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CO_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 CO_2 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 CO_2 balance required the introduction of substantial biome-specific closure terms. Nonclosure was taken as an indication that respiratory processes, advection, and non-CO_2 carbon fluxes are not presently being adequately accounted for.

Nomenclauture:

DOC = dissolved organic carbon;
fNPP = foliage component of NPP;
GPP = gross primary production (GPP > 0 denotes photosynthetic uptake);
mNPP = missing component of NPP;
NBP = net biome production (NBP > 0 denotes biome uptake);
NECB = net ecosystem carbon balance (NECB > 0 denotes ecosystem uptake);
NEE = net ecosystem exchange (NEE > 0 denotes ecosystem uptake);
NEP = net ecosystem production (NEP > 0 denotes ecosystem uptake);
NPP = net primary production (NPP > 0 denotes ecosystem uptake);
R_a = autotrophic respiration ($R_a > 0$ denotes respiratory losses);
R_e = ecosystem respiration ($R_e > 0$ denotes respiratory losses);
R_h = heterotrophic respiration ($R_h > 0$ denotes respiratory losses);
rNPP = root component of NPP;
R_s = soil respiration ($R_s > 0$ denotes respiratory losses);
VOC = volatile organic compounds;
wNPP = wood component of NPP

Keywords: carbon cycle, CO_2, 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_e) 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 CO_2 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 CO_2 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 CO_2 that is used for photosynthesis. The synthesis of new plant tissue from CO_2, 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

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

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 (CH_4), 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,

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

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 CH_4, 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

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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

$$\mathrm{NPP} = \mathrm{NEP} + R_h. \tag{3}$$

The sum of R_h and R_a represents the total ecosystem respiration (R_e) and the sum of the belowground fraction of R_a 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).

$$\mathrm{GPP} = \mathrm{NEP} + R_e. \tag{4}$$

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.*, 2002; 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:

$$\begin{aligned}\mathrm{NECB} = {} & \mathrm{NEP} \\ & - \text{nonrespiratory } CO_2 \text{ losses} - \text{non-}CO_2 \text{ losses} \\ & + \text{import from bordering ecosystems.}\end{aligned} \tag{5}$$

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_s, R_h, and R_a), derived from single or multiple direct measurements (GPP, NPP, NEP, R_e, R_h, and R_h) or modelled (GPP, NPP, NEP, R_e, R_s, R_h, and R_a).

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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 up-scaled root respiration (Hanson *et al.*, 2000) or chamber measurements after trenching or girdling. Directly measured estimates of R_a 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_e 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 CO_2 storage and advection, nocturnal NEE measured on calm nights (u^* threshold) is not used to estimate R_e. 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_e are both likely to be underestimated.

When data are available for at least two flux components, the identities given by Eqns (1)–(4) can be used to estimate a missing flux (e.g. R_a can be calculated from the difference between R_e and R_h). Flux estimates obtained by applying these equations were also included in the database. However, modelled GPP, NPP, NEP, R_e, R_s, R_h, and R_a 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

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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 CH_4 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 R_a or the sum of NEP and R_h was set to TNPP_5 despite the absence of lower-level NPP estimates. The imbalance between GPP and R_a was

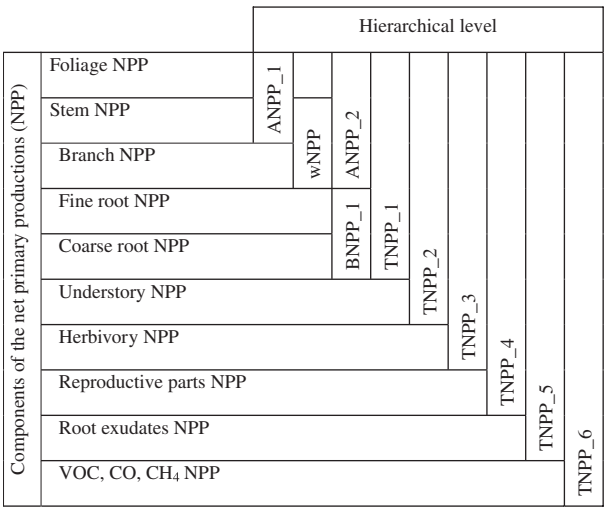

Fig. 1 Hierarchical framework for net primary production (NPP) where 11 components of the NPP are hierarchically combined in nine aggregation levels of NPP.

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 CH_4 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 cutoff diameters are expected to disappear when total belowground NPP (BNPP_1) is used].

Uncertainty of the measured CO_2 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 CO_2-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, $\pm 350\,g\,C\,m^{-2}\,yr^{-1}$ (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 $\pm 700\,g\,C\,m^{-2}\,yr^{-1}$. 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

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Table 1 Method-specific reduction factors for GPP, NPP, NEP, R_e, R_s, R_h and R_a determined by expert judgment

Method	GPP	NPP	NEP	R_e	R_s	R_h	R_a	Reduction factor
Eddy covariance and data assimilation	x		x					0.2
Eddy covariance	x		x	x	x			0.3
Measured increment and litterfall		x						0.3
Chamber based					x			0.4
Measured and modelled increment and litterfall		x						0.6
Process-model based	x	x	x	x				0.6
Chamber + girdling						x		0.8
Chamber + root excised						x		0.8
Chamber + trenching						x		0.8
Radiocarbon						x		0.8
Chamber based							x	0.8
Alkali absorption					x			0.8
Chamber + gap based						x		0.9
Process-model based					x	x	x	1.0
Flux component based	x	x	x	x	x	x	x	1.0

The reduction factors account for the precision of a method and are multiplied with the absolute range of the uncertainty of the fluxes (Table 2) to get the uncertainty of a specific observation.
NPP, net primary production; NEP, net ecosystem production; GPP, gross primary production.

