RESEARCH PAPER

Tissue-specific carbon concentration, carbon stock, and distribution in *Cunninghamia lanceolata* (Lamb.) Hook plantations at various developmental stages in subtropical China

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Abstract

· *Key message* Carbon (C) concentrations in *Cunninghamia lanceolata* (Lamb.) Hook plantations differed significantly among tissue types and were greater for aboveground than belowground tissues. Plantation C stock increased with a developmental stage from young to mature to overmature, but at all stages, the majority occurred as soil organic carbon (SOC) and was more influenced by belowground fine roots than by aboveground litterfall.

· *Context* Failing to account for tissue-specific variation in the C concentration can result in inaccurate forest C stock estimates.

· *Aims* We aimed to quantify the relative magnitudes of C stock for Chinese fir plantations at different developmental stages. Specifically, we focused on assessing tissue-specific C concentrations and C dynamics return of above- and belowground litterfall.

· *Methods* Carbon traits (C concentration, C flux, C stock, and distribution at tree and ecosystem scales) were quantified in a chronosequence of Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) monoculture plantation stands at young (10), mature (22), and overmature (34 years old) developmental stages.

· *Results* Carbon concentrations differed significantly among tissue types, with mean values of $48.5 \pm 0.1\%$ and $42.5 \pm 0.2\%$ for above- and belowground biomass, respectively. The aboveground tissue C concentration, tree- and plantation-scale C stock, and SOC stock depended on developmental stage. Carbon return in litterfall, tree C stock, and SOC increased from the young to the overmature stage. SOC stock accounted for the majority of plantation C stock at all developmental stages (78.3, 59.6, and 55.7% in the young, mature, and overmature stages, respectively) and was more highly influenced by belowground fine roots than aboveground litterfall. Carbon stocks in Chinese fir plantations were 86, 129, and 153 t ha^{-2} at the young, mature, and overmature stages.

· *Conclusion* Prolonging Chinese fir rotation increases C sequestration potential and should be the focus of forest management strategies. The tissue-specific C concentrations provide detailed information for more accurate biomass C stock estimates for Chinese fir plantations and other subtropical coniferous forests. They indicate that current guidelines result in an overestimation of belowground biomass C stocks. Using the standard 0.47 biomass to C conversion factor, the belowground C stock would have

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been overestimated by 7.6–13.0% for the Chinese fir developmental stages investigated, while tree C stock would be underestimated by 0.08–3.24%. Therefore, developing species- and tissue-specific conversion factors are required for supporting C plantation and forest C accounting strategies.

1 Introduction

Substantial increases in atmospheric CO_2 concentrations due to human activities and the drive to mitigate global climate warming have increased interest in carbon sink enhancement (Law and Harmon 2011). Forest ecosystems mitigate elevated CO_2 concentrations by locking up carbon (C) in tree tissues and increasing soil C sequestration by direct or indirect effects on C dynamics (Lorenz and Lal 2014). Forests are the largest global terrestrial C stock at 861 Pg, accounting for more than 75% of terrestrial C and approximately 40% of the C exchange between the atmosphere and the terrestrial biosphere each year (Pan et al. 2011; Schlesinger 1997), thus playing an important role in the global C cycle and reducing the greenhouse effect (IPCC 2013). The concept of a "carbon plantation" has been proposed, referring to an intensively managed forest aimed at maximizing CO_2 sequestration through timber harvesting (Onigkeit et al. 2000). In 2017, China accounted for 23.2% and 27.6% of global primary energy consumption and CO_2 emissions from combustion-related activities, respectively (BP 2018). Major ecological restoration projects initiated by the Chinese government since the late 1970s, including large-scale afforestation and reforestation, have provided an estimated annual C sink of 74 Tg C year^{-1} in the project areas, making a substantial contribution to CO_2 mitigation in China (Fang et al. 2014). China's forest biomass C stock has increased by 30% between the 1970s and 2000s, with almost equal contributions from planted and natural forests (Lu et al. 2018). In its intended nationally determined contribution to the Paris Agreement of the UN Framework Convention on Climate Change (UNFCCC), China stated aims to increase its forest C sinks by increasing the forest stock volume by 4.5 billion m^3 by 2030 compared with 2005 levels (Department of Climate Change 2015). Actions to achieve this include afforestation, restoring farmland to forest, and protecting natural forests. Therefore, accurate assessments of sequestered C and the C distribution in different forest ecosystems are needed for estimation of national C inventories to monitor progress in the use of forest ecosystems for climate change mitigation.

One of the most prominent methodologies for estimating forest C stocks is the Intergovernmental Panel on Climate Change (IPCC) Guidelines (2006) which contains C fraction values in aboveground forest biomass on a dry matter basis for different tree parts/types in tropical, subtropical, temperate,

and boreal forest domains based on measurements for a limited number of tree species and geographical settings. Species- and tissue-specific C fraction values should be used where available to reduce uncertainties (Martin et al. 2015; Thomas and Malczewski 2007; Thomas and Martin 2012), yet previous studies indicate considerable variability in measured C concentrations. Zhang et al. (2009) estimated a relative error of − 6.7 to + 7.2% in C stock for 10 temperate tree species in north-east China if inter- and intra-specific variation in C concentration were ignored. In evaluation of C stock along a chronosequence of *Larix olgensis* A. Henry in the Lesser Khingan Mountains in north-east China, considerable differences in C concentration were measured between different forest tissues, ranging from 40.8% C in fine roots to 49.9% in foliage, with the greatest variation in the fine roots (Ma et al. 2014). Assessment of the variation in C concentrations within the same tree species, between different tissues and at different growth stages, is therefore important for estimating the potential for forest C capture and storage. These measurements have further implications for the design of forest management strategies for promoting C sequestration through a selection of the tree rotation length, harvesting procedure, and managing of tree harvest residues.

Quantifying the soil organic carbon (SOC) stock and understanding the processes controlling its dynamics are also important for understanding changes in C fluxes and the overall C sequestration capacity of forest ecosystems. The individual and relative contributions of leaf and root litter to SOC sequestration are not fully understood despite numerous laboratory microcosm and field litter manipulation experiments. The input of aboveground litterfall has been demonstrated to significantly influence SOC concentration, but different studies have yielded contrasting results. Leaf litter addition in a 2-year leaf manipulation experiment in a Costa Rican tropical rain forest resulted in a 31% increase in surface soil C concentration (Leff et al. 2012), whereas similar addition studies in tropical, subtropical, and temperate forests have reported no significant change or a reduction in SOC due to a priming effect on SOC mineralization (e.g., Pisani et al. 2016; Sayer et al. 2011; Wu et al. 2018). Belowground root litter, in contrast, is increasingly regarded as an important contributor to stable SOC pools (Rasse et al. 2005). Litter manipulation experiments in a *Platycladus orientalis* (Linn.) Franco conifer plantation in subtropical China showed a significant decrease in SOC concentration (up to 28%) 2 years after root exclusion,

but no effect of litter removal and addition (Wu et al. 2018). Based on litter addition to soils in microcosm experiments, Hu et al. (2016) reported that there is greater C incorporation into the soil from fine roots than from leaf litter addition. While fine roots are more resistant to mineralization due to their chemical composition, leaf litter C is more labile and more readily lost as CO_2 through microbial respiration (Steffens et al. 2015). The apparently high variability in the interaction between above- and belowground litter and SOC stores and processing reported in different studies indicates that quantification of these C stores and fluxes is required to assess C sequestration in major forest ecosystems.

In China, estimates in Fang et al. (2014) indicate that the contribution of planted forests to the country's forest C sink has increased threefold from 5% in the 1970s to 15% in the 2000s. Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) is the most widespread and commercially important timber species in subtropical China, with fast growth (normal rotation length is 20–25 years), high yield, and excellent wood quality (Ma et al. 2007). The species is widespread in 17 provinces ranging from 20 to 34°N latitude and 100 to 120°E longitude (Yu 1997). The total plantation area and stand volume of Chinese fir are 1.10×10^7 ha^{-1} and 726 million m^3, accounting for 15.8% and 29.2% of the total plantation area and volume in China, respectively (SFA 2014), and 6.1% of global forest plantation area. Despite the increasing contribution of Chinese fir to forest plantation area, many comprehensive reviews of C fractions in different tree species (e.g., Thomas and Martin 2012) do not include Chinese fir. Thus, there is a need to report species-, tissue-, and development-stage-specific C fractions to generate more accurate "Tier 3" estimates of C stocks in Chinese fir plantations.

Several previous studies have assessed various aspects of C storage and dynamics in chronosequences of Chinese fir plantations and how they are affected by forest management. For example, comparison of C storage in first-generation Chinese fir plantation stands and natural evergreen broadleaved forest indicated that the total ecosystem C storage at all plantation ages was significantly higher than in natural forest, primarily due to greater tree biomass C offsetting reduced mineral soil C storage (Chen et al. 2013). An initial decrease in SOC stock with stand age was also reported by Yu et al. (2014) based on measured soil C inputs and outputs in first-generation Chinese fir plantations. SOC was reduced further by 10% between the first and second rotations (Yang et al. 2005) and 15% between the second and third rotations (Zhang et al. 2004). Tissue-specific C concentrations and their variability at different developmental stages have not been considered previously, but are important for the conversion from tree biomass to tree C stock for Chinese fir species. Furthermore, little is known about the effects of

above- and belowground litter on the SOC stock at different stand developmental stages.

