (Schulze, 2005). The mean ecosystem characteristics for each of the selected biomes are given in Table 5. The unexpected high latitude of the tropical forests is caused by the high number of Hawaiian sites with latitude around 20 °N. The low leaf area index for temperate semiarid evergreen forests is not robust and most likely due to the low number of observations for this biome. Maximum LAI (in most cases, LAI refers to tree LAI and does not include the LAI of the understory or the herb layer), tree height, basal area, tree density, and biomass do not follow a clear trend but overall higher biomass accumulation is observed in forests from the poles to the equator with the highest accumulation in temperate-humid evergreen forests. Within a climatic zone, forests in the humid biomes accumulate in general more biomass compared with forests in semiarid biomes. Despite the exclusion of recently disturbed sites, there is a 50-year gap between the mean and median age of the trees in the temperate humid evergreen biome, which indicates a skewed age distribution. Unrepresentative sampling in the presence of both intensively managed and old-growth stands (mostly located in the Pacific Northwest of the United States) in this biome likely explains the lower median age of the evergreen biome.

Global patterns in GPP, NPP, and NEP. The global pattern in GPP shows a clear dependency on the climatic conditions (Fig. 3). Temperature and precipitation which are both sensitive to effects of continentality and topography were thought to give a more meaningful representation of climate than latitude, longitude, and elevation. Climatic conditions explain 71 ± 2% of the variability in GPP \[ P<0.01 \text{ for GPP = } f(\text{temperature}) \times f(\text{precipitation}), \text{ where } f \text{ is a power function}. \] In line with the basic ecological principles (e.g. Liebig’s ‘Law of the Minimum’), the GPP of ecosystems that are already limited by low precipitation sums (<800 mm) or low mean annual temperatures (<5 °C) do not benefit from higher mean annual temperatures or precipitation, respectively. Given a sufficient amount of precipitation (>800 mm), GPP increases with increasing temperatures (Fig. 3, top panel). A similar relationship between temperature
and GPP has been reported for different types of terrestrial vegetation such as tundra, forest, and grasslands (Law et al., 2002). Given a nonrestrictive mean annual temperature (>5 °C), GPP benefits from higher annual precipitation sums. However, the beneficial effect of precipitation appears to saturate above 1500 mm (i.e. for tropical forests, there was no correlation between precipitation and GPP, see Fig. 3, bottom panel). This apparent saturation could originate from the use of precipitation as the independent variable instead of plant available water. At high precipitation sites, run-off is a major component of the hydrological balance and hence evapotranspiration remains almost constant beyond annual precipitation sums of 1500 mm (Schulze, 2005). At temperatures between 5 and 15 °C, some of the dryer forests even have higher GPP than wetter forests (Fig. 3), likely because the dryer sites experience less cloudiness and hence more sunshine (Table 4).

Although an effort was made to use consistent NPP data (TNPP_1), the observed relationships between climatic variables and NPP are more scattered than earlier reported relationships (Lieth & Whittaker, 1975; Scurlock & Olson, 2002). Some of the scatter in our data set is caused by including chronosequences (i.e. the ‘line’ at 25 °C or at 1200 mm in Fig. 4, top and bottom panel, respectively) in the analyses. Nevertheless, temperature and precipitation explain 36 ± 5% of the variability in NPP [P < 0.01 for NPP = f(temperature) × f(temperature), where f is a power function]. Similar to the results for GPP, the NPP of ecosystems does not respond to increasing temperatures or precipitation when the ecosystem is limited either by precipitation (<800 mm) or temperature (<5 °C), respectively (Fig. 4, top and bottom panel). For mean annual temperatures ranging from 5 to 10 °C, NPP increases with increasing temperature but appears to saturate beyond 10 °C (Fig. 4, top panel). Although low NPP values are observed at sites with low precipitation, there is no clear correlation between NPP and precipitation above precipitation of 1500 mm (Fig. 4, bottom panel). Schuur (2003) reported that NPP decreased beyond the 1500 mm threshold, but our results are not conclusive. This saturation or decrease could be the effect of using precipitation instead of plant available water as the independent variable in the figures. Similar to our observations for GPP, some of the dryer forests at intermediate mean annual temperatures (between 5 and 15 °C) have higher

