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RESEARCH PAPER

How temperature, precipitation and stand age control the biomass carbon density of global mature forests

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ABSTRACT

Aim To understand: (1) how temperature, precipitation and stand age control the above-ground biomass carbon density (BCD_a) of mature forests and its macroecology patterns across latitudes; (2) the age threshold for old-growth forests at a global scale.

Location Global forests.

Methods We compiled a database (897 sites) of mature forests between 80 and 1200 years old. The site data include latitude, longitude, mean annual temperature, mean annual precipitation, forest type, stand age, BCD_a, living biomass (above- and below-ground biomass) carbon density and total (living plus dead) biomass carbon density. Based on the site data, we performed regression analyses to show how BCD_a changes with climate and forest stand age.

Results At a global scale, the highest BCD_a of mature forests occurred mainly in the mid-latitude regions where mean annual temperatures were 8–10 °C and mean annual precipitation was between 1000 and 2500 mm. The average BCD_a of forests in the stand age class of 450–500 years was higher than those in the other stand age classes. For forests between 80 and 450 years old, which form the majority of mature forests, carbon accumulation was faster in dead biomass than in living biomass.

Main conclusions The highest BCD_a of mature forests is located in mid-latitude regions with cool temperatures and moderate precipitation. The age threshold for old-growth forests at a global scale should be 450–500 years, which is much older than the previously documented age of 100–200 years. This older age threshold for old-growth forests is probably one of the primary reasons why recent works have concluded that old-growth forests are still carbon sinks.

Keywords

Above-ground biomass carbon density, carbon sink, climate change mitigation, ecological zone, major forest biome, old-growth forest, precipitation, stand age, temperature.

INTRODUCTION

Above-ground biomass carbon density (BCD_a) is the carbon stock per area in all living biomass above the soil, including stems, branches, leaves and seeds (IPCC, 2003). According to the IPCC (2003), 'forest' is a land-use type spanning more than 0.05–1 ha with trees that have the potential to be taller than 2–5 m and a canopy cover of more than 10–30%. Forest ecosystems contain a stock of 289–363 Pg C in biomass (IPCC, 2000; FAO, 2010; Pan *et al.*, 2011), accounting for 77% of the global terrestrial vegetation carbon (IPCC, 2000). In addition, forests play an essential role in uptake of carbon from the atmosphere, at a rate of approximately 2.4 Pg C year^{-1} (Pan *et al.*, 2011).

Due to the large carbon sequestration capacity of forests, a series of forest management activities, such as LULUCF (land use, land-use change and forestry) and REDD+ (reducing emissions from deforestation and forest degradation and other activities), have been implemented to mitigate the effects of climate

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change. Assessing the efficiency of these activities requires a reliable reference for the highest carbon density of forests. Mature forests are conventionally considered to have a higher carbon density than younger forests (IPCC, 2006), but the global patterns of carbon stocks in mature forests and their drivers require improved understanding (Keith *et al.*, 2009; Liu *et al.*, 2012).

Climate and stand age have been identified as factors that control the BCD_a of mature forests and its spatial patterns (Pregitzer & Euskirchen, 2004; Stegen *et al.*, 2011). One of the climatic factors is temperature. For example, a positive relationship between BCD_a and temperature was found for boreal and temperate forests (Keith *et al.*, 2009), while a negative relationship was identified for humid tropical forests (Stegen *et al.*, 2011). Precipitation is another critical climatic factor driving BCD_a. For example, the BCD_a of temperate mature forests and tropical dry forests is mainly constrained by water deficiency, as demonstrated by a positive relationship between BCD_a and precipitation (Stegen *et al.*, 2011).

Stand age controls the duration of forest carbon accumulation (Pregitzer & Euskirchen, 2004) and consequently the spatial pattern of forest BCD_a. When stand age is not considered, some contradictory conclusions might be drawn. According to IPCC (2006), the BCD_a increases from boreal to temperate and then tropical forests. However, this result is based on existing global forests, 64% of which have not reached the mature stage (FAO, 2010). A recent study utilizing data from mature forests found that temperate mature forests located in mid-latitude regions have the highest BCD_a without considering the effect of stand age (Keith *et al.*, 2009). Therefore, an improved understanding is required for how stand age controls BCD_a and its pattern after forests achieve the mature stage at a global or regional scale (Keith *et al.*, 2009; Stegen *et al.*, 2011; Liu *et al.*, 2012).

The ecological basis for using mature forests to understand the global patterns of carbon accumulation is based on the hypothesis that mature forests have a relatively high and stable carbon density (Hudiburg *et al.*, 2009; Keith *et al.*, 2010; Liu *et al.*, 2012). With increasing stand age, carbon is initially accumulated and then reaches a steady state in pools of living biomass (above- and below-ground biomass), dead biomass (dead wood and litter) and soil. At the same time, the carbon sequestration rate of forests first increases then decreases (Goulden *et al.*, 2011) and finally approaches zero. Accordingly, the developmental stage of forests can be divided into young (stand initiation and stem exclusion) and mature (understorey re-initiation and old growth) stages (Odum, 1969; Oliver & Larson, 1990; Spies, 2004). The mature stage is when the growth of timber has reached a stage when the merchantable timber volume begins to decrease or the quality begins to degrade (Meng, 2007). Old growth is the later substage of the mature forest. Old-growth forests can be distinguished from younger forests by their composition of old trees, large dead trees and coarse woody debris, and are considered to have reached a neutral state of carbon exchange with the atmosphere (Odum, 1969; Oliver & Larson, 1990; Spies, 2004).