Based on these previous findings, we hypothesized that the C concentration differs significantly among different tissues and developmental stages in Chinese fir plantations. We also hypothesized that the C stock at the tree and plantation scales, litterfall C return dynamics, and SOC stock vary substantially among developmental stages. The main aims of this study were therefore to (1) determine the relative tissue-specific C concentration in tree tissues, (2) compare the C return dynamics of above- and belowground litterfall, and (3) assess the relative magnitudes of C stocks at the tree and plantation scales for Chinese fir plantations at different developmental stages in subtropical China.

2 Materials and methods

2.1 Site description

The location for the research was Xinkou National Forest Farm, Sanming County (26° 10′ N, 117° 27′ E), in western Fujian Province, subtropical China. It is characterized by a mid-subtropical marine monsoon climate. The mean annual air temperature is 19 °C with the lowest mean monthly temperature of 7.7 °C in January and the highest mean monthly temperature of 28.2 °C in July. The mean annual rainfall is 1749 mm (most rainfall occurs from March to June accounting for 48% of the annual total) and mean annual relative humidity is 83%. Annual mean sunshine is 1840 h, and the frost-free period is 300 days (data obtained from the meteorological station onsite). The elevation is 205–500 m above sea level, and the soil is a silty oxisol according to the US taxonomy system, derived from sandstone and shale parent materials. Further details of the site are given in Zhou et al. (2015).

To enable comparison of relative C stocks and dynamics within a chronosequence of Chinese fir while minimizing other confounding factors such as climate, geology, and soil, three monoculture Chinese fir stands were selected for the research, representing young (10 years), mature (22 years), and overmature (34 years) developmental stages. In each stand, three plots (20 m × 20 m) were established (Table 1). The young and mature stages were located on southwest-facing slopes, while the overmature plots had a northerly aspect. The dominant understory shrubs and herbs were similar in the different stages, and included *Callicarpa kochiana*, *Maesa japonica*, *Ilex pubescens*, *Woodwardia japonica*, *Selaginella moellendorf*, and *Alpinia japonica* (Zhou et al. 2015). Plantations at different developmental stages were established in 2003, 1991, and 1979 from seedlings after clearcut harvesting and slash-and-burn of the surface biomass. In all stands, weeding was conducted twice in the first 3 years and then once every 4 years thereafter. The young stage had an

Table 1 General information about the study plots in Chinese fir plantations

Plot no.	Stage	Latitude (N)	Longitude (E)	Elevation (m.a.s.l)	Slope (°)	Aspect	Mean tree height (m)	Mean DBH (cm)	Canopy density fraction
1	Young	26° 10′ 11.4″	117° 28′ 18.3″	225	11	Southwest	10.5	12.1	0.7
2	Young	26° 10′ 11.6″	117° 28′ 15.2″	258	7	Southwest	9.84	10.2	0.6
3	Young	26° 10′ 12.8″	117° 28′ 14.2″	250	19	Southwest	9.22	11.4	0.7
4	Mature	26° 10′ 8.1″	117° 28′ 22.0″	225	26	Southwest	17.9	17.8	0.7
5	Mature	26° 10′ 9.4″	117° 28′ 21.5″	243	28	Southwest	16.8	17.5	0.6
6	Mature	26° 10′ 9.5″	117° 28′ 23.0″	266	20	Southwest	17.6	18.8	0.6
7	Overmature	26° 09′ 59.5″	117° 28′ 4.3″	219	33	North	21.5	23.4	0.6
8	Overmature	26° 10′ 0.0″	117° 28′ 5.4″	217	30	North	20.6	22.3	0.5
9	Overmature	26° 09′ 58.8″	117° 28′ 2.7″	232	30	North	21.1	20.7	0.5

initial density of 2400 stems ha^{-1}. The mature and overmature stages were thinned to densities of 1650 and 1300 stems ha^{-1} in 2003 and 1995, respectively, by removing alternate rows and cutting the crowns of thinned trees on site.

2.2 Sampling and biomass production for tree species

In each plot, the diameter at breast height (DBH) and height of every tree were measured in November 2012, and trees were divided into five growth categories (dominant, subdominant, medium, suppressed, and nearly dead trees), based on the DBH and height and their growth forms. Five trees from each category were felled and all roots were excavated. Bole disks were obtained from the trunk base and DBH was measured at 1-m intervals. For live tissues (live foliage, live branches, and live cones), the biomass was estimated by power equations of the form $W = a(D^2H)^b$. Senescent tissues in the canopy (senescent foliage, branches, and cones) were modeled using linear equations as follows: $W = a(D^2H) + b$, where W is the dry weight (kg), D is the diameter (cm), H is the height (m) of each sample tree, and a and b are constants. The equation for each tissue at each developmental stage is shown in Table 1 of Zhou et al. (2016a). The stand biomass for each tissue was calculated as the sum of the biomass of all trees in the plot. All underground roots were excavated and were divided into fine roots (< 0.2 cm), small roots (0.2–0.5 cm), intermediate roots (0.5–2 cm), large roots (2–5 cm), bole roots (> 5 cm), and stump. Sub-samples of all above- and belowground tissues from each felled tree in every plot were taken for C determination (see Section 2.5).

2.3 Aboveground and belowground litter production

Litterfall was collected using litter traps (1 m × 1 m) installed at three randomly selected locations in each plot. Samples were collected mid-month throughout 2012. All aboveground litterfall was divided into leaves, branches, and cones and weighed. Sub-samples were oven-dried to a constant weight

at 80 °C for 48 h. Litterfall production (t ha^{-1}) was calculated by correcting the fresh litterfall masses for moisture content.

Fine roots (< 2 mm in diameter) are very dynamic and play a substantial role in soil C flux; therefore, fine roots were sampled using the sector method. Based on DBH, height, and growth status, three trees in each plot were chosen for fine root collection. A circle of radius 1 m around the trunk of each sample tree was divided into 60° sectors and a soil block was excavated from a different sector in July and October 2013 and January and April 2014. To investigate the fine root vertical distribution, each soil block was divided into 0–20-, 20–40-, and 40–60-cm depths from the top of the organic soil horizon after the removal of surface litter. Thus, a total of 324 soil blocks (27 sample trees × 3 soil depths × 4 sampling occasions) were collected. All of the blocks were taken to the laboratory and treated as follows. First, roots > 2 mm diameter were carefully isolated from the soil and then washed gently with deionized water to remove soil, without disrupting the small root tips. Second, the remaining soil block was wet sieved through a 0.5-mm mesh to collect broken roots which were also cleaned with deionized water. Third, the separated roots from each soil block were stored at 4 °C for determination of the fine root biomass and necromass at a later date. Living and dead fine roots were separated on ice in a cooler by visual inspection of the color of bark and xylem, resilience, and brittleness, as described by Liu et al. (2014). All fine roots were then oven-dried at 70 °C for 48 h and the dry weight was obtained as the "fine root biomass" according to Eq. 1 (Wu 2011), where r is the radius (m) of the soil block:

$$\text{Fine root biomass (living or dead fine roots)} \left(\text{t ha}^{-2} \right)$$
$$= \frac{\text{dry weight of living (or dead) fine roots per sector}}{\frac{\pi r^2}{6}}$$
$$\times 10^{-2} \tag{1}$$

2.4 Soil sampling

In each plot, soil samples were collected with a soil corer (200 cm^3) at five randomly chosen locations at 3 depths (0–20 cm, 20–40 cm, and 40–60 cm) in December 2012. Roots in the soil samples were removed by hand, and then soil samples from the same depth and the same plot were combined into a single sample to yield 27 soil samples in total (3 stand stages × 3 plots × 3 depths). The soil samples were prepared for SOC determination by air-drying for 48–72 h, homogenization, and passing through a 2-mm sieve. Following the method of Robertson et al. (1974), the same soil cores were dried at 105 °C to constant weight in order to calculate soil bulk density (BD).

2.5 Determination of carbon concentrations in tree tissues and soil

From the tree materials, after biomass measurements, three sub-samples of the same tissue type were taken for determination of the C concentration. For aboveground litterfall, C concentration was measured in sub-samples of each component (leaves, branches, and cones) from each monthly sample, resulting in a total of 1620 sub-samples (3 stand ages × 3 plots × 5 litter traps × 3 components × 12 months). For fine roots, C concentration was measured in 648 sub-samples of living and dead roots (27 sample trees × 3 soil depths × 2 tissue types × 4 sampling occasions). The sub-samples were dried in an oven to constant weight (48 h) and finely ground and homogenized. Powdered sub-samples (ca. 50 mg) were analyzed by instantaneous combustion using a CN elemental analyzer (ELEMENTAR Vario EL III, Hesse, Germany). The C concentration is expressed as mg of C mass per 100 mg of dry mass (%). No carbonates were detected in the soil samples, as evaluated by the addition of 2 M HCl; accordingly, the total C in the soil was equal to the SOC concentration.

