



Rotation age extension synergistically increases ecosystem carbon storage and timber production of Chinese fir plantations in southern China

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ABSTRACT

Afforestation is an effective method to increase carbon (C) sinks and address climate change. It is crucial to understand how the stand growth affects C sequestration capacity, especially when the trade-offs with timber production from plantations have not been fully examined. We used a chronosequence approach to estimate C storage in Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook.) plantations (including the trees, understory, litter, and soils) at seven stand ages (3, 8–11, 16, 21, 25, 29, and 32 years). Ecosystem C storage increased nonlinearly from 76.4 to 282.2 t ha⁻¹ with stand age and was fitted with a logistic model that had a maximum C storage and age of 271.9 t ha⁻¹ and 33 years, respectively, to reach 95% of the maximum stored C. The C increment was mainly contributed by an increase in tree biomass, which ranged from 2.8 to 177.7 t ha⁻¹ and comprised 4–64% of the total ecosystem C. Live root C (sum of the stump, coarse, and fine root C) showed a logistic increase from 2.0 to 26.3 t ha⁻¹ with stand age and constituted 2.5–9.3% of ecosystem C. Understory plants and litter represented a small pool (<2% of ecosystem C). The C storage in shrubs and litter slightly increased, while that in herbs decreased as the stands aged. Soil C storage was an important and relatively stable pool, ranging from 69.6 to 130.1 t ha⁻¹. Stand volume was also best fitted with a logistic model with a maximum value of 552.6 m³ ha⁻¹. Additionally, the time needed to reach 95% of the maximum volume was 25 years. Hence, extending the rotation age to over 30 years for Chinese fir plantations could potentially maximize the synergistic benefits of C storage to mitigate climate change and obtain timber products for economic profit.

1. Introduction

Forest ecosystems are the largest terrestrial carbon (C) sink that plays an important role in the global C cycle via C sequestration, and thus, are crucial for mitigation of climate change (Dixon et al., 1994; FAO, 2020). It is estimated that the global forest area is 4.06 billion ha, and the total forest C stock (including soil pool at 1 m depth) was 662 Gt in 2020 (FAO, 2020). To increase forest capacity for climate change mitigation, afforestation and reforestation have been promoted as effective methods to increase C sequestration (Winjum and Schroeder, 1997; Peichl and Arain, 2007; Taylor et al., 2007).

In 2020, planted forests covered approximately 0.29 billion ha,

accounting for approximately 7% of the global forested area (FAO, 2020). In China, forest C storage increased from 4.10 ± 0.56 Gt C (1973–1976) to 9.65 ± 0.60 Gt C (2009–2013) (Sun and Liu, 2020) and was projected to reach 12.87 Gt C in 2020 (Jin et al., 2020). Such increase is mainly due to afforestation and reforestation projects, which led to the storage of 5.73 Gt C in planted vegetation (Guo et al., 2013; Sun and Liu, 2020; Jin et al., 2020). While forest area expansion contributed 60% of the increase in China's forest C sinks (Fang et al., 2014), age-related tree growth has also increased forest C storage. Therefore, an understanding of the forest C dynamics as the tree stand develops is critical for accurate estimates of total ecosystem C stocks and the assessment of C storage potential in plantations.

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Forest C stock contains various pools, including aboveground vegetation, belowground roots, litter, and soils (Samuelson et al., 2017; Sun and Liu, 2020). In addition to the highest potential of C storage in aboveground tree biomass (stem, branches, and foliage) (Peichl and Arain, 2007), the root biomass comprises approximately 20% of underground tree biomass as well (IPCC, 2006). Therefore, underground tree roots are an important part of the forest C pool and should not be ignored when estimating forest C storage. Apart from the tree layer, there are substantial C pools in understory plants, litter (10%), and soil (45%) (FAO, 2020). However, the estimation of C stored in roots (including fine roots) and soil is usually neglected because the determination of these pools is arduous. Less information on C storage in roots and soils has hampered conducting accurate estimations of forest C stocks, and thus, a better understanding of forest C dynamics (Pan et al., 2004).

The stand age affects forest C storage (Wang et al., 2003; Pregitzer and Euskirchen, 2004; Zerva et al., 2005; Peichl and Arain, 2006; Bradford and Kastendick, 2010; Seo et al., 2013) and is usually considered for forest C management (Alexandrov, 2007; Cook-Patton et al., 2020). Living tree biomass increases with stand age following a sigmoidal curve, i.e., ecosystem and tree C storage increase after planting and then remain stable as the stand ages (Taylor et al., 2007; Zhang et al., 2012). In contrast, knowledge of the variation in soil C storage with stand age is controversial; it may be age-independent (Cheng et al., 2014), where it may either increase or decrease with stand age (Cao et al., 2012; Chen et al., 2013; Zhao et al., 2014). The inconsistent knowledge on soil C storage with stand age might be attributed to forest types, tree species, climate, land-use history, management regime, and soil properties (Paul et al., 2002; Liao et al., 2010; Yang et al., 2011; Zhang et al., 2019). Additionally, the input of fine roots and leaf litter from trees and understory plants varies with stand age, and soil C storage might occur in deeper soil layers rather than in the more often investigated topsoil (Gleixner et al., 2009; Chen et al., 2013). Therefore, the age-related changes in fine root biomass and soil C storage at different soil depths and the relative importance of the contribution of fine roots and litterfall to soil C warrants further examination. Furthermore, if the trajectory of C storage dynamics could be expressed as a function of stand age, the functions can be used to predict potential C sequestration in plantations and to determine suitable rotation length to achieve maximum C storage (Xu et al., 2010; Samuelson et al., 2017).

The proxies for biomass C allocation, such as the root-to-shoot ratio and biomass allocation fractions (the ratios of tree biomass components (stems, branches, foliage, and roots) to total tree biomass) can be used to estimate C storage in easily measurable means, i.e., in stems or aboveground biomass. Such approaches have already been incorporated in terrestrial ecosystem C modeling (Zhang et al., 2015). While the isometric allocation hypothesis suggests that the component biomass is isometrically scaled with total biomass across plant species (Euquist and Niklas, 2002; Niklas, 2005) and community types, the optimal partitioning hypothesis suggests that biomass allocation varies with the environment to capture nutrients, water, and light resources for optimum growth (Chapin et al., 1989). In addition to climate and soil conditions, stand age affects biomass C allocation in tree components (Zhang et al., 2015). The ratios of foliage, branches, and roots to total tree biomass have been reported to decrease, while that of stems increased with stand age in different forest types across biogeographical regions (Zhang et al., 2015). As a forest develops, the canopy gradually becomes denser, and the space available for branches, foliage, and root to expand becomes limited. Biomass C allocation is also altered in response to the changes in microclimate and soil nutrient conditions with stand age (Taylor et al., 2007; Cao et al., 2012), however, additional information is required to fully comprehend the mechanism of this alteration with stand age.