Recent studies, however, have demonstrated that mature, and even old-growth forests, could still sequester a large amount of carbon. For example, boreal–temperate and tropical old-growth forests have been reported to account for about 10% (Luyssaert *et al.*, 2008) and 29% (Pan *et al.*, 2011) of the carbon sink in global forests, respectively. The above-ground biomass of tropical mature rain forests in Africa (Lewis *et al.*, 2009) and the Amazon (Phillips *et al.*, 1998) and the soil of subtropical old-growth forest in China (Zhou *et al.*, 2006) are all carbon sinks.

There are several reasons for the debate on whether mature forests, even old-growth forests, are carbon neutral or carbon sinks. The first is whether those forests called mature or old growth are old enough to achieve a steady state, which involves decades to hundreds of years of succession. The age thresholds of mature and old-growth forests are conventionally regarded as 80–100 (Odum, 1969; Jarvis *et al.*, 1989; Keith *et al.*, 2009) and 200 years (Devall, 1998; Pregitzer & Euskirchen, 2004; Hudiburg *et al.*, 2009), respectively. While 80–100 years may be enough for the BCD_a of planted forests to achieve the stable state (Odum, 1969), additional years are needed for natural forests and for dead biomass and soil of planted forests (Luyssaert *et al.*, 2008). Second, no single age threshold exists for global old-growth forests (Wirth *et al.*, 2009). Old-growth forests are considered as the climax ecosystems (Clements, 1916), which means that forests in similar climate and disturbance regimes achieve the old-growth stage at similar stand ages. Therefore, the age threshold of old-growth forests should be region specific.

To understand the critical role played by existing forests in carbon assimilation, we collected site data for forests with stand ages of 80 years or more, covering most of the global forest biome types (i.e. general ecosystem classes, such as tropical forest and tropical rain forest). Specifically, we aim to examine: (1) the dependence of mature forest BCD_a and its spatial patterns on climate and stand age; (2) the age threshold of the old-growth forests at a global and a regional scale, and how this age can be used to define old-growth status of forests. This work will set a baseline for evaluating the carbon sequestration potential of the global forests and the efficiency of the LULUCF and REDD+ activities.

MATERIALS AND METHODS

Datasets

Major forest biome and ecological zone data

We used the Global Ecological Zone map developed by the FAO (2001) to determine the forest biome type for each forest site. To be clear, we used 'major forest biome' to represent a higher-level classification of the 'global ecological zone', which is composed of boreal, temperate, subtropical and tropical forests (Woodward *et al.*, 2004). A lower-level classification of global ecological zone (termed 'ecological zone'), which is embedded within major forest biomes, was also used. The boundaries of the lower level of the ecological zone were delineated principally on the basis of potential vegetation distribution maps (Köppen,

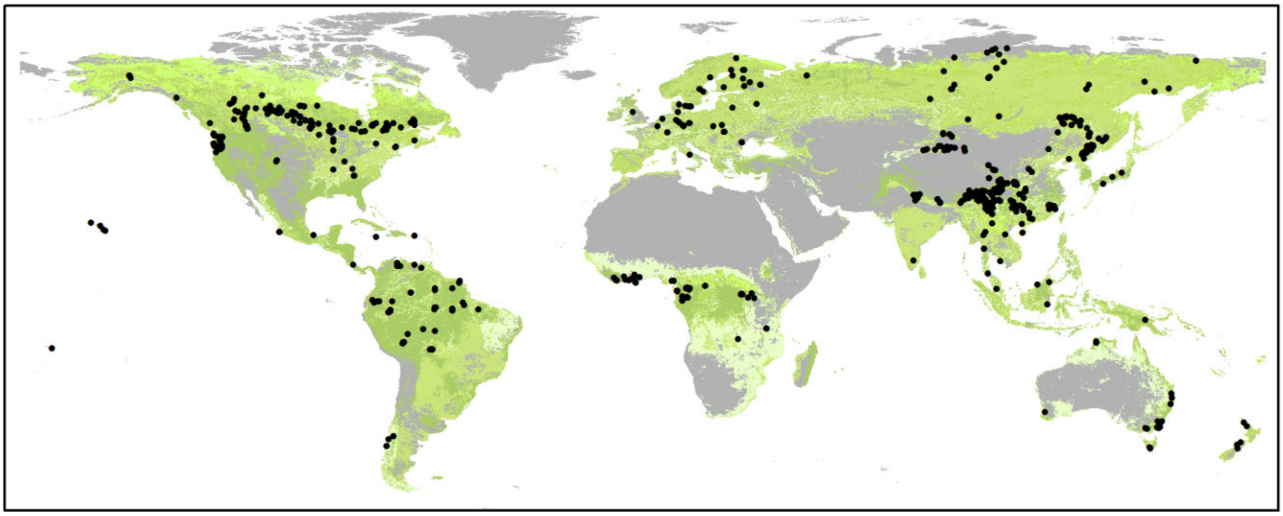

Figure 1 The spatial distribution of global mature forests. The mature forest sites (black dots) include 118 from Keith *et al.* (2009), 79 from Lewis *et al.* (2009), 112 from Luyssaert *et al.* (2007), 279 from Luo (1996), 96 from Ma *et al.* (2012), 3 from our field work and 210 from other literature. The regions in green represent the forest area obtained from Global Land Cover data (Fritz *et al.*, 2003): closed evergreen forests (dark green), closed deciduous forests (light green) and open or burned forests (pale).

1931; Trewartha, 1968; FAO, 2001). The 12 ecological zones in which our collected forest sites are mainly located include: boreal coniferous forest, boreal mountain system, boreal tundra woodland, temperate continental forest, temperate mountain system, temperate oceanic forest, subtropical humid forest, subtropical mountain system, tropical dry forest, tropical moist deciduous forest, tropical mountain system and tropical rain forest.

