

Different patterns of ecosystem carbon accumulation between a young and an old-growth subtropical forest in Southern China

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Received: 7 August 2009 / Accepted: 24 July 2010 / Published online: 26 March 2011
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Abstract Using long-term (22 years) measurements from a young and an old-growth subtropical forest in southern China, we found that both forests accumulated carbon from 1982 to 2004, with the mean carbon accumulation rate at $227 \pm 59 \text{ g C m}^{-2} \text{ year}^{-1}$ for young forest and $115 \pm 89 \text{ g C m}^{-2} \text{ year}^{-1}$ for the old-growth forest. Allocation of the accumulated carbon was quite different between these two forests: the young forest accumulated a significant amount of carbon in plant live biomass, whereas the old-growth forest accumulated a significant amount of carbon in the soil. From 1982 to 2004, net primary productivity (NPP) increased for the young forest, and did not change significantly for the old-growth forest. The increase in NPP of the young forest resulted from recruitment of some dominant tree species characteristic of the subtropical mature forest in the region and

an increase in tree density; decline of NPP of the old-growth forest was caused by increased mortality of the dominant trees.

Keywords Carbon · Mortality · Recruitment · Net primary productivity · Net ecosystem production

Introduction

Old-growth forests are considered to be carbon neutral that is the amount of carbon uptake by photosynthesis is equal to the release through plant and soil respiration (Odum 1969; Mellilo et al. 1996). This theory has been used in forest growth models (Ryan et al. 1996). However, increasing evidence shows that old-growth, undisturbed forests can still accumulate carbon even as net primary productivity (NPP) declines (Carey et al. 2001; Zhou et al. 2006; Luyssaert et al. 2008). A recent study showed that old-growth forests in boreal and temperate regions account for about 10% of net carbon uptake by all forests globally (Luyssaert et al. 2008). About half of primary forests are located in subtropical and tropical regions, and the rate of net carbon uptake by these forests and their response to increasing CO_2 levels has been shown to be much higher than those of temperate or boreal forests (Wang and Polglase 1995). Therefore, total net carbon uptake by old-growth forests may account for more than 10% of total land carbon uptake globally.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-011-9914-2) contains supplementary material, which is available to authorized users.

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Pregitzer and Euskirchen (2004) showed that temperate and tropical forests accumulated carbon in both plant living biomass and soil organic matter at a stand age >100 years, but that NPP peaked between 11 and 30 years for temperate, and between 50 and 100 years for tropical forests. Therefore, either the rate of litter production or decomposition of soil organic matter must decrease after NPP peaks, if the amount of carbon in plant and soil continues to increase. This has yet to be observed in the field.

Two processes, recruitment and mortality, control the dynamics of plant live biomass. Carey et al. (2001) argued that recruitment in an old-growth forest with complex age structure can have a significant impact on its NPP and net ecosystem productivity (NEP). In other words, continuing recruitment and mortality will result in the mean age of trees being much younger than the stand age since last disturbance. Here, we compare the ecosystem carbon dynamics of a young forest with that of an old-growth forest to show how tree dynamics will affect NPP and NEP, and how old-growth forests remain a carbon sink.

Many unmanaged subtropical and tropical forests experiencing little disturbance can be considered as old-growth forests, and have high species diversity and complex age structure. Tropical forests account for 40% of the total biomass carbon in live plants (Dixon et al. 1994) and 30–50% of total NPP of the terrestrial biosphere (Field et al. 1998), and have been estimated to be a significant carbon sink globally (Rayner et al. 1999). However, direct measurements of the carbon balance (both plant and soil) of tropical forests are rare. A recent study found that primary tropical forests in the Amazon basin accumulated a significant amount of carbon in plant biomass (Philips et al. 1998), and measurements from long-term plots in the neotropics showed that the increase in standing biomass growth rate resulted from higher stem recruitment rate than stem mortality rate (Lewis et al. 2004).

The aim of this study was to compile and analyse data on standing biomass, litter production, soil carbon dynamics, and mortality and recruitment rates of trees for a young and an old-growth subtropical forest in southern China to address two questions: (1) will the old-growth forest continue to accumulate carbon and (2) is carbon allocation pattern significantly different between the young and old-growth forests?

We compare the carbon accumulation pattern in plant live biomass of the young forest with that of the old-growth forest, use the measurements to estimate components of NPP and NEP for these two forests to understand difference in carbon accumulation patterns, and discuss two possible mechanisms for the change in carbon accumulation pattern from a young to an old-growth forests in the region.

Materials and methods

Study area

The forests we studied are located in the Dinghushan Biosphere Reserve (23°10'N, 112°32'E) in southern China. The reserve was established in 1950 to protect natural monsoon evergreen broadleaved forests (MEBF) (Zhou et al. 2006). The local climate is moist and warm with mean annual precipitation of 1,680 mm and mean annual temperature of 22.3°C. The bedrock is sandstone and shale. Soils are classified as ultisols with a pH 4.0–4.9 in the top 5 cm (Buol et al. 2003).

