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REGULAR ARTICLE

Ecosystem carbon stocks in a forest chronosequence in Hunan Province, South China

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Abstract

Background and aims Forest ecosystems represent an important carbon sink. A few studies have reported carbon stocks in a forest chronosequence, the carbon stock pattern variation and proportion of each compartment remain poorly understood. The objectives of this study were to quantify carbon stocks of each compartment of forest ecosystem and access their contribution to forest carbon stocks with forest succession.

Methods Totally, 32 plots (20 m × 50 m) in different stages of forest succession were investigated, including 11 replicates for *Masson* pine forest at the early stage, 9 for pine-broadleaved mixed forest at the middle stage, and 12 for evergreen broadleaved forest at succession climax, to quantify carbon stocks in trees, shrubs, herbaceous plants, litter and coarse woody debris (CWD), and soil.

Results The total ecosystem carbon stocks ranged from 193 to 257 Mg ha^{-1}, of which vegetation carbon stocks ranged from 94 to 129 Mg ha^{-1}. Tree biomass carbon stocks increased but shrub biomass carbon stocks decreased during forest succession. The increment of tree biomass carbon stocks was far more than that of shrub, resulting in the increases of vegetation carbon stocks during forest succession. Debris carbon stocks ranged from 4.2 to 5.6 Mg ha^{-1}, with no significant variation across the forest chronosequence. The soil carbon stocks (top 100 cm) ranged from 96 to 132 Mg ha^{-1}. Soil carbon stocks increased significantly during the forest chronosequence, of which soil carbon accumulation occured mainly in the topsoil (0–30 cm). There were no significant differences among the proportions of forest ecosystem carbon stocks in the chronosequence. The averages of proportions of vegetation biomass, debris and soil carbon were 46.7 %, 2.1 % and 51.2 %, respectively.

Conclusions Our results present robust evidence for the increasing carbon sequestration across forest succession chronosequence. Furthermore, tree growth and carbon accumulation in topsoil layer contribute equivalently to carbon sequestration during forest succession in subtropical China.

Keywords Forest succession · Carbon stock · Soil organic carbon · Forest ecosystem · Subtropical forest · Biomass

Introduction

Given global warming and increasing atmospheric CO_2 concentration, concerns regarding climate change mitigation strategies have increased in recent years. Carbon (C) sequestration by forests is considered one effective

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mitigating pathway (Dixon et al. 1994; Pan et al. 2011). Globally, forests are the largest C pool representing a C stock of 861Pg or 45.7 % of terrestrial C, more than double the amount of C in the atmosphere (FAO 2006; Pan et al. 2011), and function as an important C sink. Forest C stocks vary in time and space (Pan et al. 2011), and by changes in forest composition through the process of forest succession (Thuille and Schulze 2006; Alberti et al. 2008; Stoy et al. 2008; Wang and Epstein 2013; Zeng et al. 2013).

Ecological succession is the observed process of change in species composition and stand structure of an ecological community over time. A rich literature exists demonstrating the changes of plant productivity (Goulden et al. 2011), biological diversity (Amici et al. 2013), soil fertility (Gomoryova et al. 2007), and plant nutrition (Batterman et al. 2013) following forest community succession. Recently, a few studies on successional changes in forest C stocks have been reported (Alberti et al. 2008; De Simon et al. 2012; Novara et al. 2013; Zeng et al. 2013). Most of these studies are from Europe and the Americas and relate to dynamics of soil C stocks and microbial biomass (Foote and Grogan 2010; De Simon et al. 2012; Deng et al. 2013; Novara et al. 2013). However, there remains a lack of investigations aimed at quantifying the aboveground and belowground C stocks associated with successional change, especially in Asia (Zeng et al. 2013).

Choice of research methods plays a very important role in accurately calculating changes in forest C stocks over time. Many methods are available to quantify forest C stocks (Guo et al. 2010; Talbot et al. 2014). Of these, the most commonly used method was forest survey (Lü et al. 2010; Wang et al. 2013). To calculate fine and coarse root biomass, De Simon et al. (2012) used a coefficient of aboveground biomass. Alberti et al. (2008) also estimated root biomass using a root:shoot biomass ratio of 0.24. Although a few documents reported C stocks as forests change with succession, there is still lack of knowledge describing the partition of C stocks within forest ecosystems.

In the subtropical zone of China, the primary natural evergreen broadleaved forests were destroyed over the past centuries by human activities. Recently, forest restoration in China has gained considerable attention. After disturbance cessation, the communities tends to restore slowly to their native state. Some areas where plantations had been created have been clearcut, abandoned, and are now returning, through natural succession, to evergreen broadleaved forests. Accurate quantification of changes in C stock in forests undergoing natural succession can further improve our understanding of the role of forests in C sequestration. However, such studies are very challenging because of uncertainties in estimates in spatial and temporal variations of C stocks and fluxes (IPCC 2000). One promising approach is to examine forest C budgets and temporal trends using chronosequences (space for time substitution) (Walker et al. 2010).

Using this chronosequence approach, we selected 32 plots (20 m × 50 m for each) in a series of stands at different stages of development across a forest chronosequence covering a period of approximately 100 years, with the aim to test the hypothesis that C stocks in forest ecosystems would increase with forest succession stages. These successional forests included *Masson* pine forest (PF), pine-broadleaved mixed forest (MF), and evergreen broadleaved forest (BF). In particular, the specific objectives of this study were: (1) to quantify C stocks of each compartment of forest ecosystem, and (2) to access the contribution of each compartment to forest ecosystem C stocks.

Materials and methods

Site description and plots selection

The study was conducted in Hunan Province (108°47′–114°15′ E, 24°38′– 30°08′ N) situated in mid-subtropical zone of China (Fig. 1). Hunan Province is located at the transition zone from the Yunnan-Guizhou plateau to the lower mountains and hills on the southern side of the Yangtze River at an elevation of 21–2122 m above sea level. The climate of this region is humid mid-subtropical monsoon. The mean annual precipitation is 1200–1700 mm, of which about 68 % – 84 % falls between April and October. The average annual air temperature is 16–18 °C with mean minimum in January and mean maximum in July (Cao and Li 2012). The soil is red-yellow, which developed mostly from the parent rocks of slate and shale, and classified as Plinthudults accroding to US Soil Taxonoy.