Table 2 Absolute range ($g\,C\,m^{-2}\,yr^{-1}$) of GPP, NPP, NEP, R_e, R_s, R_h and R_a under the assumption that measurements are absent

Component flux	Uncertainty
GPP	$500 + 7.1 \times (70–\text{latitude})$
NPP	$350 + 2.9 \times (70–\text{latitude})$
NEP	350 if latitude > 23
	700 if latitude < 23
R_e	$500 + 7.1 \times (70–\text{latitude})$
R_s	$200 + 8.6 \times (70–\text{latitude})$
R_h	$100 + 2.9 \times (70–\text{latitude})$
R_a	$100 + 4.3 \times (70–\text{latitude})$

Values determined by expert judgment.
NPP, net primary production; NEP, net ecosystem production; GPP, gross primary production.

(s_{ij}) was further reduced by accounting for the length of the time series. Thus,

$$s_{ij} = \left(p_i \times RF_j\right) \Big/ \sqrt{l_{ij}},$$

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 where estimated with method j.

A similar approach was followed to estimate the uncertainty of GPP, NPP, R_e, R_a, R_h, and R_s. 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) 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 (F_i) was calculated as the weighted mean:

$$F_i = \frac{\sum_{j=1}^{k} l_{ij} \times F_{ij}}{\sum_{j=1}^{k} l_{ij}}.$$

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

$$s_i = \sqrt{\frac{\sum_k l_{ij} \times \left(s_{ij}\right)^2}{\sum_k l_{ij}}} \Big/ \sqrt{n_i},$$

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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 $8 \times 8\,\text{km}^2$ 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_e, R_a, R_h 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_e), the missing component was calculated based on the relationship between the respiration components. A similar procedure was used to calculate R_e when GPP and NEP were measured. The uncertainty of the calculated component was calculated by error propagation. In theory R_a and/or R_h 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 ($R_a = \text{GPP} - \text{TNPP_5}$ or $R_h = \text{TNPP_5} - \text{NEP}$) 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

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and temporal averaging may not apply to specific sites or specific years (Gower *et al.*, 1996).

Robustness of the CO_2 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 $\pm 10\%$, the CO_2 balance was considered robust. CO_2 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 CO_2 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 CO_2 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 Eqns (1), (3) and (4) introduced. The equations can be rewritten as follows:

$$\begin{aligned} \mathrm{GPP} + \delta\mathrm{GPP} &= \mathrm{NPP} + \delta\mathrm{NPP} + R_a + \delta R_a, \\ \mathrm{NPP} + \delta\mathrm{NPP} &= \mathrm{NEP} + \delta\mathrm{NEP} + R_h + \delta R_h, \\ \mathrm{GPP} + \delta\mathrm{GPP} &= \mathrm{NEP} + \delta\mathrm{NEP} + R_e + \delta R_e. \end{aligned}$$

The CO_2 balance was further constrained by introducing the soil respiration (R_s). Following the definitions of the respiration components the following inequalities apply:

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

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 $(|\delta\mathrm{GPP}| + |\delta\mathrm{NPP}| + |\delta\mathrm{NEP}| + |\delta R_e| + |\delta R_a| + |\delta R_h|)^2$ was minimal and the CO_2-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 CO_2 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 mediterranean 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

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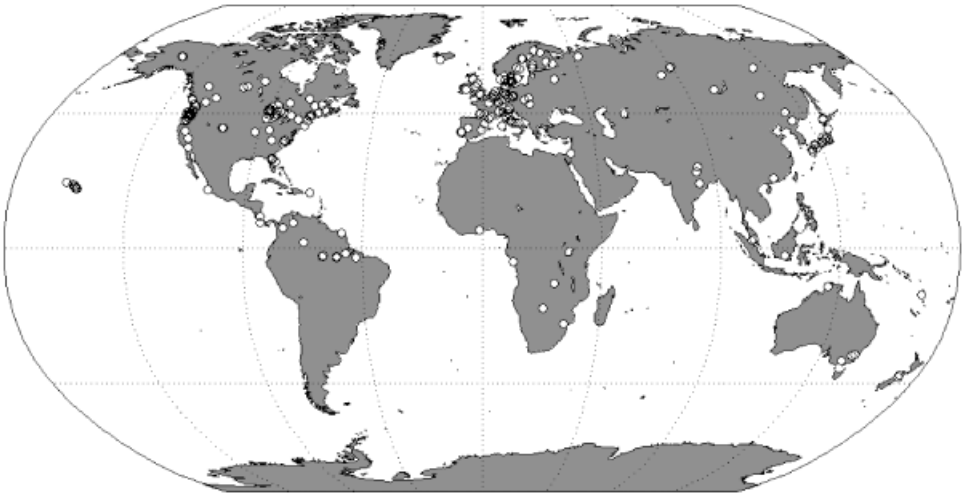

Fig. 2 Geographical distribution of the sites contained in the database.

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). Semiarid forests, particularly tropical semiarid forests (covering almost 30% of the global forested biomes) appear under-studied. 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 semiarid 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 CO_2 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 CO_2 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 CO_2 balance for boreal humid evergreen and temperate semiarid evergreen was acceptable and for the other biomes (i.e. boreal semiarid evergreen, boreal semiarid deciduous and mediterranean warm evergreen forests), CO_2 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_h and 33% of the R_a 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-CO_2 and nonrespiratory CO_2 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 CO_2 fluxes differ among biomes?

