

Article

Carbon Storage Dynamics of Secondary Forest Succession in the Central Loess Plateau of China

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Abstract: *Research Highlights:* This study comprehensively revealed the carbon sequestration characteristics of secondary forests in the central Loess Plateau during vegetation succession. *Background and Objectives:* The secondary succession of Loess Plateau forests is of great significance in global climate change, but their carbon storage dynamics are poorly understood. The study objectives were to clarify the pattern of changes and contribution level of carbon stocks in various components of ecosystem during succession. *Materials and Methods:* We selected 18 plots for *Pinus tabulaeformis* Carr. forest at the early stage of succession, 19 for pine-broadleaved mixed forest at the middle stage, and 12 for *Quercus*-broadleaved mixed forest at the climax stage to determine the tree, shrub, herb, fine root, litter, coarse wood debris (CWD), and soil carbon stocks. *Results:* Ecosystem carbon stocks increased from 160.73 to 231.14 Mg·ha⁻¹ with the succession stages. Vegetation (including tree, shrub and herb) and soil were the two largest carbon pools, and carbon was mainly sequestered in tree biomass and shallow soil (0–50 cm). In the early stage, soil contributed more carbon stocks to the ecosystem than vegetation, but with succession, the soil contribution decreased while vegetation contribution increased, finally reaching a balance (46.78% each) at the climax stage. Fine root, litter, and CWD contributed little (average 6.59%) to ecosystem carbon stocks and were mainly involved in the turnover of vegetation biomass to soil carbon. *Conclusions:* Our results provide direct evidence for carbon sequestration of secondary forests on the Loess Plateau. The dynamic results of carbon storage provide an important basis for forest restoration management under climate change.

Keywords: carbon stocks; secondary succession; Loess Plateau; *Quercus* forests

1. Introduction

Forest ecosystem carbon storage accounts for approximately 56% of terrestrial ecosystem carbon storage, of which forest vegetation carbon storage accounts for more than 80% of global vegetation carbon storage and the forest soil carbon pool accounts for more than 40% of the global soil carbon pool [1–4]. As the most important component of terrestrial ecosystems, forest ecosystems play an irreplaceable role in mitigating atmospheric CO₂ concentrations and regulating the global carbon cycle. Statistical evidence indicates that from 1850 to 1998, the global amount of CO₂ emitted due to land use change was as high as 136 ± 55 Gt C, of which 87% was derived from forest changes and 27.32% occurred in China [5,6]. Therefore, the governments of China and other signatory countries are making efforts to protect forest resources, advocate afforestation and improve forest coverage to increase forest carbon sinks and mitigate global climate change [7].

Generally, the carbon storage of forests is closely related to their succession development [3]. Secondary succession occurs in disturbed areas and is characterized by changes in plant coverage, composition, biomass, soil nutrient level, and soil erodibility [8]. The distribution of carbon stocks in various components of ecosystems is one of the important characteristics of secondary succession [3]. Understanding the carbon stocks and dynamics of forest ecosystems during succession is extremely important for governments or managers to develop forest management strategies [9–11].

Secondary forests as carbon sinks are mainly attributed to increases in their biomass carbon storage capacity with succession [12]. In the early and middle stages of secondary succession, the structure and composition of forest vegetation change dramatically, which in turn affects their carbon dynamics [13]. Moreover, some studies have shown that vegetation succession can also affect soil carbon dynamics and even improve degraded soil properties [14–16]. Therefore, understanding the vegetation and soil carbon storage dynamics during the forest succession process is crucial to evaluating ecosystem carbon storage [13,17]. At present, some studies have been conducted on the status of vegetation and soil carbon stocks under forest succession [18]. However, regarding soil carbon storage, the existing research has mainly focused on the surface soil (0–30 cm). There are few reports on deep soil after long-term vegetation restoration.