Measurements were taken from two forests: a monsoon evergreen broadleaf forest (MEBF) that has not been disturbed for at least 400 years (Wang and Ma 1982; Shen et al. 2001), and a young pine forest (PF) that was regenerated naturally after clear cutting about 80 years ago. These two forests are located within 1 km². Because of their close proximity, both forests can be considered to experience similar climate and other environmental changes. A permanent plot of 10,000 m² was established in each forest in 1978.

PF forests occupy the periphery of the reserve. An experimental site of 40,000 m² was located on a south-facing slope at an elevation of about 200 m above sea level. The sampling plot (2,000 m²) was located in the centre of the permanent plot in 1982. The forest was initially a single species stand of *Pinus massoniana*, but was gradually invaded by other species, particularly *Schima superba*, a dominant species in MEBF. From 1982 to 2004, *Pinus massoniana* remained as the dominant species by both biomass and number of individuals in this forest.

MEBF is located in the central area of the reserve. The sampling plot is the same as the permanent plot (10,000 m²) at an elevation of 200–300 m above sea

level on a south-facing slope. The forest canopy consists of three distinct vertical layers, the upper canopy is dominated by species, including *Castanopsis chinensis*, *Canarium tramdenum*, *Schima superba*, and *Engelhardtia roxburghiana*, the sub-canopy is mainly composed of *Cryptocarya concinna* and *Machilus chinensis*, whilst the lowest canopy layer consists of shrubs.

Biomass inventory

Biomass inventories were conducted in 1978, 1982, 1992, 1994, 1999, 2004 in MEBF and in 1982, 1990, 1995, 2004 in PF. At each inventory, diameter at breast height (1.3 m) or DBH, height, species identity and spatial coordinates of each tree with DBH >1 cm and tree height >1.5 m were measured. Measurements of DBH and height for each tree were used to calculate above and below ground biomass using the empirical allometric relationships obtained by harvest of trees from the forests described by Wen et al. (1997) (see Supporting material S1).

For changes of canopy structure and biomass, we divided the forest canopy into three layers: an upper layer consisting of big trees (>16 m); a middle layer of smaller trees (8–15 m) and a lower layer consisting of mainly shrubs (1.5–8 m). We classified each tree into each of those three layers using the height of a mature tree of that species.

Measurements of fine litter and coarse woody debris production

Fifteen litter fall traps of 1 m² were placed randomly in the permanent plot in each forest. Fine litter production was collected monthly for each forest from 1982 to 2004. After air-drying, the litter was oven dried at 80°C for at least 72 h, and then weighted.

Coarse woody debris (CWD) includes standing dead trees (snags) and fallen branches and stems (logs). Total amount of CWD pool was measured for both forests in 2003, and only for MEBF in 1992 and 1999. For each CWD inventory, the permanent plot was subdivided into 20 by 20 m subplots. The fallen branches and stems were considered to be CWD if diameter was >2.5 cm and length >1 m. The measured diameter and length were used to calculate the volume of woody tissue, and samples were taken for estimating wood density after drying in the oven at

80°C for at least 72 h. Total biomass of logs was estimated from the estimates of biomass volume and density. Biomass of branches and stems of snags were estimated using the biomass allometric relationship (see Table S1).

Soil carbon measurements

Surface soil samples excluding the O horizon were collected primarily in September, at the end of the rainy season. Plant residues, including roots, were discarded, and soils were then milled to pass a 2 mm sieve. Soil organic carbon was determined using the wet oxidation method (Soil and Plant Analysis Council 1999).

The permanent plot was subdivided into 10 by 10 m subplots, and about one-third of the subplots were randomly selected for soil core sampling. About five to ten 30 mm diameter soil cores were collected from the top 20 cm soil in each of the randomly selected subplots seven times from 1978 to 1995 and annually from 1996 to 2003.

Three field campaigns were conducted to measure the vertical distribution of soil organic carbon content in the top 60 cm of soil of the permanent plots in 1978, 1996 and 2001 from each of these two forests. The soil vertical profile was arbitrarily divided into four layers: 0–10 cm, 10–20 cm, 20–40 cm and 40–60 cm. Each composite soil sample consisted of five soil cores, and one composite sample was collected from each of four layers from the randomly selected 5–15 subplots in each of the forests. The vertical soil organic carbon data from all three field campaigns were pooled and fitted to a power function to estimate the mean and standard error of the soil carbon from 20 to 60 cm (see Zhou et al. 2006, for further details).

Estimation of total net primary production and net ecosystem production

Following the methodology outlined by Curtis et al. (2002), NPP of a forest ecosystem, P_n , can be calculated as

$$P_n = \Delta B + L + H \\ = \Delta B_a + \Delta B_b + L_a + L_w + L_b + H, \quad (1)$$

where ΔB is the change of standing live plant biomass in g C m⁻² year⁻¹, as estimated by successive

inventories, and is further partitioned into above ground (leaves, branches and stems) increase (ΔB_a) and below ground (both coarse roots and fine roots) increase (ΔB_b), L is the total litter production ($\text{g C m}^{-2} \text{ year}^{-1}$) and is partitioned into above ground fine litter production (L_a), below ground litter production (L_b) and the above ground coarse woody litter production that is not captured by litter traps (L_w). L_a was measured using litter traps, L_b is estimated (see below) and L_w is estimated from inventories of CWD (see Tang and Zhou 2005). In estimating NPP, we ignore the contribution from other components (H), such as herbivore consumption, emission of volatile organic components and organic carbon leaching, which together may account for up to 10% of total NPP (see Clark et al. 2001). Throughout this article, we assume a constant carbon fraction of 50% for plant biomass or litter (Tang and Zhou 2005).

