



Relationships between net primary productivity and stand age for several forest types and their influence on China's carbon balance

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ABSTRACT

Affected by natural and anthropogenic disturbances such as forest fires, insect-induced mortality and harvesting, forest stand age plays an important role in determining the distribution of carbon pools and fluxes in a variety of forest ecosystems. An improved understanding of the relationship between net primary productivity (NPP) and stand age (i.e., age-related increase and decline in forest productivity) is essential for the simulation and prediction of the global carbon cycle at annual, decadal, centennial, or even longer temporal scales. In this paper, we developed functions describing the relationship between national mean NPP and stand age using stand age information derived from forest inventory data and NPP simulated by the BEPS (Boreal Ecosystem Productivity Simulator) model in 2001. Due to differences in ecobiophysical characteristics of different forest types, NPP-age equations were developed for five typical forest ecosystems in China (deciduous needleleaf forest (DNF), evergreen needleleaf forest in tropic and subtropical zones (ENF-S), deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), and mixed broadleaf forest (MBF)). For DNF, ENF-S, EBF, and MBF, changes in NPP with age were well fitted with a common non-linear function, with R^2 values equal to 0.90, 0.75, 0.66, and 0.67, respectively. In contrast, a second order polynomial was best suitable for simulating the change of NPP for DBF, with an R^2 value of 0.79. The timing and magnitude of the maximum NPP varied with forest types. DNF, EBF, and MBF reached the peak NPP at the age of 54, 40, and 32 years, respectively, while the NPP of ENF-S maximizes at the age of 13 years. The highest NPP of DBF appeared at 122 years. NPP was generally lower in older stands with the exception of DBF, and this particular finding runs counter to the paradigm of age-related decline in forest growth.

Evaluation based on measurements of NPP and stand age at the plot-level demonstrates the reliability and applicability of the fitted NPP-age relationships. These relationships were used to replace the normalized NPP-age relationship used in the original InTEC (Integrated Terrestrial Ecosystem Carbon) model, to improve the accuracy of estimated carbon balance for China's forest ecosystems. With the revised NPP-age relationship, the InTEC model simulated a larger carbon source from 1950–1980 and a larger carbon sink from 1985–2001 for China's forests than the original InTEC model did because of the modification to the age-related carbon dynamics in forests. This finding confirms the importance of considering the dynamics of NPP related to forest age in estimating regional and global terrestrial carbon budgets.

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1. Introduction

Forests are locally and globally important ecosystems that provide habitat, timber resources, carbon storage and recreational opportunities (Hicke et al., 2007). As a key parameter quantifying the exchanges of energy and mass by vegetation (Running and Coughlan, 1988), net primary productivity (NPP) is defined as the difference between accumulative photosynthesis and accumulative autotrophic

respiration by green plants per unit of time and space (Lieth and Whittaker, 1975). In general, forest ecosystem NPP accounts for 35% of global and 65% of terrestrial ecosystem NPP (Gower et al., 1996; Waring and Schlesinger, 1985), respectively. A slight change in NPP of forests will significantly influence atmospheric CO₂ concentration and, consequently, climate change. Therefore, it is important to quantify carbon storage and fluxes for different vegetation types and developmental stages and to analyze mechanisms involved in carbon cycling to better monitor the processes that regulate the uptake, storage, and release of CO₂ (Law et al., 2001). A forest ecosystem's net carbon accumulation over the decadal time frame depends more on disturbances than on climate and CO₂ concentration (Chapin et al., 2002; Pregitzer and Euskirchen, 2004). Carbon stored in forest ecosystems over the long term will be released rapidly and in considerable amounts into the atmosphere following disturbances (Page et al., 2002). Forest age (i.e., time since disturbances) and structure are critical factors determining forest ecosystem carbon storage and fluxes (Turner et al., 1995; Caspersen et al., 2000; Law et al., 1999, 2001; Song and Woodcock, 2003; Litvak et al., 2003; Kashian et al., 2006). Many components of the forest carbon cycle are related to forest age, including biomass of coarse woody debris (Bond-Lamberty et al., 2002), stand water use (Delzon and Loustau, 2005), soil carbon (Peltoniemi et al., 2004), live biomass increment and litter decomposition (Bradford et al., 2008), size structure (Sano, 1997; Hoshino et al., 2001), NPP (Gower et al., 1996; Ryan et al., 1997; Murty and McMurtrie, 2000; Chen et al., 2002), net ecosystem productivity (NEP)/net biome productivity (Litvak et al., 2003; Song and Woodcock, 2003), and biophysical properties (McMillan and Goulden, 2008). Due to the high variation in stand age, efforts to estimate ecosystem carbon fluxes for large areas must take into account forest age structure (Murty and McMurtrie, 2000; Song and Woodcock, 2003), especially the quantitative analysis of forest NPP changes with stand age among forest types (Chen et al., 2003). However, because of difficulties in obtaining long-term observations of disturbances, quantitative research on the temporal trends of carbon balance related to stand age at regional and/or global scales is rare. Most process-based models ignored the effects of disturbances on NPP and terrestrial carbon sequestration (e.g. Harmon, 2001; Euskirchen et al., 2002; Dean et al., 2004; Thornley and Cannell, 2004), mainly because of the lack of spatial data on NPP and age distributions (Chen et al., 2002).

An improved understanding of carbon dynamics of vegetation and soils by considering stand age is needed for regional and national carbon balance assessments, particularly as major changes in the forest carbon stock are related to changes in the age class distribution (Peltoniemi et al., 2004). Most evaluations of forest carbon cycling and storage were based on age classes or only one forest type. Relationships between carbon cycle components and stand age have typically been developed for single-species, even-aged forests (Pearson et al., 1987), which indicated that biomass accumulation peaked in 40–60 years. Pregitzer and Euskirchen (2004) performed a meta-analysis of published chronosequence data to explore the dependence of forest NPP on age by age classes for tropical, temperate, and boreal forest biomes. They found that peak NPP in boreal forest occurred in the 71–120 year age class. However, large uncertainties exist for the collected data owing to varying methodologies used by a multitude of investigators and stand ages roughly grouped into five age classes (Pregitzer and Euskirchen, 2004). By analyzing the relationship between forest carbon fluxes and age, Bradford et al. (2008) found that all components of the carbon cycle increased with stand age except the net ecosystem carbon balance, and the relationship of NPP-stand age behaved as an exponential function for all forest plots in three sites of the southern Rocky Mountains. A large number of inventory plots were used in Oregon and Northern California to create a peak function (three parameters, log-normal) to fit the relationship

of NPP and stand age. This approach indicated that the maximum NPP of forests approached between 60 and 155 years (Hudiburg et al., 2009). Chen et al. (2002) used stand yield tables to develop a non-linear function of NPP against age for Canadian boreal black spruce forest, with coefficients in the function related to the site index (tree height of a 50-year old stand). It is more important to explore the relationship between NPP and stand age among a variety of forest ecosystems. Previous studies demonstrated that forest NPP declines with increasing stand age (Gower et al., 1996; Murty and McMurtrie, 2000; Smith and Long, 2001; Zaehle et al., 2006). But very few have shown that the old-growth forests serve as a global carbon source (Carey et al., 2001; Acker et al., 2002; Knohl et al., 2003; Law et al., 2003; Desai et al., 2005; Zhou et al., 2006; Luysaert et al., 2008). Meanwhile, other studies found that the decrease in NPP with age was not general and decline of NPP was not markable in old stands in some ecoregions (Hudiburg et al., 2009).

The NPP-age function can be generalized in a process-based model for simulating regional terrestrial ecosystem carbon dynamics by incorporating forest type, climate, and disturbance effects (Chen et al., 2003; Desai et al., 2008). Numerous models have been used to simulate forest ecosystem processes (Cao et al., 2003; Piao et al., 2005), but these studies analyzed NPP variations of China's forests only caused by changes in climate or atmospheric CO₂ concentration. To our knowledge, the integrated effects on NPP and carbon sequestration by China's forests of climate variability, CO₂ fertilization, and stand age have not been thoroughly examined. Wang et al. (2007) used the Canadian NPP-age function with coefficients in the function adjusted according to mean annual air temperature, to explore the patterns of carbon sinks and sources in China's forests from 1901–2001. Therefore, development of new NPP-age relationships suitable for China's forest ecosystems is needed to improve modeling accuracy.