Biomass site data

We compiled a global mature forest biomass dataset comprising 897 forest sites with stand ages of 80 years or older from the existing literature and field surveys (Fig. 1). Each site includes site name, latitude, longitude, mean annual temperature, mean annual precipitation, forest type or tree species, stand age, BCD_a, living (above- and below-ground) biomass carbon density (BCD_l), and total (living and dead) biomass carbon density (BCD_t) (Table S1 in Supporting Information). The collected forest sites cover a total of 16 ecological zones (FAO, 2001), including all the global ecological zones except subtropical dry forest and subtropical grassland (Liu *et al.*, 2012). We retrieved missing latitude or longitude information for sites without such data from Google Earth according to the site name. We extracted missing mean annual temperature or mean annual precipitation data from the global climate data of WorldClim based on the site location.

Our mature forest data are all from field plot measurements. Data from modelled biomass and regional average biomass were excluded from the dataset. Biomass was derived from measurements of diameter at breast height (d.b.h.) and the height of each tree in the plot, and then one of the following three methods was used to calculate stand biomass: (1) mean tree biomass was measured, and then multiplied by the tree density of each plot; (2) allometric equations were used to calculate the biomass of each tree; (3) allometric equations were used to calculate the mean tree biomass, and multiplied by the tree density of each plot (Luo, 1996; Pan *et al.*, 2004). BCD_l is the sum of BCD_a and the below-ground biomass carbon density (BCD_b) of trees. Dead biomass is the sum of dead wood (standing dead stem and coarse woody debris) and litter. The biomass of standing dead stem is calculated by multiplying the dead stem biomass using allometric equations and their decay classes (Keith *et al.*, 2009). The biomass of coarse woody debris is obtained by measurement of wood volume, multiplied by wood density and decay class (Yatskov *et al.*, 2003; IPCC, 2006; Keith *et al.*, 2009). Litter biomass is obtained by harvesting litter in three or more $1\ m \times 1\ m$ plots, oven drying it at 65 °C and weighing (Liu *et al.*, 2011). We used the carbon fraction of 0.5 Mg C (Mg dry matter)$^{-1}$ (IPCC, 2003) to calculate biomass carbon density (BCD) from biomass.

A total of 574 out of 897 sites have stand age, as collected from published papers, open access databases and field work (Table S1). Two methods were primarily used in estimating forest stand age based on individual tree age. One method is using tree age, which is applicable to even-aged forests, mostly planted forests. The other method utilizes a weighted average. For example, choosing the oldest 10% of trees or the three oldest trees to calculate the stand age (Hudiburg *et al.*, 2009), which is appropriate for complex forest stands, mostly natural or secondary forests. Three methods were used to determine tree age. The first is counting tree rings (Goulden *et al.*, 2011); this method is normally applied to forests with obvious seasonal change, such as boreal and temperate coniferous forests (Liu *et al.*, 2011). The second is radiocarbon dating (Mueck *et al.*, 1996), which is applied to forests where seasonal rings are not present, such as subtropical and tropical broadleaf forests. The third is based on historical records of the years after afforestation or disturbances (Goulden *et al.*, 2011).

The 329 forest sites in China, mainly from the dataset of National Forest Resources Inventory (Pan *et al.*, 2004), were surveyed in permanent plots with sizes of 0.06–1 ha (Luo, 1996; Xiao, 2005; Liu *et al.*, 2012). To eliminate the effects of plot size, a method considering tree size and tree density was employed as follows. Larger plots were set for the sites with large trees and low tree density to guarantee a minimum number of 30 trees per plot (Xiao, 2005). Wood volume, which forms the majority of above-ground biomass, was measured from plots ranging from 0.01 to 0.1 ha, and then the plot size was determined by finding the stable state of wood volume along the enlarged plot size. The results showed that wood volume would stabilize when the plot size exceeds 0.05 ha. There are 323 forest sites out of 329 in China that have stand ages (Appendix S2) which are mainly based on tree ring counting and records of afforestation (Xiao, 2005). All the 897 forest sites were used to analyse the patterns of BCD_a of global mature forests, and to examine the relationships between BCD_a and climate. The 574 sites with readily available stand age data were used to examine the relationships between BCD_a, the ratio of BCD_a to BCD_l or BCD_t and stand age.

Climate data

We used climate data from WorldClim, with a spatial resolution of 30 arcsec. The surface climate data were interpolated from station point data using the method of thin-plate smoothing splines, implemented in ANUSPLIN (Hutchinson, 2001). Most station data were from records between 1950 and 2000 (Hijmans *et al.*, 2005).

Analysis of forest above-ground biomass carbon density along spatial, climatic and stand age gradients

First, by calculating the mean, minimum, maximum and standard deviation of BCD_a of mature forests for every 4° of latitude, we tested the hypothesis that mid-latitude forests have the highest BCD_a (Appendix S3). Then, using linear, polynomial and exponential regression, we examined the relationships between BCD_a of mature forests and temperature, precipitation and stand age. Finally, we determined the stand age of the forests with the highest BCD_a, and analysed the relationships between the ratio of BCD_a to BCD_l or BCD_t and stand age.

To analyse the relationships between BCD_a of mature forests and climate factors or stand age, we calculated the mean, minimum, maximum and standard deviation of the BCD_a of mature forests for every 2 °C of mean annual temperature, 200 mm of mean annual precipitation and every 50 years of stand age. We further used regression equations to examine the relationship between BCD_a of mature forests and mean annual temperature and mean annual precipitation at a global scale and for each ecological zone (Appendix S4).