2.6 Carbon stock calculations

For trees, C stocks were calculated as the biomass C concentration (%) multiplied by the dry biomass for each tissue. The tree C stock was the sum of the C stock for each tissue, including the canopy C stock of senescent tissues. Finally, the data were scaled to an area basis (t ha^{-1}).

For aboveground litterfall, the C return per month was calculated as the C concentration multiplied by the dry mass for each component. Total C return per month was the sum of the leaf, branch, and cone components. Annual C return by aboveground litterfall was estimated as the sum of values obtained each month for each component. For belowground litterfall C return, a similar calculation method was used, i.e., the C concentration was multiplied by fine root production for living and dead fine roots for all soil depths (0–60 cm) for each

sample month. Annual C return by belowground litterfall was the mean value including both living and dead fine roots for the 4 sample months, because fine roots may be present across sampling occasions.

For soil, the SOC stocks (t ha^{-1}) for each depth at various developmental stages were calculated according to Eq. 2:

$$\text{SOC stock (t ha}^{-1}) = 10^4 \left(\frac{\text{m}^2}{\text{ha}}\right) \times \text{soil depth (m)}$$
$$\times \text{BD}\left(\frac{\text{g}}{\text{cm}^3}\right) \times \frac{\text{SOC(\%)}}{100} \qquad (2)$$

The total SOC stocks for the 0–60-cm depth for each developmental stage were calculated by summing the SOC stocks at different soil depths.

For the forest ecosystem, C stock was calculated according to Eq. 3:

$$CS_f = \sum_{i=1}^{14}(CT_i BT_i) \qquad (3)$$
$$+ \sum_{j=1}^{12}\left(CL_{Fj} \times PL_{Fj} + CL_{Bj} \times PL_{Bj} + CL_{Cj} \times PL_{Cj}\right)$$
$$+ \sum_{m=1}^{3}(CSS_m)$$

where CS_f is the forest C stock (t ha^{-1}); i is the tree tissue-specific value (i.e., live foliage, live branches, live cones, senescent foliage, senescent branches, senescent cones, stem, bark, < 0.2-cm roots, 0.2–0.5-cm roots, 0.5–2-cm roots, 2–5-cm roots, > 5-cm root bole, and stumps); C_{Ti} is the C concentration of specific tree tissues (%); B_{Ti} is the biomass specific tree tissue (t ha^{-1}); j is the month of litterfall collection, CL_{Fj}, CL_{Bj}, and CL_{Cj} are C concentrations of foliage litter, branch litter, and cone litter, respectively (%); PL_{Fj}, PL_{Bj}, and PL_{Cj} are the litterfall production of foliage, branches, and cones, respectively (t ha^{-1}); m is the soil depth layer; and CSS_m is the soil C stock calculated from Eq. 2 (t ha^{-1}).

2.7 Data analysis

The data were analyzed after testing for homogeneity of variance using Levene's test. When constant variance was not satisfied, a log$_{10}$ or square transformation was used. Means were compared by least significant difference (LSD) tests and the probability level was set at $P < 0.05$. The effects of developmental stage, tissue, and their interactions on the C concentration and tree C stock were analyzed by two-way ANOVA. The effects of stand stage and seasonal dynamics on C return by above- or belowground litterfall were evaluated by two-way ANOVA. The effects of developmental stage and soil depth on SOC and soil C stock were also evaluated by two-way ANOVA. Annual litterfall C return and total tree and total soil C stock for various developmental stages were compared by one-way ANOVA. Associations between SOC stock and litterfall C return dynamics above- and belowground were

analyzed by determining Pearson correlation coefficients. All statistical analyses were conducted in SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Carbon concentration in trees

Based on a two-way ANOVA, the C concentration in aboveground tissues depended on stand stage and tissue type ($P <$ 0.001 for both), and there were no significant interaction effects ($P = 0.258$) (Table 2). The C concentration differed significantly among the three developmental stages in live tissues (foliage, branches, and cones) and litterfall components (leaves, branches, and cones), but not for senescent tissues in the canopy. Mean ($\pm$ SE) C concentrations in different aboveground tissues of Chinese fir trees across all developmental stages were $47.8 \pm 0.2\%$ in live tissues, $48.8 \pm 0.2\%$ in senescent tissues, $49.1 \pm 0.2\%$ across the different litterfall components, $48.1 \pm 0.3\%$ in the stem, and $48.3 \pm 0.4\%$ in the bark (Table 3), with a mean of $48.5 \pm 0.1\%$ for aboveground tissues. Generally, C concentration in most aboveground tissue types increased from the young to mature stage and then remained stable from the mature to the overmature stage.

The C concentration differed significantly among belowground tissues ($P < 0.001$), but was not affected by stand stage ($P = 0.640$), and there were no interaction effects ($P = 0.183$) (Table 2). Root C concentration generally increased as the root diameter increased, with the lowest concentration in fine roots ($41.0 \pm 0.2\%$) and the highest concentration in the stump ($47.5 \pm 0.3\%$). The mean C concentration for belowground tissues was $42.5 \pm 0.2\%$ (Table 4). At the tree level, the overall mean C concentration was $47.0 \pm 0.1\%$.

3.2 Carbon return dynamics by litterfall type

3.2.1 Carbon return in aboveground litterfall

Significant differences in C return by leaf, branch, and cone components of aboveground litterfall and in total C return were observed among months and developmental stages ($P < 0.001$ for all components and total), and significant interaction effects were detected between stage and month ($P < 0.001$ for leaf, branch, and total, $P = 0.014$ for cones) (Table 5). Annual aboveground litterfall C return was significantly higher in the mature and overmature stages (1.73 ± 0.27 and 1.65 ± 0.09 t ha^{-1}) than in the young stage (0.70 ± 0.03 t ha^{-1}) (Table 6). The proportion of annual C return in aboveground litterfall was highest for leaves (62.1–67.0%), followed by branches (23.6–26.6%). Cones comprise the lowest proportion of C in litterfall: 6.34, 13.4, and 12.3% in the young,

mature, and overmature stages, respectively. In the young stage, cone litterfall was collected in only a few months. Figure 1 shows that the dynamics of litterfall C return varied among stages, but generally showed a bimodal pattern, with a small peak in April–May, particularly for the overmature stand, and a large peak in August for the mature stage. These two peaks accounted for one-third of the annual C return in aboveground litterfall.

3.2.2 Carbon return in belowground litterfall

Carbon return values in live, dead, and total fine roots was significantly affected by stand stage ($P = 0.006$, < 0.001, and 0.026, respectively) and by season ($P = 0.002$, $<$ 0.001, and 0.021, respectively). However, there were no interaction effects between stage and season ($P = 0.430$, 0.060, and 0.457, respectively) (Table 5). The annual total and live fine root C return values were highest at the mature stage at 1.41 ± 0.05 t ha^{-1} and 1.11 ± 0.07 t ha^{-1}, respectively, and significantly higher than at the overmature stage. The annual dead fine root C return increased with developmental stage (from 0.13 ± 0.01 t ha^{-1} at the young stage to 0.36 ± 0.05 t ha^{-1} at the overmature stage) (Table 6). A peak in C return in total fine root biomass was detected in July and October at the mature and overmature stages, respectively, while there was no apparent seasonal peak at the young stage (Fig. 2a). An inverse seasonal pattern was observed for live and dead fine root C return (Fig. 2b, c). The maximum live fine root C return was detected in July for the mature stage and in October for the young and overmature stages, while the lowest C return in dead fine roots was in July in all stands (Fig. 2c).

3.3 Carbon stock

3.3.1 Carbon stock in trees

The tree C stock depended significantly on stand stage, tissue type, and their interaction (Table 2). Tree C stock increased significantly with stand stage and was 17.75 ± 1.19, 49.75 ± 1.65 and 65.84 ± 2.59 t ha^{-1} for the young, mature, and overmature stages, respectively (Table 7). Carbon stock in the aboveground tissues increased significantly with stand developmental stage, accounting for 77.3–90.9% of the total tree C stock. Root C stock differed significantly with stand developmental stage; it was in the following order: mature > overmature > young stages. The stem C stock accounted for the largest percentage of the aboveground C stock, ranging from 53.0 to 68.8%, followed by the bark and live foliage C stock (8.1–15.1% and 7.8–13.6%, respectively). C stock was greater in live tissues than in senescent canopy tissues at all developmental stages (total C stocks 3.69–9.84 t ha^{-1} and 0.66–2.87 t ha^{-1}, respectively).