Chinese fir (*Cunninghamia lanceolata* (Lamb) Hook.) is the first native tree species that is the most widely planted for timber production in

subtropical China. It has a planting history of more than a thousand years (Xiang et al., 2020). According to the data from the China Forest Resources Report (2014–2018), the area of Chinese fir plantations reached 0.14 billion ha, accounting for 6.33% of the total plantation area in China. These plantations not only provide a large amount of timber (852 million m³), but they also sequester large amounts of C (National Forestry and Grassland Administration, 2019). Chen et al. (2013) investigated variations in the biomass C of trees and understory plants and soil C storage with stand age in Chinese fir plantations in Fujian province. They attempted to determine if soil C storage could recover to the levels observed in natural evergreen broadleaved forests. Changes in ecosystem C storage and the volume of stand timber in Chinese fir plantations as a function of stand age have not been previously explored. Furthermore, an exploration of fitting statistical models by using stand age as a predictor of C storage is lacking. This study aimed to: (1) quantify C storage in an entire ecosystem of Chinese fir plantations and its components (including aboveground tree biomass, roots, fine roots, understory, litter, and soil) at seven stand ages; (2) develop statistical models to describe the trajectory of change in C storage in the entire ecosystem and stand timber volume as a function of stand age; and (3) use the findings thus acquired to determine a feasible rotation length for maximum synergistic benefits of C sequestration and timber production.

2. Materials and methods

2.1. Study area

The study area is located in Huitong County (26°41'–26°47' N, 109°35'–109°38' E), Hunan Province, China. The altitude of the study sites ranges from 330 to 482 m above mean sea level. The area is located in a typical subtropical humid monsoon climatic zone with an average annual temperature of 16.8 °C and annual rainfall of 1268 mm (Ouyang et al., 2018). The soil in the study area is developed from slate and shale parent rock and is classified as an Alliti-Udic Ferrosol (well-drained clay loam red soil) (Institute of Soil Science, Chinese Academy of Science, 2001). The climax vegetation in the study area is a subtropical evergreen broad-leaved forest.

The study area is the central production area of a Chinese fir plantation. A large area of Chinese fir plantations was established here in the 1960s to meet the huge timber demand during the economic growth. Since the 1980s, the plantations have become mature and have been gradually harvested for log timber with a rotation length of 25 years. The areas are reforested within a year after harvest. Chinese fir plantations in this study were second-generation plantations that were established by the planting of seedlings of the same variety as the harvested timber. The residues of harvest, including branches, bark, needles, and roots, were burnt on site, and the site was prepared manually. During the first 3 years after planting, herbs and shrubs were manually cut to facilitate seedling growth. Cut biomass was left on the site to enrich the soil. No further silvicultural activities were carried out on the plantations. The site conditions were consistent before afforestation. Understory plants included shrubs of Japanese Maesa (*Maesa japonica*), Chinaroot Smilax (*Smilax china*), and Holly (*Ilex purpurea*). Herbs of Alder (*Woodwardia japonica*), Old World forked fern (*Dicranopteris linearis*), and Parasitic Cyclosoru (*Cyclosorus parasiticus*) were also present.

2.2. Plot selection and stand investigation

Chinese fir plantations at seven stand ages (i.e., 3, 8–11, 16, 21, 25, 29, and 32 years) that spanned a complete rotation length were selected in this study based on a space-for-time (chronosequence) approach (Wu et al., 2020). Chronosequence is a common approach to investigating the temporal dynamics of plant community and soil development across multiple time scales; it is especially suitable to understand the development of forests with age (Walker et al., 2010). Differences in soil

conditions among the plots were considered in plot selection to improve the reliability of this approach. A total of 28 permanent 400 m² plots (20 m × 20 m) were set up in 2016. There were four replicates for each stand age, and each stand contained four plots. Because only one plot was available for the 8-year-old plantation, three plots were set up in the 11-year-old stands. These four plots were pooled together to represent an 8–11-year-old age class. The 28 plots were distributed at various slope positions and aspects, and the distance between the plots was at least 100 m. Details of the experimental design for plot selection have been described by Wu et al. (2020) and Chen et al. (2021). In each plot, the diameter at breast height (DBH, at 1.3 m), total height (H), height up to the lowest live branches, and crown width were measured using a caliper, tapeline, diameter tape, and height indicator, respectively. Stand characteristics and tree size distribution in Chinese fir plantations across the seven stand ages are presented in Table S1 and Fig. 1, respectively. The change in stand density with stand age was the result of self-thinning. The relationship between stand density and average DBH is consistent with the results of Wu et al. (2001), who reported that stand density inherently changes with average DBH in Chinese fir plantations due to self-thinning.

2.3. Plant and soil sample collection

All plant and soil samples were collected at three sampling positions (the upper, middle, and lower slope) within each plot in July 2017. At first, a well-grown Chinese fir tree with average DBH and H at each sampling position was selected to collect samples. Stem samples (approximately 100 g) were collected at breast height using an increment core. Fresh leaves (approximately 100 g) and branches (approximately 500 g) were collected from three standard branches at the upper, middle, and lower crowns of a healthy tree. We manually excavated roots growing in four directions from each sample tree and then cut off the root system to collect coarse root samples. Coarse root samples (approximately 500 g) were collected from each plot. For fine root samples, in each 20 m × 20 m plot, a soil core (with an inner diameter of 5 cm and a length of 15 cm) (Beijing New Landmark Soil Equipment Co., Ltd) was used to manually drill a soil column with a depth of 0–60 cm at three locations (i.e., the upper, middle, and lower slope). Fine roots were separated from the soil core for further analysis.

A 2 m × 2 m shrub-subplot and a 1 m × 1 m herb-subplot were selected at each sampling site. All shrubs in the shrub-subplot were harvested and separated into stems, leaves, and roots. Mixed samples from three sampling positions in the same plot were then weighed, and ~100 g of a randomly selected sample of each component was taken to