Fig. 3  The top panel shows the gross primary production (GPP) according to the mean annual temperature, the size and color of the marker is a measure for the annual precipitation sum (mm). The bottom panel shows the GPP according to the annual precipitation sum, the size and color of the marker is a measure for the mean annual temperature (°C). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.
NPP than wetter forests at similar temperatures, likely because these dryer sites have a higher GPP. Despite tropical forests having the highest observed GPP values, the highest NPP values were observed in the temperate forests. High autotrophic respiration and/or non-CO₂ losses in tropical forests compared with the other biomes could explain this observation, but this then raises the question why these factors are particularly important in tropical humid forests.

Similar to earlier studies (Law et al., 2002), NEP was found independent from the mean annual temperature and precipitation sum (Fig. 5). Climate explained just 5 ± 1% of the variability in NEP \(P = 0.03\) for \(\text{NEP} = f(\text{temperature}) \times f(\text{precipitation})\), where \(f\) is a power function. However, the highest NEP values are observed in temperate humid forests. This may be related to forest management, which is more intensive in this biome. Forest management targets to increase the production of woody biomass. Therefore, it is to be expected that the effect of forest management is reflected in the CO₂ balance as thinning and harvesting result in a higher wNPP and a lower heterotrophic respiration due to the removal of woody biomass before it dies and decomposes in situ. Mean wNPP in temperate humid forests is among the highest values observed (Table 3), which supports the idea that management is the cause of the high-observed NEP values. However, an effect of management on \(R_h\) is not seen in the data (Table 3). Although some of the higher NEP values in temperate forests might be due to management, management in itself neither explains the magnitude of the NEP value nor whether the ecosystem is a CO₂ source or sink. The global pattern of NEP values of unmanaged forest across biomes (Fig. 6) is similar to that of forests in general (Fig. 5) and shows that also unmanaged forests are most often carbon sinks. This finding indicates that preservation of unmanaged forest ecosystems could be just as important as reforestation efforts in mitigating climate change through carbon sequestration.

Across European forests, the absence of a latitudinal trend in GPP, in the presence of a latitudinal trend in NEP was the foundation for the hypothesis that respiration was the main determinant of the CO₂ balance at the regional scale (Valentini et al., 2000). However, the current analysis at larger spatial scale shows exactly the opposite (i.e. a global pattern in GPP in the absence of a global pattern in NEP).
findings suggest that on the global scale GPP is mainly climate driven ($R^2 = 0.72$, $P < 0.01$) and only marginally sensitive to nonclimatic conditions. In contrast, the global pattern in NEP was found be insensitive to climatic conditions ($R^2 = 0.05$, $P = 0.03$) and was, therefore, expected to be mainly determined by nonclimatic conditions such as successional stage, management, site history and site disturbance. We hypothesize that different drivers determine the carbon fluxes at different spatial scales (i.e. the magnitude of NPP on the global scale can is likely driven by the climatic conditions, whereas the site level NPP is also determined by site quality and management).

Fig. 5 The top panel shows the net ecosystem production (NEP) according to the mean annual temperature, the size and color of the marker is a measure for the annual precipitation sum (mm). The bottom panel shows the NEP according to the annual precipitation sum, the size and color of the marker is a measure for the mean annual temperature ($^\circ$C). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

Fig. 6 Global relationship between net ecosystem production (NEP) and mean annual temperature in unmanaged forests. The size and color of the marker is a measure for the annual precipitation sum (mm). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.
Despite the difference in drivers between GPP and NEP, a linear relationship between GPP and NEP has been reported across terrestrial vegetations (Law et al., 2002). If we confine our data set to a similar range in GPP as in Law et al. (2002; 600–2200 g C m$^{-2}$ yr$^{-1}$), a similar relationship is observed (Fig. 7). However, increasing GPP beyond 2200 g C m$^{-2}$ yr$^{-1}$ does not result in a further increase of NEP (Fig. 7). Although below a GPP of 2200 g C m$^{-2}$ yr$^{-1}$ there is a tendency of higher NEP with higher GPP, this relationship has limited predictive power. At any GPP, the range of possible NEP values is so wide that it is even not possible to predict whether the forest will be a carbon source or sink ($R^2 = 0.28$ for a quadratic regression model, $P < 0.01$).