Below ground root litter production (L_b) was not measured, and is estimated using the following relationship:

$$L_b = a_3 L_a \quad (2)$$

The coefficient a_3 as estimated by Yan et al. (2006b) is 1.17 ± 0.12 for PF and 1.62 ± 0.36 for MEBF.

Above ground NPP, P_a ($\text{g C m}^{-2} \text{ year}^{-1}$), is estimated as

$$P_a = \Delta B_a + L_a + L_w. \quad (3)$$

NEP, P_e ($\text{g C m}^{-2} \text{ year}^{-1}$) can be estimated as the sum of changes in plant live biomass, litter (both fine and coarse litter), CWD carbon pool and soil organic carbon. That is

$$P_e = \Delta B + \Delta W + \Delta D + \Delta S, \quad (4)$$

where ΔB is the change of live plant biomass (both above ground and below ground), ΔW is the change in CWD pool as estimated from measurements, ΔD is change in litter pool (both above ground and below ground) and ΔS is change in soil organic carbon. The unit for all terms in Eq. 4 is $\text{g C m}^{-2} \text{ year}^{-1}$.

Both ΔB and ΔS can be estimated from measurements. Direct measurements of litter pool (ΔD) in the field are difficult, and we assume that $\Delta D = 0$ in this study. Change in CWD pool over successive years is estimated as follows.

Assuming that the decay of CWD carbon is first-order with a decay constant of k (year^{-1}), we can model the CWD carbon pool dynamics as

$$\frac{dW}{dt} = L_w - kW, \quad (5)$$

where W is the CWD pool size (g C m^{-2}) and L_w is the CWD input per year ($\text{g C m}^{-2} \text{ year}^{-1}$) that is estimated from the woody biomass of dead trees between two successive biomass inventories, and t is the time (year). The solution of Eq. 5 is given by

$$W_{t+1} = \frac{L_w}{k} - \left(\frac{L_w}{k} - W_t \right) e^{-k} \quad (6)$$

Therefore

$$\Delta W = W_{t+1} - W_t = \left(\frac{L_w}{k} - W_t \right) (1 - e^{-k}) \quad (7)$$

The amount of CWD was only measured once in 2003, and was very low (10 g C m^{-2}) in PF. We calculated ΔW for PF by assuming the total amount of CWD is zero in 1982 and the coarse woody litter inputs (L_w) from the successive biomass inventories. Because of the low amount of CWD in PF, any error in the assumed amount of CWD in 1978 for PF is unlikely to have any significant effects on our results.

Results

Standing plant biomass and tree number dynamics

Our estimates show that total standing live biomass increased by 152% in PF from 1982 to 2004, but decreased by 17% in MEBF from 1978 to 2004 (Fig. 1a). By fitting the data using a weighted least squares method (Table 1), we estimated the linear trend of biomass change to be $286 \pm 46 \text{ g dry matter m}^{-2} \text{ year}^{-1}$ for PF, and $-180 \pm 144 \text{ g dry matter m}^{-2} \text{ year}^{-1}$ for MEBF. The trend in biomass is statistically significantly different from zero for PF from 1982 to 2004 (t test, $P < 0.05$) but not in MEBF from 1978 to 2004. The tree density remained relatively constant for MEBF, but increased by more than 10-folds for PF (Fig. 1b).

Structural change and biomass dynamics

To understand how changes in tree density affect the plant biomass in PF and what caused the decline in tree biomass in MEBF, we analysed the change in biomass and composition of forest canopies (Fig. 2).

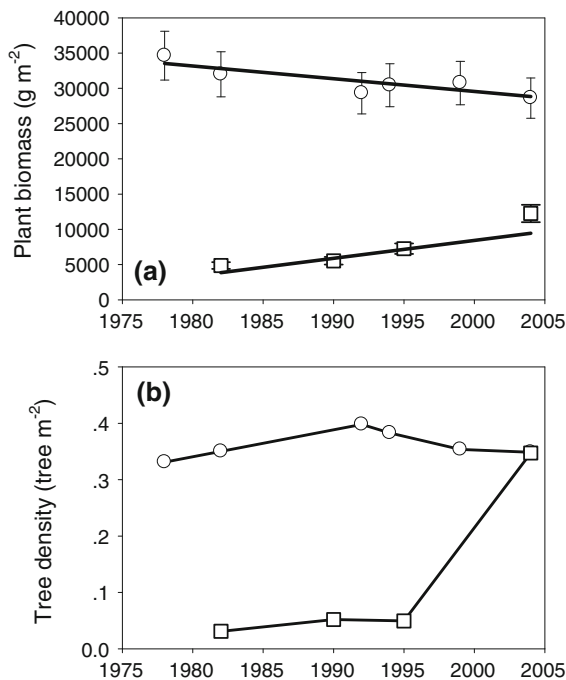


Fig. 1 Change in total plant dry matter (panel **a**), and tree density (panel **b**) for PF (square) and MEBF (circle). Lines on the upper panel are fitted using the weighted least squares method and the error bar represents one standard error of the mean