Table 2 Two-way ANOVA results for the C concentration in above- and belowground tissues, carbon stock in trees, SOC concentration, soil bulk density, and carbon stock in soil

Source	Df	Mean square	F value	P value
Carbon concentration				
Stage	2	88.571	15.780	< 0.001***
Aboveground tissue	10	59.308	10.566	< 0.001***
Stage × aboveground tissue	20	6.667	1.188	0.258
Carbon concentration				
Stage	2	2.057	0.457	0.634
Belowground tissue	5	228.965	50.898	< 0.001***
Stage × belowground tissue	10	6.577	1.462	0.156
Carbon stock in tree				
Stage	2	199.812	494.547	< 0.001***
Tissue	8	570.015	1410.825	< 0.001***
Stage × tissue	16	91.696	226.953	< 0.001***
SOC				
Stage	2	12.838	4.866	0.020*
Soil depth	2	168.222	63.764	< 0.001***
Stand stage × soil depth	4	3.938	1.493	0.246
Soil bulk density				
Stage	2	0.007	0.585	0.567
Soil depth	2	0.022	1.944	0.172
Stand stage × soil depth	4	0.011	0.969	0.449
Carbon stock in soil				
Stage	2	80.305	4.571	0.025*
Soil depth	2	939.935	53.500	< 0.001***
Stand stage × soil depth	4	7.312	0.416	0.795

$*P < 0.05$, $***P < 0.001$

3.3.2 Carbon stock in soil

A two-way ANOVA indicated that SOC concentration and soil C stock were significantly affected by stand stage ($P = 0.020$, 0.025) and soil depth ($P < 0.001$, < 0.001), but there were no significant interaction effects (Table 2). Soil bulk density did not vary significantly with stand stage and soil depth. Soil density increased as the soil depth increased for all stand stages, and the mean soil density was significantly greater in the young and overmature stages (1.32 and 1.34 g cm^{-3}) than in the mature stage (1.29 g cm^3) (Fig. 3a). SOC concentration decreased significantly with soil depth ($P < 0.05$). For the surface soil layer at 0–20 cm, it ranged from 12.6 g kg^{-1} in the young stage to 16.5 g kg^{-1} in the mature stage, and in the lower soil layer (40–60 cm), it ranged from 5.13 to 7.81 g kg^{-1} as the stand stage increased. The mean

Table 3 Carbon concentration (%) in various aboveground tissue types at different developmental stages of Chinese fir plantations

Developmental stage	Live foliage	Live branch	Live cone	Senescent foliage	Senescent branch	Senescent cone	Stem	Bark	Litterfall leaf	Litterfall branch	Litterfall cone
Young	47.9 ± 0.3b	45.8 ± 0.4b	47.0 ± 0.5b	48.9 ± 0.3a	47.6 ± 0.4a	48.2 ± 0.2a	47.5 ± 0.4b	47.2 ± 0.5b	48.1 ± 0.7b	46.9 ± 0.6b	49.3 ± 0.6b
Mature	49.2 ± 0.4a	47.4 ± 0.4a	51.0 ± 1.7a	49.4 ± 0.2a	48.2 ± 0.3a	50.7 ± 0.4a	49.4 ± 0.7a	48.5 ± 0.3ab	50.3 ± 0.1a	49.0 ± 0.7a	49.9 ± 0.4b
Overmature	49.1 ± 0.2a	47.4 ± 0.3a	47.5 ± 0.1ab	49.4 ± 0.3a	48.3 ± 0.8a	50.3 ± 0.7a	47.8 ± 0.3b	49.0 ± 0.8a	49.0 ± 0.6ab	47.8 ± 0.6ab	51.5 ± 0.7a
Mean	48.8 ± 0.2	46.8 ± 0.2	48.5 ± 0.8	49.2 ± 0.2	47.9 ± 0.3	50.1 ± 0.5	48.1 ± 0.3	48.3 ± 0.4	49.1 ± 0.3	47.9 ± 0.4	50.2 ± 0.3

Values are means ± SE. Different lowercase letters in the same column indicate significant differences among developmental stages for the same tissue type (LSD-HSD test at $P < 0.05$)

Table 4 Carbon concentration (%) in roots at various developmental stages of Chinese fir plantations

Developmental stage	Fine root (< 0.2 cm)	Small root (0.2–0.5 cm)	Intermediate root (0.5–2 cm)	Coarse root (2–5 cm)	Root bole (> 5 cm)	Stump	Mean
Young	42.4 ± 0.2a	45.2 ± 1.1a	46.0 ± 0.9a	46.3 ± 1.1a	44.7 ± 0.4b	47.8 ± 0.3a	43.7 ± 0.3a
Mature	40.1 ± 0.3b	44.7 ± 1.1a	45.8 ± 0.3a	46.3 ± 0.9a	46.3 ± 0.3a	48.2 ± 0.3a	41.6 ± 0.4b
Overmature	40.3 ± 0.3b	45.4 ± 0.5a	45.4 ± 0.4a	46.0 ± 0.4a	45.7 ± 0.5ab	46.5 ± 0.2b	42.0 ± 0.4b
Mean	41.0 ± 0.2	45.1 ± 0.6	45.8 ± 0.5	46.2 ± 0.5	45.6 ± 0.3	47.5 ± 0.3	42.5 ± 0.2

Values are means ± SE. Different lowercase letters in the same column indicate significant differences among developmental stages for the same tissue type (LSD-HSD test at $P < 0.05$)

SOC was significantly lower at the young stage (8.49 g kg^{-1}) than at the mature stage and overmature stage (10.4 g kg^{-1} and 10.7 g kg^{-1}, respectively) (Fig. 3b).

For each soil layer and the total soil depth, C stock increased as the developmental stage increased. The total soil C stock increased significantly from 67.1 t ha^{-1} in the young

Table 5 A two-way ANOVA results for carbon return by above- and belowground litterfall

Source	Df	Mean square	F value	P value
Carbon return by leaf				
Stage	2	0.020	13.077	< 0.001***
Month	11	0.016	10.321	< 0.001***
Stage × month	22	0.008	5.060	< 0.001***
Carbon return by branch				
Stage	2	0.003	13.346	< 0.001***
Month	11	0.002	10.493	< 0.001***
Stage × month	22	0.001	4.943	< 0.001***
Carbon return by cone				
Stage	2	0.002	24.981	< 0.001***
Month	11	0.000	4.876	< 0.001***
Stage × month	22	0.000	2.271	0.014*
Carbon return by total aboveground litterfall				
Stage	2	0.055	18.701	< 0.001***
Month	11	0.034	11.592	< 0.001***
Stage × month	22	0.017	5.644	< 0.001***
Carbon return by live fine roots				
Stage	2	0.561	6.377	0.006**
Season	3	0.597	6.794	0.002**
Stage × season	6	0.091	1.030	0.430
Carbon return by dead fine roots				
Stage	2	0.184	25.448	< 0.001***
Season	3	0.081	11.176	< 0.001***
Stage × season	6	0.017	2.388	0.060
Carbon return by total fine roots				
Stage	2	0.375	4.282	0.026*
Season	3	0.341	3.892	0.021*
Stage × season	6	0.086	0.985	0.457

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

stage to 85.0 t ha^{-1} in the overmature stage. Carbon stock decreased significantly from the shallowest to the deepest soil depths for all developmental stages ($P < 0.05$); it was 32.8–39.0 t ha^{-1} at 0–20 cm and 14.0–21.1 t ha^{-1} at 40–60 cm (Fig. 3c). The correlations between SOC concentrations and the different components of aboveground and belowground litter C return were all positive, but were significant only for belowground litter C return (Table 6).

3.3.3 Total carbon stock in Chinese fir plantations

Total C stocks in Chinese fir plantations increased as the stand stage increased; they were 86, 129, and 153 t ha^{-1} in the young, mature, and overmature stages, respectively (Fig. 4). Significant differences were detected between the young and overmature stages ($P < 0.05$). The majority of C occurred in the soil pools (78.3, 59.6, and 55.7% in the young, mature, and overmature stages, respectively), with the proportion decreasing with stand age. Soil C stocks amounted to 67.1, 76.9, and 85.0 t ha^{-1} at each stage, while tree C stocks (including roots) were 17.9, 50.5, and 66.1 t ha^{-1} at each stage, respectively. The aboveground litterfall C stock for 1 year was a negligible component of the stand C stock, ranging from 0.8 to 1.3%.

4 Discussion

4.1 Carbon concentration variation

For accurate estimates of tree C stocks, both inter- and intra-species variation and tissue-specific variation should be considered. In the chronosequence of Chinese fir plantations, studied C concentration of most tissue types, particularly aboveground tissues, increased from the young to mature stage and then remained stable from the mature to the overmature stage. The increase of C concentration from the young to mature stage may be due to the significant positive correlation reported between C concentration and DBH and tree height by Weber et al. (2018) and could be associated with larger, fast-growing trees. Significant differences in tissue C

Table 6 Annual carbon return by aboveground and belowground litterfall and its correlation with SOC concentration in Chinese fir plantations at different developmental stages

Item	Aboveground litterfall carbon return (t ha^{-1})				Belowground litterfall carbon return (t ha^{-1})		
	Leaf	Branch	Cone	Total	Live fine root	Dead fine root	Total fine root
Young stage	0.47 ± 0.03b	0.19 ± 0.01b	0.04 ± 0.01b	0.70 ± 0.03b	1.06 ± 0.06ab	0.13 ± 0.01b	1.19 ± 0.04b
Mature stage	1.08 ± 0.20a	0.42 ± 0.01a	0.23 ± 0.05a	1.73 ± 0.27a	1.11 ± 0.07a	0.30 ± 0.03a	1.41 ± 0.05a
Overmature stage	1.06 ± 0.05a	0.39 ± 0.05a	0.20 ± 0.01a	1.65 ± 0.09a	0.87 ± 0.06b	0.36 ± 0.05a	1.23 ± 0.05b
The Pearson correlation coefficient with SOC	0.242	0.201	0.199	0.229	0.739**	0.398*	0.840**

Note: Different lowercase letters in a column indicate significant differences among stand stages according to LSD-HSD test at $P < 0.05$. Values = means ± SE. Correlation coefficients of SOC with litterfall stock in aboveground and belowground parts are shown in the final row of the table

$**P < 0.01$, $*P < 0.05$

concentrations have been reported in some tree species for some tissues, but not for others. For example, for *Quercus variabilis* C concentration in branches increased from young to middle-aged trees but were not significantly different in near-mature and mature trees, while there was no significant difference in C concentration between leaf, stem, and root tissues at different ages (Jiang et al. 2017). In *Robinia pseudoacacia* L. plantations, no significant difference in C concentrations was measured between roots and stems in 5-,

10-, 15-, and 20-year-old trees, but there was a significant increase in leaf C concentration in trees older than 5 years (Li et al. 2013). Overall, our tissue C concentration results for Chinese fir suggest that, for C sequestration purposes, it is advantageous to promote rapid tree growth to at least the mature stage.