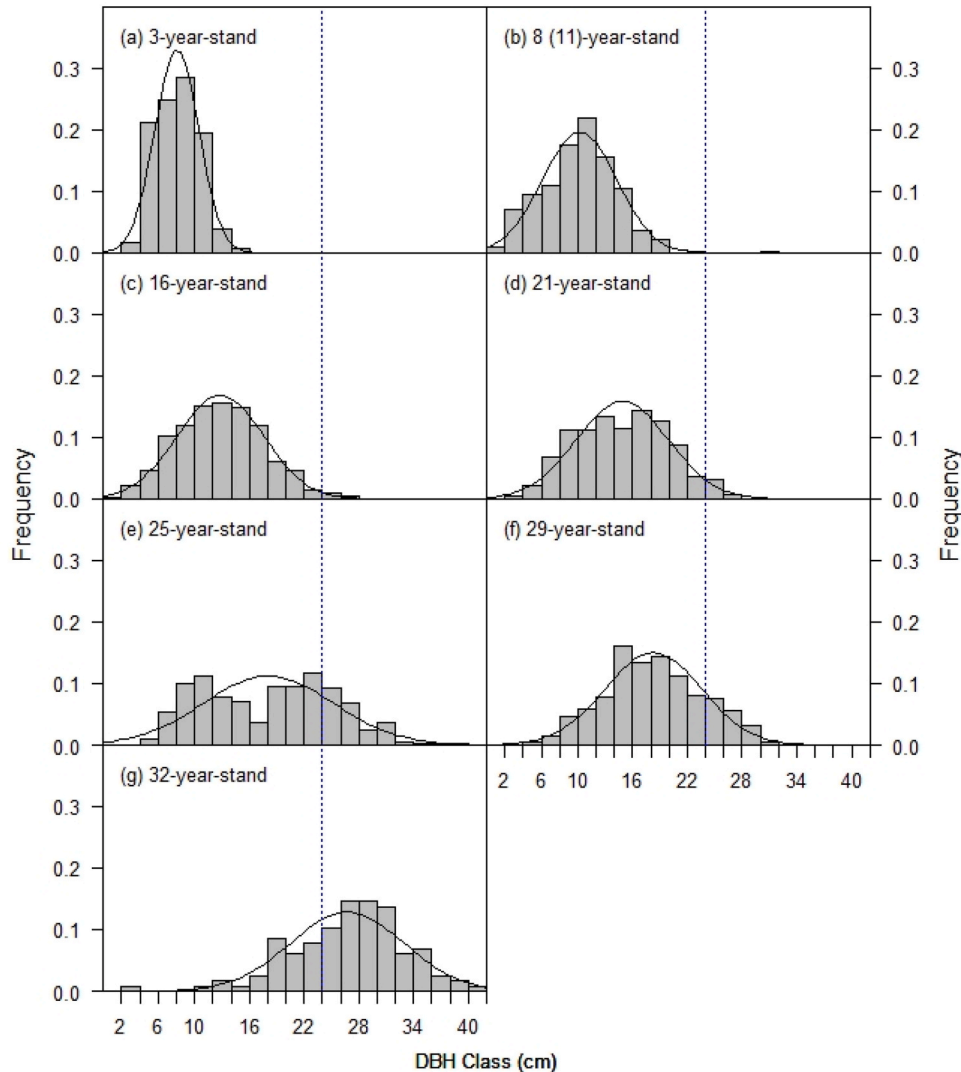


Fig. 1. Frequency distribution of diameter at breast height (DBH) with an interval of 2 cm in Chinese fir plantations of different stand ages. The blue dashed line indicates the value that separates the large trees (DBH > 25 cm) in the stands from others.

the laboratory. All herbs in the herb-subplot were harvested and separated into leaves and roots; the processing steps that followed were the same as those for shrubs. Litter samples (~100 g) were collected from an area of 0.25 m² (0.5 m × 0.5 m) in the shrub-subplot. The plant samples were dried for 48 h at 60 °C, weighed to determine the dry-to-wet mass ratio, and were ground in a Wiley mill (2-mm mesh) for determination of the C concentration.

After litter collection, the soil in the organic layer from the shrub-subplot (0.5 m × 0.5 m) was collected with a small shovel and immediately packed into a sampling bag. A 60 cm-deep soil pit was excavated manually in the same shrub-subplot (0.5 m × 0.5 m) to collect soil samples. Soil bulk density samples were collected from depths of 0–10, 10–30, and 30–60 cm using a steel soil core with an inner diameter of 7 cm and a length of 10 cm (Fig. S1). After removing the soil attached to the outside of the corer, all soil inside it was put into a sampling bag immediately and sealed. Fresh soil samples (~500 g) were collected from each depth mentioned above in the same shrub-subplot as well. Samples from the same depth from a single plot were mixed thoroughly. All soil samples were immediately brought back to the laboratory for further processing and chemical analysis.

2.4. Chemical analysis

The soil samples used for the determination of bulk density were oven-dried at 105 °C and weighed to obtain their dry weight. Stones were removed from the sample before weighing the sample; the volume of the stones was determined by the drainage method. Soil bulk density (BD, g cm⁻³) was determined by the following equation (Nuszdorfer, 1981):

$$BD = (W_{\text{soil}} - W_{\text{stone}}) / (V_t - V_{\text{stone}}) \quad (1)$$

Where W_{soil} (g) denotes the weight of the soil; W_{stone} (g) denotes the weight of stones; V_t (cm³) denotes the volume of the steel soil corer (384.65 cm³ in this study), V_{stone} (cm³) denotes the volume of stones. To determine the pH value, organic matter content, C, total N, and total P, another portion of the soil sample was air-dried for a week and sieved through a 2-mm mesh to remove gravel and coarse organic matter. Soil pH was measured in a soil/water (deionized) mixture with a ratio of 1:2.5 using an FE20 pH meter (Mettler Toledo Instrument Co., Ltd., Shanghai, China). The concentration of organic C in plant and soil samples was determined by K₂Cr₂O₇-H₂SO₄ caefaction (Institute of Soil Science, 1978), where the conversion factor for soil organic matter to C was 0.56. Total N concentration was measured using the Semi-micro-Kjeldahl method (Institute of Soil Science, Chinese Academy of Science, 1978). Total P concentration was determined using the Mo-Sb colorimetric method (Institute of Soil Science, 1978). The C concentrations in each plant organ are presented in Table S2, and the physical and chemical properties of soil are shown in Table S3.

2.5. Carbon storage and stand volume estimation

The biomass of full trees and their components in the plots was estimated with the allometric equations developed for Chinese fir plantations at different stand ages (Xiang et al., 2020). The biomass of all trees in each plot was summed to calculate the biomass in the stand and the biomass of each organ in a unit area. C storage in each component (i. e., stem, branch, leaf, coarse root, and fine root) was estimated by multiplying their biomass and corresponding C concentration and then summing it up to the stand level. The method to estimate C storage for shrubs, herbs, and litter was similar to that for trees, i. e., the C storage in each component was estimated by multiplying biomass and C concentration. Tree volume was calculated using the following formula:

$$V = 0.000058777042 \times DBH^{1.9699831} \times H^{0.89646157} \quad (2)$$

The values thus obtained were summed to obtain the stand volume

for each plot. Trees with DBH larger than 25 cm were considered to be large-diameter trees, and their volume was determined in each plot.

Soil organic C storage (S_{soil} ; t ha⁻¹) in the mineral layers from the three depths (0–10, 10–30, and 30–60 cm) and in the organic layer was calculated using the following equation:

$$S_{\text{soil-mineral layer}} = C_{\text{soil}} \times BD \times D \times 10^{-1} \quad (3)$$

$$S_{\text{soil-organic layer}} = C_{\text{soil}} \times W/A \times 10^{-1} \quad (4)$$

Where C_{soil} (g kg⁻¹) denotes soil organic C concentration; BD (g cm⁻³) denotes the soil bulk density; D (cm) denotes the soil depth; W (g) denotes the dried weight of soil sample in the organic layer; A (cm²) denotes the area of shrub-subplot; 10^{-1} is the conversion factor.