In MEBF, trees in the canopy layer accounted for over 90% of total stand biomass, but decreased as a fraction of all stems from 57 to 29%; whilst the fractions of biomass and numbers of trees in the small tree layer increased from 3 to 8%, and from 34 to 55%, respectively. The biomass fraction of individuals in the shrub layer remained low (<0.5%), but the tree density increased from 9 to 16% from 1978 to 2004. PF changed from a nearly pure *Pinus massoniana* forest in 1982 to a mixed forest with three distinctive layers in 2004. Individuals in the shrub layer accounted for 30% of total density and 3% of stand biomass, and trees in the middle layer accounted for 54% of total tree density and 5% of standing biomass in 2004.

In PF the net increase in biomass m⁻² was dominated by trees in the canopy layer, but the increase in tree density was dominated by individuals in the small tree and shrub layers. In MEBF net biomass loss of trees in the canopy layer is larger than the net biomass increase from small trees and shrubs over three of the five inventory periods (Fig. 3). As a

result, the number of trees in the canopy layer decreased from 1978 to 2004, the number of small trees increased over three of five inventory period, and the number of shrub trees increased only from 1982 to 1992, and decreased over all other periods. Thus, change in the standing biomass of both forests is dominated by change in biomass of trees in the canopy layer, and the change in tree density is dominated by trees in the canopy layer in MEBF and in the small tree and shrub layers in PF.

Above ground litter production and soil carbon dynamics

Annual above ground litter production, L_a increased from 124 to 297 g C m⁻² year⁻¹ in PF from 1982 to 2004, and decreased from 355 to 299 g C m⁻² year⁻¹ in MEBF from 1982 to 2004 (Fig. 4). Only the trend for PF is statistically significantly different from zero (t test, $P < 0.05$). By 2004, the amount of annual above ground litter production was not significantly different between these two forests.

Soil carbon did not change in PF, but increased significantly in MEBF (t test, $P < 0.05$) (Fig. 5). The linear trend was estimated to be 25 ± 48 g C m⁻² year⁻¹ in PF and 182 ± 45 g C m⁻² year⁻¹ in MEBF. This trend is quite different from the change in live plant biomass in these two forests (see Fig. 1).

Estimates of net primary productivity and its components

NPP was estimated as the sum of changes of standing biomass, litter fall and CWD production from 1982 to 2004. Change in standing plant biomass (both above ground and below ground) was estimated from successive inventories (Fig. 1a). Above ground litter was measured (Fig. 4), and below ground litter was estimated using Eq. 2.

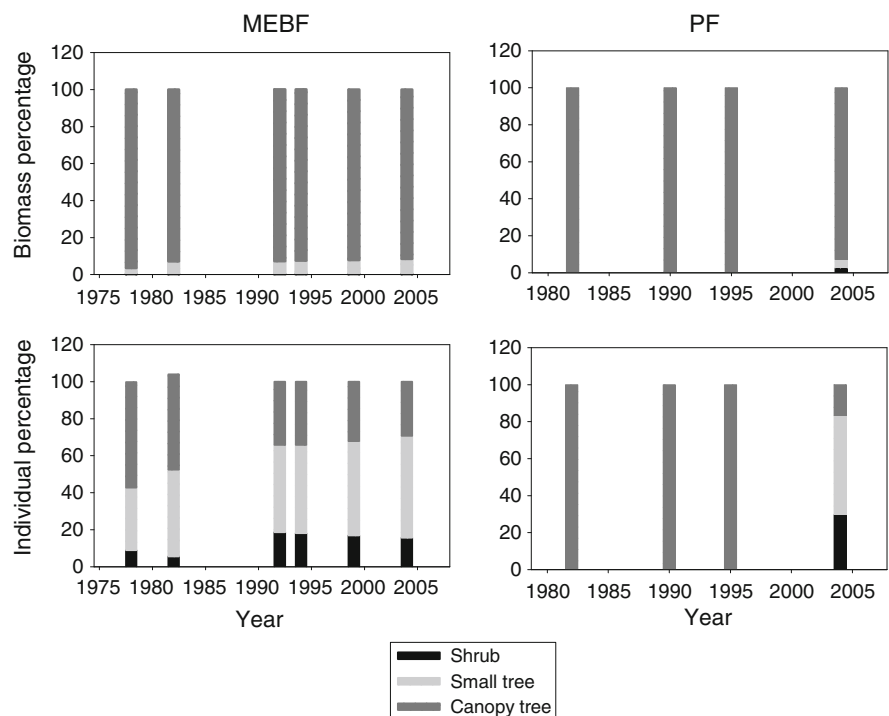
CWD production was estimated as follows: Based on the study of Tang and Zhou (2005), we estimated that the annual CWD production (L_w) is 1.4 ± 1.3 g C m⁻² year⁻¹ from 1982 to 2004 for PF. Based on the measurements of successive inventories, we estimated that L_w is 80 ± 4 g C m⁻² year⁻¹ from 1992 to 1994, 172 ± 6 g C m⁻² year⁻¹ from 1994 to 1999 and 284 ± 10 g C m⁻² year⁻¹ from 1999 to 2004 in MEBF. We also estimated that the mean annual decay rate of CWD (k) is 0.15 year⁻¹ using