Our results for stem C concentration for Chinese fir (47.5–49.4%) differed from estimates for temperate tree species (Zhang et al. 2009). They were smaller than those for
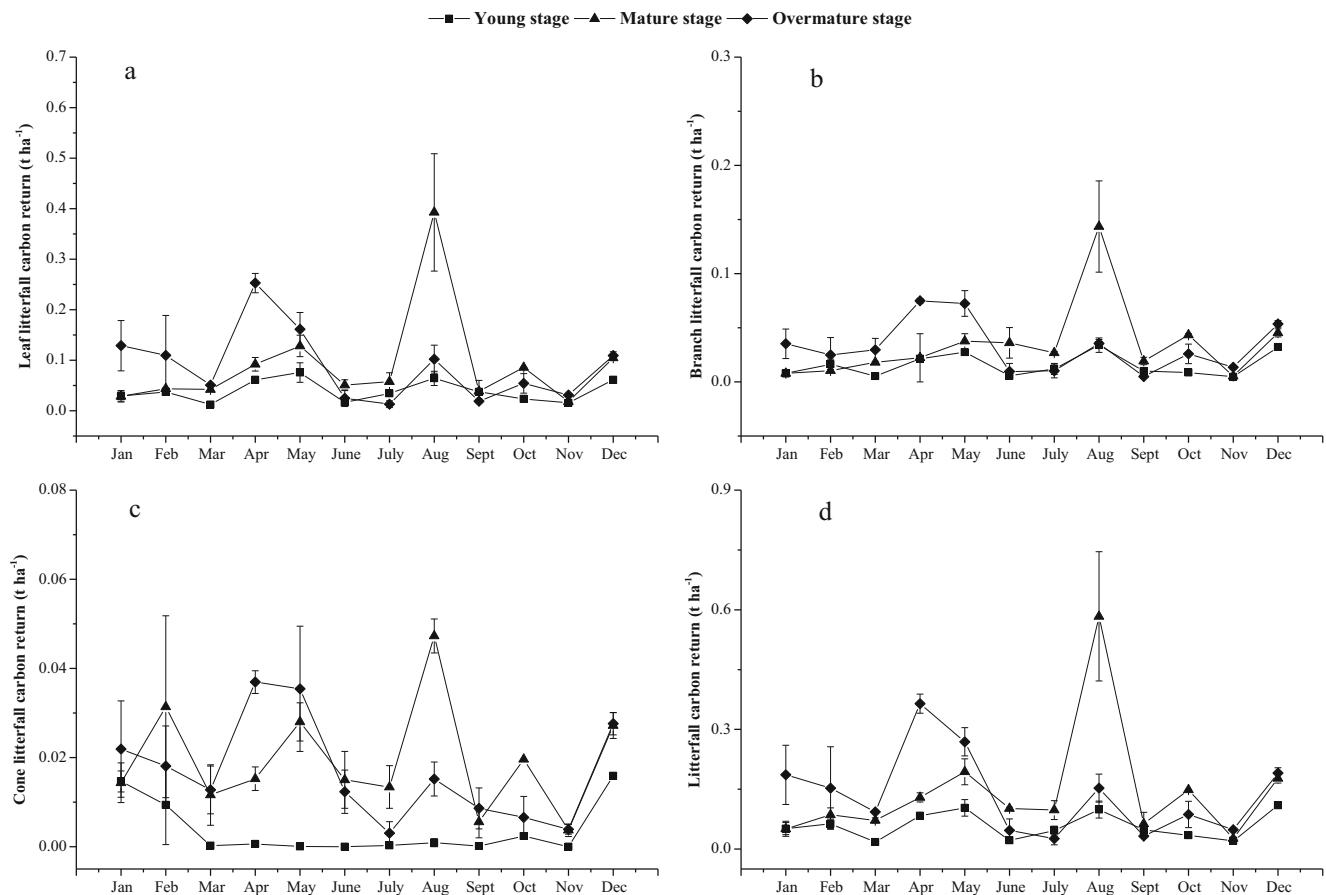

Fig. 1 Monthly carbon return in different litterfall components at various developmental stages in Chinese fir plantations: **a** leaf, **b** branch, **c** cone, and **d** total aboveground litterfall. Values are means ± SD ($n = 3$). Different *y*-axis scales
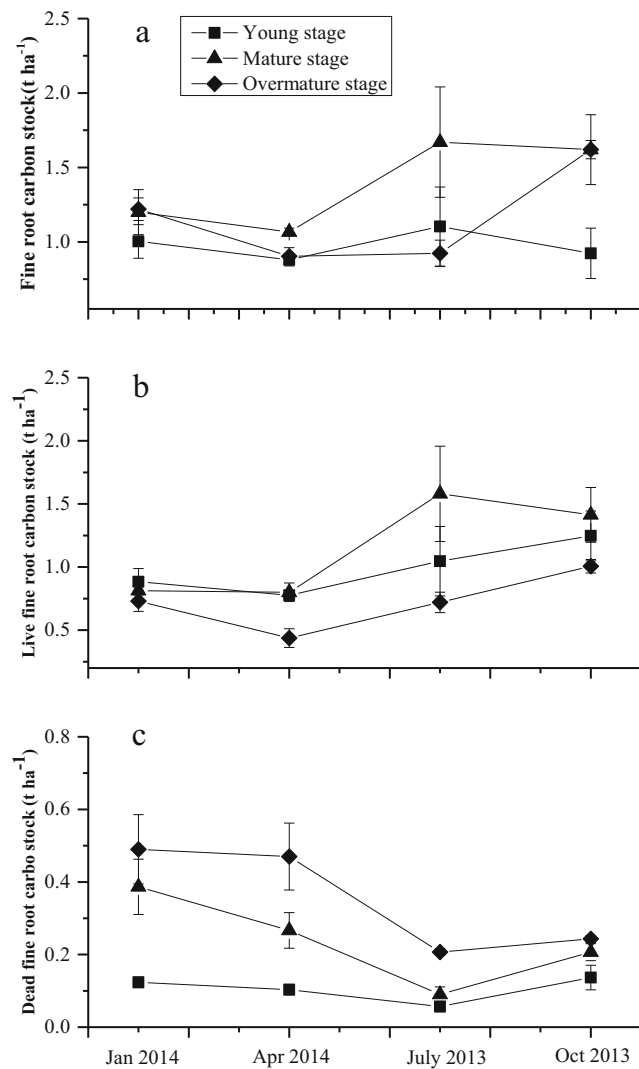
Fig. 2 Seasonal dynamics of **a** total, **b** live, and **c** dead fine root carbon return at various developmental stages in the 0–60-cm soil layer in Chinese fir plantations. Values are means ± SE ($n = 3$). Different y-axis scales in **c**

Phellodendron amurense Rupr. (55.6%), *Pinus koraiensis* Sieb. et Zucc. (52.6%), *Fraxinus mandshurica* Rupr. (53.2%), and *Juglans mandshurica* Maxim. (52.8%), but similar to those obtained for *Larix gmelinii* Rupr. (46.7%), *Acer mono* Maxim. (46.6%), and *Betula platyphylla* Suk. (45.9%) (Zhang et al. 2009). Substantial differences in C concentration within a species have been reported among 16 white birch populations in bark (45.2–49.9%), in fine roots (41.5–46.2%), and at the mean tree level (44.6–47.8%) (Wang et al. 2015). However, no studies have examined the C concentration among provenances of Chinese fir species and this is a topic for further investigation.