Climate and stand characteristics across biomes. Mean climate, stand characteristics and CO_2 fluxes of the biomes are based on the observations contained in the

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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

Table 3 Mean carbon fluxes, NPP components, sum of closure terms [$\Sigma(\delta\text{Flux}) = |\delta\text{GPP}| + |\delta\text{NPP}| + |\delta R_e| + |\delta R_a| + |\delta R_h|$] and their standard deviation for the different biomes. The SD refer to the variability surrounding the mean values

	Boreal humid	Boreal semiarid		Temperate humid		Temperate semiarid	Mediterranean warm	Tropical humid
	Evergreen	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Evergreen	Evergreen
GPP	973 ± 83	773 ± 35	1201 ± 23	1762 ± 56	1375 ± 56	1228 ± 286	1478 ± 136	3551 ± 160
NPP	271 ± 17	334 ± 55	539 ± 73	783 ± 45	738 ± 55	354 ± 33	801 ± NA	864 ± 96
fNPP	73 ± 9	47 ± 5	109 ± 11	159 ± 19	235 ± 13	56 ± 11	134 ± NA	316 ± 32
wNPP	205 ± 28	110 ± 20	304 ± 36	280 ± 29	329 ± 47	117 ± 20	389 ± NA	212 ± 52
rNPP	69 ± 9	157 ± 31	112 ± 22	235 ± 14	207 ± 20	172 ± 19	278 ± NA	324 ± 56
NEP	131 ± 79	40 ± 30	178 ± NA	398 ± 42	311 ± 38	133 ± 47	380 ± 73	403 ± 102
R_e	824 ± 112	734 ± 37	1029 ± NA	1336 ± 57	1048 ± 64	1104 ± 260	1112 ± 100	3061 ± 162
R_a	489 ± 83	541 ± 35	755 ± 31	951 ± 114	673 ± 87	498 ± 58	615 ± NA	2323 ± 144
R_h	381 ± 40	247 ± 26	275 ± 31	420 ± 31	387 ± 26	298 ± 16	574 ± 98	877 ± 96
$\Sigma(\delta\text{Flux})$	439 ± 122	176 ± 81	163 ± 90	216 ± 102	206 ± 95	713 ± 314	359 ± 131	774 ± 225
R_e/GPP	0.88 ± 0.09	0.97 ± 0.04	0.86 ± 0.01	0.77 ± 0.03	0.77 ± 0.04	0.87 ± 0.22	0.76 ± 0.07	0.88 ± 0.04
R_e/GPP	0.85 ± 0.14	0.95 ± 0.06	0.86 ± 0.02	0.76 ± 0.04	0.76 ± 0.06	0.96 ± 0.38	0.76 ± 0.10	0.86 ± 0.06

The R_e/GPP 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

	Boreal humid	Boreal semi-arid		Temperate humid		Temperate semiarid	Mediterranean warm	Tropical humid
	Evergreen	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Evergreen	Evergreen
Mean winter temperature (°C)	−9 ± 7	−18 ± 6	−20 ± 8	4 ± 5	2 ± 9	0 ± 5	10 ± 3	23 ± 4
Mean summer temperature (°C)	13 ± 4	13 ± 4	13 ± 4	17 ± 4	20 ± 5	14 ± 3	23 ± 3	24 ± 3
Precipitation sum winter (mm)	205 ± 110	52 ± 33	47 ± 31	449 ± 337	183 ± 164	356 ± 182	239 ± 212	685 ± 664
Precipitation sum summer (mm)	144 ± 88	183 ± 105	156 ± 86	194 ± 234	356 ± 259	81 ± 99	106 ± 127	469 ± 395
Net radiation sum winter ($W\,m^{-2}$)	46 ± 48	46 ± 31	33 ± 29	147 ± 92	150 ± 100	152 ± 141	196 ± 47	361 ± 55
Net radiation sum summer ($W\,m^{-2}$)	216 ± 35	359 ± 102	348 ± 108	473 ± 104	425 ± 78	502 ± 95	550 ± 102	437 ± 47
Mean winter air humidity (%)	86 ± 16	83 ± 19	79 ± 22	84 ± 11	79 ± 11	85 ± 18	74 ± 7	82 ± 4
Mean summer air humidity (%)	72 ± 12	71 ± 6	70 ± 6	67 ± 12	77 ± 5	50 ± 6	60 ± 8	77 ± 6

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

	Boreal humid	Boreal semiarid		Temperate humid		Temperate semiarid	Mediterranean warm	Tropical humid
	Evergreen	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Evergreen	Evergreen
Latitude (°)	58 ± 7	59 ± 5	61 ± 5	44 ± 8	44 ± 9	44 ± 2	40 ± 4	14 ± 8
Max LAI ($m^2 m^{-2}$)	4.1 ± 3.0	3.4 ± 1.8	3.5 ± 1.5	7 ± 2.9	6.1 ± 3.5	1.8 ± 1.0	3.5 ± 1.2	5.2 ± 1.2
Tree height (m)	14 ± 7	8 ± 2	19 ± 5	20 ± 12	19 ± 7	10 ± 5	12 ± 8	28 ± 9
Basal area ($m^2 ha^{-1}$)	28 ± 12	26 ± 10	28 ± 4	42 ± 24	31 ± 15	8 ± 2	24 ± 14	23 ± 13
Tree density (number ha^{-1})	3767 ± 5652	4230 ± 3018	1451 ± 720	1399 ± 1985	1723 ± 2439	506 ± 326	2136 ± 2815	385 ± 221
Stand age (years)	72 ± 52	121 ± 67	78 ± 31	91 ± 141	75 ± 50	94 ± 86	45 ± 34	>100
Aboveground biomass ($g C m^{-2}$)	5761 ± 3708	4766 ± 2498	7609 ± 2438	14 934 ± 13 562	10 882 ± 5670	6283 ± 5554	5947 ± 1808	11 389 ± 5824
Belowground biomass ($g C m^{-2}$)	1388 ± 836	1604 ± 925	1352 ± 645	4626 ± 4673	2565 ± 2609	2238 ± 1728	3247 ± 2212	2925 ± 2284