Table 1 Trends with time for plant live biomass, above ground fine litter production, soil organic carbon and estimated NPP for the young and old-growth forests

	PF	MEBF
Plant live biomass ($\text{g C m}^{-2} \text{ year}^{-1}$)	$143 \pm 23^*$	-90 ± 72 (1978–2004)
Above ground fine litter production ($\text{g C m}^{-2} \text{ year}^{-1}$)	$5 \pm 1^*$	-5 ± 3
Soil organic carbon ($\text{g C m}^{-2} \text{ year}^{-1}$)	24 ± 48 (1978–2003)	$182 \pm 45^*$ (1978–2003)
NPP ($\text{g C m}^{-2} \text{ year}^{-1}$)	$26 \pm 2^*$	-6.6 ± 5.5

The trend was obtained by fitting a linear line to the estimates using the weighted least square method. All trends are for the period 1982–2004 unless otherwise specified

* Significantly different from zero (t test, $P < 0.05$)

Fig. 2 Fraction of biomass (*upper panels*) or individuals (*lower panels*) for canopy tree, small tree and shrub layers in the young and old-growth forests

Eq. 7 from 1992 to 2003 in MEBF. Based on the study of Tang and Zhou (2005), we assumed that the CWD is 817 g C m^{-2} in 1982 in MEBF, we then estimated that L_w is $131 \text{ g C m}^{-2} \text{ year}^{-1}$ using Eq. 6 for the period 1982–1992 in MEBF.

The estimated NPP of PF increased from $311 \text{ g C m}^{-2} \text{ year}^{-1}$ in 1982 to $973 \text{ g C m}^{-2} \text{ year}^{-1}$ in 2004 (Fig. 6). Biomass increase and litter production account for one-third and two-thirds of total NPP, respectively; the contribution to NPP by L_w is very small in PF (<1%). The ratio of below ground/total NPP varies between 38 and 49% over the period.

Mortality is a significant component of NPP in MEBF (Fig. 6d). L_w accounts for 11–70% of total above ground NPP from 1982 to 2004. An increase in tree mortality results in a decrease in above ground live biomass (Table 1) and an increasing relative contribution of L_w to NPP over the period (Fig. 6d).

Below ground NPP includes two components: change in root (both fine and coarse roots) biomass and below ground litter production. From 1982 to 2004, the root biomass decreased at an average rate of $-19 \text{ g C m}^{-2} \text{ year}^{-1}$ as estimated from the allometric relationship (Fig. 6e). Below ground litter

Fig. 3 Net change in live tree biomass (*upper panel*) and tree density (*lower panel*) for canopy tree (black), small tree (light grey) or shrub (dark grey) layer of the two forests for each inventory interval. Positive value represents an increase and negative value represents a decrease over two successive inventories

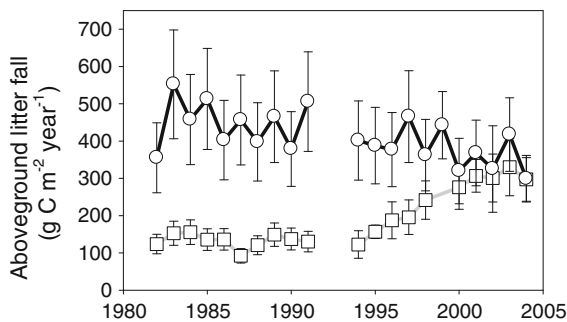
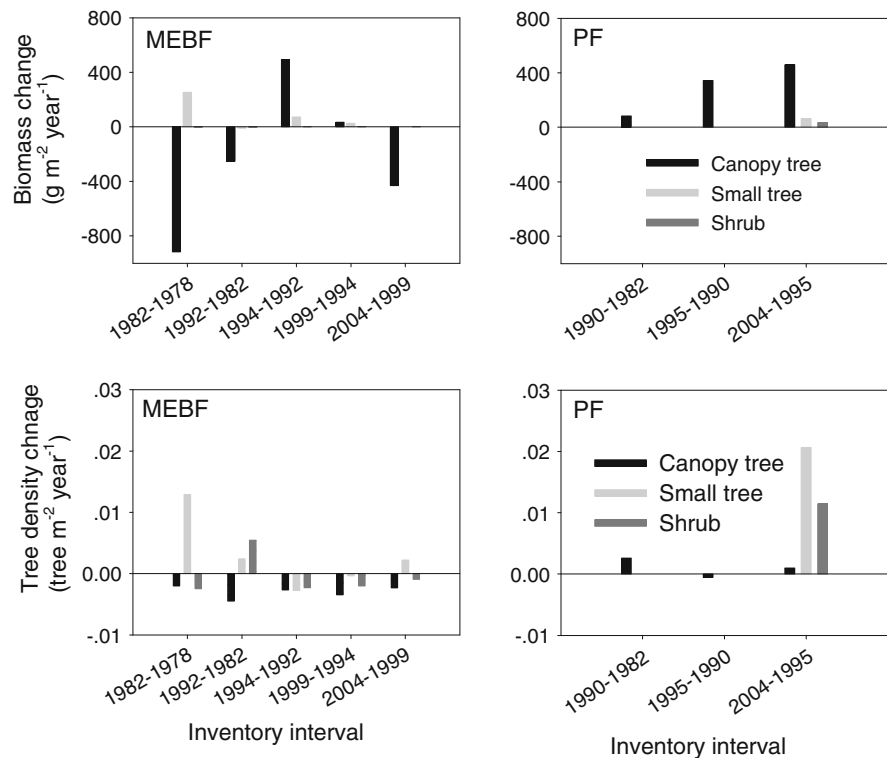