The carbon cycle of forest ecosystems is closely related to the dynamic balance between vegetation carbon storage and soil carbon storage [19], and the return of vegetation biomass carbon to soil affects the efficiency of this cycle. The carbon restitution of litters and fine roots are two main pathways of vegetation carbon return [19] that directly determine the carbon turnover rate. Studies have shown that the carbon storage of litter is synchronous with changes in soil organic carbon storage, and an increase in litter causes the accumulation of soil organic carbon [20,21]. Fine roots return organic carbon to soil through their secretion and decomposition, which is the most direct path for plants to input photosynthetic products into the soil. Although fine roots accounted for less than 30% of the total root biomass in a forest ecosystem, their net productivity accounted for 30% to 80% of the total forest productivity [22]. In addition, some studies have reported that the organic matter and carbon returned to soil through fine roots every year even exceed the contribution of litters [23].

Coarse woody debris (CWD) is an important source of detritus following disturbances and contributes to the structure and function of forest ecosystems [24]. Recently, many ecological characteristics and processes of CWD have been studied, including wildlife habitat, nutrient cycling, water storage, and carbon storage [25]. CWD has a slow decomposition rate and can last for decades or even hundreds of years, thus forming a long-term carbon pool. According to Pan's research [11], dead wood accounts for approximately 8% of the world's forest carbon stocks, and the stock of dead wood varies depending on the forest-forming tree species and the forest type [26]. However, these variations are often not taken into account in the estimation of ecosystem carbon stocks, thus leading to little knowledge of the extent to which CWD carbon dynamics affect the ecosystem carbon balance [27].

Excessive deforestation has led to severe carbon emissions and soil erosion on the Loess Plateau of China. In recent decades, the Chinese government has taken various measures to slow greenhouse gas emissions and soil erosion on the Loess Plateau. Specifically after the implementation of the Natural Forest Protection Project (NFPP) and the Grain to Green Project (GTGP), the areas covered with secondary forests at different recovery stages have rapidly increased. By 2015, the forest area of the Loess Plateau had reached about 3.17 million ha, accounting for 15.2% of China's forest area [28–32]. Therefore, this development is of great significance in combatting global climate change. Especially in the center of Loess Plateau, the forest ecosystems constitute 28.79% of the land base and have gained much attention in the discussion of global C cycling [14–16,33]. While most of these studies have focused on the vegetation and soil carbon stocks of secondary forests, there have been few studies on litter, CWD and fine roots, and to some extent, the carbon stocks of the entire forest ecosystem have been underestimated. Furthermore, there are few reports on the carbon distribution patterns of the entire forest ecosystem at different succession stages on the central Loess Plateau.

Accordingly, in this paper, the study of carbon stock characteristics of the secondary forests in different succession stages on the central Loess Plateau includes not only vegetation and soil but also litter, CWD and fine roots to lay a foundation for fully revealing the carbon dynamics of secondary forests on the Loess Plateau. The specific purposes of this study are as follows: (1) to explore whether the secondary succession of forests on the central Loess Plateau is a carbon sink or a carbon source and determine the pattern of changes in ecosystem carbon stocks with secondary succession; (2) to quantify the C stocks of various components of the forest ecosystem; and (3) to clarify the contribution level of various components of the ecosystem carbon stocks.

2. Materials and Methods

2.1. Site Description and Plot Selection

The study was conducted in the Huanglong-Qiaoshan forest region ($35.4795^{\circ}\sim 35.6118^{\circ}$ N, $109.2048^{\circ}\sim 109.5322^{\circ}$ E), which is located in the Ziwuling mountains of the central Loess Plateau of China (Figure 1). The region belongs to a transition zone from a warm temperate semi-arid to a semi-humid climate at an elevation of 1100–1750 m above sea level [34]. The mean annual temperature is 8–9 °C, with a maximum in August and a minimum in February [34]. The mean annual precipitation is 588–630 mm [34], of which approximately 70.4% falls between June and September [35]. The mean annual relative humidity is 63%–68% [33]. The mean annual frost-free period is approximately 180 days [35]. The soil is largely loessal, having developed from primitive or secondary loess parent materials, which are evenly distributed 50–130 m deep above red earth consisting of calcareous cinnamon soil [14].