The values are the mean ± the standard deviation of the observed values for the sites included in the CO_2-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 [$P<0.01$ for GPP = f(temperature) × f(precipitation), where f 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

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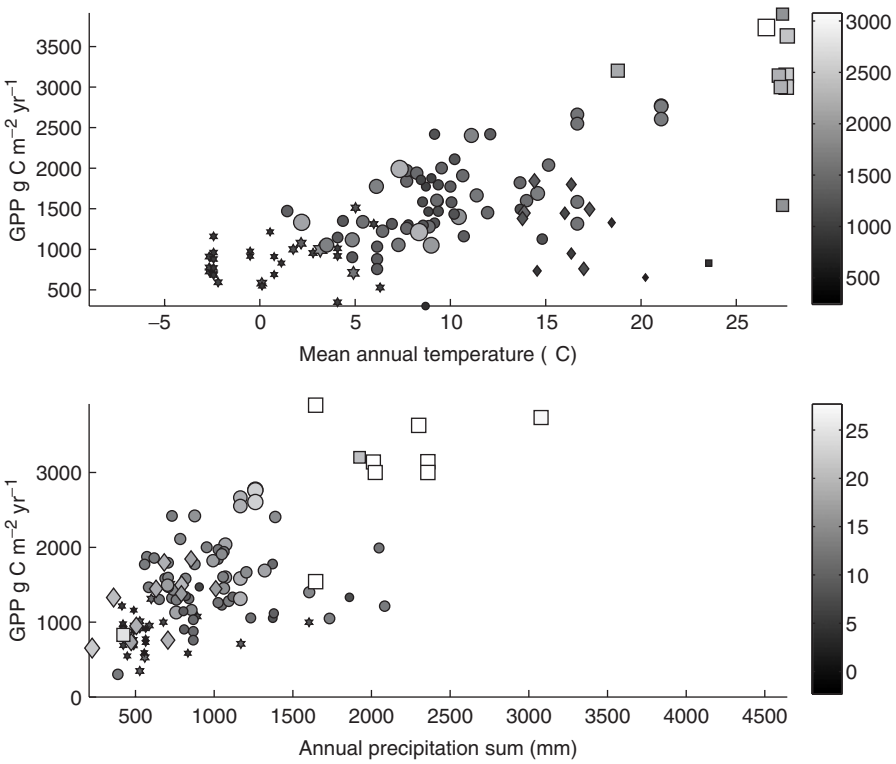

Fig. 3 The top panel shows the gross primary production (GPP) according to the mean annual temperature, the size and color of the marker is a measure for the annual precipitation sum (mm). The bottom panel shows the GPP according to the annual precipitation sum, the size and color of the marker is a measure for the mean annual temperature (°C). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

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(precipitation), 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

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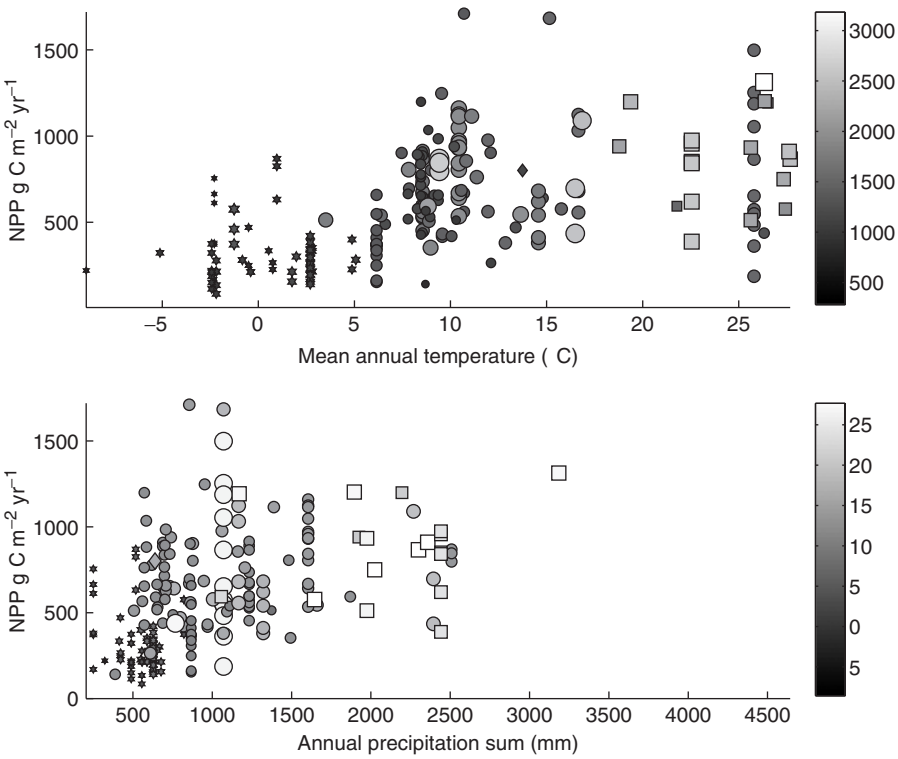

Fig. 4 The top panel shows the net primary production (NPP) according to the mean annual temperature, the size and color of the marker is a measure for the annual precipitation sum (mm). The bottom panel shows the gross primary production (GPP) according to the annual precipitation sum, the size and 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-CO_2 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 $5 \pm 1\%$ of the variability in NEP [$P = 0.03$ for NEP = f(temperature) $\times$ f(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 CO_2 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 CO_2 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 CO_2 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). Our