Fig. 4 Annual above ground litter production for PF (squares) or MEBF (circles). One standard error of the mean is shown for each estimate

production accounts for most of the below ground NPP and its inter-annual variation in MEBF.

The ratio of below ground NPP/total NPP varies from 50 to 60% for MEBF from 1982 to 2004 (Fig. 6f), which is higher than the mean ratio for PF over the same period, as a result of relatively larger amount of below ground litter production in MEBF.

The linear trend for NPP from 1982 to 2004 was estimated to be 26 ± 2 g C m⁻² year⁻¹ for PF and -6.6 ± 5.5 g C m⁻² year⁻¹ for MEBF (see Fig. 7

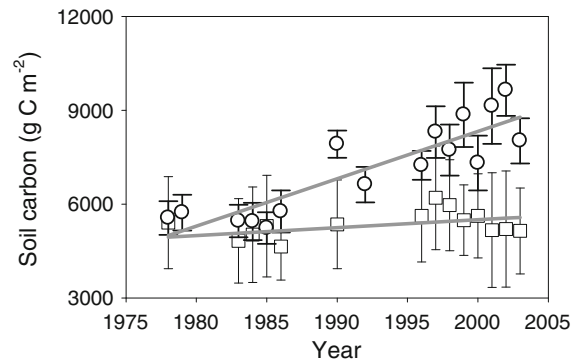
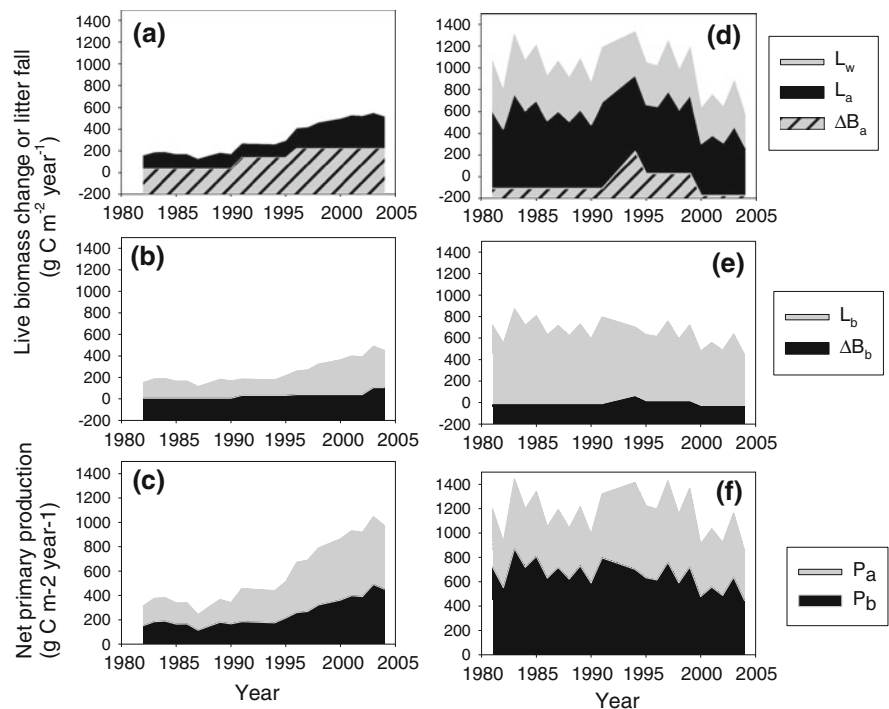


Fig. 5 Mean (and standard error) for top 60 cm soil carbon in PF (open square) and MEBF (open circle) from 1978 to 2003. Trend lines fitted using weighted least squares for each forest

and Table 1 for comparing with changes in other pools or fluxes). The linear trend is statistically significantly different from zero for PF only (*t* test, $P < 0.05$). The mean of the estimated NPP is 550 ± 54 g C m⁻² year⁻¹ for PF and 1165 ± 198 g C m⁻² year⁻¹ for MEBF over the period 1982–2004. The NPP of MEBF is not statistically significantly different from that in PF by 2004. However, the below ground allocation of total NPP in the old-growth forest is much greater than that in the young forest (Fig. 6c, f).