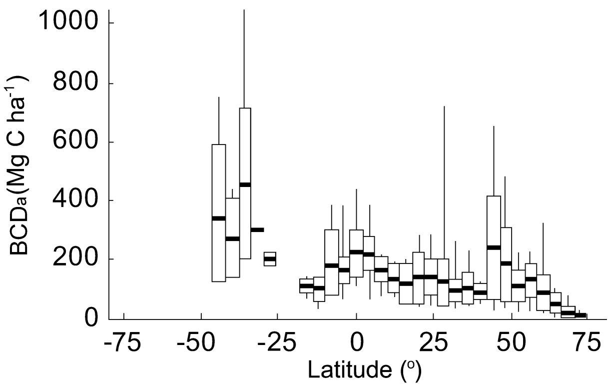

Figure 2 The latitudinal above-ground biomass carbon density (BCD_a) patterns of global mature forests. The mean (the horizontal bold line), standard deviation (the box), minimum and maximum (the vertical thin line) BCD_a of mature forests are shown for every 4° of latitudinal bands.

RESULTS

Effect of climate on the BCD_a of mature forests and its spatial pattern

Three low (70° N, 25° N, 20° S) and three high (0°, 45° N, 40° S) bands of BCD_a of mature forests are shown across latitudes (Fig. 2). The regions with the highest BCD_a are mostly located in mid-latitude regions, e.g. south-east Australia, south-east Tibet and the Oregon coast of North America, with BCD_a of 752, 718, 653 Mg C ha^{-1}, respectively. However, the mean and the lower bound of the BCD_a of mature forests generally decreases from the equator to poles in the Northern Hemisphere. For example, the mean BCD_a values of the 0, 20, 40, 60 and 75° N bands are 223, 138, 89, 86 and 8 Mg C ha^{-1}, respectively, and the lower bounds of the BCD_a of the 0, 20, 40, 60 and 75° N bands are 111, 40, 51, 18 and 3 Mg C ha^{-1}, respectively.

At a global scale, when the temperature is lower than 8 °C the relationship between BCD_a of mature forests and mean annual temperature is positive. When the temperature is near 10 °C, the BCD_a of mature forests reaches its maximum. And when the temperature is over 10 °C, the BCD_a of mature forests shows a weak negative trend (Fig. 3a). In addition, when precipitation is less than 1000 mm, the relationship between BCD_a of mature forests and mean annual precipitation is positive. When precipitation ranges from 1000 to 2500 mm, the BCD_a of mature forests reaches its maximum. When precipitation is above 2500 mm, the relationship becomes negative (Fig. 3b).

The relationships between BCD_a of mature forests and temperature and precipitation at the global scale are also applicable for each major forest biome. For example, BCD_a increases with temperature for boreal forests, and increases with precipitation for temperate and tropical forests when precipitation is less than 1500 mm. The temperate forests with a mean annual temperature of 8–10 °C and mean annual precipitation of 1500–2000 mm obviously have a higher BCD_a than do tropical forests (Fig. 4).

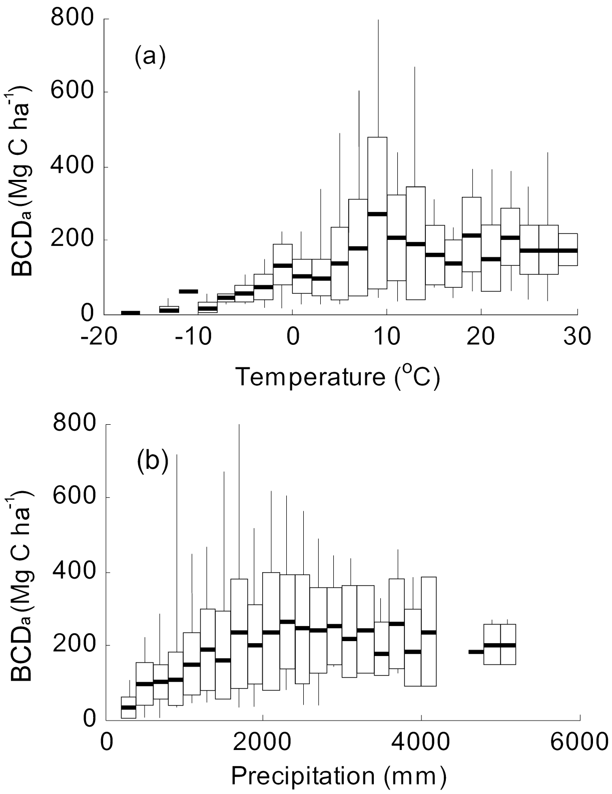

Figure 3 The relationship between above-ground biomass carbon density (BCD_a) of global mature forests and (a) mean annual temperature, (b) mean annual precipitation. We analysed the BCD_a of mature forests for every 2 °C of mean annual temperature and every 200 mm of mean annual precipitation. The bold bar is the average BCD_a, the top and bottom of the box is the average + stand deviation and average – stand deviation, respectively. The vertical fine line is the variance of BCD_a.

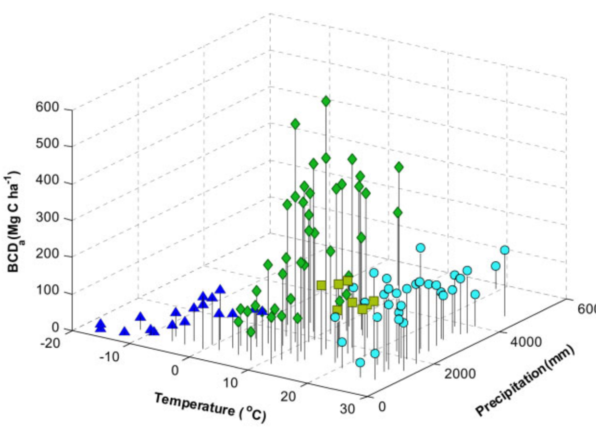

Figure 4 The above-ground biomass carbon density (BCD_a) of mature forests in relation to mean annual temperature and mean annual precipitation. Each point is the average BCD_a of all the sites for every 3 °C mean annual temperature and every 300 mm mean annual precipitation. The forests are divided into four major forest biomes: boreal (blue triangle), temperate (green diamond), subtropical (yellow-green square), and tropical forests (cyan circle).