Effect of the growth strategy and water availability. The differences in CO$_2$ fluxes between growth strategies were tested individually for each flux in each biome (one-way ANOVA, assuming equal variances and using growth strategy as a factor). Out of the potential 42 tests (seven biomes x six fluxes), 19 tests could not be performed due to the absence of one of the growth strategies within the biome (i.e. no data available of deciduous forests in the humid tropics). In general, the fluxes between evergreen and deciduous forests did not differ within the same climate zones (ANOVA, $P > 0.15$; see Figs 8–10). Five exceptions were observed (ANOVA, $P \leq 0.10$): GPP and $R_e$ are higher in evergreens compared with deciduous forests in the temperate humid zone, GPP and $R_e$ are higher in deciduous forests in the boreal semiarid zone (based on few observations) and NEP is lower in deciduous than in evergreen mediterranean warm forests (based on few observations). Current statistical evidence, thus justifies merging growth strategies and hence limiting the stratification of biomes to the climatic zones. Nevertheless, we opted to present biomes that distinguish growth strategies to acknowledge other ecological differences and because 19 out of 42 tests could not be performed.

In general fluxes are lower in semi-arid ecosystems compared with humid ecosystems (Figs 3–5). In the temperate zone, this difference is significant at the 0.05 level for GPP, NEP, and $R_h$, while for NPP the difference is significant at the 0.10 level.

CO$_2$ balances
Where is the CO$_2$ going? Eddy covariance studies have indicated uncertainties concerning the correct interpretation of CO$_2$ fluxes measured on calm nights (Goulden et al., 1996; Malhi & Grace, 2000). These uncertainties are exceptionally important in tropical rain forests where typically about 80% of all nighttime data is collected during calm nights. The uncertainties are caused by CO$_2$ storage below the canopy, advective losses of CO$_2$ and higher random uncertainties during calm nights (Araujo et al., 2002; Kruijt et al., 2004; Richardson et al., 2006) and it is often unclear how to deal with night-time flux measurements in tropical forests (however, see Saleska et al., 2003). Two different approaches for replacing night-time measurements at low turbulence were reported to result in at least 100% difference of the annual NEP (Kruijt et al., 2004). Consequently, the reported NEP’s for tropical forests are likely to be an overestimate of the true CO$_2$ uptake. Based on the current estimates of NEP in tropical humid evergreen forests, the equivalent of 10% of the CO$_2$ influx by photosynthesis remains in the ecosystem (Fig. 8). Wood growth accounts for 50% of the carbon sink. However, the importance of woody biomass as a long-term sink of carbon in tropical humid forests is still under debate (cf. Phillips et al., 1998; Clark, 2002;
Fig. 8 Observed CO₂ balance for the mediterranean warm and tropical humid biome. These CO₂ balances were not closed and therefore the identities given by Eqns (1)–(4) do not apply. The width of the arrows is proportional to the fluxes and all units are in g C m⁻² yr⁻¹. (n) refers to the number of observations; 25–75% refers to the 25th an 75th percentiles of the observations. Flux values were obtained from the same data but a different bootstrap-run and can therefore be slightly different from the values reported in Table 3.