The native vegetation is evergreen broadleaved forest typical of subtropics, with *Castanopsis spp.* and *Quercus spp.* as the major species. At the early stage of forest succession after plantation abandonment, the secondary forest consists mainly

Fig. 1 Sites of the Masson pine forest (PF, ■), the pine and broadleaved mixed forest (MF, ●) and the evergreen broadleaved forest (BF, ▲) in Hunan province, subtropical China

of *Masson* pine (*Pinus massoniana*). With secondary forest development, deciduous tree species join the stand, such as liquidambar (*Liquidambar formosana*), sassafras (*Sassafras tzumu*), basswood (*Tilia tuan*), and camphor tree (*Cinnamomum camphora*). At climax, evergreen broadleaved tree species such as *Castanopsis spp.*, *Quercus spp.*, *Cyclobalanopsis spp.* become dominant. Based on this successional pattern, pure *Masson* pine forests (PF), pine-broadleaved mixed forest, and evergreen broadleaved forest (BF) were selected to represent the early, medium, and regional climax stages. Previous reports demonstrated that these three stages represent a typical chronosequence of forest succession in subtropical China (Huang et al. 2011; Zeng et al. 2013; Zhang et al. 2013). We selected 32 plots having no evidence of recent disturbance. Distance between stands representing each forest type was more than 1 km (Fig. 1). The main characteristics of each chronosequence are reported in Table 1.

Aboveground and belowground biomass

The 32 plots included 11 replicates for PF, 9 for MF, and 12 for BF. The area of each plot was 1000 m^2 (20 m × 50 m). In October 2011, all plots were intensively surveyed, recording community structure, elevation, slope, forest age, and canopy density. Diameter at breast height (DBH, DBH $\geq$ 5 cm at 1.3 m) and height of each tree were measured for all trees in each plot. To quantify total biomass and biomass of different compartments (e.g., stem, branch, leaf and root) of each tree, allometric growth equations for each tree species were used. For equation simulation, at least 10 standard trees of every tree species were selected and harvested. The allometric growth equations for dominant and other tree species were listed in Table 2. We used these allometric growth equations to calculate the aboveground biomass (stem, branch and leaf) of every tree and the total aboveground biomass for every plot.

The coarse root ($\geq$ 2 mm) biomass of dominant and other tree species was also calculated using allometric

Table 1 Characteristics of the studied chronosequences

Community	*Masson* forest (PF)	Pine-broadleaved mixed forest (MF)	Evergreen broadleaved forest (BF)
Successional stage	I	II	III
Age (years)	20–30	20–50	40–100
Slope (°)	5–20	5–15	5–36
Elevation (m)	205–548	192–758	218–1004
Canopy density (%)	50	65	70
Stand density (stems ha^{-1})	986	1148	1055
Stone in soil (%, weight)	1.5	4.1	14.1
Soil taxonomy	Ultisol	Ultisol	Ultisol
Dominant species			
Tree layer	*Pinus massoniana*	*Pinusmassoniana* *Liquidambar formosana* *Sassafras tzumu* *Cinnamomum camphora*	*Castanopsis fargesii* *Schima superb* *Quercus spp.* *Lithocarpus glabra* *Machilus pauhoi* *Cyclobalanopsis glauca*
Shrub layer	*Loropetalum chinense* *Quercus fabri* *Clerodendrum cyrtophyllum*	*Maesa japonica* *Ilex aculeolata* *Eurya nitida*	*Maesa japonica* *Eurya nitida* *Sapium discolor* *Quercus fabri*
Herb layer	*Miscanthus floridulu* *Dicranopteris linearis* *Parathelypteris nipponica*	*Woodwardia japonica* *Dicranopteris linearis* *Dryopteris spp.* *Carex nemostachys*	*Dicranopteris linearis* *Urena lobata* *Diplopterygium chinense* *Carex nemostachys* *Lophatherum gracile* *Arthraxon hispidus* *Polygonum spp.*

growth equations. More than 10 standard trees of every tree species were selected and harvested to simulate equations (same with selected trees for aboveground biomass calculation). The coarse root biomass of individual standard trees of each species was determined through excavating a soil cylinder (Xiang et al. 2011). A soil cylinder extending from the ground projection of the crown was excavated at a verticle depth of 60 cm. Soil was carefully excavated at 20-cm-depth intervals and sifted through a wire sieve (20-mm mesh) to separate roots. Stumps and attached taproots were pulled out, and soil residue remained on roots was removed by brushing and washing. All harvested roots were weighted and divided into four classes according to the method of Xiang et al. (2011). Subsamples of each class were brought to the laboratory and dried at 65 °C to constant weight. Moisture content was determined and used to calculate the dry mass for each class, and the total root biomass was achieved by combining all classes.

Measurements of fine root (<2 mm) biomass were made using the soil coring method (Helmisaari et al. 2007). Using a stainless-steel cylinder of a diameter of 10 cm and a height of 20 cm, ten soil cores were collected randomly from the 0–20 and 20–40-cm mineral soil layers of each plot. Fine roots were separated from the soil by washing and then dried at 65 °C for 48 h, in order to calculate dry biomass on an area basis. The density of fine root biomass was calculated from the mean dry biomass of fine root sampled (B_{fr}) and the volume of the stainless-steel cylinder (V), using the following equation: $D_{fr} = B_{fr} / V$. The total biomass of roots is equal to the sum of coarse root and fine root biomass.