The objectives of this study were to 1) develop generalized functions describing the relationship between NPP and stand age for several typical forest ecosystems in China through the use of forest age information derived from national inventory data and NPP simulated by the Boreal Ecosystem Productivity Simulator (BEPS) model and 2) investigate the effect of the newly refined NPP-age relationship on the estimation of the carbon budgets of China's forests for the past 100 years.

2. Data and methods

2.1. Spatially explicit data

A land cover map of China in 2001 was used to parameterize the models (BEPS and InTEC) for each pixel. This map was produced from a nationwide land-use map at a 30-m resolution interpreted from Landsat TM images and a 1:2 500 000 vegetation map (Liu et al., 2005; Feng et al., 2007). The fused land cover map had high accuracy after validation with ground-based data (Feng, 2004). The land cover map was classified into seven forest types, including Deciduous needleleaf forest (DNF), Evergreen needleleaf forest in temperature zone (ENF-N), Evergreen needleleaf forest in tropic zone and subtropics zone (ENF-S), Deciduous broadleaf forest (DBF), Evergreen broadleaf forest (EBF), Mixed forest: ENF and DBF (MF), and Mixed broadleaf forest: DBF and EBF (MBF). The representation species of DNF, ENF-S, DBF and EBF were boreal/temperate *Larix* forest, subtropical *Pinus massoniana* forest, montane *Populus-Betula* deciduous forest, Sclerophyllous evergreen *Quercus* forest, respectively. Fig. 1 shows the spatial distribution of forest ecosystems in China. The forested area identified by remote sensing data covers 1.39 million km², accounting for 14.5% of the total landmass of China. This is lower than the value of 1.59 million km² published by the State Administration of Forestry

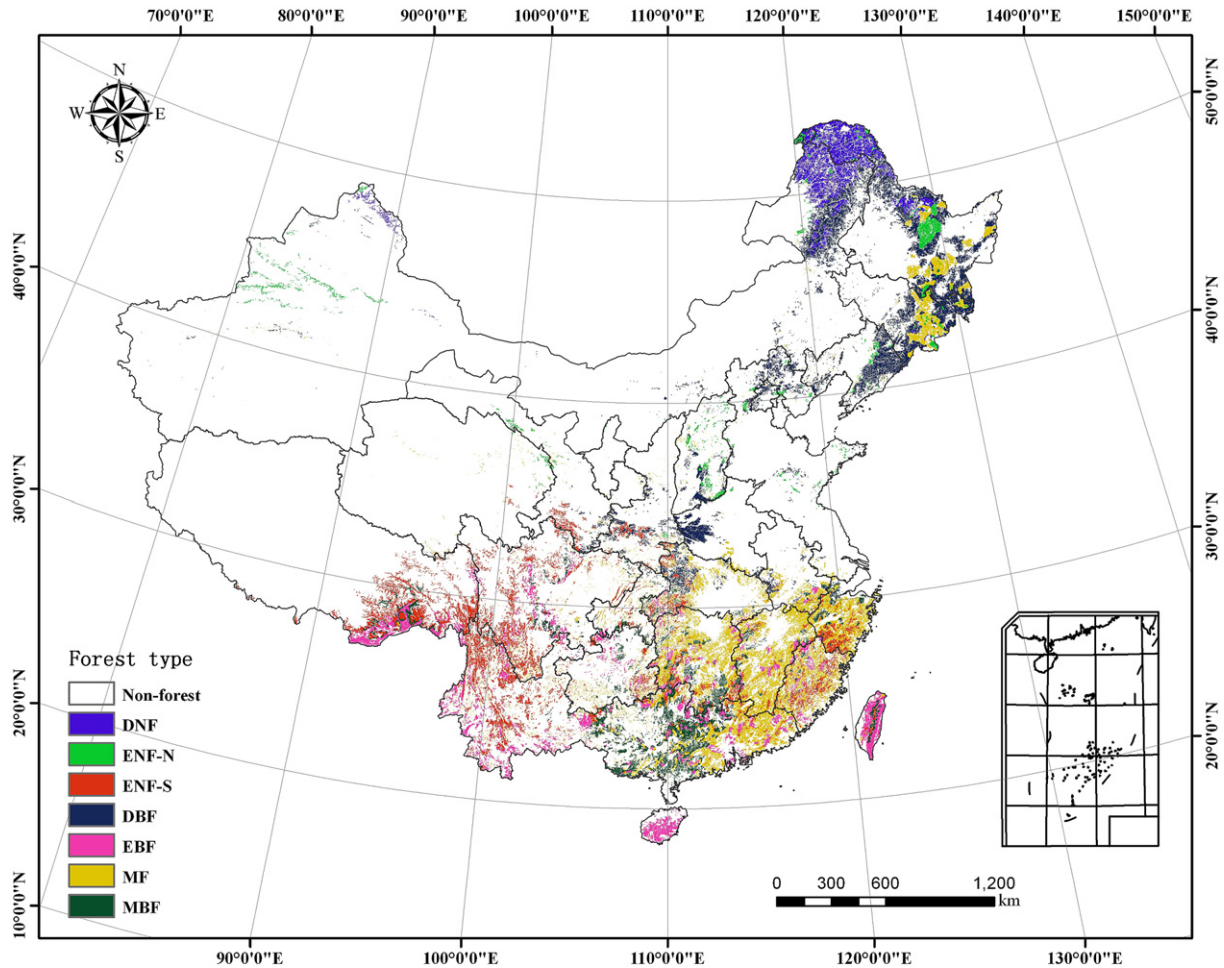


Fig. 1. Spatial distribution of forest ecosystems in China in 2001.

report (State Forestry Administration, 1999), because of differences in defining forest density.

A China-wide annual NPP map for 2001 was used for this study. The map was produced by Feng et al. (2007) using the daily BEPS model. BEPS is a process-based, remote sensing-driven ecological model, modified from FOREST-BGC (Running and Coughlan, 1988) and designed to simulate NPP of terrestrial ecosystems at regional/global scales (Liu et al., 1997, 1999). Inputs into BEPS include land cover, leaf area index (LAI), available water capacity, and daily meteorological variables (maximum and minimum temperatures, precipitation, relative humidity, and incoming solar radiation) (Liu et al., 2002). The majority of all meteorological data (680 stations) were interpolated to individual 1-km pixels using ANUSPLIN (Hutchinson, 2002), a method that has proven to be more accurate than other interpolation methods, including GRDS Surfer and ARC GRID (Price et al., 2000; Feng, 2004). The remaining data were used to validate the accuracy of the climate map (Feng et al., 2007). The BEPS model has been used to simulate NPP of terrestrial ecosystems for many regions (Liu et al., 1997, 2002; Matsushita and Tamura, 2002; Feng et al., 2007) extensively evaluated at the site level in China (Sun et al., 2004; Zhou et al., 2007; Zheng et al., 2007; Chen et al., 2007). BEPS does not require information about forest age but it can simulate the variations of forest NPP with stand ages indirectly through remotely sensed LAI variation with age. A nationwide forest stand age map in 2001 was constructed from the fourth national forest inventory datasets taken between 1989 and 1993 in 32 provinces (FRSC, 1994; Wang et al., 2007).