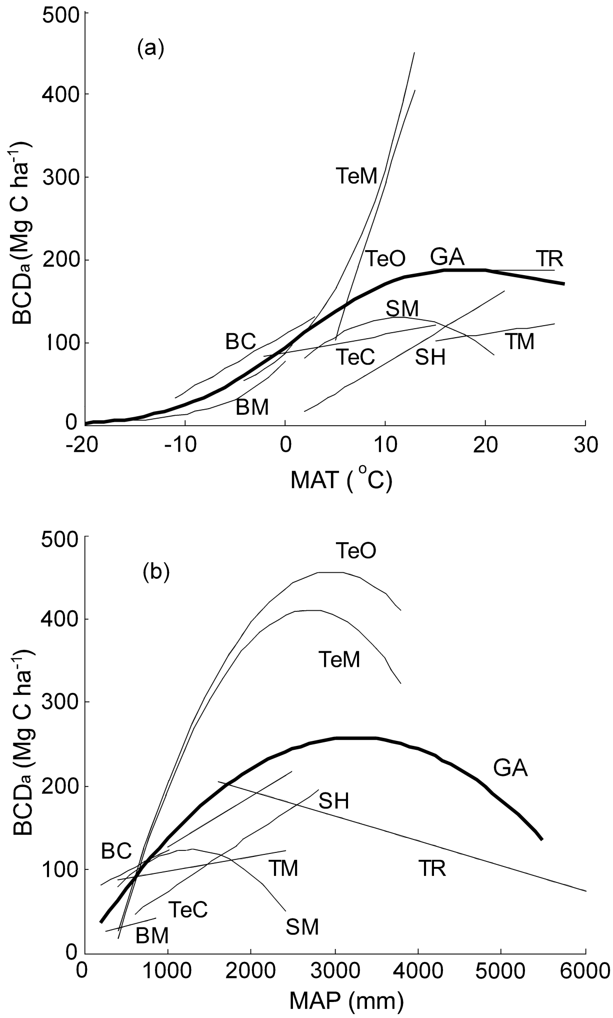

Figure 5 The relationship between above-ground biomass carbon density (BCD_a) and mean annual temperature (MAT) (a) or mean annual precipitation (MAP) (b) at a global and ecological zone scale. Abbreviations: GA, global average; BM, boreal mountain system; BC, boreal coniferous forest; TeM, temperate mountain system; TeC, temperate continental forest; TeO, temperate oceanic forest; SM, subtropical mountain system; SH, subtropical humid forest; TR, tropical rain forest; TM, tropical moist deciduous forest.

Among the 12 ecological zones, a linear positive relationship exists between BCD_a and mean annual temperature in boreal coniferous forest ($R^2 = 0.12$, $P < 0.0001$, $n = 150$), temperate oceanic forest ($R^2 = 0.19$, $P = 0.0066$, $n = 37$), subtropical humid forest ($R^2 = 0.21$, $P = 0.0032$, $n = 40$) and tropical dry forest ($R^2 = 0.63$, $P = 0.0188$, $n = 8$) (Fig. 5a). A nonlinear relationship exists between BCD_a and mean annual temperature in the boreal mountain system ($R^2 = 0.56$, $P < 0.0001$, $n = 24$), temperate mountain system ($R^2 = 0.39$, $P < 0.0001$, $n = 194$) and subtropical mountain system ($R^2 = 0.04$, $P = 0.0393$, $n = 144$). A linear positive relationship occurs between BCD_a and mean annual precipitation in subtropical humid forest ($R^2 = 0.12$, $P = 0.0275$, $n = 40$), tropical moist deciduous forest ($R^2 = 0.39$, $P = 0.0014$,

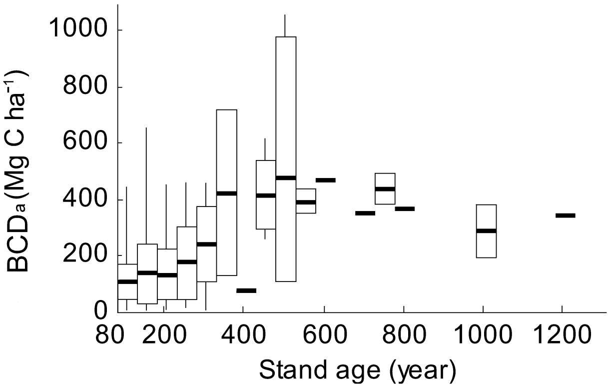

Figure 6 The relationship of above-ground biomass carbon density (BCD_a) and stand age for mature forests (50-year interval for statistics). Symbols are the same as in Fig. 2.

$n = 23$), the tropical mountain system ($R^2 = 0.78$, $P = 0.0015$, $n = 9$) and tropical rain forest ($R^2 = 0.10$, $P < 0.0001$, $n = 166$) (Fig. 5b). A nonlinear relationship exists between BCD_a and mean annual precipitation in the temperate mountain system ($R^2 = 0.60$, $P < 0.0001$, $n = 194$) and temperate oceanic forest ($R^2 = 0.30$, $P = 0.0026$, $n = 37$).