Table 2 Allometric growth equations used to estimate tree biomass

Tree species		*Pinus massoniana*	R^2
Pinus massoniana	Stem	$0.01844 \times (D^2H)^{0.993}$	0.971
	Branch	$0.18488 \times (D^2H)^{0.5904}$	0.768
	Leaf	$0.11272 \times (D^2H)^{0.50819}$	0.787
	Root	$0.00394 \times (D^2H)^{1.00337}$	0.912
Sassafras tzumu	Stem	$0.01022 \times (D^2H)^{1.04436}$	0.982
	Branch	$0.12428 \times (D^2H)^{0.62607}$	0.895
	Leaf	$0.04917 \times (D^2H)^{0.51635}$	0.979
	Root	$0.17616 \times (D^2H)^{0.66359}$	0.962
Liquidambar formosana	Stem	$0.0052 \times (D^2H)^{1.1567}$	0.997
	Branch	$0.0387 \times (D^2H)^{0.731}$	0.995
	Leaf	$0.0192 \times (D^2H)^{0.7729}$	0.993
	Root	$0.0057 \times (D^2H)^{0.989}$	0.993
Cinnamomum camphora	Stem	$0.01305 \times (D^2H)^{1.04777}$	0.964
	Branch	$0.01661 \times (D^2H)^{0.9779}$	0.736
	Leaf	$0.00608 \times (D^2H)^{0.84549}$	0.584
	Root	$0.04058 \times (D^2H)^{0.87911}$	0.563
Castanopsis fargesii	Stem	$0.07159 \times (D^2H)^{0.86747}$	0.999
	Branch	$0.05602 \times (D^2H)^{0.78411}$	0.994
	Leaf	$0.01915 \times (D^2H)^{0.74925}$	0.991
	Root	$0.04803 \times (D^2H)^{0.78908}$	0.999
Cyclobalanopsis glauca	Stem	$0.06035 \times (D^2H)^{0.91847}$	0.987
	Branch	$0.03508 \times (D^2H)^{0.88521}$	0.984
	Leaf	$0.00435 \times (D^2H)^{0.93164}$	0.979
	Root	$0.03949 \times (D^2H)^{0.86376}$	0.991
Machilus pauhoi	Stem	$0.0659 \times (D^2H)^{0.86398}$	0.999
	Branch	$0.0335 \times (D^2H)^{0.814}$	0.999
	Leaf	$0.03105 \times (D^2H)^{0.715}$	0.998
	Root	$0.10691 \times (D^2H)^{0.693}$	0.998
Schima superb	Stem	$0.00543 \times (D^2H)^{1.16277}$	0.880
	Branch	$0.0062 \times (D^2H)^{0.99113}$	0.795
	Leaf	$0.05977 \times (D^2H)^{0.59053}$	0.730
	Root	$0.0566 \times (D^2H)^{0.81718}$	0.931
Other tree species	Stem	$0.045 \times (D^2H)^{0.894}$	0.944
	Branch	$0.019 \times (D^2H)^{0.851}$	0.944
	Leaf	$0.046 \times (D^2H)^{0.501}$	0.944
	Root	$0.007 \times (D^2H)^{1.033}$	0.944

D and H are diameter at 1.3 m height (cm) and tree height (m), respectively

To estimate understory vegetation (herbaceous plant and shrub) biomass, we used the destructive harvesting method. Three 2 m × 2 m shrub subplots and one 1 m × 1 m herbaceous plant quadrat per subplot were randomly selected within each 20 m × 50 m plot. Shrubs were harvested and separated into leaves, branches, and stem; all herbaceous plants were clipped at ground line from each quadrat. After sampling, all plant materials (including roots) collected with these subplots were transported to the laboratory and then dried at 65 °C to constant weight and meassured their biomass.

Litter and coarse woody debris (CWD) biomass

In this study, debris included aboveground litter and CWD. Aboveground litter, defined as litter on the soil surface, was quantified by collecting all the litter and twigs (< 2 cm diameter) within a randomly-selected 1 m × 1 m subplot in each plot (the same as the herb quadrat). After sampling, all plant materials collected within these subplots were dried at 65 °C to constant weight prior to measuring their biomass.

The amounts of CWD (> 2 cm diameter) in the three 10 m × 10 m subplots in each plot were measured. CWD biomass was calculated as the product of CWD volume and decay class-specific densities (Iwashita et al. 2013). Each piece of CWD was assigned to one of five decay classes modified from Keller et al. (Keller et al. 2004). Decay classes 1–4 were successively more decomposed tree CWD, and tree fern CWD comprised a fifth decay class. Densities (dry mass/volume) for each decay class were quantified on representative samples from crosssections of debris collected in situ using the water displacement method, except decay class 1 which was equal to live wood density.

Soil sampling

Soil sampling was conducted in five soil layers, 0–10, 10–20, 20–30, 30–50, and 50–100 cm, using a stainless-steel cylinder of a diameter of 5 cm. In each 20 m × 50 m plot, eight soil cores were randomly collected after the removal of the litter layer and mixed to effectively form one soil sample. All samples were passed through a 2-mm sieve, and the organic fragments (plant material and root residues) were removed. Each sample was air-dried and stored at room temperature for chemical analysis. The soil bulk density of the different soil layers was measured using a soil bulk sampler with a 5.0 cm diameter and 5.0 cm high stainless-steel cutting ring (3 replicates) in each plot. Locations for soil bulk sampler were randomly selected. The original volumes of each soil core and its dry mass after drying at 105 °C were measured. The coarse fractions (soil fraction >2 mm) of each sample were also recorded.

Chemical analysis

All plant materials, including the compartments (stem, branch, leaf, coarse and fine roots) of tree species, shrub (branch, leaf and root), herbaceous plant, litter, and CWD, and soil samples were dried and ground to 0.25 mm before chemical analysis for organic C concentration. C concentrations of plant and soil samples were measured with a C/N analyzer (Elementar, Germany).

C stock calculation

C stocks of tree layers are the sums of each tree species biomass per unit area multiplied by their C concentrations using the equation:

$$CS_{\text{tree}}\left(\text{Mg}\,ha^{-1}\right) = \sum_{i,j=1}^{n} B_{i,j} \times \text{Cconc}_{i,j} + B_{\text{fine root}} \times \text{Cconc}_{\text{fine root}}$$

where CS_{tree} is the C stock of trees (Mg ha^{-1}), $B_{i,j}$ is the compartment j biomass of tree speice i per unit area (Mg ha^{-1}), $Cconc_{i,j}$ is the C concentration of comonent j of tree specie i, $B_{fine\ root}$ is the fine biomass per unit area (Mg ha^{-1}), $Cconc_{fine\ root}$ is the C concentration of fine root, i is the kind of tree species, and j is the stem, branch, leaf, and coarse root.