2.2. Methods

2.2.1. Developing the functions of net primary productivity and stand age

Following the methodology used in the InTEC (Integrated Terrestrial Ecosystem Carbon) model (Chen et al., 2000c), the relationship between NPP and stand age was fitted as (Chen et al., 2003):

$$NPP(\text{age}) = A \left(1 + \frac{b(\text{age}/c)^d - 1}{\exp(\text{age}/c)} \right) \quad (1)$$

where parameter A determines the general magnitude of NPP, b , c , and d are parameters determining the rate of NPP changing with age and were initially found to be related to the site index (Chen et al., 2003). Due to insufficient site index data for the application of this relationship to large areas, the site index was replaced with the mean annual air temperature (T_a) (Chen et al., 2003; Wang et al., 2007). Originally, the parameters b , c and d in Eq. (1) as functions of T_a were derived from maps of annual mean T_a and annual total NPP at a known age (80 years) in 1994 (Chen et al., 2003). In regional applications of this relationship, it is assumed that these parameters will be solely determined by T_a and do not vary with forest types. In Chen et al. (2003), Eq. (1) was normalized against the maximum NPP at a given T_a to allow it to vary between 0 and 1. The absolute value of NPP at a given age was iteratively

simulated as the product of the normalized productivity of forests at different ages, initial NPP and interannual variability of NPP caused by variations of climate, atmospheric concentration and nitrogen deposition. The initial NPP was tuned according to NPP in a recent reference year modeled using the BEPS model (see Section 2.2.2).

T_a in Canada is considerably lower than that in China, so we found that the shape of the normalized forests' NPP curve at $T_a > 15^\circ\text{C}$ was considerably distorted. To address this problem, we analyzed NPP-age relationships for typical forest ecosystems in China using NPP simulated by the BEPS model and stand age derived from inventory data in 2001. The ideal approach to understanding age-dependent trends in NPP involves the simultaneous study of a carefully selected age sequence of stands—the so-called chronosequence approach. However, no long-term inventory NPP data is available in China. The chronosequence approach is inevitably impractical at regional scales due to the cost of establishing the many replicate chronosequences. The maps of NPP simulated using the BEPS model and an inventory stand age in 2001 were to investigate the dependence of NPP on age for China's forests at regional scales. Due to the uncertainties in simulated NPP and inventory and their relatively coarse resolutions, the correlations of NPP with ages identified in this way may include some uncertainties. Nevertheless, they can be used as the first order of approximations of NPP changes with ages to constrain the uncertainties in simulated carbon balance at regional scales.

For each forest type, the mean value of NPP for a specific age was calculated based on NPP and the stand-age map in 2001. If there were fewer than 10 pixels for a specific age of a forest type, the age was rejected, because a limited number of pixels may not represent this age group. The non-linear curve tool of Origin 7.5 software was used to fit Eq. (1) according to mean NPP and stand age. If Eq. (1) was not the best function for describing the changes in NPP with age, other functions were employed.

2.2.2. Application for carbon sinks and sources of China's forests

The processes driving the forest carbon cycle vary with stand age and forest types (Hudiburg et al., 2009), and estimates of regional carbon fluxes from modeling efforts depend in large part on our ability to accurately characterize stand age and forest types across the region (Turner et al., 2007). Wang et al. (2007) used the InTEC model to calculate the distribution of annual carbon sources and sinks of China's forest ecosystems from 1901 to 2001 using the original NPP-age curves which were constructed using Canadian data. These NPP-age curves developed in Canada may not properly represent changes of NPP with age for China's forests owing to differences in factor affecting forest growth, including climate, soil, forest species and nitrogen deposition rate. It is therefore necessary to develop NPP-age relationships suitable for applications in China's forests to improve estimate of carbon budget. The refined NPP-age functions will be substituted into the InTEC model to investigate the spatio-temporal distributions of carbon uptakes of China's forests.

InTEC model is a regional forest carbon-budget model that integrates the effects of disturbance (fire, insect-induced and mortality) and non-disturbance factors (growing season length and temperature, abiotic decomposition factors, annual precipitation, atmosphere CO_2 concentration, and nitrogen deposition) on carbon sequestration by forests (Chen et al., 2000a,b,c). It includes three main modules: (1) sensitivities of the gross primary productivity (GPP) to various non-disturbance factors through scaling the Farquhar's leaf-level photosynthesis model (Farquhar et al., 1980) up to the canopy level using a sunlit-shaded leaf stratification approach (2) a modified soil biogeochemical model based on CENTURY (Parton et al., 1993) with forest-related detritus pools added to the model and (3) a set of empirical NPP-age relationships to represent the regrowth pattern of forests following disturbances. An NPP map

in a reference year (2001) and a forest age map are required model inputs. The annual NPP value in 2001 was used as the benchmark to determine the initial NPP. After the initialization of NPP, the model was run forward to simulate annual NPP and carbon budget during the period from 1901 to 2001 with the consideration of the integrated effects of forest age and non-disturbance factors on forest carbon cycling. The inputs to the model include spatially distributed data of climate, soil texture, nitrogen deposition and vegetation parameters derived from remote sensing (LAI and land cover). The spatial distribution of the model was set as 1 km in this study. Detailed descriptions of the InTEC model structure, variables, and data processing methods are referred to Chen et al. (2000a,b,c). The InTEC model has been used in China in several studies (Wang et al., 2007; Shao et al., 2007; Ju and Chen, 2008).

3. Results

3.1. Validation of NPP map

The simulated NPP by BEPS was validated using NPP database created by Luo (1996) based on field measurements, which has been widely used to validate forest NPP, such as Pan et al. (2004), Feng et al. (2007), Peng et al. (2009). For each plot, the information on latitude, longitude, elevation, forest type, stand age, forest components' biomass, and corresponding NPP was available. Table 1 shows the comparison of simulated NPP with Luo's NPP data for different provinces. The simulated NPP was in good agreement with Luo's NPP, with a correlation coefficient of 0.77 ($P < 0.01$). Variability of simulated NPP among different forest types was slightly lower than that of observed NPP.

3.2. Spatial pattern of simulated net primary productivity

The simulated annual mean NPP of China's forest ecosystems in this study was $562\text{ g C m}^{-2}\text{ yr}^{-1}$. Total NPP was $0.78\text{ Pg C (1 Pg} = 10^{15}\text{ g)}$,

Table 1

Comparison of simulation NPP with ground-based NPP for four forest types (Unit: $\text{g C m}^{-2}\text{ yr}^{-1}$).

| Forest Type | Sample accounts | Province | Ground-based NPP | | Simulation NPP | |
|-------------|-----------------|----------------|------------------|-------|----------------|-------|
| | | | Mean | Std | Mean | Std |
| DNF | 8 | Heilongjiang | 401.8 | 120.1 | 424.7 | 48.1 |
| | 9 | Xinjiang | 458.0 | 107.7 | 436.0 | 45.3 |
| | 17 | Inner Mongolia | 374.1 | 93.8 | 152.4 | 88.9 |
| ENF-S | 9 | Anhui | 677.3 | 223.4 | 444.6 | 156.5 |
| | 18 | Fujian | 776.2 | 220.1 | 678.8 | 149.6 |
| | 9 | Guangdong | 696.6 | 195.8 | 642.3 | 158.9 |
| | 36 | Guangxi | 609.8 | 228.4 | 559.8 | 171.1 |
| | 54 | Guizhou | 565.3 | 197.3 | 537.3 | 183.6 |
| | 12 | Jiangxi | 863.5 | 237.7 | 595.6 | 152.5 |
| | 13 | Sichuan | 455.0 | 174.6 | 356.1 | 192.5 |
| DBF | 16 | Tibet | 484.0 | 153.8 | 308.0 | 217.9 |
| | 43 | Yunnan | 450.9 | 133.3 | 607.9 | 231.0 |
| | 12 | Hebei | 492.9 | 72.3 | 382.8 | 139.4 |
| | 29 | Heilongjiang | 538.3 | 178.4 | 509.4 | 135.3 |
| | 26 | Jilin | 652.6 | 222.3 | 459.3 | 189.1 |
| | 9 | Inner Mongolia | 549.6 | 219.6 | 444.9 | 154.4 |
| | 170 | Shanxi | 431.2 | 128.8 | 339.3 | 143.9 |
| | 12 | Sichuan | 482.6 | 146.2 | 612.2 | 146.7 |
| | 9 | Xinjiang | 240.9 | 105.5 | 166.9 | 92.1 |
| | 21 | Guangxi | 955.6 | 214.8 | 858.9 | 178.8 |
| EBF | 100 | Guizhou | 674.5 | 211.6 | 749.8 | 188.4 |
| | 43 | Hunan | 948.0 | 189.9 | 773.8 | 166.3 |
| | 11 | Tibet | 560.0 | 118.5 | 425.2 | 313.4 |
| | 31 | Yunnan | 654.7 | 215.4 | 927.7 | 373.9 |
| MBF | 6 | Guizhou | 723.8 | 181.7 | 688.3 | 216.1 |