The stand age having the highest BCD for mature forests

Stand age is an important factor controlling forest BCD. For forests younger than 450 years, the average BCD_a of mature forests increases with stand age. When the stand age is over 450 years, the average BCD_a starts to decrease (Fig. 6). For forests with a stand age of between 80 and 500 years, the average BCD_a increases by 1.03 Mg C ha^{-1} year^{-1}. For forests with a stand age of between 500 and 1200 years, the average BCD_a decreases by 0.21 Mg C ha^{-1} year^{-1}.

For the forests with stand ages from 80 to 500 years, the ratio of BCD_a to BCD_l is approximately 0.8, which is consistent with IPCC results (IPCC, 2003). When the age of the forest stand increases from 80 to 450 years, the ratio of BCD_a to BCD_t decreases from 0.7 to 0.55, while the ratio of the other parts (root, dead wood and litter) to BCD_t increases from 0.3 to about 0.45 (Fig. 7). This means that both the BCD_a and the BCD_t of mature forests increase with stand age, while carbon accumulation is quicker in dead biomass than in living biomass for forests with a stand age between 80 and 450 years.

At the major forest biome scale, the BCD_a of boreal, temperate and subtropical forests mainly increases as stand age increases from 80 to 200, 80 to 500 and 80 to 300 years, respectively. The average BCD_a of the 200-, 500- and 300 year-old forests for the three major forest biomes, including boreal, temperate and subtropical forests, are about two, four, three times those of the 80-year-old forests, respectively (Fig. 8).

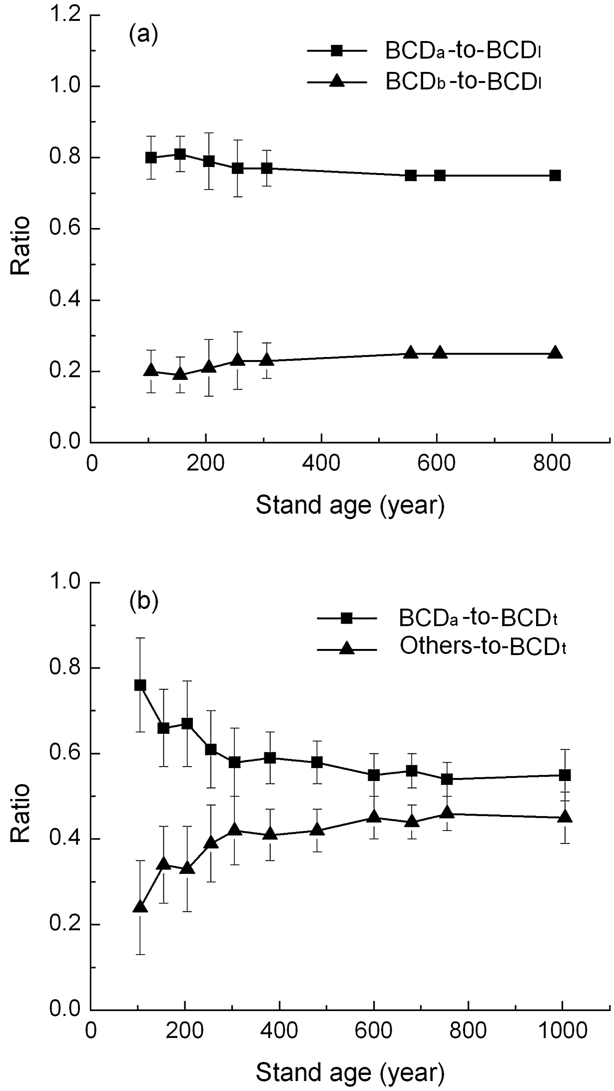

Figure 7 (a) The ratio of the above-ground biomass carbon density (BCD_a) to the living biomass carbon density (BCD_l) and the ratio of the below-ground biomass carbon density (BCD_b) to BCD_l along forest age. (b) The ratio of the BCD_a to the total biomass carbon density (BCD_t) and the ratio of the other parts (roots, dead wood and litter) to BCD_t along forest age (50-year interval for statistics). The data shown in the figure have been smoothed.

DISCUSSION

Climate dependence of BCD_a of mature forests

Climate determines the BCD_a of mature forests and its spatial patterns. The highest BCD_a of mature forests mainly occurs in the mid-latitude regions with temperatures around 10 °C (Figs 2–4), followed by low-latitude regions and finally high-latitude regions. This result is in line with the previous documented findings that global mature forests have the highest BCD_a in temperate and tropical regions (Luyssaert *et al.*, 2007; Keith *et al.*, 2009; Stegen *et al.*, 2011). Along the latitudinal gra-