Shrub C stocks were calculated as:

$$CS_{\text{shrub}}\left(\text{Mg}\,ha^{-1}\right) = \sum_{i=1}^{n} B_i \times \text{Cconc}_i$$

where CS_{shrub} is the C stock of shrub (Mg ha^{-1}), B_i is the compartment i biomass of shrub per unit area (Mg ha^{-1}), $Cconc_i$ is the C concentration of compartment i of shrub, and i is the stem, branch, and root.

Herbaceous plantaceous plant C stocks were calculated according to the following equation:

$$CS_{\text{herb}}\left(\text{Mg}\,ha^{-1}\right) = \sum_{i=1}^{n} B_i \times \text{Cconc}_i$$

where $CS_{herbaceous\ plant}$ is the C stock of herbaceous plantaceous plant (Mg ha^{-1}), B_i is the compartment i biomass of herbaceous plantaceous plant per unit area (Mg ha^{-1}), $Cconc_\text{i}$ is the C concentration of compartment i of herbaceous plantaceous plant, and i is the aboveground and belowground compartments.

Litter C stock is the biomass of litter per unit area multiply by its C concentration.

C stocks of CWD were calculated as:

$$CS_{CWD}\left(\mathrm{Mg}\,ha^{-1}\right) = \sum_{i=1}^{n} V_i \times D_i \mathrm{Cconc}_i$$

where CS_{CWD} is the C stock of CWD (Mg ha^{-1}), V_i and D_i are the volume and density of CWD in decay class i, respectively, $Cconc_i$ is the C concentration of CWD in decay class i, and i is the decay class.

Soil C stocks were calculated by the following equation:

$$CS_{CWD}\left(\mathrm{Mg}\,ha^{-1}\right) = \sum_{i=1}^{n} BD_i \times \mathrm{Cconc}_i \times D_i$$

Where CS_{soil} is the C stock of soil (Mg ha^{-1}), BD_i is the soil bulk density in i layer (g cm^{-3}), $Cconc_i$ is the soil organic C (Harper et al. 2012) concentration in i layer (%), D_i is the soil thickness of i layer (cm), and i is the layer number of topsoil.

Forest C stock is the sum of C stocks of tree, shrub, herbaceous plant, litter, CWD and soil.

Statistical analysis

One-way ANOVA was used to evaluate the differences among tree, shrub, herbaceous plant, litter and CWD biomass C stocks in PF, MF and BF stands. Two-way ANOVA was used to evaluate differences among soil C stocks in different layers soil in PF, MF and BF stands. Tukey's honestly significant difference test was performed when there were significant differences at $p < 0.05$. Analyses were performed using SPSS Statistics Release15.0 (SPSS Inc.).

Results

Vegetation biomass C stocks

Tree biomass C sotck in BF (127.4 Mg ha^{-1}) was significantly greater than in PF (90.4 Mg ha^{-1}) and MF (91.8 Mg ha^{-1}), of which branch and root biomass C stocks in tree layers in BF were significantly greater than in PF (Fig. 2a). In contrast, shrub biomass C stock in BF (0.6 Mg ha^{-1}) was much lower than that in PF (1.9 Mg ha^{-1}, Fig. 2b). The increases of C stocks in trees were much larger than the decreases of C stocks in shrubs across the forest chronosequence, resulting in more vegetation biomass C stock in BF compared to PF and MF.

The proportion of tree biomass C stock to vegetation biomass C stock increased significantly with forest succession. The proportions of shrub and herbaceous plant biomass C stocks in BF were significantly lower compared to that in PF and MF. The average proportions of tree, shrub and herbaceous plant biomass C stocks were approximately 97.3 %, 1.2 % and 1.5 %, respectively.

Debris and soil C stocks

Litter C stocksshowed no significant variation across different succession stages. There were significant differences among CWD C stocks in PF, MF and BF. The largest CWD C stock was in BF, followed by MF. The lowest CWD C stock occurred in PF. The significant

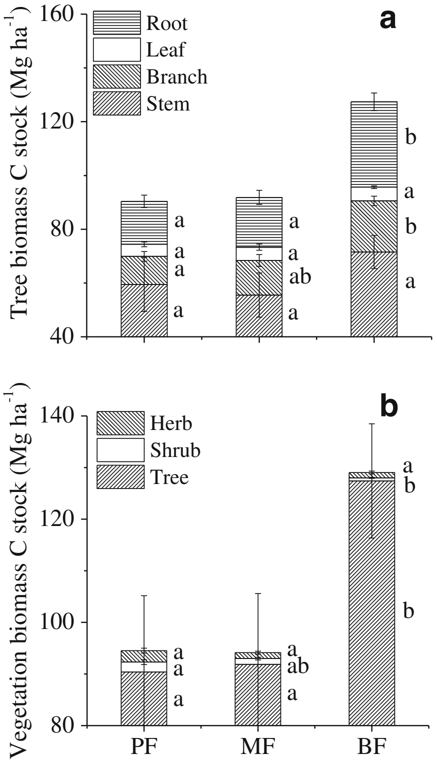

Fig. 2 Vegetation (including tree) biomass carbon stocks of various components in the Masson pine forest (PF), the pine and broad-leaf mixed forest (MF) and the evergreen broadleaved forest (BF) in Hunan province, subtropical China. **a**, Tree biomass carbon stock; **b**, Vegetation biomass carbon stock. Lowercase letters indicate significant differences of vegetation (tree) biomass carbon stocks of same components at different succession stages at p = 0.05 (ANOVA using Tukey's honestly significant difference test)

increase of CWD C stocks offset the decrease of litter C stocks with forest succession, resulting in no significant differences in debris C stocks among PF (4.6 Mg ha^{-1}), MF (4.2 Mg ha^{-1}) and BF (5.6 Mg ha^{-1}, Fig. 3).