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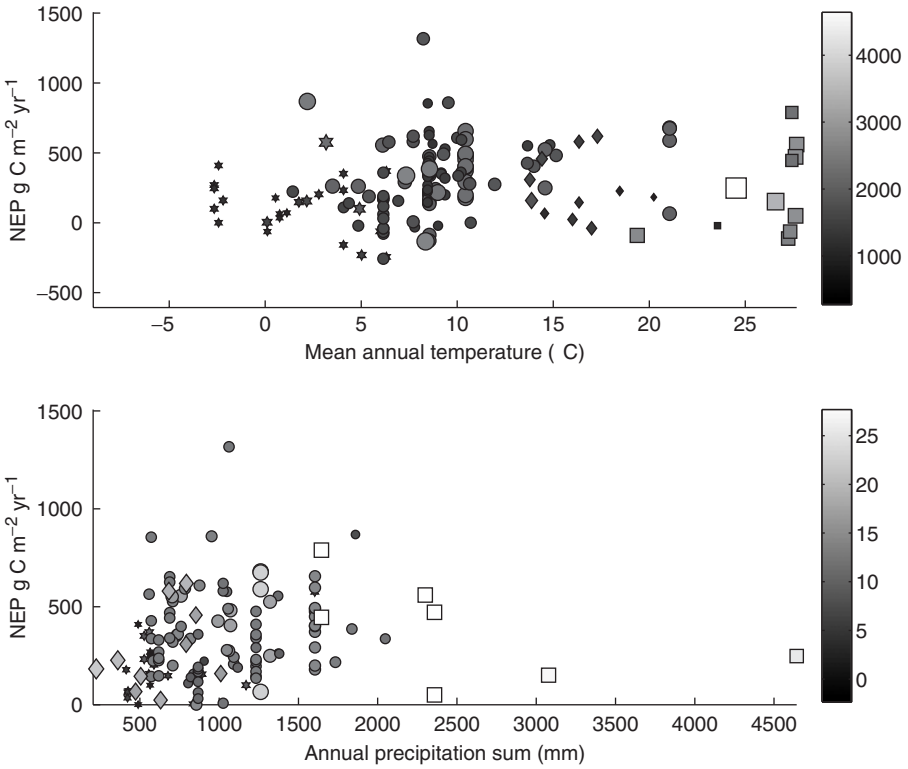

Fig. 5 The top panel shows the net ecosystem production (NEP) according to the mean annual temperature, the size and color of the marker is a measure for the annual precipitation sum (mm). The bottom panel shows the NEP according to the annual precipitation sum, the size and color of the marker is a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

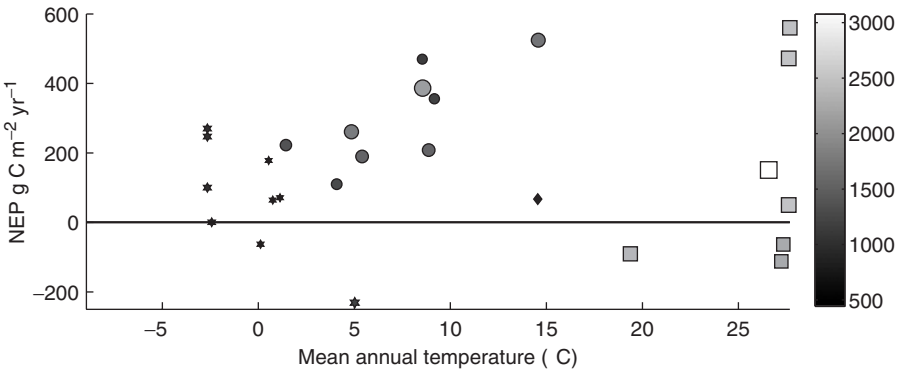

Fig. 6 Global relationship between net ecosystem production (NEP) and mean annual temperature in unmanaged forests. The size and color of the marker is a measure for the annual precipitation sum (mm). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

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).

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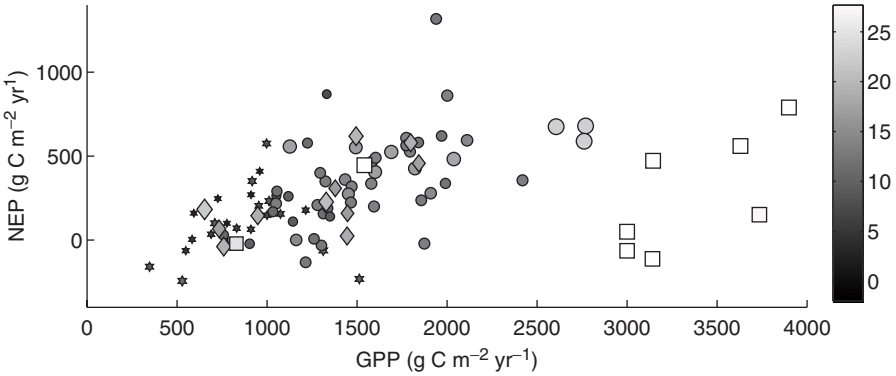

Fig. 7 Relationship between net ecosystem production (NEP) and gross primary production (GPP) across biomes. The size and color of the marker is a measure for the mean annual temperature (°C). Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

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 × 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;