Fig. 6 Estimates of NPP and its components, coarse woody debris input (L_w), above ground litter input (L_a), change in above ground live tree biomass (ΔB_a), root litter input (L_b), and change in below ground root biomass (ΔB_b), above ground NPP (P_a) and below ground NPP (P_b) for PF (a–c) and MEBF (d–f) from 1982 to 2004



Net ecosystem production: where is the accumulated carbon stored?

We used Eq. 4 to estimate mean NEP and their uncertainties by assuming $\Delta D = 0$ for both forests. Estimates of the change in standing plant live biomass (ΔB) and in soil carbon (ΔS) are estimated from the successive inventories for each of these two forests (Figs. 1, 5) from 1982 to 2004. Change in

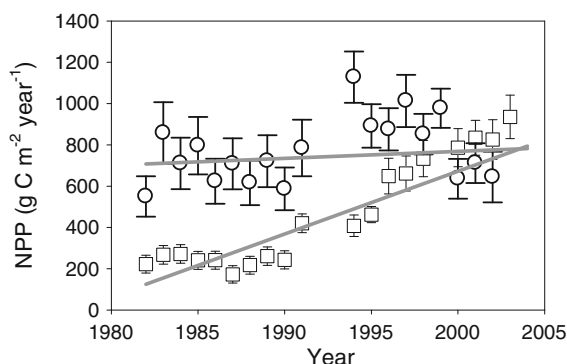


Fig. 7 Total NPP (and standard error) for MEBF (circle) and PF (square) for the period 1982–2004. Trend lines fitted using weighted least squares. One standard error for each data point was used as the weight for the regression

CWD pool sizes (ΔW) are estimated as follows: The measured CWD pool size is 10 g C m^{-2} for PF in 2003 (Tang and Zhou 2005). Therefore, ΔW in PF is unlikely to be significant, and is assumed to be zero from 1982 to 2004. For MEBF, we estimated ΔW from the measured CWD pool sizes in 1992, 1999 and 2003 and the estimate of CWD pool size of 817 g C m^{-2} for 1982 based on the study by Tang and Zhou (2005).

For PF, the rate of soil carbon accumulation is positive for live plant biomass for the first two periods and negative for the last two periods (Fig. 8). The rate of carbon accumulation in plant live biomass is greater than the rate of carbon loss from soil. The mean NEP is $227 \pm 59 \text{ g C m}^{-2} \text{ year}^{-1}$ for PF (Table 2), and therefore the ecosystem is a carbon sink with most carbon is accumulated in the standing plant live biomass.

For MEBF, the rate of carbon accumulation is negative for two of three periods in plant live biomass, and the rate of carbon accumulation is positive in the soil after 1982 (Fig. 8). The mean NEP is $115 \pm 89 \text{ g C m}^{-2} \text{ year}^{-1}$ for MEBF (Table 2), and therefore MEBF also is a carbon sink, with most carbon being accumulated in the soil.

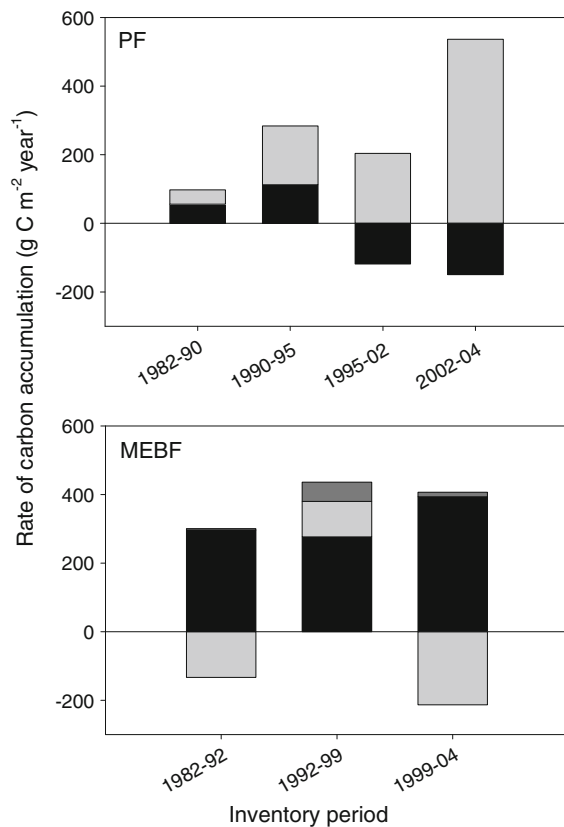


Fig. 8 Changes in the rates of carbon accumulation in soil (black bar), plant (light grey bar) and coarse woody debris (dark grey bar) carbon pools over successive inventory periods for PF and MEBF. Positive value represents carbon accumulation and negative value represents carbon loss. For PF, accumulation rate of coarse woody debris is assumed to be zero

Discussion

This study shows significant differences in components of NPP between young and old-growth subtropical forests in the south China region. From 1982 to 2004, the young pine-dominated forest (PF) was invaded by tree species characteristic of old-growth forests in the region, the number of trees m^{-2} increased several fold and their NPP increased (Fig. 3). For the old-growth forest (MEBF), death of large trees in the canopy layer resulted in invasion by small trees that were much less productive (or lower NPP), and the total NPP of the stand decreased (Fig. 3). Since age-related tree biomass dynamics has not been incorporated in many models for estimating forest carbon budgets at regional or global scales (Sitch et al. 2003), such models are likely to give