Soil C stock in MF (131.9 Mg ha^{-1}) was significantly higher than that in PF (95.8 Mg ha^{-1}), with no significant difference between BF (122.1 Mg ha^{-1}) and MF (Fig. 4 and 5a). Soil C stocks at the depths of 0–10, 10–20, and 20–30 cm varied significantly, but showed no variation between the layers of 30–50 and 50–100 cm (Fig. 4). The C stock at the depth of 0–30 cm accounted for 55.6 to 65.8 % of total C stocks in top 1 m soils in all forest ecosystems and increased gradually with forest succession stages.

The contribution of each components to forest ecosystem C stocks

Vegetation biomass and soil both contributed about 50 % of the total ecosystem C stocks, with no significant variation of their contributions across the three kinds of forests (Fig. 5). The average contributions of vegetation biomass, debris, and soil to forest ecosystem C stocks were 46.7 %, 2.1 % and 51.2 %, respectively.

Discussion

Vegetation biomass C stocks across the forest succession

Vegetation biomass C stocks of forests in subtropical region of China increased with forest succession as indicated by the result that vegetation biomass C stock in BF was significantly higher than in PF and MF, which is consistent with results from other studies (Alberti et al. 2008; De Simon et al. 2012; Wang and Epstein 2013). Wang and Epstein (2013) reported that there was a carbon source-sink transition during secondary succession in a Virginia valley. Alberti et al. (2008) found that forest carbon stock increased at a mean rate of 1.18 Mg ha^{-1} yr.$^{-1}$ during a secondary succession in the Eastern Prealps of Italy. De Simon et al. (2012) reported that beech and spruce forests acted as carbon sink, although net ecosystem productions of beech and spruce forests decreased at the early stages of a chronosequence. The changes of tree species composition were the one of the main causes resulting in the increases of vegetation biomass carbon stocks across the forest succession. Forests consisting of broadleaved tree species possess more biomass carbon stocks than those

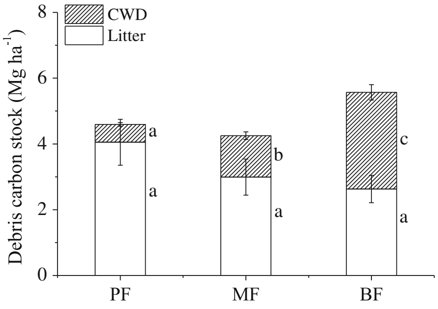

Fig. 3 Debris carbon stocks in the Masson pine forest (PF), the pine and broad-leaf mixed forest (MF) and the evergreen broadleaved forest (BF) in Hunan province, subtropical China. Lowercase letters indicate significant differences of debris carbon stocks of same component at different succession stages at $p = 0.05$ (ANOVA using Tukey's honestly significant difference test)

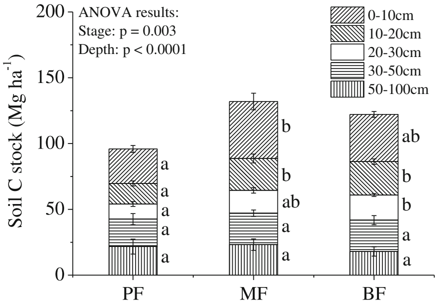

Fig. 4 Soil carbon stocks in the Masson pine forest (PF), the pine and broad-leaf mixed forest (MF) and the evergreen broadleaved forest (BF) in Hunan province, subtropical China. Lowercase letters indicate significant differences of soil carbon stocks in same depth at different succession stages at $p = 0.05$ (ANOVA using Tukey's honestly significant difference test)

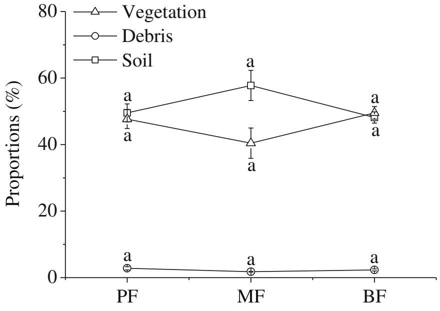

Fig. 5 Proportions of every compartment to ecosystem carbon stocks in the pine forest (PF), the pine and broad-leaf mixed forest (MF) and the evergreen broadleaved forest (BF) in Hunan province, subtropical China. Lowercase letters indicate significant differences among proportions of every compartment carbon stocks at different succession stages at $p = 0.05$ (ANOVA using Tukey's honestly significant difference test)

consisting of coniferous tree species (Chen et al. 2005; Glenday 2006). Moreover, plant function diversity and tree species richness positively corelated to biomass carbon stock of forest (Guo and Ren 2014). More diverse ecosystems might accumulate more carbon as a result of increased photosynthetic inputs (Catovsky et al. 2002). The translation of tree species composition (from coniferous to broadleaved tree species) and the enhance of plant diversity resulted in the increase of vegetation biomass carbon stocks across the forest succession. These results indicated that the secondary forest succession can promote to carbon sequestration into vegetation biomass, act as carbon sink, and it can be an important strategy to reduce the concentration of atmospheric carbon dioxide and alleviate global climate change.

As the key compartment of vegetation biomass carbon stocks, tree biomass carbon stocks increased significantly as succession developed. Tree biomass carbon stocks in a forest chronosequence in this study ranged from 90 to 127 Mg ha^{-1}. These values were well within the ranges of tree biomass carbon stocks (26–286 Mg ha^{-1}) reported for subtropical and tropical forests (Fang et al. 2003; Glenday 2006; Zhang et al. 2007; Zeng et al. 2013; Sun and Guan 2014). The ratio of tree biomass carbon stock to vegetation biomass carbon stocks ranged from 95 to 99 %, increased significantly with forest succession, which was consistent with the results from subtropical and tropical forests (80–99 %) (Chen et al. 2005; Glenday 2006; Zhang et al. 2007; Lü et al. 2010; Zeng et al. 2013; Sun and Guan 2014). The results from the present study and those from other previous studies indicate that the tree layer plays an important role in forest biomass accumulation and carbon sequestration as forest succession develops in subtropical and tropical areas. Given the importance of tree layer in carbon sequestration, we should accelerate the fast recovery of tree species composition and their carbon sequestration function to alleviate the global climate change.