Several studies have examined tissue-specific variation in C concentrations in tropical and subtropical species, but most studies have focused on temperate/boreal species. Across Chinese fir trees of different, ages we measured C

concentrations of 48.0% in live tissues, 49.1% in senescent canopy tissues, 49.1% in litterfall, and 48.3% in bark, resulting in an overall aboveground tree concentration of 48.6%. The C concentration in roots (42.5%) was lower than that in aboveground woody parts, consistent with previous results for mangrove species (Rodrigues et al. 2015), *Camellia oleifera* (Zheng et al. 2008), and *Pinus pinaster* Ait. (Bert and Danjon 2006). As shown in Table 8, compared with previous estimates, our estimates for the tissue C concentration in Chinese fir species were lower than that for corresponding parts in *Pinus elliottii* and *Pinus pinaster* Ait. (Bert and Danjon 2006). The foliage C concentration in our study (48.8%) was similar to those observed for *Camellia oleifera* and *Cyclobalanopsis glauca*, i.e., 49.4% and 49.7%, respectively. Fine roots had a lower C concentration (42.5%) than those of *Pinus elliottii* (52.2%) and *Pinus massoniana* (56.5%) (Zheng et al. 2008). For bark, the C concentration in this study (48.3%) was greater than those for *Quercus petraea* (46.9%) and *Quercus pyrenaica* (45.8%) (Castaño-Santamaría and Bravo 2012). However, the stem C concentration in Chinese fir (48.1%) was lower than those of 10 temperate tree species (49.9%, on average) (Zhang et al. 2009) and was within the range obtained for 32 tropical tree species (44.4–49.4%) (Elias and Potvin 2003). Yang et al. (2006) reported that the C concentrations in the stem, bark, foliage, and branches were 56.3%, 56.2%, 53.7%, and 51.9%, respectively, and the C concentrations in the fine root, small root, intermediate root, coarse root, and bole root were 51.7%, 51.4%, 52.2%, 51.8%, and 52.4%, respectively, in a 33-year-old Chinese fir plantation in Sanming County, Fujian Province, China. The greater mean C concentration (55.6%) reported compared with our study (48.5%) can be explained by the use of a more aggressive C analysis procedure using potassium dichromate and hydration heating. Together, these studies demonstrate that the C concentration varies substantially across tissues within a tree species, and therefore, the tissue-specific tree C concentration should be evaluated when assessing tree C stocks.

4.2 Carbon stock

4.2.1 Plantation carbon stock

Since a previous study of Chinese fir plantations reported that the vegetation C stock was predominantly in the trees (92.8–98.2%), with understory vegetation, including shrubs and herbs, only accounting for 0.4–3.6% of the total plantation C stock (Lan et al. 2016), the understory C stock was not considered in our study. We summed tree C stock, annual litterfall C return, and soil C stock and found that C stock increased with developmental stage in the individual components and in the Chinese fir plantation overall. Our results of developmental stage effects on ecosystem C

Table 7 Tree carbon stock (t ha^{-1}) distribution in tree species at different developmental stages of Chinese fir plantations

Developmental stage	Live foliage	Live branch	Live cone	Senescent foliage	Senescent branch	Senescent cone	Stem	Bark	Aboveground	Root	Total
Young	1.89 ± 0.13c	1.22 ± 0.10c	0.58 ± 0.04c	0.97 ± 0.08b	0.62 ± 0.06a	0.12 ± 0.01a	7.35 ± 0.53c	1.13 ± 0.09b	13.87 ± 1.04c	3.88 ± 0.23c	17.75 ± 1.19c
Mature	3.30 ± 0.12b	2.19 ± 0.09b	1.80 ± 0.14a	0.34 ± 0.02c	0.16 ± 0.01b	0.16 ± 0.01a	27.94 ± 0.77b	6.38 ± 0.23a	42.27 ± 1.38b	7.47 ± 0.28a	49.75 ± 1.65b
Overmature	5.42 ± 0.27a	3.45 ± 0.17a	0.97 ± 0.04b	2.10 ± 0.14a	0.72 ± 0.05a	0.05 ± 0.02b	41.36 ± 1.48a	6.08 ± 0.36a	60.14 ± 2.38a	5.70 ± 0.21b	65.84 ± 2.59a
Mean	3.54 ± 0.52	2.29 ± 0.33	1.12 ± 0.18	1.14 ± 0.26	0.50 ± 0.09	0.10 ± 0.02	25.55 ± 4.97	4.53 ± 0.86	38.76 ± 6.79	5.67 ± 0.53	44.45 ± 7.13

Values are means ± SE. Different lowercase letters in the same column indicate significant differences among Chinese fir plantations of different ages at $P < 0.05$

sequestration were consistent with some previous studies in plantation forests (e.g., Lan et al. 2016; Pang et al. 2017). The most likely explanation for the observed increased C stocks is silvicultural management. Forest thinning, as conducted in the mature and overmature plantation stands in this study, has been shown to stimulate tree growth in Chinese fir plantations (Zhou et al. 2016b) and thus is expected to enhance tree C stock, litterfall, and organic C return to the soil.

Compared with other forests, our estimate for the Chinese fir plantation C stock (122 t ha^{-1}) was lower than that for a *Larix olgensis* A. Henry natural forest (184 t ha^{-1}, mean value of 7- to 48-year-old plantations) (Ma et al. 2014). The C stocks in the Chinese fir plantation in our study were greater than
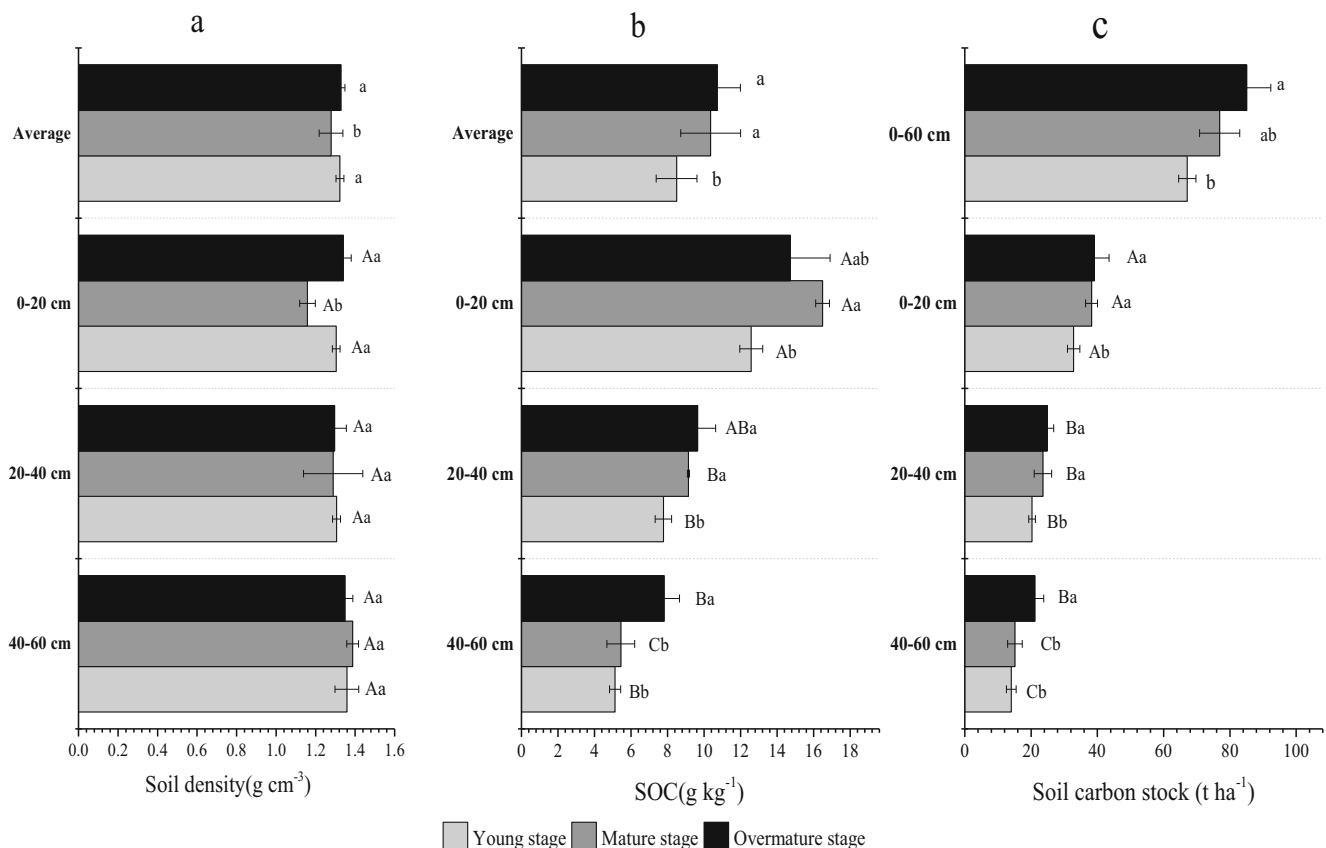