2.6. Statistical analysis

The relationships between stand age (x) and C storage (y) of ecosystem, tree, stem, root, and stand volume (y) were fitted using linear and nonlinear functions, including Michaelis-Menten ($y = ax/(1 + bx)$), Chapman-Richard ($y = a(1 - e^{-(bx)^c})$), asymptotic exponential ($y = a(1 - e^{-(bx)})$) and $y = a - be^{(-cx)}$, and logistic $y = a/(1 + e^{(b-x)/c})$ functions. Linear ($y = ax + b$) and second-order polynomial ($y = ax^2 + bx + c$) functions were tested to examine the relationship between stand age (x) and C storage (y) in shrubs, herbs, litters, tree components (branches, leaves, and fine roots), as well as large tree volume in the stand (y). The best-fit models for C storage and stand volume were selected based on the significance (p value) of the parameters (a , b , and c) and functions, adjusted R^2 , and root mean squared error (RMSE). The stand age needed to reach 95% of the maximum C storage in the ecosystem and the tree biomass and the stand volume were derived from the most optimally fitted model. As no model could fit significantly, a one-way analysis of variance (ANOVA) was used to examine the differences in soil C storage, soil organic C concentrations, and fine root C storage across the plantations of different stand ages. All statistical analyses were performed using the statistical software R 4.0.5 (R Development Core Team, 2021).

3. Results

3.1. Dynamics of ecosystem C storage and allocation with stand age

The C storage in Chinese fir plantation ecosystems (including tree, shrub, herb, litter, and soil) increased nonlinearly with stand age and ranged from 76.4 to 282.2 t ha⁻¹ (Fig. 2a). A logistic model with stand age as the predictor fitted well ($R^2 = 0.79$, $p < 0.001$) with the changes in ecosystem C storage. The maximum ecosystem C content estimated by the logistic model was 271.9 t ha⁻¹ and the time to reach 95% of this ecosystem C was 33 years (Table 1).

Ecosystem C accumulation in Chinese fir plantations as the stand ages was primarily contributed by tree biomass C and constituted 3.7–64.3% of total C (Fig. S2a). The soil was an important C pool, but the proportion of C stored in it decreased from 94.8 to 33.5% with stand age and then became stable at 37.9%. The C pools were low in understory plants (0.6%) and litters (1.0%). While C storage in herbs decreased with stand age, ranging between 0.2 t and 1.3 t ha⁻¹, C storage in shrubs and litter increased initially and then slightly decreased (Fig. 3b–d).

3.2. Variations in tree biomass C storage in the different plant organs

Tree biomass C (sum of the stem, branch, leaf, stump, and coarse and fine roots) in Chinese fir plantations increased nonlinearly from 2.8 to 177.7 t ha⁻¹ and was fitted with a logistic model using stand age as the predictor (Fig. 2b). The maximum value of stored C from the logistic model was 163.1 t ha⁻¹ and the time to reach 95% of this maximum was 31 years (Table 1).

As the stand grew older, C stored in the stem, total roots, and coarse

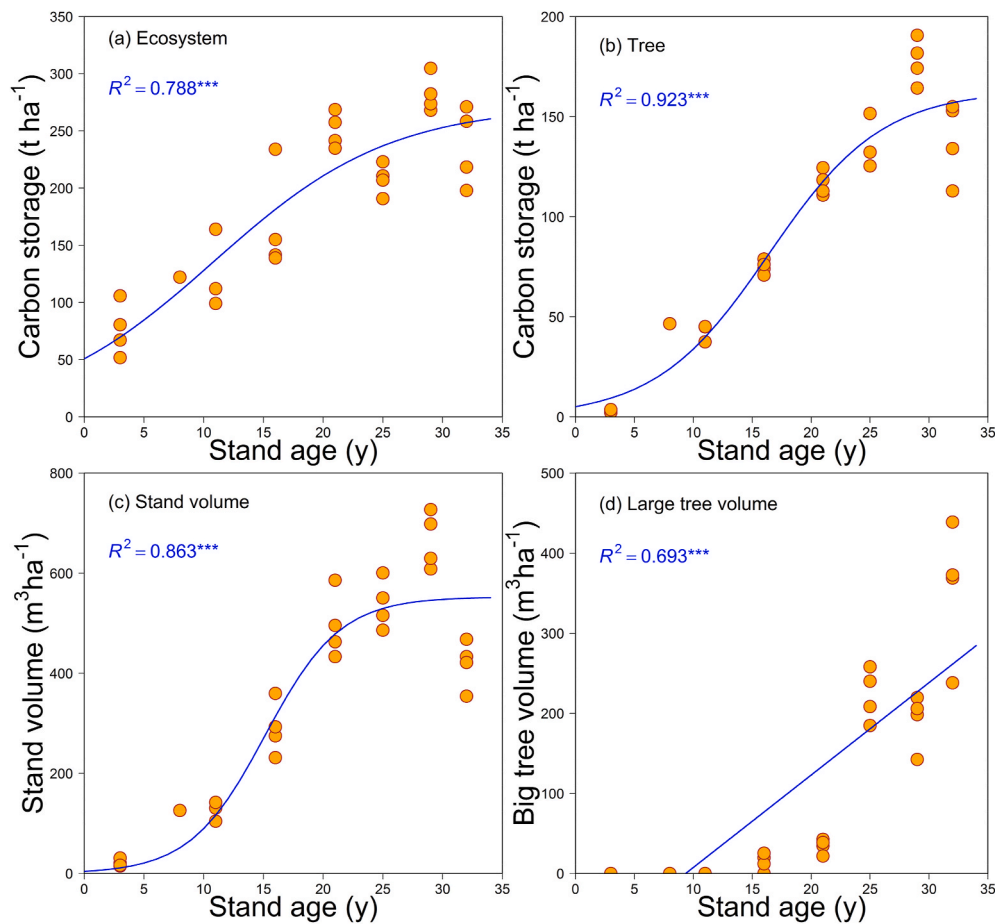


Fig. 2. Observed carbon storage in (a) ecosystem, (b) total trees, (c) stand volume, and (d) large-tree volume in Chinese fir plantations plotted against stand ages. The findings are drawn with fitted curves indicated by determining coefficients and significance level ($*p < 0.05$, $**p < 0.01$, and $***p < 0.001$).