Our results showed that shrub biomass carbon stocks decreased significantly in the forest chronosequence. This may be the result of increasing overstory canopy closure and tree density with forest succession, because canopy closure had a strong influence on standing crop of understory plant, and tree density strongly constrained understroy plant standing crop (Sabo et al. 2009). The proportion of understory biomass carbon stock to vegetation biomass carbon stocks ranged from 1.3 to 4.4 %, with an average of 2.7 %, which were well within the ranges of the proportion of understory biomass carbon stock (0.1–19.8 %) reported for subtropical and tropical forests (Chen et al. 2005; Fang et al. 2003; Zhang et al. 2007; Zeng et al. 2013; Sun and Guan 2014). Although the contribution of understory plants to ecosystem carbon stocks was low in this study, there were a lot of documents showed that understory plants possess high biodiversity and the seedlings of tree species are also the important composition of understory plants (Onaindia et al. 2013). Thus, understory plants are still very important from the perspective of the long term sustainable forest ecosystem function, such as the potential of C sequestration.

C stocks in debris and soil

Although there was a trend of decrease of litter carbon stocks across the forest succession, litter carbon stocks didn't vary. It may be due to the change of litterfall production and litter decomposition rates across the forest succeseion. Litterfall productions of forests increased with forest succession (Huang et al. 2011), and with the increase of the number of mixed broadleaved tree species in mixed coniferous broadleaved forests (Huang et al. 2005). Meanwhile the rates of litter decomposition increased after the transformation of pure masson pine forest to mixed forest with broadleaved tree species (Huang et al. 2011; Song et al. 2014). The increase of litter decomposition rate offset the increase of litterfall productions, leading to similar litter carbon stocks across forest succesion. CWD carbon stocks increased significantly along the forest chronosequence. This was due to the gradually increasing mortality of masson pine with increasing forest age (Tang and Zhou 2005). The increase of CWD carbon stocks offset the decrease of litter carbon stocks, leading to no changes in debris carbon stocks with forest succession. Debris acts as a carbon source of soil and plays an important role in long-term carbon stock of forests (Manies et al. 2005). Continuous carbon supply from debris is of great significance in the accumulation of soil carbon pool. Debris carbon stocks in the forest chronosequence ranged from 4.2 to 5.6 Mg ha^{-1}, which were close to those values reported for subtropical forests (2.7–4.7 Mg ha^{-1}) in China (Zhang et al. 2007). The proportions of debris carbon stock to forest ecosystem stock ranged from 1.8 to 2.8 %, which were comparable to that of tropical seasonal rainforests (2.0–3.4 %) in Southwest China

(Lü et al. 2010), and higher than that of subtropical forests (0.3–1.2 %) in South China (Zeng et al. 2013) and tropical rainforests (0.1–0.3 %) in East Africa (Glenday 2006). The variation of proportions of debris carbon stock in our study and these reported by Zeng et al. (2013) and Glenday (2006) may be the differences of forest ages.

Soil carbon stock in MF was significantly greater than that in PF, and it showed that soil carbon stocks increased significantly as forest succession developed in this study. Although few document reported that soil organic matter pool decreased markedly at an early stage of secondary succession (Ohtsuka et al. 2010), a large of documents found that soil carbon stock increased during forest succession (Foote and Grogan 2010; Huang et al. 2011; Deng et al. 2013; Novara et al. 2013). The changes of soil C stocks were the result of the accumulation of soil organic C with forest succession (Deng et al. 2013). These changes were closely related to plant succession that can influence the litter quality and the decomposition rate following the alteration of plant communities (Novara et al. 2013). Leaf litter is a primary source of soil organic carbon (Cusack et al. 2009), and Fine roots are also an important source of soil organic carbon (Chen et al. 2002). Owing to the incease of litterfall production and litter decomposition rate, total carbon products of input to belowground from decomposed litter increased significantly with forest succession (Huang et al. 2011), resulting in the increase of the concentration of soil organic C and the accumulation of soil organic C stock. These results indicated that soil was also an important carbon sink during forest succession, and it can also be a strategy to reduce the concentration of atmospheric carbon dioxide.

Contribution to forest ecosystem C stock

There were no significant differences among the proportions of vegetation carbon stocks in PF, MF and BF. Similarly, the proportions of soil carbon stocks in PF, MF and BF didn't differ. The results suggest that the contributions of vegetation biomass and soil carbon stocks to forest carbon stocks didn't vary across the forest succession. It is owing to the the simultaneous increase of the C stocks in vegetation biomass and soil across the forest succession. The proportions of vegetation biomass and soil carbon stocks were close to 50 %, and it indicates that vegetation and soil play equivalent improtant roles in carbon sequestration across the forest succession. However, the result is inconsistent with few document. The rates of biomass carbon sequestration were much higher than the rates of soil carbon sequestration in oak (*Quercus robur*) and Norway spruce (*Picea abies*) in Denmark, Sweden and the Nethelands, suggested biomass carbon plays more important role in carbon sequestration (Vesterdal et al. 2006). Alberti et al. (2008) also found that the dominant sink for atmospheric carbon within secondary mixed ash and sycamore forests seems to be live wood while the soil plays a much smaller role during a second succession. In contrast, our results showed that soil play the same role with vegetation in carbon sequestration across the forest succession in subtropical China. These values indicated that the contributions of vegetation and soil to forest ecosystem C stocks may vary in different forest type and region. The different results may depend on a few of factors controlled soil carbon stock and carbon sequestration in forest ecosystem, such as tree species composition (Tang and Li 2013), forest age (Deng et al. 2013), and climate (Marin-Spiotta and Sharma 2013). The role of vegetation in carbon sequestration is indisputable, however, the contribution of soil to C sequestration in forest ecosystem is still questionalbe with forest succession. In the future, we should strengthen the research of soil C stock and its contribution to forest ecosystem C stock, especially in the process of forest succession and vegetation restoration.