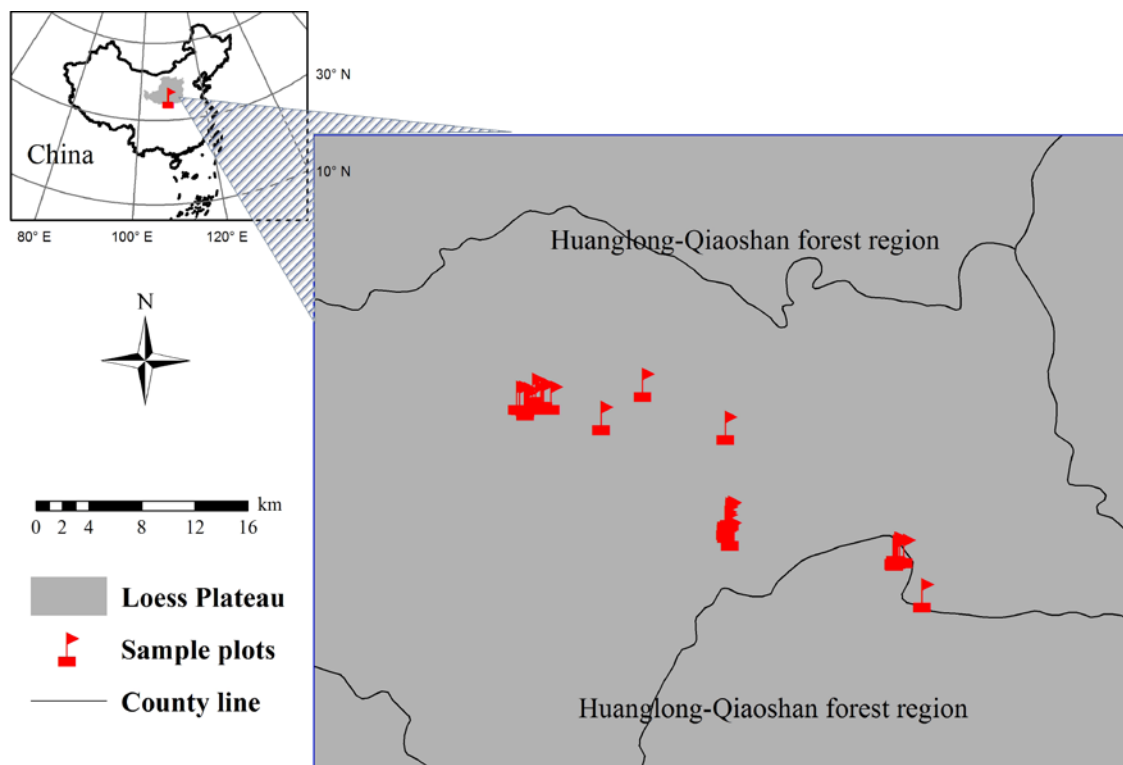


Figure 1. Representation of the study site.

The zonal vegetation is warm temperate deciduous broadleaved forest, with *Quercus acutissima* Carruth. and *Quercus wutaishanica* Mayr. as the dominant species. In the early stage of succession, after fire or man-made destruction, the secondary forest is mainly composed of a pioneer tree species, *Pinus tabulaeformis*. With secondary succession, in the middle stage, some broadleaved trees begin to move in gradually, mainly *Populus davidiana* Dode. and *Betula platyphylla* Suk. In the climax community

stage of succession, *Quercus* tree species become dominant. Many previous studies have indicated that these three stages form a representative sequence in the Ziwuling forests on the Loess Plateau of China [14,36,37]. Based on this sequence, the pure *Pinus tabuliformis* forest (PF), pine-broadleaved mixed forest (PBF) and *Quercus*-broadleaved mixed forest (QBF), representing the early, middle and climax stages of succession, respectively, were chosen in this forest region. We selected 49 plots that had not been disturbed artificially in recent decades. These plots were established as long-term monitoring sites by team members between 2004 and 2016 and consisted of 18 replicates for the PF, 19 for the PBF, and 12 for the QBF. Each plot was 20 m × 30 m. The distance between plots in the same succession stage was greater than 0.1 km, and the distance between stands of the three succession stages was greater than 5 km.