Table 1

Parameters (with standard error in parenthesis) for the best-fitted functions of ecosystem carbon (C) storage (t ha^{-1}), C storage in trees (t ha^{-1}), stand volume ($\text{m}^3 \text{ha}^{-1}$), and large tree volumes ($\text{m}^3 \text{ha}^{-1}$) in Chinese fir plantations using stand age (y) as the predictor.

| Variables | Function | a | b | c | R^2 | RMSE | Time to reach 95% of the maximum (years) |
|---------------------|---------------------------|-------------------------|------------------------|----------------------|-------|--------|--|
| Ecosystem C storage | $y = a/(1 + e^{(b-x)/c})$ | 271.912 (25.035) *** | 10.851 (2.050)*** | 7.383 (2.006)** | 0.788 | 34.382 | 33 |
| C storage in trees | $y = a/(1 + e^{(b-x)/c})$ | 163.096 (9.910)*** | 16.422 (1.036)*** | 4.804 (0.875) *** | 0.923 | 16.451 | 31 |
| Stand volume | $y = a/(1 + e^{(b-x)/c})$ | 552.551 (30.087) *** | 15.140 (0.920)*** | 3.135 (0.846)** | 0.864 | 83.593 | 25 |
| Large tree volume | $y = ax + b$ | 11.541 (1.507)* | -107.791 (32.743) * | | 0.693 | 76.910 | |

roots increased as per the logistic functions, while that in the branches and leaves increased linearly (Fig. S3). The C stored in the fine roots initially increased, reach a peak, and then slightly decreased with stand age, but the difference was not significant across plantations of different stand ages (Fig. S3f). Stems were the largest contributors to tree biomass C, which ranged from 16.7 to 73.9% of total C. Branches, leaves, and roots shared a roughly similar proportion of tree biomass C, ranging from 4.0 to 12.1%, 4.5–15.4%, and 5.6–14.3%, respectively.

The ratio of root-to-shoot biomass ($B_{\text{root}}/B_{\text{shoot}}$) decreased sharply from ~ 2.2 in 3-year-old stands to 0.3 in 8- or 11-year-old stands, and, eventually stabilized at about 0.2 in developed stands (Fig. S2b). The ratio of aboveground to stem ($B_{\text{abv}}/B_{\text{stem}}$) biomass only slightly decreased in stands before they became 21-year-old and then remained stable at 1.2 (Fig. S2b).

3.3. Variations in soil C storage with stand age

Soil organic C concentration in the organic layer increased with stand age ($p > 0.05$), but there were no obvious trends in 0–10 cm, 10–30 cm, or 30–60 cm (Fig. S4). Soil carbon stored in the stand aged 21 years was the highest; it was significantly higher than the C stored in stands aged 3 and 25 years but was not significantly different as compared to C in other plantations (Fig. 3a). The average soil C storage in each stand ranged from 69.6 to 130.1 t ha^{-1} (Fig. 3a).

3.4. Changes in stand volume with stand age

The stand volume in Chinese fir plantations increased nonlinearly with stand age with the average values ranging from 20.8 to $666.0 \text{ m}^3 \text{ha}^{-1}$ for each stand; these values were significantly ($R^2 = 0.86$, $P < 0.001$) fitted using a logistic model (Fig. 2c). The maximum stand

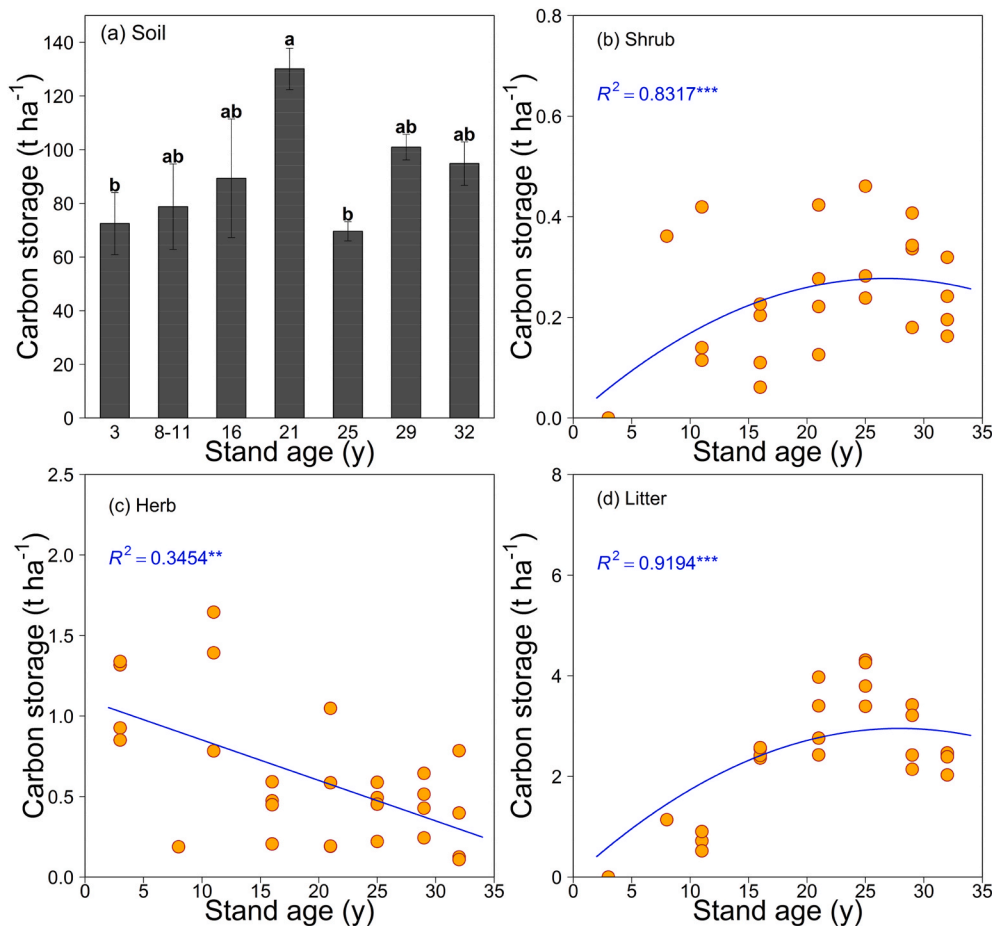


Fig. 3. Soil carbon storage (a) (sum of the organic layer and mineral layer (0–60 cm) in Chinese fir plantations. Values are presented as the mean \pm standard error. Different letters indicate significant differences in soil carbon storage across different stand ages ($p < 0.05$). Observed carbon storage in (b) shrub, (c) herb, and (d) litter in Chinese fir plantations plotted against stand ages, together with fitted curves indicated by determining coefficients and significance level ($*p < 0.05$, $**p < 0.01$, and $***p < 0.001$).

volume estimated from the logistic model was $552.6 \text{ m}^3 \text{ ha}^{-1}$, and the time to reach 95% of this maximum was 25 years (Table 1). When stands grew for 25 years, the number of large-diameter ($>25 \text{ cm}$ in DBH) trees rapidly increased, and the increase in the volume of large-diameter trees was linear (Table S1; Fig. 2d).