Fig. 3 Soil bulk density **a**, SOC concentration **b**, and soil carbon stock **c** at various soil depths and developmental stages of Chinese fir plantations. Values are means ± SE ($n = 3$). Different lowercase letters indicate significant differences among stages at the same soil depth, and different uppercase letters indicate significant differences among soil depths at the same stage. All means were compared using LSD post hoc tests at $P < 0.05$
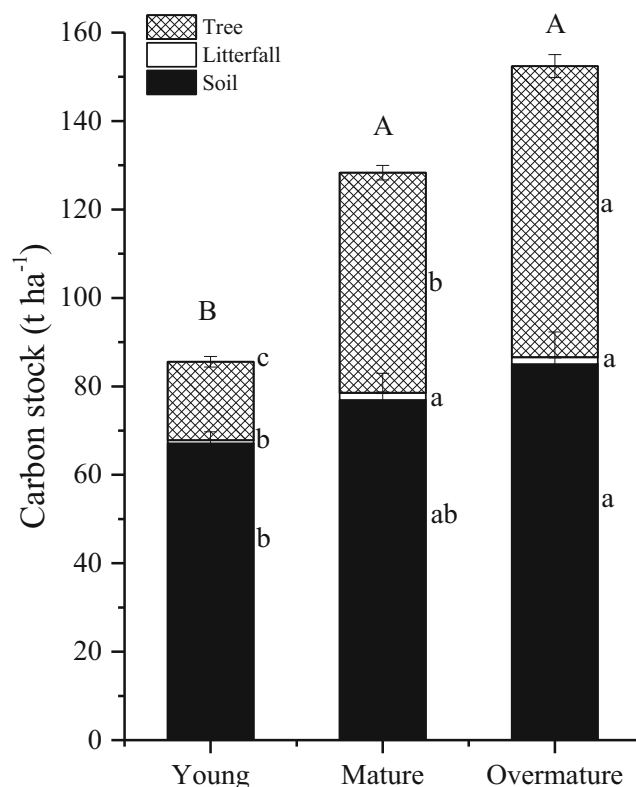
Fig. 4 Mean carbon stock in various parts of Chinese fir plantations at various developmental stages. The tree stock includes above- and below-ground biomass, and litterfall refers to the annual C return in aboveground litterfall. Values are means ± SE ($n = 3$) Different lowercase letters indicate significant differences among stand stages for the same tissue/soil stock, and different uppercase letters indicate significant differences among stands in the total plantation C stock. All means were compared using LSD post hoc tests at $P < 0.05$

those for 12-, 25-, and 36-year-old *Picea asperata* plantations (78.6, 104, and 90.6 t·ha^{-1}, respectively) in the eastern Tibetan Plateau, China (Pang et al. 2017), and lower for similar age Chinese fir stands (34 years, this study 153 t ha^{-1} vs. 33 years 228 t ha^{-1}) in the same region as our study (Sanming County, China) (Yang et al. 2006). However, our measured plantation C stocks were similar to those for Chinese fir (103 t ha^{-1}), *Pinus elliottii* (104 t ha^{-1}), and *Camellia oleifera* (113 t ha^{-1}) plantations in the hilly red soil region of southern China (Zheng et al. 2008).

There are several explanations for the substantial variation in reported forest C stock in China, both for individual forests and for the national forest C stock. Firstly, forest density and forest management practices (e.g., thinning and residue management) may affect C stocks in live trees, coarse woody debris, and the forest floor. In this study, the canopy density decreased with stand age (Table 1) due to thinning in the mature and overmature stages which is related to increased availability of space and light for the remaining trees to grow more rapidly, thus enhancing plantation C stocks. Decreasing canopy density might be expected to result in decreased soil

organic carbon stocks due to increased decomposition of litter, as demonstrated in the field for *C. lanceolata* needle litter (Ma et al. 2017). However, in this study, the significant increase in aboveground litterfall C return from the young to the thinned mature and overmature stages appears to have offset this effect. Secondly, the C stock in a forest will be affected by the biomass which will vary between climatic zones, with lower forest growth rates and biomass in colder regions in northern China and at high altitude. Thirdly, the sectors included in estimates of total forest C stocks are not consistent between studies. Most studies included C stocks in live trees, understory vegetation, litterfall, and soil, but some studies also included removed trees, fallen and standing dead wood, and the litter layer. Furthermore, the soil depths examined ranged from 20 to 100 cm, leading to high variation in soil C estimates among studies.

4.2.2 Tree carbon stock

In this study, biomass was multiplied by the tissue-specific C concentration to convert biomass to C stock. The tree C stock for Chinese fir species was 17.9 t ha^{-1} for the young stage, 50.5 t ha^{-1} for the mature stage, and 66.1 t ha^{-1} for the overmature stage. The average tree C stock in our study across the three developmental stages investigated (44.9 t ha^{-1}) was lower than the average forest vegetation C stock (57.1 t ha^{-1}) and the *Pinus massoniana* C stock in Guangxi Province (53.9 t ha^{-1}), but similar to those for temperate coniferous forests (43.2 t ha^{-1}) and warm temperate coniferous forests (48.0 t ha^{-1}) (Zhou et al. 2000). The tree C stock in our study was lower than that for Chinese fir species at the fast-growing stage (11 years old, 35.0 t ha^{-1}) at Hunan Huitong Ecological Station in southern China under a subtropical monsoon climate (26° 50′ N, 109°45′ E). The tree C stock in the mature stage was lower than for a 23-year-old Chinese fir plantation (85.9 t ha^{-1}) and a 20-year-old Panamanian *Tectona grandis* teak plantation (120 t ha^{-1}) (Kraenzel et al. 2003). Additionally, the tree C stock in the 34-year-old stand in our study was lower than that in a 32-year-old Chinese fir plantation (119 t ha^{-1}) in northern Guangxi Province, China (Lan et al. 2016). However, the tree C stock at the young stage in our study was consistent with estimates for a Chinese fir monoculture plantation in Guangdong Province, China (20.7 t ha^{-1}) (Lin et al. 2014).

Variations in tree C stocks were mainly determined by the forest age, type, density, and rotation length. Generally, tree C stock increases as the stand age increases in Chinese fir (Lan et al. 2016), *Larix olgensis* A. Henry plantations (Ma et al. 2014), and *Prunus davidiana* (Carr.) Franch, *Caragana korshinskii* Kom., and *Hippophae rhamnoides* plantations (Dang et al. 2017). Nevertheless, many tree C stock estimates have been obtained using a constant factor for the conversion of biomass to C stock, ignoring tissue-specific C stock. For the

Table 8　Comparison between our results and those of previous studies for tissue-specific carbon concentrations in different tree species

Biome	Species	Age (years)	C concentration (%)							Location	Reference
			Foliage	New branch	Old branch	Stem	Bark	Coarse root	Fine root		
Subtropical forest	Cunninghamia lanceolata	10	47.9	45.8	47.6	47.5	47.2	46.3	42.4	China	This reference
Subtropical forest	Cunninghamia lanceolata	22	49.2	47.4	48.2	49.4	48.5	46.3	40.1	China	This reference
Subtropical forest	Cunninghamia lanceolata	34	49.1	47.4	48.3	47.8	49.0	46.0	40.3	China	This reference
Temperate/boreal forest	Pinus pinaster Ait.	50	53.6	–	–	–	55.9	51.3	–	France	Bert and Danjon (2006)
Temperate/boreal forest	Pinus koraiensis Sieb. et Zucc.	41	56.4	54.5	53.8	52.6	–	52.8	50.4	China	Zhang et al. (2009)
Temperate/boreal forest	Phellodendron amurense Rupr.	57	54.3	54.9	55.4	55.6	–	53.6	50.0	China	Zhang et al. (2009)
Temperate/boreal forest	Juglans mandshurica Maxim.	57	51.5	49.9	52.6	52.8	–	50.2	48.0	China	Zhang et al. (2009)
Temperate/boreal forest	Larix gmelinii Rupr.	49	49.2	50.4	47.9	46.7	–	46.9	46.5	China	Zhang et al. (2009)
Temperate/boreal forest	Acer mono Maxim.	52 and 57	49.1	47.6	47.0	46.6	–	45.0	44.5	China	Zhang et al. (2009)
Temperate/boreal forest	Fraxinus mandshurica Rupr.	52 and 57	50.6	52.5	52.6	53.2	–	51.7	48.0	China	Zhang et al. (2009)
Temperate/boreal forest	Betula platyphylla Suk.	57 and 58	48.9	49.8	46.5	45.9	–	45.7	44.4	China	Zhang et al. (2009)
Temperate/boreal forest	Fraxinus mandshurica Rupr.	52 and 57	50.6	52.5	52.6	53.2	–	51.7	48.0	China	Zhang et al. (2009)
Subtropical forest	Quercus petraea	ca. 60	–	–	–	Sapwood 45.5 Heartwood 46.0	46.9	–	–	Spain	Castaño-Santamaría and Bravo (2012)
Subtropical forest	Quercus pyrenaica Willd.	ca. 60	–	–	–	Sapwood 45.6 Heartwood 45.8	45.8	–	–	Spain	Castaño-Santamaría and Bravo (2012)
Tropical forest	Pinus elliottii	15	58.9	Coarse 56.7 Fine 55.3	–	54.9	53.3	Root (>2 cm) 56.6 Root (0.2–2 cm) 54.9	52.2	China	Zheng et al. (2008)
Tropical forest	Cunninghamia lanceolata	15	50.4	Coarse 46.0 Fine 45.7	–	47.6	49.0	Root (>2 cm) 48.7 Root (0.2–2 cm) 47.0	45.0	China	Zheng et al. (2008)
Tropical forest	Camellia oleifera	15	49.4	Coarse 51.8 Fine 50.2	–	51.2	51.3	Root (>2 cm) 48.8 Root (0.2–2 cm) 47.0	45.5	China	Zheng et al. (2008)
Tropical forest	Pinus massoniana	15	44.7	Coarse 54.9 Fine 53.7	–	60.7	53.9	Root (>2 cm) 59.7 Root (0.2–2 cm) 58.0	56.5	China	Zheng et al. (2008)
Tropical forest	Cyclobalanopsis glauca	15	49.7	Coarse 48.6 Fine 47.9	–	47.7	48.9	Root (>2 cm) 48.7 Root (0.2–2 cm) 47.5	46.9	China	Zheng et al. (2008)

young, mature, and overmature developmental stages of the Chinese fir stands investigated in this study, the underground C stock would be overestimated by 7.6%, 13.0%, and 8.1%, respectively, while the overall tree C stock would be underestimated by 0.08%, 3.24%, and 1.76% and overestimated by 6.3%, 2.9%, and 4.5%, respectively, if 0.47 (IPCC 2006) and 0.5 (IPCC 2003) were used as the biomass to C conversion factor. Nevertheless, the overall mean tree C fractions for the different Chinese fir developmental stages was 46.5%, 47.1%, and 47.4%, respectively, which is very similar to the default tree biomass C fraction of 0.47 in IPCC (2006).