Table 2 Net primary production (NPP), net ecosystem production (NEP) and their components for young and old-growth forests from 1982 to 2004

	PF	MEBF
Above ground litter production (L_a)	198 (42)	412 (109)
Below ground litter production (L_b)	208 (24)	667 (150)
CWD input (L_w)	1 (1)	176 (3)
Change in plant biomass (ΔB)	143 (23)	-90 (72)
Change in CWD pool (ΔW)	0 (0)	23 (28)
Change in soil carbon (ΔS)	25 (48)	182 (45)
NPP ($P_n = L_a + L_b + L_w + \Delta B$)	550 (54)	1,164 (198)
NEP ($P_e = \Delta B + \Delta W + \Delta S$)	227 (59)	115 (89)

Unit is $\text{g C m}^{-2} \text{ year}^{-1}$. The number in brackets represents one standard error

biased estimates of the carbon uptake by mature forests.

Using a different method, Yan et al. (2006b) estimated that NPP for PF and MEBF were 475 and 1,148 $\text{g C m}^{-2} \text{ year}^{-1}$, respectively, in 2003/2004. They assumed that the live tree biomass was at steady state for PF. If we assumed that live tree biomass did not change in 2003 and 2004, our estimates of NPP would be 645 and 1,067 $\text{g C m}^{-2} \text{ year}^{-1}$ for PF and MEBF in 2004, respectively. The difference in NPP estimates between the two studies largely results from changes in live tree biomass (both growth and mortality). When changes in tree biomass are considered, our estimates of NPP are 973 and 855 $\text{g C m}^{-2} \text{ year}^{-1}$ for PF and MEBF, respectively.

From 1982 to 2004, the soil accumulated carbon at a mean rate of 182 $\text{g C m}^{-2} \text{ year}^{-1}$ in MEBF, which is similar to the carbon accumulation rate by old forests (>200 years) in the boreal and temperate region, but where the carbon is stored is quite different (Luyssaert et al. 2008). Our results also showed that the young forests (PF) accumulated a significant amount of carbon in live plant biomass, whilst the old-growth forest (MEBF) accumulates carbon in the soil. This is different from the findings of Philips et al. (1998) for primary tropical forests in the Amazon, where mature forests continued to accumulate carbon in plant live biomass. This study also showed that CWD production contributed to 6–31% of total NPP in MEBF from 1982 to 2004.

As the changes in the amount of carbon in plants, CWD and soil are all estimated from measurements with uncertainties quantified, we consider our results

robust in terms of the carbon storage pattern changes along the forest successional gradient. Only below ground litter production is modelled [using Eq. 2 developed for these forests previously by Yan et al. (2006b)], but this should not affect our conclusions. However, it may have significant impact on the ecologic mechanism to explain the shift in carbon allocation pattern, as the values of parameters in Eq. 2 were estimated using 1 year of observation of soil respiration and litter production only and may be subject to large uncertainties when extrapolated to other years.

We postulate two possible causes for this shift in carbon storage pattern as forests age. One is that the below ground competition for nutrients intensifies as forests become older, particularly for phosphorus (see Yan et al. 2006a). Pioneering species, such as *Pinus massoniana* have a more efficient nutrient acquisition strategy than some dominant tree species in the late successional forests, such as *Castanopsis chinensis* (see Yan et al. 2006a). As tree biomass increases, more nutrients from the soil are accumulated in the woody tissue during succession, the cycling of limiting nutrients slows down, and competition for soil nutrients among trees intensifies. Some of the dominant tree species with less efficient nutrient acquisition strategy will become more nutrient limited than other tree species, particularly some small trees and shrubs. As the small trees and shrubs are not as productive as the dominant species in the late succession forest, the total NPP of the forest will decline, as postulated by Gower et al. (1996). The second cause is that the increased N deposition in the region over the last three decades may have also contributed to the shift in the carbon storage pattern. All three forests were exposed to similar high N deposition over the last two decades; N deposition rate at Dinghushan mountain region has been increasing steadily, from $5.6 \text{ g N m}^{-2} \text{ year}^{-1}$ in 1992 to $7 \text{ g N m}^{-2} \text{ year}^{-1}$ in 2004 (unpublished data). It is possible that increasing N deposition may have accelerated P limitation, which is in agreement with the theoretical study by Perring et al. (2008), and is supported by the results from the studies of litter decomposition in these forests. Mo et al. (2006) showed that N addition $>10 \text{ g N m}^{-2} \text{ year}^{-1}$ increased litter decomposition rate in PF and MF, but slowed down the litter decomposition rate, and soil C decomposition in MEBF. As a result, soil

accumulates carbon in MEBF, but not in the other two forests.

Acknowledgments This study was funded by NSFC projects 30725006 and 40730102. We thank many researchers and supporting staff for their sustained contributions in data collections, and the funding support and supervision from the Chinese Ecosystem Research Network (CERN). The authors confirm that all the experiments and studies comply with the current Chinese laws.

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