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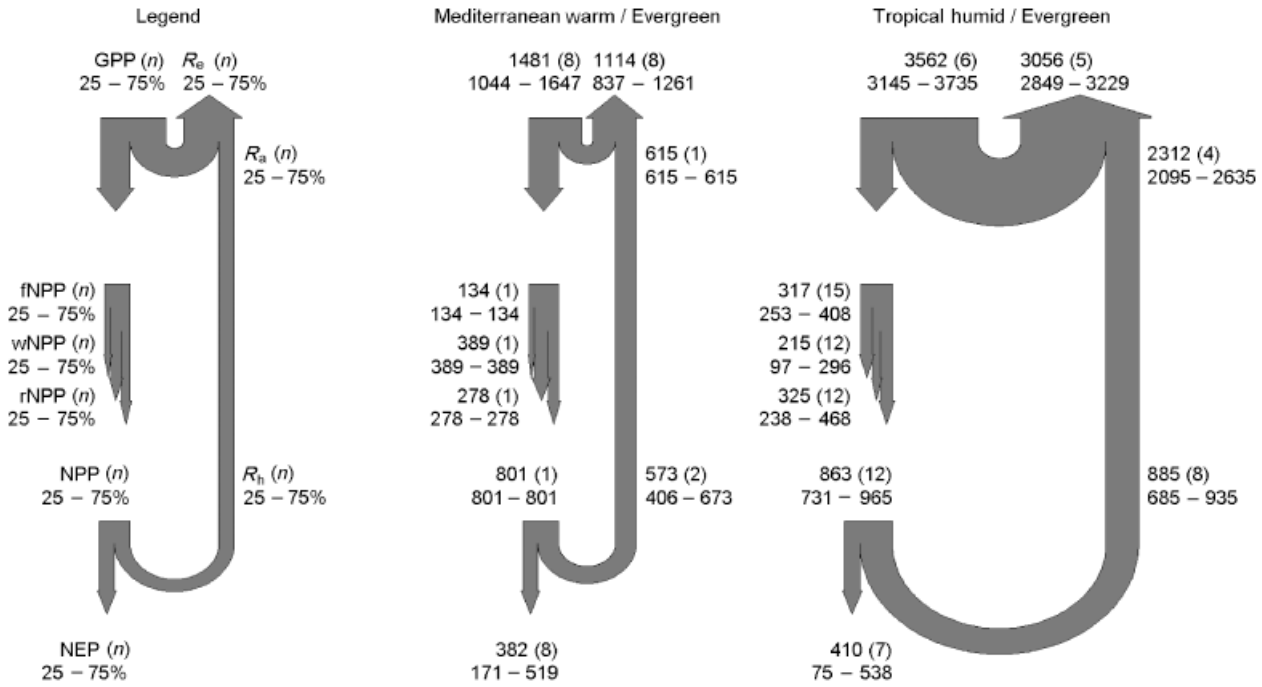

Fig. 8 Observed CO_2 balance for the mediterranean warm and tropical humid biome. These CO_2 balances were not closed and therefore the identities given by Eqns (1)–(4) do not apply. The width of the arrows is proportional to the fluxes and all units are in $g\,C\,m^{-2}\,yr^{-1}$, (*n*) refers to the 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.

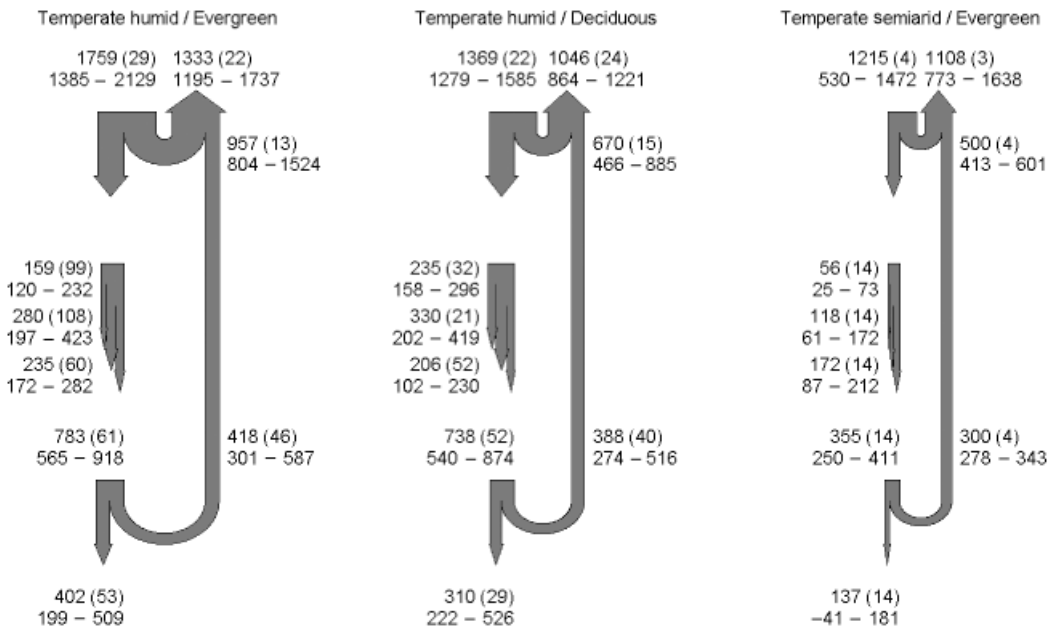

Fig. 9 Observed CO_2 balance for the temperate biomes. These CO_2 balances were not closed and therefore the identities given by Eqns (1)–(4) do not apply. The width of the arrows is proportional to the fluxes and all units are in $g\,C\,m^{-2}\,yr^{-1}$. The legend of the figures is given in Fig. 8. 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.