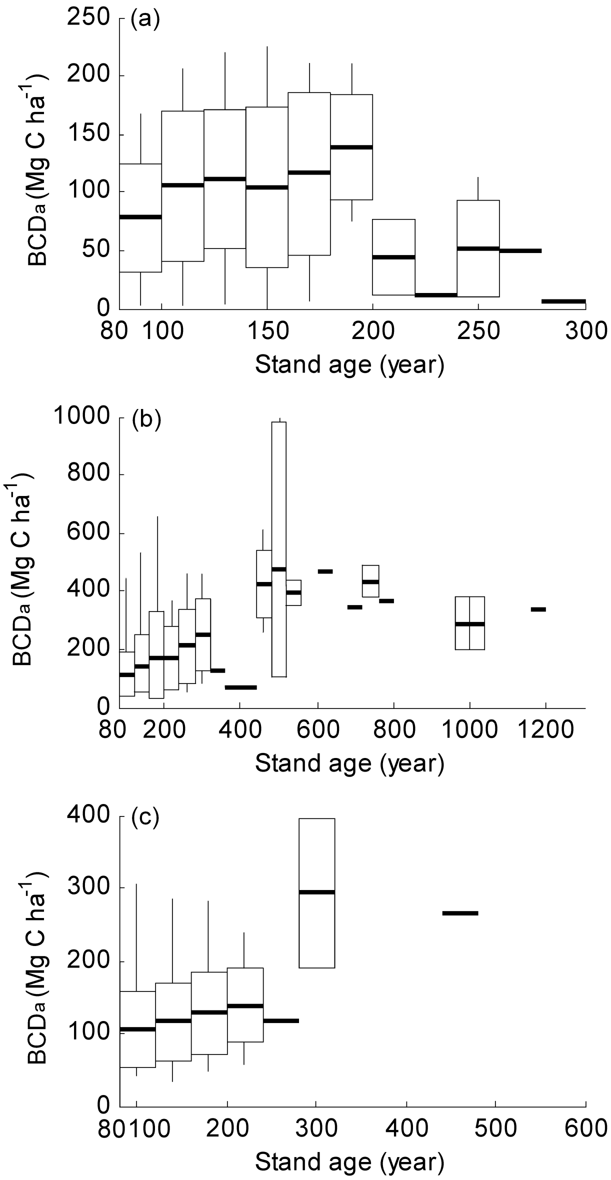

Figure 8 The relationship of above-ground biomass carbon density (BCD_a) and stand age for mature forest sites in three major forest biomes: (a) boreal (20-year interval for statistics), (b) temperate (40-year interval for statistics), (c) subtropical (40-year interval for statistics). Symbols are the same as in Fig. 2.

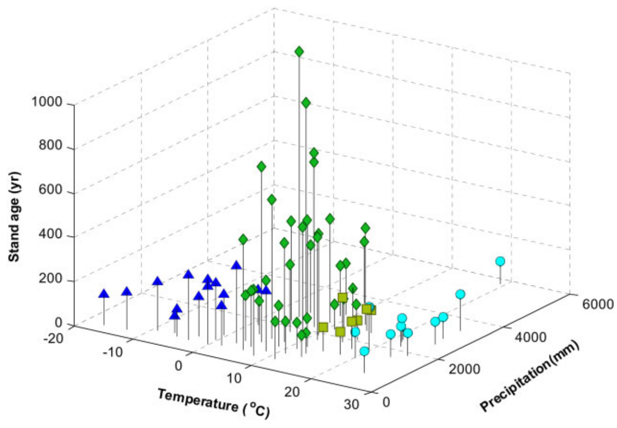

Figure 9 Stand ages of mature forests in relation to mean annual temperature and mean annual precipitation. Each point is the average stand age of all the sites for every 3 °C mean annual temperature and every 300 mm mean annual precipitation. The forests are divided into four major forest biomes: boreal (blue triangle), temperate (green diamond), subtropical (yellow-green square), and tropical (cyan circle) forests. The maximum stand age of mature forests reflects tree longevity (Bigler & Veblen, 2009; Stephenson *et al.*, 2011).

dient the lower bound of BCD_a of mature forests generally declines from tropical to temperate and boreal forests, which is consistent with the pattern exhibited by the existing global forests (IPCC, 2006). The possible reason behind the latitudinal patterns is that BCD_a of forests is controlled by the years (or stand age) and the rate of carbon sequestration. For global mature forests, the mature forests in mid-latitude regions have an older stand age than other regions (Fig. 9). For most of the existing forests that have not achieved a mature state (FAO, 2010), their BCD_a pattern is related to declining rate of carbon sequestration from tropical to temperate and boreal forests (Chapin *et al.*, 2002).

The BCD_a of mature forests and its spatial patterns may change with climate fluxes. The relationship between the BCD_a of mature forests and temperature is positive in those regions with a mean annual temperature < 8 °C, and negative in those regions with a mean annual temperature > 10 °C. We postulate that increased temperatures would lead to increased BCD_a for boreal and temperate mature forests (located in high latitudes) and decreased BCD_a for tropical mature forests (located in low latitudes). If forest types and precipitation remain unchanged, every 1 °C increase in temperature would increase BCD_a by 7.8 Mg C ha^{-1} for mature forests distributed in areas with a mean annual temperature lower than 8 °C (Fig. 3), but decrease the BCD_a of wet tropical forests (Stegen *et al.*, 2011), and decrease BCD_a by 29.8 Mg C ha^{-1} for African rain forests (Liu *et al.*, 2012). Similar trends were reported from the long-term site observations and dendrochronology studies in boreal and temperate forests (McMahon *et al.*, 2010; Beck *et al.*, 2011).

The relationship between the BCD_a of mature forests and precipitation suggests that increased precipitation would boost BCD_a for temperate continental forests, subtropical dry forests and tropical moist deciduous forests. If forest types and temperature remain unchanged, every 100 mm of precipitation increase would increase BCD_a by 11.1 Mg C ha^{-1} for mature forests receiving less than 1000 mm of mean annual precipitation, while BCD_a would decrease by 3.2 Mg C ha^{-1} for those mature forests receiving more than 2500 mm of mean annual precipitation (Fig. 5). Supportive site observation studies have been reported that a doubling of annual precipitation increased tree ring width by 120% for temperate mature forests (Dobbertin *et al.*, 2010). In addition, the BCD_a is different among mature forests growing under similar temperature or precipitation regimes, as revealed by the large standard deviation (SD) and the broad range of variance (Fig. 3). This implies that besides temperature and precipitation, some other factors, such as stand age (Goulden *et al.*, 2011), soil nutrients (Chapin *et al.*, 2002) and elevation (Zhu *et al.*, 2010), may also affect the BCD_a.