Conclusion

Our study investigates the changes in carbon stocks of each compartment in successional forest ecosystems in subtropical China. We found that total forest ecosystem carbon stocks in the chronosequence increased significantly and the carbon accumulation was due to the increase of vegetation biomass and soil carbon stocks. There were no significant differences among the proportions of forest carbon stock in the forest chronosequence. Our results indicated that forest ecosystem sequestered atmosphere carbon during forest succession and became a carbon sink, and vegetation and soil play equivalent roles in carbon sequestration in forest ecosystems across the forest succession in subtropical China.

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References

Alberti G, Peressotti A, Piussi P, Zerbi G (2008) Forest ecosystem carbon accumulation during a secondary succession in the eastern Prealps of Italy. Forestry 81:1–11. doi:10.1093/forestry/cpm026

Amici V, Santi E, Filibeck G, Diekmann M, Geri F, Landi S, Scoppola A, Chiarucci A (2013) Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. J Biogeogr 40:2335–2347. doi:10.1111/Jbi.12182

Batterman SA, Hedin LO, van Breugel M, Ransijn J, Craven DJ, Hall JS (2013) Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502:224–227. doi:10.1038/Nature12525

Cao XY, Li JP (2012) Evaluation of carbon storage and its economic value of *Pinus massoniana* ecosystem in Hunan. Issues For Econ 32:114–117

Catovsky S, Bradford MA, Hector A (2002) Biodiversity and ecosystem productivity: implications for carbon storage. Oikos 97:443–448. doi:10.1034/j.1600-0706.2002.970315.x

Chen H, Harmon ME, Sexton J, Fasth B (2002) Fine-root decomposition and N dynamics in coniferous forests of the Pacific northwest, USA. Can J For Res 32:320–331. doi:10.1139/x01-202

Chen GS, Yang YS, Xie JS, Guo JF, Gao R, Qian W (2005) Conversion of a natural broad-leafed evergreen forest into pure plantation forests in a subtropical area: effects on carbon storage. Ann For Sci 62:659–668. doi:10.1051/forest.2005073

Cusack DF, Chou WW, Yang WH, Harmon ME, Silver WL (2009) Controls on long-term root and leaf litter decomposition in neotropical forests. Global Chang Biol 15:1339–1355. doi:10.1111/j.1365-2486.2008.01781.x

De Simon G, Alberti G, Delle Vedove G, Zerbi G, Peressotti A (2012) Carbon stocks and net ecosystem production changes with time in two Italian forest chronosequences. Eur J Forest Res 131:1297–1311. doi:10.1007/s10342-012-0599-4

Deng L, Wang KB, Chen ML, Shangguan ZP, Sweeney S (2013) Soil organic carbon storage capacity positively related to forest succession on the loess plateau, China. Catena 110:1–7. doi:10.1016/j.catena.2013.06.016

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190

Fang YT, Mo JM, Peng SL, Li DJ (2003) Role of forest succession on carbon sequestration of forest ecosystem in lower subtropical China. Acta Ecol Sin 23:1685–1694

FAO (2006) Global forest resource assessment 2005. Food and agricultural Organization of the United Nations. Rome, Italy

Foote RL, Grogan P (2010) Soil carbon accumulation during temperate forest succession on abandoned low productivity agricultural lands. Ecosystems 13:795–812. doi:10.1007/s10021-010-9355-0

Glenday J (2006) Carbon storage and emissions offset potential in an east African tropical rainforest. Forest Ecol Manag 235:72–83. doi:10.1016/j.foreco.2006.08.014

Gomoryova E, Ujhazy K, Hrivnak R, Strelcova K, Gomory D (2007) Soil properties and microbial activity changes along spruce forest succession in an abandoned grassland. Pol J Ecol 55:457–467

Goulden ML, McMillan AMS, Winston GC, Rocha AV, Manies KL, Harden JW, Bond-Lamberty BP (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Chang Biol 17:855–871. doi:10.1111/j.1365-2486.2010.02274.x

Guo Q, Ren H (2014) Productivity as related to diversity and age in planted versus natural forests. Global Ecol Biogeogr 23:1461–1471. doi:10.1111/geb.12238

Guo ZD, Fang JY, Pan YD, Birdsey R (2010) Inventory-based estimates of forest biomass carbon stocks in China: a comparison of three methods. Forest Ecol Manag 259:1225–1231. doi:10.1016/j.foreco.2009.09.047

Harper RJ, Okom AEA, Stilwell AT, Tibbett M, Dean C, George SJ, Sochacki SJ, Mitchell CD, Mann SS, Dods K (2012) Reforesting degraded agricultural landscapes with eucalypts: effects on carbon storage and soil fertility after 26 years. Agric Ecosyst Environ 163:3–13. doi:10.1016/j.agee.2012.03.013

Helmisaari HS, Derome J, Nojd P, Kukkola M (2007) Fine root biomass in relation to site and stand characteristics in Norway spruce and scots pine stands. Tree Physiol 27:1493–1504

Huang CC, Ge Y, Zhu JR, Yuan WG, Qi LZ, Jiang B, Shen Q, Chang J (2005) The litter of *Pinus massoniana* ecological public-welfare forest in Zhejiang Province and its relationship with the community characters. Acta Ecol Sin 25:2507–2513

Huang YH, Li YL, Xiao Y, Wenigmann KO, Zhou GY, Zhang DQ, Wenigmann M, Tang XL, Liu JX (2011) Controls of litter quality on the carbon sink in soils through partitioning the products of decomposing litter in a forest succession series in South China. Forest Ecol Manag 261:1170–1177. doi:10.1016/j.foreco.2010.12.030

IPCC (2000) Land use, land-use change, and forestry. Special report of the intergovernmental panel on climate change Cambridge University Press, Cambridge

Iwashita DK, Litton CM, Giardina CP (2013) Coarse woody debris carbon storage across a mean annual temperature gradient in tropical montane wet forest. Forest Ecol Manag 291:336–343. doi:10.1016/j.foreco.2012.11.043

Keller M, Palace M, Asner GP, Pereira R, Silva JNM (2004) Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. Global Chang Biol 10:784–795. doi:10.1111/j.1529-8817.2003.00770.x