4. Discussion

4.1. Ecosystem C storage in Chinese fir plantations

Ecosystem C storage in Chinese fir plantations of different stand ages varied from 76.4 to 282.2 t ha^{-1} . The total average ecosystem C storage was 183.56 t ha^{-1} , which was within the range of 182.29 – 245.16 t ha^{-1} (Fu, 2016) and 97.62 – 283.43 t ha^{-1} (Chen et al., 2013) reported previously in Chinese fir plantations in Fujian province. However, it was higher than the average values (68.8 – 157.9 t ha^{-1}) in different forest types in Hunan (Chen et al., 2019). This indicates that Chinese fir plantations have a high C sequestration capacity as compared to other forests in the same region. A nonlinear increase to achieve saturation of ecosystem C storage with stand age observed in this study is consistent with the findings of previous studies (Taylor et al., 2007; Chen et al., 2013; Ming et al., 2014; Samuelson et al., 2017). This result supports the theoretical idea from models that mature or old forests are close to an equilibrium in net ecosystem production, and their total C storage remains rather stable (Odum, 1969; Bond-Lamberty et al., 2004).

There are two possible explanations for the variation in ecosystem C storage and its allocation in plant organs in Chinese fir plantations of different stand ages. At first, the accumulation of ecosystem C in Chinese fir plantations was mainly contributed by an increase in tree biomass C, which was implied by the finding that the trends in tree biomass C as a

function of stand age were consistent with the trends in ecosystem C, which increased steadily before maturity and then became stable. Tree biomass C constituted 3.7–64.3% of the total ecosystem C and increased from 2.8 to 177.7 t ha^{-1} with the stand age. This changing pattern agrees with the results reported for other even-aged plantations (Peichl and Arain, 2006; Chen et al., 2013; Zhang et al., 2014; Justine et al., 2017). As a stand developed, stems and roots were the top two C pools in the tree biomass. Their C storage exhibited a logistic growth pattern with stand age, while branches and leaves increased linearly with stand age. These variations are in accordance with previous studies conducted in other forests (McConnaughay and Coleman, 1999; Mokany et al., 2006; Litton et al., 2007; Wang et al., 2008). As the stands develop, a large proportion of C is allocated to stems and roots to support entire trees (Litton et al., 2004; Weiner, 2004). Secondly, in contrast to the continued increase in C in mature or old natural forests due to the regrowth of subdominant trees as part of understory regeneration, Chinese fir plantations gradually form a closed canopy and intercept more light, thereby limiting the amount of light reaching the understory plants (von Arx et al., 2012). As a result, C storage by understory plants (shrubs and herbs) and litters accounted for a small proportion ($<2\%$) of ecosystem C (Fig. S2a).

4.2. Soil C storage in Chinese fir plantations

Soil C storage is an important C pool and accounted for a large proportion (representing 33.5–94.8% of ecosystem C) in Chinese fir plantations; the average soil C stored in plantations of each stand age varied from 69.6 to 130.1 t ha^{-1} (Fig. S2a; Fig. 3a). These values were within the range of soil C observed in Chinese fir plantations of different age classes across Hunan (77.7 – 106.5 t ha^{-1} at a depth of 0–100 cm)

(Chen et al., 2017), Guangxi (80.1–145.4 t ha⁻¹ at a depth of 0–50 cm) (Lan et al., 2016), and other subtropical forests (60.3–123.9 t ha⁻¹) (Chen et al., 2017). The differences could be due to the depth of soil sampling, site conditions, or stand characteristics (Chen et al., 2013, 2017).

Soil C storage in Chinese fir plantations did not exhibit an obvious change with stand age, but there were significant differences across plantations of different stand ages. Soil C storage was the greatest in the 21-year-old stand and the lowest in the 25-year-old stand (Fig. 3a). Soil C in forests is derived from the decomposition of aboveground litter, belowground fine roots, and exudates (Chen et al., 2013; Jackson et al., 2017). Spatial heterogeneity of sites could also affect soil C storage. Our study showed that C input from litters and roots was balanced by C output from microbial decomposition in soil, therefore, soil C storage remained relatively stable with stand age, which was in accordance with other studies (Yang et al., 2011). Understory plants contributed <2% of the total ecosystem C. Regardless of the small contribution of the understory plants, they must be maintained to improve soil C storage and healthy productivity (Jackson et al., 2017).

4.3. Reconciling timber production with ecosystem C storage in Chinese fir plantations

Plantations provide multiple ecosystem services, including C and timber production (Mbabazi, 2011; Baral et al., 2016). Reconciling the trade-offs between these services is a challenge. Ecosystem C storage and stand volume in Chinese fir plantations were best fitted by a logistic model using stand age as the predictor in this study (Table 1; Fig. 2). However, the time required to reach 95% of their maximum values differed; it was 33 years for ecosystem C, which was longer than that of stand volume (25 years) (Table 1). This result is consistent with the report by Jiang et al. (1982) that Chinese fir plantations reach their maximum timber production (450 m³ ha⁻¹) at a stand age of 25–30 years. The decline in stand volume at stand ages of 29–33 years might be due to the self-thinning, as it greatly reduces the stand density and degrades the site. A study by Micky et al. (2021) found that low stand density led to a decrease in stand volume. As the differences in sites had been accounted for during plot selection, the changes in biomass caused by stand density were the main reason for the decrease in stand volume. Harvesting at 25 years to maximize timber production would cause adverse effects on ecosystem C sequestration. At present, the price for large-diameter timber from Chinese fir is 3 × higher than the price for small-diameter timber. Furthermore, our study showed that the number of large-diameter trees and stand volume increased with stand age (Fig. 1; Fig. 2c). Therefore, extending the rotation age to >30 years would increase the synergistic benefit of maximum ecosystem C storage and timber production from large-diameter trees in Chinese fir plantations.

4.4. Limitations of this study

The chronosequence approach is appropriate to study forest structure and functions that follow the same trajectory across long time scales (Walker et al., 2010). However, it is difficult to control the heterogeneities across the sampling site and to account for differences in the commencing conditions of forests. These parameters are crucial as they inevitably lead to variations in stand density and soil carbon storage. Long-term observations at the same locations in experimental forests are important to investigate the patterns of change in forest structure and ecosystem functions (i.e., carbon storage and stand volume).

5. Conclusions

The stand age is an important factor that affects C storage and allocation in Chinese fir plantation ecosystems. Ecosystem C storage nonlinearly increased with stand age and was fitted using a logistic model.

Chinese fir plantations have high C sequestration capacity, and thus, they can play a significant role in mitigating global climate change. Our findings indicated that the accumulation of ecosystem C was mainly driven by an increase in tree biomass C as the stand developed. In addition, forest soil was an important C pool, which remained rather stable with stand age. An extension of rotation age can increase the synergistic benefit of maximum ecosystem C storage and timber production by enhancing the growth of large-diameter trees in Chinese fir plantations.

Credit author statement

W.H.X. designed the research; W.H.X., L.X., P.F.L., S.O.Y., L.C., Y.L.Z., X.W.D., Z.H.Z. and H.L.W. performed experiments, conducted field-work, collected and analyzed data. X.H.X. and L.X. wrote the manuscript. W.H.X., Y.T.H., L.X.Z. and W.F.X. revised the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115426>.