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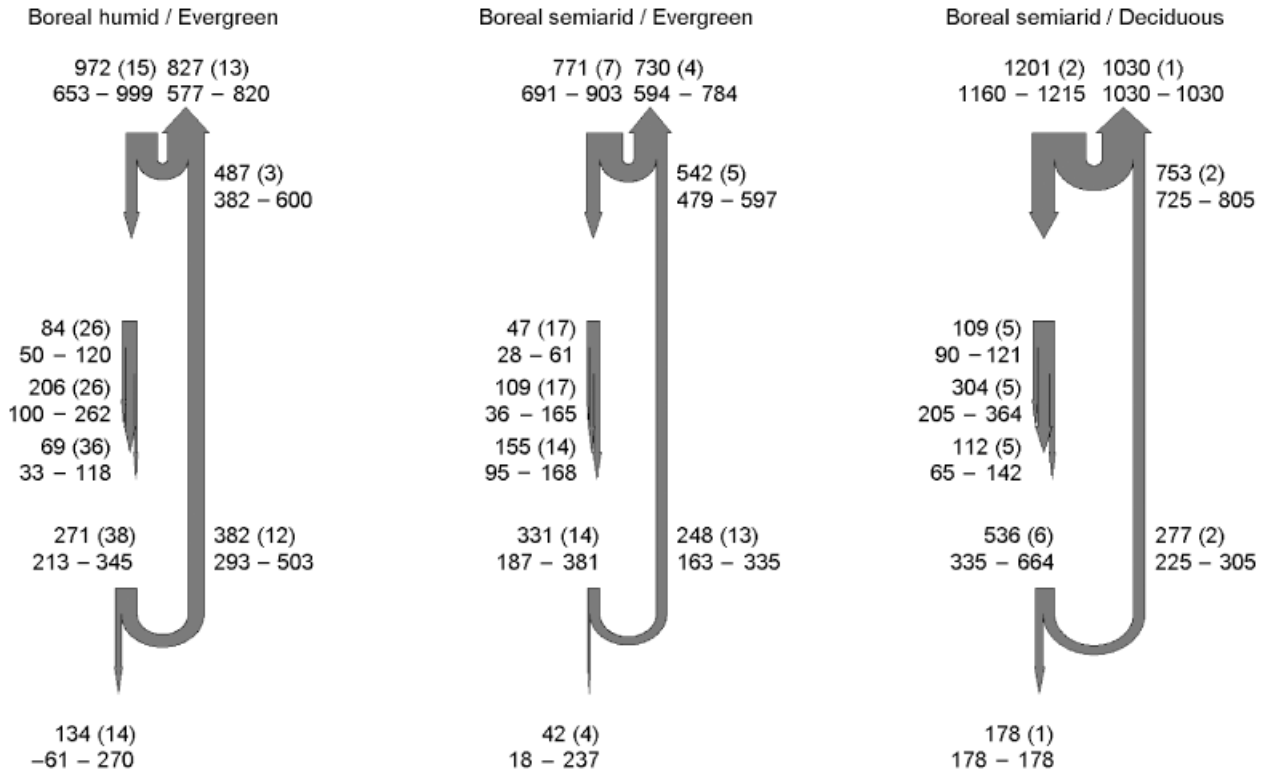

Fig. 10 Observed CO_2 balance for boreal biomes. These CO_2 balances were not closed and therefore the identities given by Eqns (1)–(4) do not apply. The width of the arrows is proportional to the fluxes and all units are in $g\,C\,m^{-2}\,yr^{-1}$. The legend of the figures is given in Fig. 8. Flux 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-CO_2 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 CO_2 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 semiarid forests are close to a CO_2-neutral state, which means that an equal amount of CO_2 that was taken up by photosynthesis is released by auto- and heterotrophic respiration (Fig. 9). In temperate humid deciduous and temperate semiarid 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 semiarid evergreen forests. However, the boreal semiarid 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 semiarid deciduous and tropical humid in a second group and boreal semiarid evergreen and temperate semiarid 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

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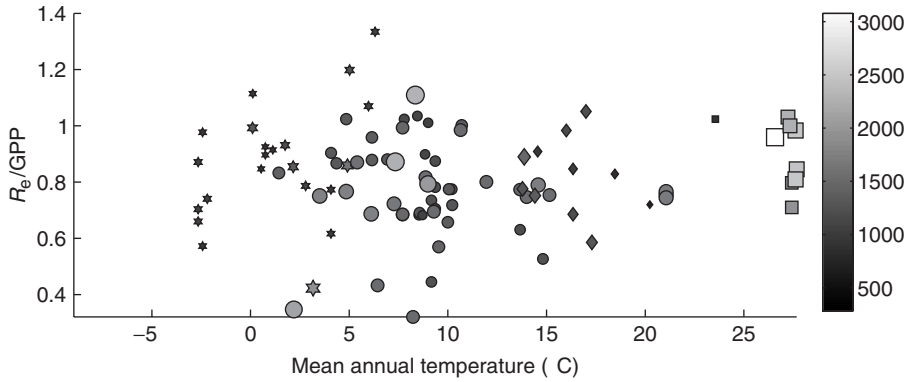

Fig. 11 Global patterns in R_e/gross primary production (GPP) according to the mean annual temperature and annual precipitation sum. The size and the color of the marker are measures for the absolute flux value. Stars, boreal; circles, temperate; diamonds, Mediterranean; and squares, tropical forests.

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 CO_2 balance. In Figs 8–10, weighted mean CO_2-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 CO_2 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 R_a 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 CO_2 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 CO_2 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)

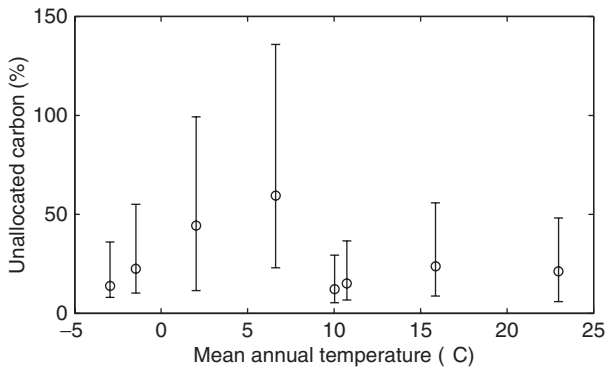

Fig. 12 Relationship between the unallocated carbon, calculated as the sum of the closure terms for gross primary production (GPP), net primary production (NPP), net ecosystem production (NEP), R_e, R_a and R_h and the mean annual temperature. Biomes from left to right: boreal semiarid deciduous, boreal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

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 CO_2 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 CO_2 balances and to estimate regional and global carbon budgets more accurately than currently possible.