2.2. Vegetation Biomass

In July 2016, all 49 plots in the three stages of succession were investigated, and the forest type, stand age, canopy density, stand density, elevation, slope, soil type and community structure were recorded (Table 1). The field measurement followed the protocol of “Observation Methodology for Long-term Forest Ecosystem Research” of the National Standards of the People’s Republic of China [38]. The diameter at breast height (DBH) and height were measured for all trees with a DBH greater than 5 cm in each plot. The tree biomass was quantified by species-specific allometric biomass equations (Table 2). The understory vegetation (shrub and herb) biomass was estimated by full excavation methods. Three 5 m × 5 m shrub subplots were randomly selected in each sample plot. One 1 m × 1 m herb quadrat was randomly selected within every subplot. Shrubs were harvested and separated into leaves, branches, and roots; herbs were harvested and separated into their aboveground and belowground components. The understory vegetation samples were transported to the laboratory and dried at 65 °C to constant weight for biomass and C fraction determinations.

Table 1. Stand characteristics of the three succession stages in the Huanglong-Qiaoshan forest region.

Forest Type	<i>Pinus tabuliformis</i> Forests (PF)	Pine-Broadleaved Mixed Forest (PBF)	<i>Quercus</i> -Broadleaved Mixed Forest (QBF)
Successional stage	I	II	III
Stand age (a)	20–30	20–60	30–100
Canopy density (%)	65–70	65–75	75–85
Stand density (trees·ha ⁻¹)	1755 ± 83	1729 ± 66	1580 ± 61
Elevation (m)	1100–1200	1100–1200	1100–1200
Slope (°)	10–20	10–25	10–25
Mean tree height (m)	13.3	15.1	16.5
Mean DBH (cm)	14.6	15.3	17.2
Soil type	Gray cinnamon soil	Gray cinnamon soil	Gray cinnamon soil
Dominant species			
Trees	<i>P. tabuliformis</i>	<i>P. tabulaeformis</i> <i>Populus davidiana</i>	<i>Q. acutissima</i> <i>Q. wutaishanica</i> <i>Betula platyphylla</i> <i>Malus baccata</i> (L.) Borkh.
Shrubs	<i>Spiraea salicifolia</i> L. <i>Lonicera japonica</i> Thunb.	<i>Sophora davidii</i> (Franch.) Skeels <i>Lespedeza bicolor</i> Turcz. <i>Smilax china</i> L.	<i>Sophora davidii</i> (Franch.) Skeels. <i>Rosa rubus</i> Lévl. et Vant. <i>Rosa xanthina</i> Lindl. <i>Celastrus orbiculatus</i> Thunb. <i>Euonymus alatus</i> (Thunb.) Sieb. <i>Viburnum dilatatum</i> Thunb.
Herbs	<i>Carex uda</i> Maxim.	<i>Elymus dahuricus</i> Turcz. <i>Rubia cordifolia</i> L.	<i>Carex uda</i> Maxim. <i>Imperata cylindrica</i> (L.) Beauv. <i>Tripolium vulgare</i> Nees. <i>Patrinia scabiosaefolia</i> Fisch. ex Trev. <i>Cephalanthera erecta</i> (Thunb. ex A. Murray) Bl.

Table 2. Species-specific allometric equations used to quantify the biomass of the tree components.