The definition and age threshold of old-growth forests

The definition of old-growth forests has long been debated. Some studies have tried to differentiate old-growth forests from younger forests using forest characteristics (Spies, 2004; Blasi *et al.*, 2010) such as a more complex structure and greater species diversity (Blasi *et al.*, 2010; Keeton *et al.*, 2010). A more straightforward method to define old-growth forests is to use an age threshold. For example, 80, 100, 154 and 120–200 years were used for planted forests in east Asia (Kira & Shidei, 1967; Odum, 1969), natural forests in Australia (Jarvis *et al.*, 1989; Keith *et al.*, 2009), boreal forests in Canada (Goulden *et al.*, 2011) and boreal and temperate forests (Smithwick *et al.*, 2002; Pregitzer & Euskirchen, 2004; Luyssaert *et al.*, 2008; Hudiburg *et al.*, 2009), respectively. These studies illustrate that there is no unanimous age threshold for old-growth forests at a global scale or regional scale.

Based on our analysis of the 574 sites, the age threshold of old-growth forests is 450–500 years at a global scale, and 200, 500 and 300 years for boreal, temperate and subtropical forests, respectively. At a global scale, the 450–500-year-old forests have the highest BCD_a for global mature forests. We postulate that 450–500 years could be treated as the age for forests to achieve a carbon neutral state, and used as the age threshold of old-growth forests on a global scale. This age is much older than the value of 80–200 years used in previous hypotheses (Kira & Shidei, 1967; Odum, 1969; Pregitzer & Euskirchen, 2004; Luyssaert *et al.*, 2008; Goulden *et al.*, 2011). At a regional scale, the age thresholds are different for boreal, temperate and subtropical forests because of markedly different factors, such as climate, species composition (Van Tuyl *et al.*, 2005), stand structure (Blasi *et al.*, 2010) and tree longevity (Fig. 9).

The different age thresholds of the old-growth forests for the major forest biomes may help us to resolve why previous studies have found that increased net primary productivity from boreal to temperate and subtropical forests failed to result in increased biomass (Clark, 2004; Keeling & Phillips, 2007). There could be two reasons for this: (1) increased temperature leads to increased respiration (Clark, 2004; Larjavaara & Muller-Landau, 2012); and (2) the longevity and mortality of trees in each major forest biome is different (Stephenson *et al.*, 2011). The non-uniform age threshold for old-growth forests at a global scale shows that regional or major forest biome-specific studies are needed.

Why old-growth forests are carbon sinks

The controversy about why old-growth forests are still carbon sinks (Phillips *et al.*, 1998; Zhou *et al.*, 2006; Luyssaert *et al.*, 2008; Lewis *et al.*, 2009) can be explained by re-examining the definition of old-growth forests. We found that the stand age of those forests with the highest BCD_a is much older than the age threshold of old-growth forests as proposed in previous studies (Pregitzer & Euskirchen, 2004; Goulden *et al.*, 2011). This discrepancy could be caused by the failure of the conventionally held age threshold, taking into account re-disturbance and long-term climatic change (Fisher, 1990; Muller-Landau, 2009). The relationship between the BCD_a of mature forests and climate showed that climate change would break the equilibrium of a stable carbon density in old-growth forests (Fig. 5). Increased temperature will lead to carbon sinks in ecological zones such as boreal continental forests, temperate continental forests and tropical mountain forests. Other climate change factors, such as elevated CO_2 concentration and nitrogen deposition, can also increase carbon exchange between old-growth forests and the atmosphere (Muller-Landau, 2009; Yu *et al.*, 2011).

The potential contribution of forest management to global carbon balance

The BCD_a of mature forests is two to four times that of existing global forests (Liu *et al.*, 2012). The BCD increases as a forest grows from 80 to 400 years, and the mean annual increase rate of BCD_a of mature forests is in accordance with the long-term inventory results (Phillips *et al.*, 1998; Baker *et al.*, 2004; Luyssaert *et al.*, 2008). This means that the BCD increases from global existing forests to mature forests and old-growth forests. However, the BCD of old-growth forests is an idealized reference for estimating the potential contribution of existing global forests to take up carbon. A sustainable strategy of forest management is to increase forest BCD while considering wood removal (IPCC, 2006).

The non-standard plot sizes around the world in this study could also cause uncertainty in assessing forest BCD_a. For example, in the forest sites in China the plot sizes are designated as 0.06–0.1 ha (Xiao, 2005), which are close to those used in USA (USDA, 2011) and Canada (Louisiana Pacific Canada Ltd, 2000). For forest sites smaller than 1.0 ha, BCD_a would be overestimated due to a skewed tree size distribution to the end of large trees (Brown *et al.*, 1995). Therefore, when we conservatively use the BCD_a of mature forests as a reference, the carbon sequestration potential of the global existing forests is 313.4 Pg C under sound conservation and management (Liu *et al.*, 2012).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1 Global mature forest site dataset.
Table S2 Allometric equations used in biomass calculations of our mature forest sites.
Table S3 The statistical results for above-ground biomass carbon density (BCD_a) of mature forest sites at every 4° of latitude.
Table S4 The relationship between above-ground biomass carbon density of mature forests and mean annual temperature and mean annual precipitation in each ecological zone.
Appendix S1 Global mature forest site dataset.
Appendix S2 The field work and used allometric equations in our mature forest sites.
Appendix S3 The relationship between above-ground biomass carbon density (BCD_a) of mature forests and latitude.
Appendix S4 The relationship between above-ground biomass carbon density (BCD_a) of mature forests and mean annual temperature and mean annual precipitation in each ecological zone.

BIOSKETCH

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