accounting for 35% of national total NPP for all terrestrial ecosystems (except water bodies, $2.235 \text{ Pg C yr}^{-1}$). High NPP values ($>600 \text{ g C m}^{-2} \text{ yr}^{-1}$) were mainly found in forested areas of southern China. In Tibetan and needleleaf forests of northeastern China, NPP was normally lower than $200 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Means and standard deviations of NPP for different forests are shown in Fig. 2. The productivity of broadleaf forests was generally higher than that of needleleaf forests. EBF had the highest NPP ($747 \text{ g C m}^{-2} \text{ yr}^{-1}$), which was nearly three times higher than that of ENF-N ($146 \text{ g C m}^{-2} \text{ yr}^{-1}$). Mean NPP of ENF-S was much larger than that of ENF-N but close to that of DBF. MF had a mean NPP value of $575 \text{ g C m}^{-2} \text{ yr}^{-1}$, in the between of broadleaf and needleleaf forests. Furthermore, the mean NPP of MBF was also high, second only to that of EBF.

3.3. Spatial pattern of stand age

Overall, stand age across the entire study area ranged from 1 to 307 years. In southeastern China, stand age varied from 1 to 40 years old, and forests here also had the highest productivity. Forests with stand age in excess of 120 years were located mainly in Sichuan Province. Meanwhile, forests in northeastern China were mainly between the ages of 40 and 120 years, decreasing from 100 to 120 years in western areas to 40–60 years in eastern areas.

The age class histogram of all forest ecosystems (Fig. 3) indicated that the area of different age classes exhibited notable variability. The stand age distribution peaked in the 20–40 year age class (about $56.82 \times 10^4 \text{ km}^2$), accounting for 41% of total forest area, and was twice as large as that in the 40–60 year age class. Only 0.44% of forests had age groups greater than 160 years. In general, 84% of forests were within the ages of 10–80 years, indicating that the majority of China's forests are young and mid-aged.

There were large differences in stand age structure among various forest ecosystems (Fig. 3). In the 20–40 year age class, MF accounted for a larger proportion than any other forest types, but DBF had a larger area in the 40–60 year age class. Areas of ENF-S, EBF, and MBF were larger in the 20–40 year age class than in any other age class. ENF-N accounted for a small proportion of all forest ecosystems in each age class, whose areas were generally below $1.0 \times 10^4 \text{ km}^2$. DNF's age structure was different from any other forest type, and leaned toward mature forests of 80–100 years.

3.4. Relationship between forest net primary productivity and age

Our study analyzed only five types of forest ecosystems in China, including DNF, ENF-S, DBF, EBF, and MBF. The forest types were

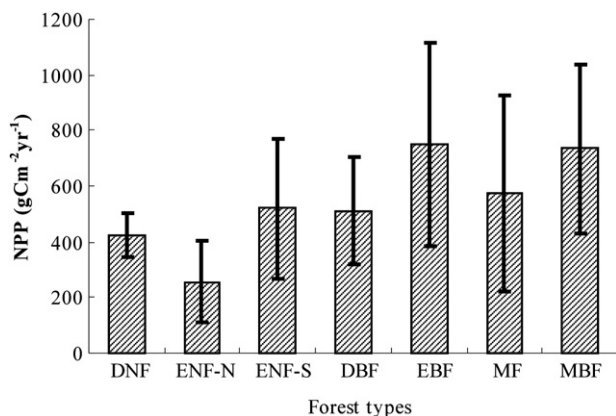


Fig. 2. Annual mean NPP of China's forest ecosystems. Error bars represent standard deviations.

determined according to the leaf form: needleleaf or broadleaf, and longevity: deciduous or evergreen.

3.4.1. Deciduous needleleaf forest

DNF was mainly distributed in the Daxing'a mountain range and a small part of Xinjiang Province (Fig. 1). After averaging for DNF pixels in 2001, annual mean temperature (MT) was $-3.4 \text{ }^\circ\text{C}$, annual total precipitation (TP) was 437 mm, and annual mean LAI (MLAI) was 2.2 (Table 2). Because the temperature in northern China was relatively low, the growing season usually ranged from the beginning of June and the end of October. In the growing season, especially the summer, daily temperature can go up to $20 \text{ }^\circ\text{C}$. The stand age ranged from 20 to 181 years on the stand age map, but a data gap existed for forests younger than 20 years. Estimation of the effects of stand age on NPP for forests younger than 20 years is important for carbon budget studies (Chen et al., 2003). With the assumption that NPP in the first growing year equals zero, a simple linear extrapolation of NPP was performed to fill the NPP gap from 1 to 19 years.

DNF's fitted equation captures 90% of NPP change with age (Table 3). As shown in Fig. 4a, NPP initially increased rapidly and reached a peak value of $462 \text{ g C m}^{-2} \text{ yr}^{-1}$ at 54 years. During the stage of rapid growth, the increment of NPP varying with age was $8 \text{ g C m}^{-2} \text{ yr}^{-1}$. The estimated mean NPP in the first 54 years was $360 \text{ g C m}^{-2} \text{ yr}^{-1}$. After the peak, NPP gradually decreased. For 181 year-old forests, the estimated NPP was $147 \text{ g C m}^{-2} \text{ yr}^{-1}$, which was just 32% of the peak value ($462 \text{ g C m}^{-2} \text{ yr}^{-1}$).

3.4.2. Evergreen needleleaf forest in tropic and subtropical zones

ENF-S was mainly located in southeastern China, Tibetan Autonomous Region, and Yunnan Province (Fig. 1). For this type of forests, the MT and TP in 2001 were $10.7 \text{ }^\circ\text{C}$ and 1147 mm, respectively. Meanwhile, MLAI of ENF-S was 3.6, which was significantly larger than that of DNF (Table 2). Stand ages of ENF-S varied from 1 to 212 years.

ENF-S's fitted equation explains 75% of NPP change with age (Table 3). NPP simulated by the BEPS model showed large variations, increasing from $499 \text{ g C m}^{-2} \text{ yr}^{-1}$ at 40–50 years of age to $596 \text{ g C m}^{-2} \text{ yr}^{-1}$ at 50–60 years of age. Prior to reaching becoming 100 years old, ENF-S's NPP was larger than that of DNF at each stand age. The peak NPP of $620 \text{ g C m}^{-2} \text{ yr}^{-1}$ occurred at year 13, which was much earlier than that of DNF. ENF-S's NPP declined much faster after reaching peak than did NPP of DNF. After 140 years, the decline rate of NPP was lower. NPP just decreased by 5% between 140 and 212 years (Fig. 4b). NPP at the age of 212 years can still be 63% of the maximum.

3.4.3. Deciduous broadleaf forest

In 2001, the MT, TP, and MLAI for DBF were $4.5 \text{ }^\circ\text{C}$, 547 mm, and 2.5, respectively (Table 2). On the forest age map, stand age of DBF ranged from 1 to 153 years. Eq. (1) was not applicable for this forest type. Through statistical analysis, a second order polynomial equation was found to be best suited for describing the relationship between NPP and stand age for DBF (Table 3).

Seventy-nine percent of the variation of NPP caused by changing stand age was explained by the fitted equation. As shown in Fig. 4c, NPP simulated by BEPS fluctuated considerably. It was likely caused by factors other than age, including climate and site conditions within the large regions. We have therefore fitted a smooth curve through the data points to capture the main pattern of NPP variation with age. Overall, NPP rapidly increased from 1 to 100 years old, then declined slowly after the age of 122, at which the NPP approached the peak of $625 \text{ g C m}^{-2} \text{ yr}^{-1}$. Due to lack of data for DBF's NPP beyond about 150 years, we are unable to determine whether NPP would decline significantly at ages older than 150.