References

- Alexandrov, G., 2007. Carbon stock growth in a forest stand: the power of age. *Carbon Bal. Manag.* 2, 4.
- Baral, H., Guariguata, M.R., Keenan, R.J., 2016. A proposed framework for assessing ecosystem goods and services from planted forests. *Ecosyst. Serv.* 22, 260–268.
- Bradford, J.B., Kastendick, D.N., 2010. Age-related patterns of forest complexity and carbon storage in pine and aspen–birch ecosystems of northern Minnesota, USA. *Can. J. For. Res.* 40, 401–409.
- Bond-Lamberty, B., Wang, C.K., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. *Global Change Biol.* 10, 473–487.
- Cao, J., Wang, X., Tian, Y., Wen, Z., Zha, T., 2012. Pattern of carbon allocation across three different stages of stand development of a Chinese pine (*Pinus tabulaeformis*) forest. *Ecol. Res.* 27, 883–892.
- Chapin, F.S., Groves, R.H., Evans, L.T., 1989. Physiological determinants of growth rate in response to phosphorus supply in wild and cultivated *Hordeum* species. *Oecologia* 79, 96–105.
- Chen, G.S., Yang, Z.J., Gao, R., Xie, J.S., Yang, Y.S., 2013. Carbon storage in a chronosequence of Chinese fir plantations in southern China. *For. Ecol. Manag.* 300, 68–76.
- Chen, L.C., Wang, H., Yu, X., Zhang, W.D., Lü, X.T., Wang, S.L., 2017. Recovery time of soil carbon pools of conversional Chinese fir plantations from broadleaved forests in subtropical regions, China. *Sci. Total Environ.* 587, 296–304.
- Chen, L.C., Guan, X., Li, H.M., Wang, Q.K., Zhang, W.D., Yang, Q.P., Wang, S.L., 2019. Spatiotemporal patterns of carbon storage in forest ecosystems in Hunan Province, China. *For. Ecol. Manag.* 432, 656–666.
- Chen, L., Xiang, W., Ouyang, S., Wu, H., Xia, Q., Ma, J., Zeng, Y., Lei, P., Xiao, W., Li, S., Kuzyakov, Y., 2021. Tight coupling of fungal community composition with soil quality in a Chinese fir plantation chronosequence. *Land Degrad. Dev.* 32, 1164–1178.
- Cheng, X., Han, H., Kang, F., Song, Y., Liu, K., 2014. Variation in biomass and carbon storage by stand age in pine (*Pinus tabulaeformis*) planted ecosystem in Mt. Taiyue, Shanxi, China. *J. Plant Interact.* 9, 521–528.
- Cook-Patton, S.C., Leavitt, S.M., Gibbs, D., Harris, N.L., Lister, K., Anderson-Teixeira, K. J., Briggs, R.D., Chazdon, R.L., Crowther, T.W., Ellis, P.W., Griscorn, H.P., Herrmann, V., Holl, K.D., Houghton, R.A., Larrosa, C., Lomax, G., Lucas, R.,