In addition to variation in tree biomass C fraction between different species and tissue types, a further source of uncertainty in estimating C stocks in tropical forests is that the volatile C wood content is not considered in studies based on oven-dried biomass samples. From the comparison of freeze- and oven-dried wood samples of 59 Panamanian rainforest tree species, the volatile C content of wood has been shown to be non-significant at $2.48 \pm 1.28\%$ (mean $\pm$ S.D.) (Martin and Thomas 2011). Therefore, tropical forest C stock calculations based on C fractions derived from oven-dried biomass will be underestimated. Even though volatile C content has not been measured in Chinese fir trees, similar non-significant values would be expected since it is a subtropical tree species and the tree wood and foliage have aromatic properties. Hence, the mean stem wood C concentration of 48.1% across all developmental stages of a Chinese fir plantation reported in this study might actually be higher at 50.6%, a very similar value to the default C fraction of 0.5 noted in the IPCC (2003) Good Practice Guidance.

4.2.3 SOC stock

Quantifying SOC is important for understanding changes in soil properties and C fluxes in ecosystems. In this study, SOC stock (0–60 cm) increased significantly from the young stage (67.1 t ha^{-1}) to the mature and overmature stages (76.9 t ha^{-1} and 85.0 t ha^{-1}, respectively) of the Chinese fir stands. Our estimates were consistent with the values from 27- and 87-year-old Chinese fir stands reported from other studies in Fujian Province (68.6 and 76.0 t ha^{-1}; Yang et al. 2003 and Zhong et al. 2008, respectively), but were far lower than the average value of 194 t ha^{-1} for different forest ecosystems in China (Zhou et al. 2000). Similar to our results, many studies have reported that the SOC stock increases with plantation age, e.g., in rubber plantations (Nath et al. 2018). Our SOC storage estimates for the mature stage (22 years old) were consistent with those for Chinese fir at a similar age in mixed stands (68.6 t ha^{-1}) (Yang et al. 2003), but were greater than those for a pure Chinese fir stand (56.0 t ha^{-1}, soil depth 0–40 cm). However, in other Chinese fir short-rotation plantations, the overall magnitude of SOC storage was greater than in our

study, but did not show a clear trend with respect to age. Zhang et al. (2017) reported that the mean SOC storage (0–100 cm) decreased slightly from the young stage (111 t ha^{-1}) to the middle stage (92.0 t ha^{-1} for 16-year-old stands) and was greater at the mature stage (118 t ha^{-1} for 25-year-old stands) among Chinese fir. Therefore, the SOC stock can vary greatly, even in the same forest type, and depends on many factors, e.g., soil type, climate, and land use change and management (Paul et al. 2002).

Above- and belowground litterfall are the most important sources of SOC and determine the quantity and quality of SOC, especially for the soil surface layer (Wang et al. 2013). Significant differences were observed for fine root C concentration, with higher concentration under the young compared with the mature and overmature stages (Table 4). We found positive correlations between SOC stock and above- and belowground litter C return, but correlations were only significant with belowground litterfall (Table 6). These results indicate that the SOC stock was influenced mostly by the turnover and production of belowground fine roots, instead of aboveground litterfall production. We measured the mean annual aboveground litterfall production of 3.29, 3.73, and 4.88 t ha^{-1} for the same Chinese fir stands (Zhou et al. 2015) and dead fine root production of 0.36, 0.76, and 0.94 t ha^{-1} at young, mature, and overmature developmental stages, respectively. Although fine root production is often low, the fast decomposition rate and root turnover contribute more to soil organic matter than the C return from aboveground litterfall (Asaye and Zewdie 2013).

Live and dead fine root C stocks showed inverse patterns of seasonal variation in the Chinese fir plantations studied (Fig. 2) which are attributed to the tree phenological growth rhythm and seasonal climate patterns. The greatest propagation of fine roots occurred in July may be due to a high temperature before the onset of drought conditions, while another high value of fine root biomass occurred in October, which might be associated with the increase of soil moisture after dry and hot conditions. The fine root necromass showed the opposite seasonal pattern, peaking in January and April, which may be related to lower temperature conditions in winter, resulting in low forest productivity and accumulation of dead fine roots (Yang et al. 2004). These interpretations are supported by other studies in a variety of forest and climate settings in which fine root growth was reported to be positively correlated with soil temperature (Steele et al. 1997) and to tree phenology and inversely correlated with soil moisture deficit (Joslin et al. 2001). In a study of factors affecting fine root mass in four subtropical forest types in China, including a Chinese fir plantation, highest root necromass was reported at the beginning and end of the growing season, as in this study, and fine root biomass was positively correlated with air temperature and inversely with precipitation (Liu et al. 2014). Although aboveground litterfall was not significantly

correlated with SOC stock in this study, seasonal variation was also observed in C return in litterfall, particularly for the mature and overmature developmental stages. Peaks occurred in April–May and August (Fig. 1) and are attributed to environmental conditions, such as intermittent rainfall and strong winds in April and May may lead to defoliation. Typhoons often occur in August, which has caused extensive nonphysiological defoliation in the study area (Zhou et al. 2015).

SOC can be divided into active carbon (AC) and recalcitrant/passive carbon pools, which make different contributions to the atmospheric CO_2 content due to varying sequestration and release processes (Nath et al. 2018), but also interact. Understanding the nature and cycling of SOC and controlling factors is critical to inform recommendations for land use and management to maximize the uptake and stability of SOC (Malik et al. 2018). Pathak et al. (2017) reported that active soil C pools were mainly derived from nutrient input and organic compounds from aboveground litterfall that are metabolized in soils. Chemical mechanisms of SOC stabilization are suggested to be more significant than physical processes, such as protection arising from the soil texture (Krull et al. 2003). Thus, in the Chinese fir system studied, the likely presence of tannins and waxy compounds (i.e., lipids) and lignins in aboveground litterfall and roots, respectively, may increase passive C pools. The stability of SOC is also expected to increase with soil depth due to the positive association been a turnover time of microbial biomass and soil depth in mineral soils below forest (Spohn et al. 2016). Recent research suggests a significant contribution of microbial-biomass-to-stable-SOC fractions (e.g., Kallenbach et al. 2016), although most studies to date have been conducted in model soils or agricultural systems. Hence, the mechanisms controlling SOC stability at different developmental stages in Chinese fir plantations should be further studied in the near future.

5 Conclusions

While the C concentration varied substantially among above- and belowground tissues at the tree level, the overall C fraction in aboveground biomass was within the range of 0.44–0.49 for tropical and subtropical forest species recommended in IPCC Guidelines (2006). For Chinese fir species, tree C stock estimates decreased by 0.08%, 3.24%, and 1.76%, respectively, if the general conversion factor (0.47 for trees) was used. Positive correlations were found between SOC stock and C return by above- and belowground litterfall in Chinese fir plantations; however, fine root input was a more important driver of soil C sequestration than aboveground litterfall. The effects of the developmental stage were significant for C stock in trees, soil, and plantations; C stock increased according to developmental stage. Carbon stock estimates at the overmature stage were 66.1

t ha^{-1} and 153 t ha^{-1} for the tree and plantation scales, respectively, and were substantially higher than those at the young and mature stages. These results confirmed that old-growth forests sequester more C in live woody tissues and slowly decomposing organic matter in litter and soil, which should be the focus of protection strategies (Luyssaert et al. 2008). Therefore, prolonging the rotation length for Chinese fir plantations, as we reported previously (Zhou et al. 2016a), would increase not only annual nutrient turnover but also the C sink strength. Furthermore, our results are useful for national GHG inventory assessments for China to fulfil the requirements of the Paris Accord and may be a good reference for more detailed tier 3 estimates of forest biomass carbon in extensive Chinese fir plantation and other coniferous species in tropical and subtropical areas.

Data availability statement The datasets generated and/or analyzed during the current study are available in the Dryad Digital Repository (Zhou et al. 2019) at https://doi.org/10.5061/dryad.61pm78v

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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