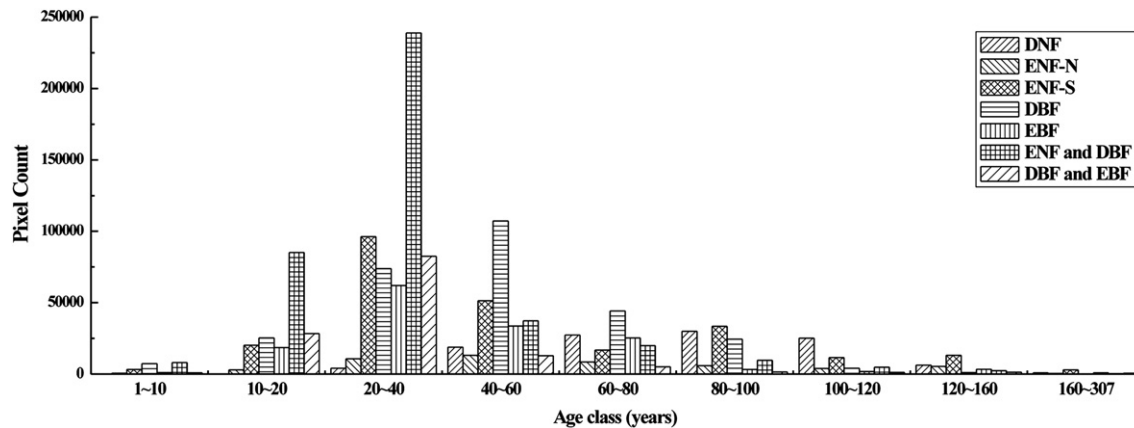


Fig. 3. Pixel counts for each stand age class for each forest ecosystem.

3.4.4. Evergreen broadleaf forest

EBF was distributed mainly in the coastal areas of southeastern China, including Hainan and Taiwan provinces (Fig. 1). The climatic conditions of the region were characterized by MT of 16.2 °C and TP of 1466 mm. The MLAI of EBF was 4.6, which was the largest among all forest types (Table 2). The range of EBF stand age from the forest age map was between 4 and 182 years. We filled the gap of NPP values at the ages of 1–3 years using a simple linear interpolation algorithm.

NPP simulated by BEPS showed relatively large fluctuation during the first 50 years. The fitted equation explained 66% of NPP variations related to forest ages (Table 3). The NPP output from the fitted equation increased rapidly in the early stage and achieved a maximum value at year 40. After that, NPP decreased at a rate of 2 g C m⁻² yr⁻¹ (Fig. 4d). NPP at the latest year (182) was 569 g C m⁻² yr⁻¹, equivalent to 64% of the maximum NPP.

3.4.5. Mixed broadleaf forest: DBF and EBF

MBF was widely distributed in southern China (Fig. 1). MT (16.9 °C) and TP (1628 mm) for MBF were higher than those of other forest types. MLAI of MBF was 4.2, which was second only to that of EBF (Table 2). The age of this type of forests ranged from 6 to 192 years. The NPP gap for forests aged from 1 to 5 years was also filled using the linear interpolation approach.

The NPP estimated by the MBF's fitted equation agreed with NPP simulated by BEPS ($R^2 = 0.67$) (Table 3). NPP simulated by BEPS reached high values at the ages of 50–60 years while the maximum NPP estimated by the fitted equation occurred at 32 years (Fig. 4e). The fitted NPP-age curve of MBF was similar to that of EBF and reached the peak NPP earlier than that of DBF. NPP at the age of 192 years declined 28% from its peak value.

3.5. Simulation of carbon balance for China's forests

As shown in Fig. 5a, the annual mean NPP of China's forests increased from 429 g C m⁻² yr⁻¹ in 1901 to 504 g C m⁻² yr⁻¹ in 2001,

Table 2
The meteorological factors and MLAI of forest ecosystems in China.

| Forest type | MT (°C) | TP (mm) | Mlai |
|-------------|---------|---------|------|
| DNF | -3.4 | 437 | 2.2 |
| ENF-S | 10.7 | 1147 | 3.6 |
| DBF | 4.5 | 547 | 2.5 |
| EBF | 16.2 | 1466 | 4.6 |
| MBF | 16.9 | 1628 | 4.2 |

an increment rate of 0.85 g C m⁻² yr⁻¹ before 1949, the mean NPP in China's forests was 436 ± 6 g C m⁻² yr⁻¹. There was a slight increment during 1950–1987, with a value of 463 ± 4 g C m⁻² yr⁻¹. After China implemented large planting projects in the 1980s and 1990s (Fang et al., 1998, 2001), the annual NPP increased to 534 ± 15 g C m⁻² yr⁻¹. NPP reached the peak of 607 g C m⁻² yr⁻¹ in 1998. In these plantations, NPP of forests are expected to increase in the first 50 years and then to decrease thereafter. As a result of the influence of plantations covering large areas, NPP in China's forests is expected to rise until the 2030s and then decline after that, and this would have considerable implications for China's forest carbon budget (Ju et al., 2007).

Soil organic carbon (SOC), aboveground biomass, litter, roots, and the total ecosystem carbon (ECO) of China's forests from 1901 to 2001 were also recalculated using InTEC. ECO of China's forests from 1901 to 2001 varied between 31.1 and 36.8 Pg C yr⁻¹. The ranges of carbon pools in SOC, aboveground biomass, litter and roots during the analysis period were 14.1–15.1, 9.2–14.4, 2.4–3.5 and 3.9–5.4 Pg C, respectively. The ECO changed a little from 1901 to 1949 and then rapidly decreased from 1950 to 1987. The minimum value of ECO occurred in 1987, equals to 31.1 Pg C yr⁻¹. Among four carbon pools in Table 4, aboveground biomass was the key carbon pool that decided the forest carbon balance, because aboveground biomass lost the largest amount of carbon, accounting for 81% of total net loss of carbon during 1901–2001. Aboveground biomass released the largest amount of carbon from 1950–1987 (4.73 Pg C) while it sequestered 3.35 Pg C from 1980–2001, due to the large planting projects taking place in China. On the centurial scale, SOC and roots sequestered carbon, although their changes were slight. Using soil profiles obtained from China's second national soil survey, conducted from 1979 to 1992, SOC stocks in the top 10, 20, 30, 50, and 100 cm of soils were estimated to be,

Table 3
The fitted NPP-age equations for each forest ecosystem in China.

| Forest type | a | b | c | d | R ² |
|-------------|--------|------|--------|------|----------------|
| DNF | 265.72 | 3.00 | 50.32 | 0.74 | 0.90 |
| ENF-S | 385.92 | 2.10 | 47.58 | 0.12 | 0.75 |
| DBF | 408.07 | 3.61 | -0.015 | | 0.79 |
| EBF | 365.60 | 4.12 | 91.57 | 0.30 | 0.66 |
| MBF | 561.65 | 2.13 | 40.23 | 0.39 | 0.67 |

Note: the pattern of NPP-age equation was $NPP(\text{age}) = a \left(1 + \frac{b(\text{age}/c)^d - 1}{\exp(\text{age}/c)} \right)$ for DNF, ENF-S, EBF and MBF; but for DBF, the equations was $NPP(\text{age}) = a + b(\text{age}) + c(\text{age})^2$