- Madsen, P., Malhi, Y., Paquette, A., Parker, J.D., Paul, K., Routh, D., Roxburgh, S., Saatchi, S., van den Hoogen, J., Walker, W.S., Wheeler, C.E., Wood, S.A., Xu, L., Griscom, B.W., 2020. Mapping carbon accumulation potential from global natural forest regrowth. *Nature* 585, 545–550.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Euqist, B.J., Niklas, K.J., 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295, 1517–1520.
- Fang, J., Guo, Z., Hu, H., Kato, T., Muraoka, H., Son, Y., 2014. Forest biomass carbon sinks in east Asia, with special reference to the relative contributions of forest expansion and forest growth. *Global Change Biol.* 20, 2019–2030.
- FAO, 2020. *Global Forest Resources Assessment 2020: Main Report*. <https://doi.org/10.4060/ca9825en>. Rome.
- Fu, R., 2016. Quantitative Estimation of Biomass and Carbon Storage for Chinese Fir Plantation. PhD thesis. Beijing Forestry University, China (in Chinese).
- Gleixner, G., Tefs, C., Jordan, A., Hammer, M., Wirth, C., Nueske, A., Telz, A., Schmidt, U.E., Glatzel, S., 2009. In: Wirth, C., et al. (Eds.), *Soil Carbon Accumulation in Old-Growth Forests*. Old-Growth Forests, p. 231.
- Guo, Z.D., Hu, H.F., Li, P., Li, N.Y., Fang, J.Y., 2013. Spatio-temporal changes in biomass carbon sinks in China's forests from 1977 to 2008. *Sci. China Life Sci.* 56, 661–671.
- Institute of Soil Science, Chinese Academy of Sciences, 1978. *Analytical Methods of Soil Physics and Chemistry*. Shanghai Scientific and Technical Publishers, Shanghai, China.
- Institute of Soil Science, Chinese Academy of Sciences, 2001. *Chinese Soil Taxonomy*. Science Press, Beijing.
- IPCC, 2006. Intergovernmental Panel on Climate Change Guidelines for National Greenhouse Gas Inventories, vol. 4. Institute for Global Environmental Strategies (IGES), Hayama, Japan, p. 83.
- Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Piñeiro, G., 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. *Rev. Ecol., Evol. Syst.* 48, 419–445.
- Jiang, Z.L., Ye, J.Z., Zhou, B.L., 1982. *Tending Felling of Chinese Fir Plantations*. China Forestry Press House, Beijing (in Chinese).
- Jin, L., Yi, Y., Xu, J., 2020. Forest carbon sequestration and China's potential: the rise of a nature-based solution for climate change mitigation. *China Econ. J.* 13, 200–222.
- Justine, M.F., Yang, W., Wu, F., Khan, M.N., 2017. Dynamics of biomass and carbon sequestration across a chronosequence of Masson pine plantations. *J. Geophys. Res.: Biogeosciences* 122, 578–591.
- Lan, S., Du, H., Zeng, F., Song, T., Peng, W., Han, C., Chen, L., Su, L., 2016. Carbon storage and allocation in *Cunninghamia lanceolata* plantations with different stand ages. *Chin. J. Appl. Ecol.* 27, 1125–1134.
- Liao, C., Luo, Y., Fang, C., Li, B., 2010. Ecosystem carbon stock influenced by plantation practice: implications for planting forests as a measure of climate change mitigation. *PLoS One* 5, e10867.
- Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. *Global Change Biol.* 13, 2089–2109.
- Litton, C.M., Ryan, M.G., Knight, D.H., 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. *Ecol. Appl.* 14, 460–475.
- Mbabwe, J., 2011. Ecosystem goods and services from plantation forests. *Int. J. Environ. Study* 68, 249–250.
- Micky, A., Andreas, B., Clara, A.F., Clara, A.F., Rasmus, A., 2021. The relationship between volume increment and stand density in Norway spruce plantations. *FOREST: Int. J. Financ. Res.* 94, 151–165.
- McConnaughey, K.D.M., Coleman, J.S., 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80, 2581–2593.
- Ming, A., Jia, H., Zhao, J., Tao, Y., Li, Y., 2014. Above- and below-ground carbon stocks in an indigenous tree (*Mytilaria laosensis*) plantation chronosequence in subtropical China. *PLoS One* 9, e109730.
- Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84–96.
- National Forestry and Grassland Administration, 2019. *China Forest Resource Report (2014-2019)*. China Forestry Publishing House.
- Niklas, K.J., 2005. Modeling below- and aboveground biomass for non-woody and woody plants. *Ann. Bot.* 95, 315–321.
- Nuszdorfer, F.C., 1981. Bulk density. In: Klinka, K., Green, R.N., Trowbridge, R., Lowe, L. E. (Eds.), *Taxonomic Classification of Humus Forms in Ecosystems of British Columbia*. B.C. Min. For. Land Management Report, pp. 49–51. No. 8.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 164, 262–270.
- Ouyang, S., Xiao, K., Zhao, Z., Xiang, W., Xu, C., Lei, P., Deng, X., Li, J., 2018. Stand transpiration estimates from recalibrated parameters for the granier equation in a Chinese fir (*Cunninghamia lanceolata*) plantation in southern China. *Forests* 9, 162.
- Pan, Y., Luo, T., Birdsey, R., Hom, J., Melillo, J., 2004. New estimates of carbon storage and sequestration in China's forests: effects of age-class and method on inventory based carbon estimation. *Clim. Change* 67, 211–236.
- Paul, K.I., Polglase, P.J., Nyakuengama, J.G., Khanna, P.K., 2002. Change in soil carbon following afforestation. *For. Ecol. Manag.* 168, 241–257.
- Peichl, M., Arain, M.A., 2006. Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. *Agric. For. Meteorol.* 140, 51–63.
- Peichl, M., Arain, M.A., 2007. Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. *For. Ecol. Manag.* 253, 68–80.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biol.* 10, 2052–2077.
- R Development Core Team, 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Samuelson, L.J., Stokes, T.A., Butnor, J.R., Johnsen, K.H., Gonzalez-Benecke, C.A., Martin, T.A., Cropper Jr., W.P., Anderson, P.H., Ramirez, M.R., Lewis, J.C., 2017. Ecosystem carbon density and allocation across a chronosequence of longleaf pine forests. *Ecol. Appl.* 27, 244–259.
- Seo, Y.O., Lee, Y.J., Lumbres, R.I.C., Pyo, J.K., Kim, R.H., Son, Y.M., Lee, K.H., 2013. Influence of stand age class on biomass expansion factor and allometric equations for *Pinus rigida* plantations in South Korea. *Scand. J. For. Res.* 28, 566–573.
- Sun, W., Liu, X., 2020. Review on carbon storage estimation of forest ecosystem and applications in China. *For. Ecosyst.* 7, 4.
- Taylor, A.R., Wang, J.R., Chen, H.Y.H., 2007. Carbon storage in a chronosequence of red spruce (*Picea rubens*) forests in central Nova Scotia, Canada. *Can. J. For. Res.* 37, 2260–2269.
- von Arx, G., Dobbertin, M., Rebetez, M., 2012. Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agric. For. Meteorol.* 166–167, 144–155.
- Wang, C., Benbond-Lamberty, Gower, S.T., 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. *Global Change Biol.* 9, 1066–1079.
- Wang, X.P., Fang, J.Y., Zhu, B., 2008. Forest biomass and root-shoot allocation in northeast China. *For. Ecol. Manag.* 255, 4007–4020.
- Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
- Weiner, J., 2004. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol. Evol. Systemat.* 6, 207–215.
- Winjum, J.K., Schroeder, P.E., 1997. Forest plantations of the world: their extent, ecological attributes, and carbon storage. *Agric. For. Meteorol.* 84, 153–167.
- Wu, C.Z., Hong, W., Jiang, Z.L., 2001. A study on the analysis method of density change during self thinning for *Cunninghamia lanceolata* plantation. *J. Fujian College For.* 1, 6–9 (in Chinese).
- Wu, H., Xiang, W., Ouyang, S., Xiao, W., Li, S., Chen, L., Lei, P., Deng, X., Zeng, Y., Zeng, L., Peng, C., 2020. Tree growth rate and soil nutrient status determine the shift in nutrient-use strategy of Chinese fir plantations along a chronosequence. *For. Ecol. Manag.* 460, 117869.
- Xiang, W., Li, L., Ouyang, S., Xiao, W., Zeng, L., Chen, L., Lei, P., Deng, X., Zeng, Y., Fang, J., Forrester, D., 2020. Effects of stand age on tree biomass partitioning and allometric equations in Chinese fir (*Cunninghamia lanceolata*) plantations. *Eur. J. For. Res.* 140, 317–332.
- Xu, B., Guo, Z., Piao, S., Fang, J., 2010. Biomass carbon stocks in China's forests between 2000 and 2050: a prediction based on forest biomass–age relationships. *Sci. China (Life Sci.)* 53, 776–783.
- Yang, Y., Luo, Y., Finzi, A.C., 2011. Carbon and nitrogen dynamics during forest stand development: a global synthesis. *New Phytol.* 190, 977–989.
- Zerva, A., Ball, T., Smith, K.A., Mencuccini, M., 2005. Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty Gley. *For. Ecol. Manag.* 205, 227–240.
- Zhang, H., Guan, D., Song, M., 2012. Biomass and carbon storage of *Eucalyptus* and *Acacia* plantations in the Pearl river Delta, South China. *For. Ecol. Manag.* 277, 90–97.
- Zhang, H., Song, T., Wang, K., Du, H., Yue, Y., Wang, G., Zeng, F., 2014. Biomass and carbon storage in an age-sequence of *Cyclobalanopsis glauca* plantations in southwest China. *Ecol. Eng.* 73, 184–191.
- Zhang, H., Song, T.X., Wang, K.L., Wang, K.X., Liao, J.X., Xu, G.H., Zeng, F.P., 2015. Biogeographical patterns of forest biomass allocation vary by climate, soil and forest characteristics in China. *Environ. Res. Lett.* 10, 044014.
- Zhang, X., Zhang, X., Han, H., Shi, Z., Yang, X., 2019. Biomass accumulation and carbon sequestration in an age-sequence of Mongolian pine plantations in Horqin sandy land, China. *Forests* 10, 197–214.
- Zhao, J., Kang, F., Wang, L., Yu, X., Zhao, W., Song, X., Zhang, Y., Chen, F., Sun, Y., He, T., Han, H., 2014. Patterns of biomass and carbon distribution across a chronosequence of Chinese pine (*Pinus stabulaeformis*) forests. *PLoS One* 9, e94966.