Lü XT, Yin JX, Jepsen MR, Tang JW (2010) Ecosystem carbon storage and partitioning in a tropical seasonal forest in southwestern China. Forest Ecol Manag 260:1798–1803. doi:10.1016/j.foreco.2010.08.024

Manies KL, Harden JW, Bond-Lamberty BP, O'Neill KP (2005) Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. Can J For Res 35:472–482. doi:10.1139/x04-179

Marin-Spiotta E, Sharma S (2013) Carbon storage in successional and plantation forest soils: a tropical analysis. Global Ecol Biogeogr 22:105–117. doi:10.1111/j.1466-8238.2012.00788.x

Novara A, Gristina L, La Mantia T, Ruhl J (2013) Carbon dynamics of soil organic matter in bulk soil and aggregate fraction during secondary succession in a Mediterranean environment. Geoderma 193:213–221. doi:10.1016/j.geoderma.2012.08.036

Ohtsuka T, Shizu Y, Nishiwaki A, Yashiro Y, Koizumi H (2010) Carbon cycling and net ecosystem production at an early stage of secondary succession in an abandoned coppice forest. J Plant Res 123:393–401. doi:10.1007/s10265-009-0274-0

Onaindia M, de Manuel BF, Madariaga I, Rodriguez-Loinaz G (2013) Co-benefits and trade-offs between biodiversity, carbon storage and water flow regulation. Forest Ecol Manag 289:1–9. doi:10.1016/j.foreco.2012.10.010

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. Science 333:988–993. doi:10.1126/science.1201609

Sabo KE, Sieg CH, Hart SC, Bailey JD (2009) The role of disturbance severity and canopy closure on standing crop of understory plant species in ponderosa pine stands in northern Arizona, USA. Forest Ecol Manag 257:1656–1662. doi:10.1016/j.foreco.2009.01.006

Song Y, GU XR, Yan HY, Mao WT, Wu XL, Wan YX (2014) Dynamics of microbes and enzyme activities during litter decomposition of *Pinus massoniana* forest in mid-subtropical area. Environ Sci 35:1151–1158

Stoy PC, Katul GG, Siqueira MBS, Juang JY, Novick KA, McCarthy HR, Oishi AC, Oren R (2008) Role of vegetation in determining carbon sequestration along ecological succession in the southeastern United States. Global Chang Biol 14:1409–1427. doi:10.1111/j.1365-2486.2008.01587.x

Sun L, Guan DS (2014) Carbon stock of the ecosystem of lower subtropical broadleaved evergreen forests of different ages in Pearl River Delta, China. J Trop For Sci 26:249–258

Talbot J, Lewis SL, Lopez-Gonzalez G, Brienen RJW, Monteagudo A, Baker TR, Feldpausch TR, Malhi Y, Vanderwel M, Araujo Murakami A, Arroyo LP, Chao K-J, Erwin T, van der Heijden G, Keeling H, Killeen T, Neill D, Núñez Vargas P, Parada Gutierrez GA, Pitman N, Quesada CA, Silveira M, Stropp J, Phillips OL (2014) Methods to estimate aboveground wood productivity from long-term forest inventory plots. Forest Ecol Manag 320:30–38. doi:10.1016/j.foreco.2014.02.021

Tang GY, Li K (2013) Tree species controls on soil carbon sequestration and carbon stability following 20 years of afforestation in a valley-type savanna. Forest Ecol Manag 291:13–19. doi:10.1016/j.foreco.2012.12.001

Tang XL, Zhou GY (2005) Coarse woody debris biomass and its potential contribution to the carbon cycle in successional subtropical forests of southern China. Chin J Plant Ecol 29:559–568

Thuille A, Schulze ED (2006) Carbon dynamics in successional and afforested spruce stands in Thuringia and the alps. Global Chang Biol 12:325–342. doi:10.1111/j.1365-2486.2005.01078.x

Vesterdal L, Rosenqvist L, van der Salm C, Groenenberg B-J, Johansson M-B, Hansen K (2006) Carbon sequestration in soil and biomass following afforestation: experiences from oak and Norway spruce chronosequences in Denmark, Sweden, and the Netherlands. In: Muys B, Hansen K (eds) Heil, G. Environmental Effects of Afforestation in North-Western Europe From Field Observations to Decision Support Springer, Berlin, pp. 19–51

Walker LR, Wardle DA, Bardgett RD, Clarkson BD (2010) The use of chronosequences in studies of ecological succession and soil development. J Ecol 98:725–736. doi:10.1111/j.1365-2745.2010.01664.x

Wang J, Epstein HE (2013) Estimating carbon source-sink transition during secondary succession in a Virginia valley. Plant Soil 362:135–147. doi:10.1007/s11104-012-1268-6

Wang QK, Wang SL, Zhong MC (2013) Ecosystem carbon storage and soil organic carbon stability in pure and mixed stands of *Cunninghamia lanceolata* and *Michelia macclurei*. Plant Soil 370:295–304. doi:10.1007/s11104-013-1631-2

Xiang WH, Liu SH, Deng XW, Shen AH, Lei XD, Tian DL, Zhao MF, Peng CH (2011) General allometric equations and biomass allocation of *Pinus massoniana* trees on a regional scale in southern China. Ecol Res 26:697–711

Zeng ZQ, Wang SL, Zhang CM, Gong C, Hu Q (2013) Carbon storage in evergreen broad-leaf forests in mid-subtropical region of China at four succession stages. J Forestry Res 24:677–682. doi:10.1007/s11676-013-0404-3

Zhang J, Ge Y, Chang J, Jiang B, Jiang H, Peng CH, Zhu JR, Yuan WG, Qi LZ, Yu SQ (2007) Carbon storage by ecological service forests in Zhejiang Province, subtropical China. Forest Ecol Manag 245:64–75. doi:10.1016/j.foreco.2007.03.042

Zhang Q, Han RC, Huang ZL, Zou FS (2013) Linking vegetation structure and bird organization: response of mixed-species bird flocks to forest succession in subtropical China. Biodivers Conserv 22:1965–1989. doi:10.1007/s10531-013-0521-5