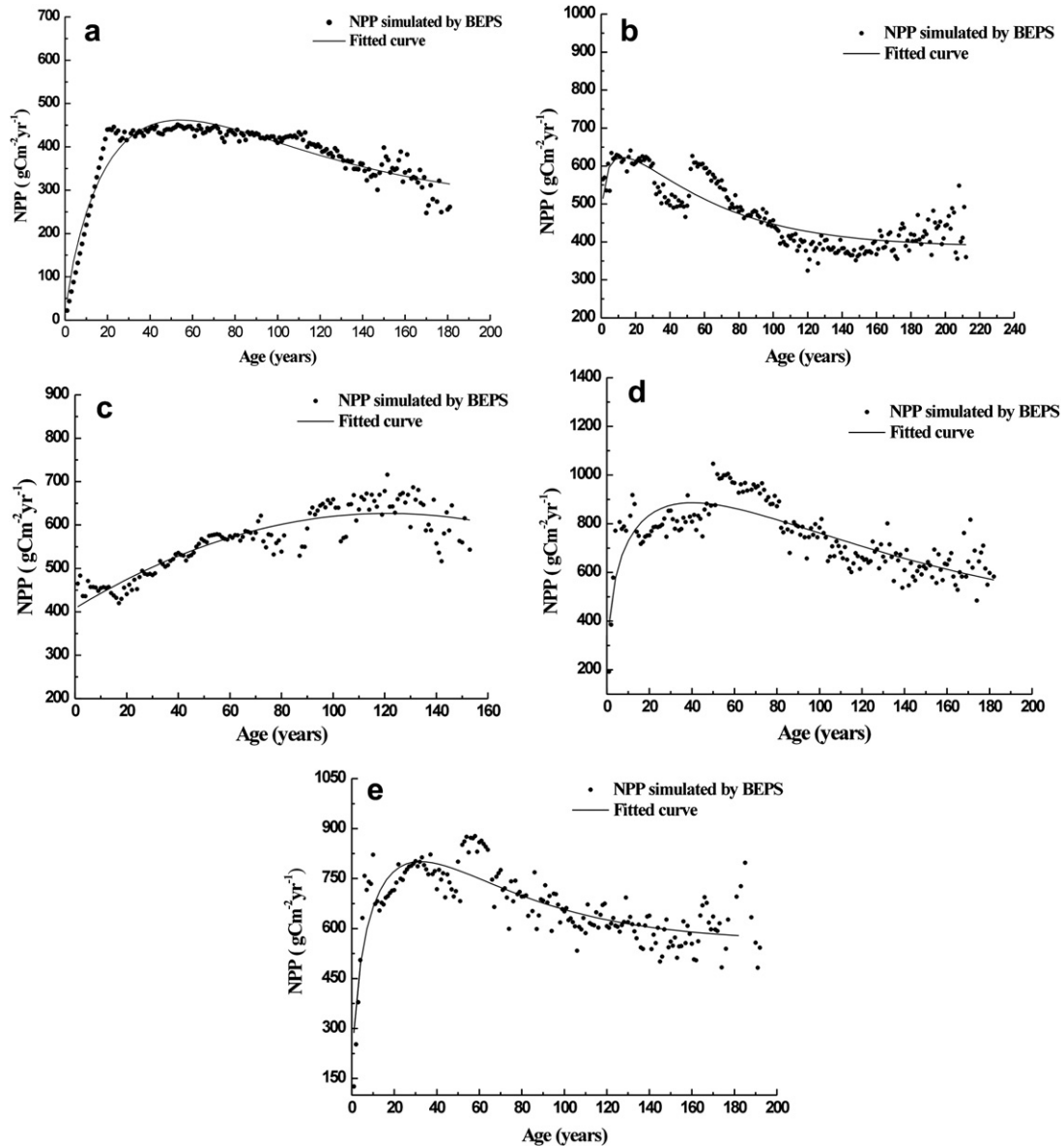


Fig. 4. The relationship between NPP and stand age for DNF(a), ENF-S(b), DBF(c), EBF (d), and MBF(e).The black points represent mean age-specific NPP simulated by the BEPS model.

18.12 ± 3.35 , 33.74 ± 5.93 , 44.48 ± 7.80 , 61.30 ± 11.40 , and 82.47 ± 19.46 Pg C for the 1980s, respectively. Meanwhile, SOC storage to a depth of 30 cm was 15.12 Pg C for forests (including shrubland) (Wang et al., 2004). In the InTEC model, the mean SOC for forests (including shrubland) was 15.04 ± 0.08 Pg C. Although the forest area and definition were slightly different, the results of the InTEC model simulation were consistent with that from soil survey.

NEP of China's forests in the three periods was also recalculated (Fig. 5c). From 1901 to 1949, the NEP of China's forests was about 5.10 ± 10.22 Tg C yr⁻¹, behaving as a relatively small carbon sink and changing to -147.14 ± 30.80 Tg C yr⁻¹ (Carbon source) from 1950 to 1987. The minimum NEP (carbon source) appeared in 1979 (-348.35 Tg C yr⁻¹). From 1988–2001, NEP increased to 259.47 ± 67.47 Tg C yr⁻¹, averaging an annual sink of 0.30 Pg C in the 1990s. Peak NEP (445.78 Tg C yr⁻¹) appeared in 1998, which was consistent with the results of NPP.

4. Discussion

4.1. Comparison with ground-based data

Reliability of the above-fitted equations was compared with the dataset from Luo (1996). The allometric equations specific for certain forest types and regions were used to calculate biomass of tree stems, branches, foliage, and roots with available information of stand DBH (diameter at breast height) and height of each age group, before adding the biomass of tree components to estimate total tree biomass (Pan et al., 2004). Plot NPP data were estimated from the plot live biomass based on the growth rates derived from stem analysis research and leaf life span (Luo et al., 2002). The stand age of a plot input into the above-fitted equations, and the resultant NPP was compared with NPP measured at the same plot. Table 5 summarizes the comparison results. For DNF and ENF-S, NPP simulated with the curved-fitted functions developed in this study