Tree species	Components	Equations	R ²	Sources
<i>Pinus tabulaeformis</i>	Stem (with bark)	$B = 0.0198 \cdot D^{2.086} H^{0.7278}$	0.9652	Zhou [39]
	Branch	$B = 0.0013 \cdot D^{2.5746} H^{0.9057}$	0.8672	
	Foliage	$B = 0.0061 \cdot D^{1.3523} H^{0.455}$	0.7543	
	Root (≥ 0.2 cm)	$B = 0.0062 \cdot D^{2.2801} H^{0.7999}$	0.8761	
<i>Populus davidiana</i>	Stem (with bark)	$B = 0.044 \cdot D^{1.7343} H^{0.8181}$	0.9782	Zhou [39]
	Branch	$B = 0.0025 \cdot D^{2.1615} H^{0.931}$	0.8594	
	Foliage	$B = 0.0217 \cdot D^{1.1963} H^{0.7073}$	0.8740	
	Root (≥ 0.2 cm)	$B = 0.0034 \cdot D^{2.1936} H^{0.9178}$	0.7795	
<i>Betula platyphylla</i>	Stem (with bark)	$B = 0.0453 \cdot D^{2.0612} H^{0.5649}$	0.9169	Zhou [39]
	Branch	$B = 0.014 \cdot D^{1.7675} H^{0.4917}$	0.8647	
	Foliage	$B = 0.0104 \cdot D^{1.5123} H^{0.4006}$	0.7616	
	Root (≥ 0.2 cm)	$B = 0.0117 \cdot D^{2.106} H^{0.5779}$	0.8371	
<i>Quercus wutaishanica</i>	Stem (with bark)	$B = 0.0584 \cdot D^{1.9514} H^{0.5743}$	0.9578	Zhou [39]
	Branch	$B = 0.0866 \cdot D^{1.7715} H^{0.5066}$	0.8564	
	Foliage	$B = 0.0142 \cdot D^{1.8764} H^{0.5377}$	0.8169	
	Root (≥ 0.2 cm)	$B = 0.0832 \cdot D^{1.77} H^{0.5053}$	0.8863	
<i>Quercus acutissima</i>	Stem (with bark)	$B = 0.0185 \cdot D^{1.8896} H^{1.0577}$	0.9306	Yang et al. [40]
	Branch	$B = 0.0159 \cdot D^{1.7693} H^{1.0081}$	0.8403	
	Foliage	$B = 0.0021 \cdot D^{1.6321} H^{0.9787}$	0.7597	
	Root (≥ 0.2 cm)	$B = 0.0099 \cdot D^{1.8212} H^{1.0295}$	0.8606	
Other hardwood tree species	Stem (with bark)	$B = 0.048 \cdot (D^2 H)^{0.8494}$	0.9970	Zhou [39]
	Branch	$B = 0.0412 \cdot (D^2 H)^{0.68}$	0.9460	
	Foliage	$B = 0.0262 \cdot (D^2 H)^{0.7727}$	0.9670	
	Root (≥ 0.2 cm)	$B = 0.0301 \cdot (D^2 H)^{0.7767}$	0.9900	
Other conifer tree species	Stem (with bark)	$B = 0.0932 \cdot (D^2 H)^{0.7743}$	0.9350	Zhou [39]
	Branch	$B = 0.0079 \cdot (D^2 H)^{0.9285}$	0.9860	
	Foliage	$B = 0.0066 \cdot (D^2 H)^{0.8187}$	0.8780	
	Root (≥ 0.2 cm)	$B = 0.0322 \cdot (D^2 H)^{0.8168}$	0.8400	

B, D and H are the biomass (kg), the diameter at a height of 1.3 m (cm) and the tree height (m), respectively;

2.3. Fine Root Biomass, Litter and CWD Biomass

The fine root (<0.2 cm) biomass was measured using a soil corer (10 cm in diameter). Ten soil cores were excavated randomly at depths of 0–20 and 20–40 cm in every plot, packed separately into Ziplock plastic bags, and brought to the laboratory. In the laboratory, the root samples were separated from the soil by rinsing them with water. All fine root samples were oven-dried at 80 °C for 48 h followed by weighing [41]. The fine root biomass was the sum of the 0–20 cm and 20–40 cm fine root dry biomass.

To quantify the litter biomass on the surface, three 1 m × 1 m quadrats were randomly selected in each sample plot (same as the herb quadrats). All the litter and twigs (<2 cm diameter) in each quadrat were collected and brought to the laboratory to be oven-dried at 65 °C to a constant weight.