Fig. 9 Observed CO₂ balance for the temperate biomes. These CO₂ balances were not closed and therefore the identities given by Eqns (1)–(4) do not apply. The width of the arrows is proportional to the fluxes and all units are in g C m⁻² yr⁻¹. The legend of the figures is given in Fig. 8. Flux values were obtained from the same data but a different bootstrap-run and can therefore be slightly different from the values reported in Table 3.
Phillips et al., 2002). Even if the non-CO₂ losses amount to 15–20% of the NPP (Clark et al., 2001; Grace & Malhi, 2002; Richey et al., 2002), the sequestration of carbon in soils and organic matter pools is expected to be an important process in tropical humid forests. Despite the summer drought in Mediterranean warm forests, the equivalent of 25% of the CO₂ accumulated through photosynthesis remains in the ecosystem (Fig. 8). In this biome, wNPP is roughly equal to NEP, which suggests declining soil organic matter pools in response to land-use change or ecosystem perturbation.

Within the different temperate biomes, large differences were observed in absolute flux values (i.e. GPP, NPP, NEP; Fig. 9). In temperate humid evergreen forests the mean annual NEP is larger than the wNPP. Roughly 70% of the NEP accumulates in the woody biomass, and therefore sequestration of carbon in soils and organic matter pools is expected to be an important process. Temperate semi-arid forests are close to a CO₂-neutral state, which means that an equal amount of CO₂ that was taken up by photosynthesis is released by autotrophic and heterotrophic respiration (Fig. 9). In temperate humid deciduous and temperate semi-arid evergreen forests, wNPP and NEP are almost equal so accumulation of the entire annual NEP can occur in the woody biomass reducing the importance of the soil and organic matter pools for carbon sequestration.

The differences among the boreal biomes are smaller than the differences among the temperate biomes. In general, the boreal humid evergreen forests have higher absolute fluxes than the boreal semi-arid evergreen forests. However, the boreal semi-arid deciduous biome is more productive than its humid counterparts. In all three boreal biomes wNPP exceeds NEP, suggesting an important contribution of decomposition of historical carbon through land-use change or ecosystem perturbation.

Carbon use, expressed as the ratio of \( R_e \) over GPP (Table 3), is significantly different between temperate humid evergreen, temperate humid deciduous, and Mediterranean warm forests in one group, boreal humid evergreen, boreal semi-arid deciduous and tropical humid in a second group and boreal semi-arid evergreen and temperate semi-arid in a third group (ANOVA, \( P<0.01 \)). High efficiencies, indicated by low \( R_e/GPP \) ratios were found in temperate humid and Mediterranean forests. The variability in carbon use across forest biomes observed from our database is larger than the previously reported variability across forests, grasslands...
and tundra (Law et al., 2002). As the drivers of NEP are not well understood it is not clear what determines these differences in carbon use but it is hypothesized that intensive managed (i.e. increasing wood production through thinning is among the causes of a more-efficient carbon use in forest biomes). We did not observe a global pattern in carbon use (Fig. 11).

Closing the CO₂ balance. In Figs 8–10, weighted mean CO₂-fluxes are plotted for different biomes without any further consideration. At intermediate temporal scales (years to decades) and in the absence of measurement and conceptual errors [Eqns (1)–(5) are to be used on the appropriate timescale], the theoretical relationships among the fluxes should hold. However, the figures indicate that this agreement is often poor. Therefore, closure of the CO₂ balance was enforced by adding an additional ‘closure term.’

The closure terms are a numerical way to approach data quality and flux uncertainty on the biome-level. An underestimation of one flux (i.e. NPP can be accounted for by adding a closure term to NPP but also by decreasing Rₐ or GPP). Therefore, it is preferable to focus on the sum of the absolute values of the closure terms (Table 3), instead of individual closure terms (not shown). For all biomes, substantial correction terms (ranging from 10% to 60% of GPP) were needed to close the CO₂ balance (Table 3). There is no relationship between the relative amount of unallocated carbon and the mean annual temperature (Fig. 12) or annual precipitation sum (not shown).