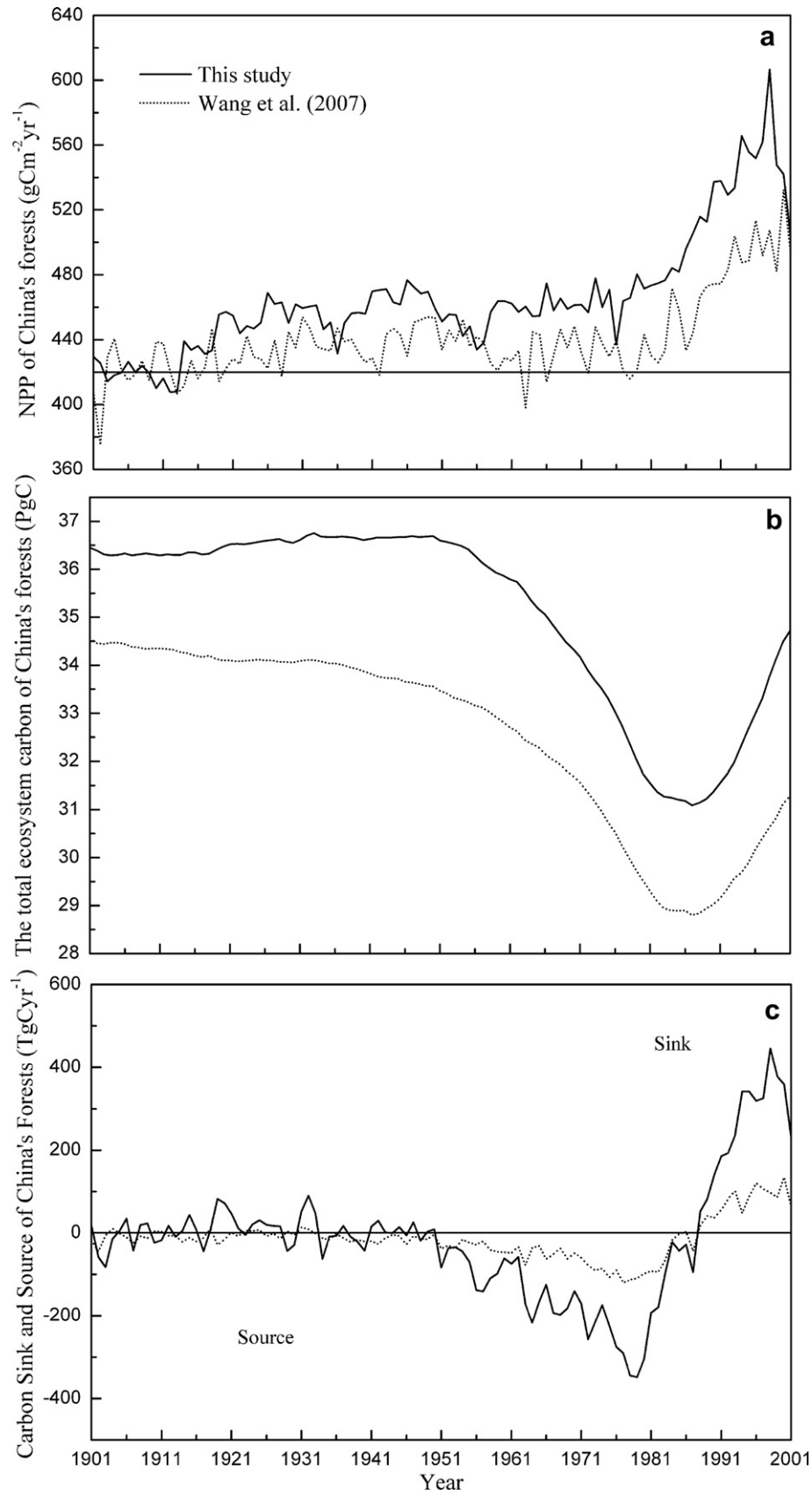


Fig. 5. Comparison of annual mean NPP (a), total ecosystem carbon (b), and annual NEP (c) of China's forests with Wang et al. (2007) describing the effect of age on carbon balance in the InTEC model. The dashed line represents results from Wang et al. (2007), while the solid line is the recalculated values achieved by the using a refined NPP-age function developed in this study.

Table 4

Cumulative carbon pools of China's forests SOC, aboveground biomass, litter and roots for three periods (1901–1949, 1950–1987, and 1987–2001).

| | 1901–1949 (Pg C) | 1950–1987 (Pg C) | 1988–2001 (Pg C) | 1901–2001 (Pg C) |
|-------------|---------------------|---------------------|---------------------|---------------------|
| SOC | 0.22 | 0.63 | −0.84 | 0.01 |
| Aboveground | −0.13 | −4.73 | 3.35 | −1.51 |
| Litter | 0.10 | −0.34 | −0.24 | −0.48 |
| Roots | 0.02 | −0.5 | 0.59 | 0.11 |
| Total | 0.21 | −4.94 | 2.86 | −1.87 |

were significantly correlated with plot-level measurements. However, simulated NPP using the fitted functions and field measured values did not correlate well for DBF, EBF, and MBF. Mean values of the relative differences between simulated and measured NPP are in the range of −12%–9%.

4.2. Age-dependent net primary productivity of forests

For individual forest types, the NPP simulated by BEPS often differ from the curve-fitted results. The difference is mainly caused by the influence of factors other than age on simulated NPP. We therefore believe that the fitted curve represents more closely the NPP-age pattern than the scattered original NPP data points. EBF and MBF show similar patterns of NPP changes through stand development, with NPP increasing to a median of approximately 664–745 g C m^{−2} yr^{−1} and a maximum of 802–888 g C m^{−2} yr^{−1} at 30–40 years old. NPP of DBF didn't show a pattern with a distinct peak followed by a decline, as seen in the other four forest types. Rather, DBF's NPP tended to increase slightly for the first 70 years and then become asymptotic at approximately 600 g C m^{−2} yr^{−1}. The age at which NPP reached the maximum value differed by forest ecosystems. The maximum NPP of evergreen forests occurred earlier than that of deciduous forests. In general, more productive forests show an earlier growth peak and a steeper growth decline (Van Tuyla et al., 2005). Previous studies indicate that NPP generally decreases in old forests to about half (Mund et al., 2002; Ryan et al., 2004) or one-third (Luyssaert et al., 2008) of its maximum value. However, other researches have found old forests to be as productive as young forest stands (Harmon, 2001; Van Tuyla et al., 2005). In our study, predicted NPP of old forests (related the latest year) declined by 28%–37% from its peak for all of forest types except DBF.

Forests in different regions within a biome also have different rates of NPP caused by many other site factors, including climate, soil, and drainage (Pregitzer and Euskirchen, 2004). Age-dependent responses of forests to temperature and rainfall vary (McMillan et al., 2008; Hudiburg et al., 2009). In our study, forests (e.g. EBF and MBF) in wetter conditions had much higher NPP at a given age than the ones (e.g. DNF) located in drier environments (Table 1 and Fig. 4). Warm, dry years resulted in a marked reduction of mid-summer CO₂ uptake by young stands, but this temperature-and drought-induced stress is much weaker in old stands, presumably with well established root systems. Meanwhile, similar declines were not observed

during cool-dry or warm-moist years (McMillan et al., 2008). Furthermore, the decline of forest growth with site quality varied with species. Biomass declined more rapidly on higher-quality sites in four of the eight studies, while in other studies, the declining rate of growth was unaffected by site quality (Ryan et al., 1997). Therefore, we believed that many factors affect the NPP change with stand age. In forest stand development, forest growth increases after stand initiation but then declines soon after full-canopy leaf area is reached (Binkley et al., 2002). Age-related changes in forest NPP have been extensively discussed, but ecophysiological causes of changing NPP have seldom been examined comprehensively. Gower et al. (1996) proposed that decreased nutrient availability and enhanced stomatal limitation were the major causes for NPP decline with stand age. Ryan et al. (1997) reviewed the hypotheses in detail and described five important aspects, including changes in photosynthesis with stand development, nutrient supply, respiration, carbon allocation, and hydrological function. This research also implied that a decline in stand leaf area usually accompanies a decline in aboveground wood growth. Murty and McMurtrie (2000) modified the G'DAY model coupled with age mechanisms in investigating the causes for age-related NPP decline. They found that when the soil N:C ratio is fixed, declining N-availability alone can explain the decline in NPP, and when soil N:C ratios are allowed to vary, increasing sapwood respiration contributes little to NPP decline. However, the decline of NPP with age can be explained as a combined effect of declining photosynthesis efficiency and declining N-availability to trees (Murty and McMurtrie, 2000). Ryan et al. (2004) used an experimental test to explore the causes of forest-growth decline with stand age and found that the decline in aboveground wood production with stand age was greater than the decline in canopy photosynthesis, suggesting increased respiratory loss with increasing stand age.

Applying one NPP-age equation for all forest types would result in large uncertainties in estimated carbon budgets because different forest types have various ecophysiological characteristics. Eq. (1) can be used to fit the decline of average NPP with age for four forest types (DNF, ENF-S, EBF, and MBF) in China. But the regression coefficients in Eq. (1) varied considerably with forest types. The NPP-fitted curves for ENF-S and EBF and MBF were similar, but ENF-S NPP increased faster than that of the latter two. Meanwhile, the change of NPP with age can be fitted best for DNF among all forest types.

4.3. Effect of the refined NPP-age curve on simulated carbon balance for China's forests

As shown in Fig. 5a, the application of the default and new NPP-age functions in InTEC produced similar temporal patterns of annual NPP from 1901 to 1985. Annual mean NPP of forests has increased dramatically since the 1980s, and the annual increase rate of NPP simulated in this study was faster than that identified in a previous study by Wang et al. (2007), who used the default NPP-age curves in InTEC. The simulated maximum NPP value appeared

Table 5

Regressive analysis and the percent difference between observed NPP and modeled NPP based on forest types. NPPmod is NPP calculated using the above-fitted equations, while NPPobs is NPP observed by Luo (1996).

| Forest type | Plot number | Linear regressive equation | R ² | Probability | Relative difference ^b |
|-------------|-------------|----------------------------------|----------------|--------------------|----------------------------------|
| DNF | 11 | NPPmod = 0.365NPPobs + 253.967 | 0.371 | 0.047 ^a | 8.5% |
| ENF-S | 82 | NPPmod = 0.189 NPPobs + 376.608 | 0.331 | 0 ^a | −4.07% |
| DBF | 100 | NPPmod = −0.036 NPPobs + 566.819 | | 0.067 | −12.04% |
| EBF | 25 | NPPmod = −0.019 NPPobs + 883.987 | | 0.292 | −4.96% |
| MBF | 55 | NPPmod = 0.011NPPobs + 756.650 | | 0.496 | 3.69% |

^a Significant at $P < 0.05$.