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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

Plot information		
Plot name	Text	Name of the plot
Biome	Text	Biome according to US Department of Agriculture (1999)
Growth strategy	Text	Evergreen, deciduous or mixed
Growth form	Text	Needle-leaved, broadleaved or mixed
Tree species	Text	Dominant tree species
Tree species	Text	Co-dominant tree species
Latitude	Number	Latitude in decimal degrees
Longitude	Number	Longitude in decimal degrees
Elevation	Number	Elevation above sea level in m
Management	Text	Relevant information on management and disturbance
Observed stand characteristics		
Basal area	Number	Basal area in $m^{-2}\,ha^{-1}$
Diameter	Number	Diameter at breast height in m
Height	Number	Mean tree height in m
Density	Number	Stand density in number of trees.ha^{-1}
Age	Number	Age of the dominant trees in years
LAI	Number	Maximal LAI in $m^2\,m^{-2}$
Method	Text	Description of the method used to determine LAI
Observed stand biomass		
Foliar biomass	Number	Foliar biomass in $g\,C\,m^{-2}$
Branch biomass	Number	Branch biomass in $g\,C\,m^{-2}$
Stem biomass	Number	Stem biomass in $g\,C\,m^{-2}$
Stump biomass	Number	Stump biomass in $g\,C\,m^{-2}$
Coarse root biomass	Number	Coarse root biomass in $g\,C\,m^{-2}$
Fine root biomass	Number	Fine root biomass in $g\,C\,m^{-2}$
Aboveground biomass	Number	Total aboveground biomass in $g\,C\,m^{-2}$
Belowground biomass	Number	Total belowground biomass in $g\,C\,m^{-2}$
Observed stand climate		
Temperature	Number	Mean annual temperature in °C
Precipitation	Number	Total annual precipitation in mm
Evaporation	Number	Total annual evaporation in mm
APAR	Number	Total annual absorbed radiation in $MJ\,m^{-2}$
PAR	Number	Total annual incident radiation in $MJ\,m^{-2}$
IPAR	Number	Total annual intercepted radiation in $MJ\,m^{-2}$
Observed flux estimate		
GPP	Number	Ecosystem GPP in $g\,C\,m^{-2}\,yr^{-1}$
NEP	Number	Ecosystem NEP in $g\,C\,m^{-2}\,yr^{-1}$
R_e	Number	Ecosystem Re $g\,C\,m^{-2}\,yr^{-1}$
NPP wood	Number	NPP of the stems/wood $g\,C\,m^{-2}\,yr^{-1}$
NPP foliage	Number	NPP of the foliage $g\,C\,m^{-2}\,yr^{-1}$
NPP branch	Number	NPP of the branches $g\,C\,m^{-2}\,yr^{-1}$
NPP stumps	Number	NPP of the stumps $g\,C\,m^{-2}\,yr^{-1}$
NPP coarse	Number	NPP of the coarse roots $g\,C\,m^{-2}\,yr^{-1}$
NPP fine	Number	NPP of the fine roots $g\,C\,m^{-2}\,yr^{-1}$
NPP repro	Number	NPP of the reproductive organs $g\,C\,m^{-2}\,yr^{-1}$
NPP herbi	Number	NPP of the herbivory $g\,C\,m^{-2}\,yr^{-1}$
NPP under	Number	NPP of the understory $g\,C\,m^{-2}\,yr^{-1}$
NPP VOC	Number	NPP of the VOC's $g\,C\,m^{-2}\,yr^{-1}$
NPP exudates	Number	NPP of the root exudates $g\,C\,m^{-2}\,yr^{-1}$
R_s	Number	Total soil respiration $g\,C\,m^{-2}\,yr^{-1}$
R_a	Number	Autotrophic respiration $g\,C\,m^{-2}\,yr^{-1}$
R_h	Number	Heterotrophic respiration $g\,C\,m^{-2}\,yr^{-1}$
Methodology	Text	Description of the different methodologies that were used to estimate the fluxes
Site climate and environment		
Temperature	Number	Monthly mean annual temperature in °C (CRU, 2006)
Precipitation	Number	Monthly precipitation sum in mm CRU (2006)
Air humidity	Number	Monthly air humidity CRU (2006)
Cloud cover	Number	Monthly average cloud cover (%) CRU (2006)
Number of wet days	Number	Monthly sum of wet days CRU (2006)
Long wave radiation (1)	Number	Monthly absorbed downward longwave radiation in $W\,m^{-2}$ Krinner *et al.* (2005)
Long wave radiation (2)	Number	Monthly net surface longwave radiation in $W\,m^{-2}$ Krinner *et al.* (2005)
Solar radiation	Number	Monthly solar radiation in $W\,m^{-2}$ Krinner *et al.* (2005)
Soil moisture	Number	Monthly soil moisture in mm Krinner *et al.* (2005)
Dry deposition	Number	Mean monthly dry deposition of $N\,g\,N\,m^{-2}$ $month^{-1}$ Krinner *et al.* (2005)
Wet deposition	Number	Mean monthly wet deposition of $N\,g\,N\,m^{-2}$ $month^{-1}$ Krinner *et al.* (2005)
NH*x* deposition	Number	Mean monthly NHx deposition of $N\,g\,N\,m^{-2}$ $month^{-1}$ Krinner *et al.* (2005)
NDVI	Number	Mean 14-day NDVI Tucker *et al.* (2005)

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