Recall that the CO₂ balances for temperate humid evergreen, temperate humid deciduous and tropical humid evergreen forests were found to be robust against the influence of individual flux estimates (see ‘Available data’). Despite robustness, 10–20% (Fig. 12) of the photosynthetic carbon uptake remains unallocated to a specific flux component, indicating that for these biomes better data in terms of accuracy and precision are needed rather than more data. Although the CO₂ balances for boreal humid evergreen and temperate semi-arid evergreen forests are reasonable robust (see ‘Available data’), 45–60% of the carbon uptake remains unallocated in these ecosystems. More and better observations of the respiratory processes and lateral fluxes at the ecosystem scale (i.e. advection, VOC, DOC) would enable us to better close the CO₂ balances and to estimate regional and global carbon budgets more accurately than currently possible.

Fig. 11 Global patterns in Rₑ/gross primary production (GPP) according to the mean annual temperature and annual precipitation sum. The size and the color of the marker are measures for the absolute flux value. Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

Fig. 12 Relationship between the unallocated carbon, calculated as the sum of the closure terms for gross primary production (GPP), net primary production (NPP), net ecosystem production (NEP), Rₑ, Rₐ, and R₉ and the mean annual temperature. Biomes from left to right: boreal semiarid deciduous, boreal semiarid evergreen, boreal humid evergreen, temperate semiarid evergreen, temperate humid evergreen, temperate humid deciduous, mediterranean warm evergreen, and tropical humid evergreen.
Conclusions

We have described a new global database of forest C fluxes and pools. This database, which quantifies CO$_2$ fluxes and pathways across a number of different levels of integration (from photosynthesis up to net ecosystem production), fills an important gap for model calibration, model validation and hypothesis testing at global and regional scales. The database contains 513 sites from eight major biomes. Estimates of the mean fluxes in temperate humid evergreen, temperate humid deciduous and tropical humid evergreen were found to be robust; in other biomes, small sample sizes and high variability among sampled sites resulted in less robust flux estimates. Closing the CO$_2$ balances required the introduction of closure terms. The value of the closure terms was taken as an indication for the existence of methodological and conceptual errors in the CO$_2$ balances. For all biomes, the correction terms needed to close biome-specific CO$_2$ balances are substantial, ranging from 10% to 60%. We believe that a better understanding of respiratory processes and lateral fluxes at the ecosystem scale is a prerequisite to closing CO$_2$ balances at the ecosystem level. This would enable us to estimate regional and global carbon budgets more accurately than currently possible. Carbon budgets of semiarid forests (boreal, temperate and tropical) would benefit most from additional data inputs.

The global patterns in GPP and NPP show clear relationships with mean annual temperature and annual precipitation. Primary production increases with increasing temperature and precipitation, but saturates beyond a threshold of 1500 mm precipitation for GPP and NPP or 10°C mean annual temperature for NPP. Global patterns in NEP were not correlated with climatic variables. We hypothesize instead that variability in NEP is mainly determined by nonclimatic conditions such as successional stage, management, site history and site disturbance.

Availability of the database

Contributions or corrections to the database, as well as requests to use the database (subject to standard ‘Fair Use’ policies), should be directed to the corresponding author (S. L.).

Acknowledgements

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Appendix A

Appendix A Data sources contained in the database.


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Appendix B

Table B1 Overview of the information contained in the database

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<th>Plot information</th>
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<tr>
<td>Biome</td>
<td>Biome according to US Department of Agriculture (1999)</td>
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<tr>
<td>Growth strategy</td>
<td>Evergreen, deciduous or mixed</td>
</tr>
<tr>
<td>Growth form</td>
<td>Needle-leaved, broadleaved or mixed</td>
</tr>
<tr>
<td>Tree species</td>
<td>Dominant tree species</td>
</tr>
<tr>
<td>Tree species</td>
<td>Co-dominant tree species</td>
</tr>
<tr>
<td>Latitude</td>
<td>Latitude in decimal degrees</td>
</tr>
<tr>
<td>Longitude</td>
<td>Longitude in decimal degrees</td>
</tr>
<tr>
<td>Elevation</td>
<td>Elevation above sea level in m</td>
</tr>
<tr>
<td>Management</td>
<td>Relevant information on management and disturbance</td>
</tr>
</tbody>
</table>