^b Relative difference is calculated as $(\text{NPPmod} - \text{NPPobs}) / \text{NPPobs} \times 100\%$.

in 1998 in this study, while NPP peaked in 2000 in the simulation by Wang et al. (2007) with a relatively low value of $532 \text{ g C m}^{-2} \text{ yr}^{-1}$. A peak in NPP in 1998 has been described in many studies and it was related to high temperature and precipitation (Cao et al., 2003; Piao et al., 2005).

ECO of China's forests in this study was slightly higher than that reported by Wang et al. (2007) (Fig. 5b). This suggests that the results of Wang et al. (2007) possibly underestimated the carbon pools of China's forests, but the change trends in both studies were similar. The minimum carbon stock in China's forests occurred in 1987 in current study, which was consistent with results from Wang et al. (2007). From 1901 to 2001, the cumulative C stocks in SOC, aboveground biomass, and roots in this study were all larger than the values of Wang et al. (2007), while the cumulative C stocks in litter was $303.65 \pm 0.05 \text{ Pg C}$, slightly lower than the value from Wang et al. (2007) ($314.65 \pm 0.05 \text{ Pg C}$).

From 1901 to 1949, the NEP of China's forests behaved as a relatively small carbon sink (Fig. 5c), while Wang et al. (2007) reported that China's forests acted as a carbon source ($21.01 \pm 7.83 \text{ Tg C yr}^{-1}$) during this period. Current NEP from 1950 to 1987 was much more negative than results from Wang et al. (2007). The carbon release by China's forests in this period was caused by many factors, including small forest areas and natural or anthropogenic disturbances (Houghton and Hackler, 2003; Wang et al., 2007). From 1988 to 1990, currently simulated NEP was consistent with values from Wang et al. (2007). During the 1980s and 1990s, terrestrial ecosystems in China were found by three methods to be a net carbon sink of $0.19\text{--}0.26 \text{ Pg C yr}^{-1}$ and analysis of the national forest inventory data suggests that forest ecosystems (including shrubland) behave as a carbon sink of $137.3 \pm 58 \text{ Tg C yr}^{-1}$ (Piao et al., 2009). The simulation in this study indicated that forest ecosystems (including shrubland) sequestered carbon at the rate of $143.1 \text{ Tg C yr}^{-1}$ over the period 1982–1999. This sink is less than that of $0.30\text{--}0.58 \text{ Pg C yr}^{-1}$ in the conterminous United States (Pacala et al., 2001) but is comparable with that of $0.14\text{--}0.21 \text{ Pg C yr}^{-1}$ in geographic Europe (Janssens et al., 2006; Ciais et al., 2006). Results of this study indicated that, after 1999, China's forests sequestered more carbon than the results of the former study (Wang et al., 2007).

4.4. Uncertainties

Considerable differences exist between simulated and ground-based NPP. This may be caused by the following two factors. First, the tree density (Litton et al., 2004) and other factors (such as site conditions, local climate, nutrient status, and the soil texture) may have differed in simulation and ground-based data in this study. Second, the approach used for calculating ground-based data may also differ in field researches. Due to lack of adequate plots, if allometric equations did not exist for a certain forest type in a region, equations from a neighboring region were adopted by Luo (1996) to produce NPP datasets (Pan et al., 2004) which was used in this study. A large uncertainty may result from inconsistency in methods used to calculate NPP. Different methods, such as the volume-biomass method and mean-density method, may cause an up to 65% difference in calculated carbon stock, even though the same sample plot data were used (Pan et al., 2004). The uncertainties in estimating carbon dynamics can be significantly reduced by increasing the sample data points (Smith and Heath, 2000; Smith et al., 2002), and therefore, we call for more ground-based NPP measurements.

Sun et al. (2004) used a modified BEPS model to explore the spatial distribution of NPP in Changbaishan Natural Reserve in China with Landsat ETM⁺ data. Modeled NPP of the forest was higher than observed NPP with a mean relative error of 8.6%, while the correlation coefficient was very high (R^2 up to 0.90) (Sun et al., 2004). Despite the possibility that BEPS slightly overestimated NPP,

the NPP-age curve pattern would have not been significantly affected.

In previous studies, the stand age of a plot was computed as the mean of the oldest 10% of trees (Spies and Franklin, 1991; Van Tuyl et al., 2005). However, the information about old forests was inadequate in inventory data. As a result, stand age was defined as a mean age of all trees in a plot in our study. In other words, the mean value of tree age in each forest pixel at 1-km resolution was treated as stand age. Obviously, our nominal 1-km² average could include a wide variety of subpixel features, such as bare ground or shrubland. The methods, which were used to estimate stand age from tree age, would have different effects on the age estimation at each developmental stage of a forest (Bradford et al., 2008), and this uncertainty still exists in our results. In addition, we just consider the variation of NPP with age for different typical forest types derived from remote sensing data due to the unavailability of spatial data of different forest species. This simplification might induce uncertainties in developed NPP-age relationships and calculated regional carbon balance since different forest species has different growth rates.

Uncertainties also exist for old forest stands. After 100 years, the BEPS-derived NPP values of all forest ecosystems fluctuated greatly with age, unlike the stable initial stage. One reason may be that the distribution of old forests was relatively sparse. Song and Woodcock (2003) found that forest NPP stays at a relatively stable level after 300 years. But in our study, the maximum field stand age in all forest types was 212 years. Therefore, we could not determine the trend in forest NPP at ages older than 200 years; although we expect that the self-renewal processes of old forests would keep their NPP less stable (Harmon et al., 1990). In particular, only 3.1% of DBF pixels are found to be older than 140 years, leaving a considerable uncertainty about the trend of NPP at older ages.

5. Conclusions

In our study, we developed relationships between NPP and stand age for several major forest types in China using average NPP simulated with the BEPS model driven by remote sensing inputs and forest age obtained from inventory data. In general, these relationships are highly significant, with R^2 values ranging from 0.66 to 0.90. The changes in NPP with age for DNE, ENF-S, EBF, and MBF can accurately be described using a complex non-linear function with different parameter values. Furthermore, the patterns of NPP variation with stand age were similar for these four forest types. However, the time at which NPP reached the peak value varied widely. Meanwhile, the NPP-age relationship for DBF differed considerably from functions of other forest types and was best fitted using a second order polynomial. The peak NPP for DBF appeared at the much older age (122 years) compared with other types, and there are not enough data to determine the curve shape after the peak, which gives rise to the fitted NPP-age relationship of this type of forests different with that of other forest types.

Using the new NPP-age functions determined in this study, we used the InTEC model to analyze changes in the carbon balance in China's forest during 1901–2001. During 1901–1949, China's forests acted as a very small sink of $5.1 \pm 10.22 \text{ Tg C yr}^{-1}$. The forests switched to a large carbon source, with a value of $147.14 \pm 30.80 \text{ Tg C yr}^{-1}$ during 1950–1987. Because of large plantation projects implemented in 1980s, China's forests behaved as a large carbon sink, with a value of $259.47 \text{ Tg C yr}^{-1}$. These results of China's forest carbon budget from this study differ considerably from the results of a previous study (Wang et al., 2007) using NPP-age relationships developed for boreal ecosystems, suggesting the importance of reliable age-NPP relationships for regional carbon balance estimation. Large uncertainties still exist in the developed

NPP-age relationships and consequently carbon balance because of uncertainties in simulated NPP and spatially distributed forest age data. Nevertheless, this is the first study in China to develop localized NPP-age relationships for regional carbon balance estimation.

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