| Observed stand characteristics | Basal area in m$^{-2}$ha$^{-1}$ |
| Source            | Diameter at breast height in m |
| Height            | Mean tree height in m |
| Density           | Stand density in number of trees.ha$^{-1}$ |
| Age               | Age of the dominant trees in years |
| LAI               | Maximal LAI in m$^{-2}$ |
| Method            | Description of the method used to determine LAI |

| Observed stand biomass | Foliar biomass in g C m$^{-2}$ |
|------------------------| Branch biomass in g C m$^{-2}$ |
| Stem biomass           | Stump biomass in g C m$^{-2}$ |
| Coarse root biomass    | Fine root biomass in g C m$^{-2}$ |
| Aboveground biomass    | Total aboveground biomass in g C m$^{-2}$ |
| Belowground biomass    | Total belowground biomass in g C m$^{-2}$ |

| Observed stand climate | Mean annual temperature in °C |
|------------------------| Total annual precipitation in mm |
| Evaporation            | Total annual evaporation in mm |
| APAR                   | Total annual absorbed radiation in MJ m$^{-2}$ |
| PAR                    | Total annual incident radiation in MJ m$^{-2}$ |
| IPAR                   | Total annual intercepted radiation in MJ m$^{-2}$ |

| Observed flux estimate | Ecosystem GPP in g C m$^{-2}$ yr$^{-1}$ |
|------------------------| Ecosystem NEP in g C m$^{-2}$ yr$^{-1}$ |
| $R_{h}$                | Ecosystem Re g C m$^{-2}$ yr$^{-1}$ |
| NPP wood               | NPP of the stems/wood g C m$^{-2}$ yr$^{-1}$ |
| NPP foliage            | NPP of the foliage g C m$^{-2}$ yr$^{-1}$ |
| NPP branch             | NPP of the branches g C m$^{-2}$ yr$^{-1}$ |
| NPP stumps             | NPP of the stumps g C m$^{-2}$ yr$^{-1}$ |
| NPP coarse             | NPP of the coarse roots g C m$^{-2}$ yr$^{-1}$ |
| NPP fine               | NPP of the fine roots g C m$^{-2}$ yr$^{-1}$ |
| NPP repro              | NPP of the reproductive organs g C m$^{-2}$ yr$^{-1}$ |
| NPP herbi              | NPP of the herbivory g C m$^{-2}$ yr$^{-1}$ |
| NPP under              | NPP of the understory g C m$^{-2}$ yr$^{-1}$ |
| NPP VOC                | NPP of the VOC's g C m$^{-2}$ yr$^{-1}$ |
| NPP exudates           | NPP of the root exudates g C m$^{-2}$ yr$^{-1}$ |
| $R_{a}$                | Total soil respiration g C m$^{-2}$ yr$^{-1}$ |
| $R_{b}$                | Autotrophic respiration g C m$^{-2}$ yr$^{-1}$ |
| $R_{c}$                | Heterotrophic respiration g C m$^{-2}$ yr$^{-1}$ |
| Methodology            | Description of the different methodologies that were used to estimate the fluxes |

Site climate and environment

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<tr>
<th>Temperature</th>
<th>Monthly mean annual temperature in °C (CRU, 2006)</th>
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<td>Monthly precipitation sum in mm CRU (2006)</td>
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<tr>
<td>Air humidity</td>
<td>Monthly air humidity CRU (2006)</td>
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<tr>
<td>Cloud cover</td>
<td>Monthly average cloud cover (%) CRU (2006)</td>
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<tr>
<td>Number of wet days</td>
<td>Monthly sum of wet days CRU (2006)</td>
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<td>Long wave radiation (1)</td>
<td>Monthly absorbed downward longwave radiation in W m$^{-2}$ Krinner et al. (2005)</td>
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<td>Long wave radiation (2)</td>
<td>Monthly net surface longwave radiation in W m$^{-2}$ KrInner et al. (2005)</td>
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<td>Wet deposition</td>
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