The CWD biomass was inventoried by its decay class in each sample plot. We assigned each piece of woody debris to one of five decay classes, which is outlined in Table 3. The diameter at each end and the length of woody debris (≥ 2 cm diameter) were measured. When the woody debris intersected a plot boundary, we only measured the parts within the boundary. The volume of each piece of woody debris was calculated by the equation for the truncated volume [25]. The samples of each decay class were collected and oven-dried at 65 °C to a constant weight for calculating the wood densities (dry mass/volume). The woody debris biomass is the product of the volume and decay class-specific densities.

Table 3. Decay class designations for coarse woody debris.

Characteristic	Decay Class				
	I	II	III	IV	V
Bark	Recently downed, intact	Beginning to peel or crack	Trace to absent	Absent	Absent
Sapwood	Present, intact	Mostly intact, partly soft	Soft and crushes under foot	Mostly absent	Absent
Heartwood (if present)	Not visible	Not visible	Visible in places	Beginning to decay	Showing signs of substantial decay

2.4. Soil Sampling

In each sample plot, nine drill points were randomly selected along the diagonal, and the surface litter of each point was cleared. Soil sampling was accomplished by a soil auger (5.0 cm in diameter) in five soil layers, 0–10, 10–20, 20–30, 30–50, and 50–100 cm, and soil samples collected in the same layer were combined. All soil samples were filtered with a 2 mm metal sieve. The roots and other debris were removed, and the samples were air-dried. Three bulk soil samples were also drilled in each soil layer using a soil core sampler (both 5.0 cm in diameter and height) and oven-dried at 105 °C to calculate the soil bulk density ($\text{g}\cdot\text{cm}^{-3}$).

2.5. Organic C Analysis and C Stock Calculation

The dried biological and soil samples of each component were ground and screened with a 2.5 mm metal sieve to analyse the organic C concentration with a C/N analyser (analytikjena Inc., Elementar, Germany).

The C stocks of the tree layer were calculated by the following formula:

$$CS_{\text{tree}}(\text{Mg}\cdot\text{ha}^{-1}) = \sum_{i,j=1}^n B_{i,j} \times C_{\text{conc}_{i,j}} \quad (1)$$

where CS_{tree} is the C stock of the tree layer ($\text{Mg}\cdot\text{ha}^{-1}$), i represents the stem, branch, foliage, and root (≥ 0.2 cm) components of the trees, j represents the different tree species, $B_{i,j}$ is the dry biomass of component i of tree species j per hectare ($\text{Mg}\cdot\text{ha}^{-1}$), and $C_{\text{conc}_{i,j}}$ is the C concentration of component i of tree species j .

The C stocks of the shrub layer were calculated as follows:

$$CS_{\text{shrub}}(\text{Mg}\cdot\text{ha}^{-1}) = \sum_{i=1}^n B_i \times C_{\text{conc}_i} \quad (2)$$

where CS_{shrub} is the C stock of the shrub layer ($\text{Mg}\cdot\text{ha}^{-1}$), i represents the foliage, branch, and root components, B_i is the dry biomass of component i per hectare ($\text{Mg}\cdot\text{ha}^{-1}$), and C_{conc_i} is the C concentration of component i .

The C stocks of the herb layer were calculated as follows:

$$CS_{\text{herb}}(\text{Mg}\cdot\text{ha}^{-1}) = \sum_{i=1}^n B_i \times C_{\text{conc}_i} \quad (3)$$

where CS_{herb} is the C stock of the herb layer ($\text{Mg}\cdot\text{ha}^{-1}$), i represents the above- and belowground components, B_i is the dry biomass of component i per hectare ($\text{Mg}\cdot\text{ha}^{-1}$), and C_{conc_i} is the C concentration of component i .

The C stocks of the fine roots were calculated as follows:

$$CS_{\text{fine root}}(\text{Mg}\cdot\text{ha}^{-1}) = B_{\text{fine root}} \times C_{\text{conc}_{\text{fine root}}} \quad (4)$$

where $CS_{\text{fine root}}$ is the C stock of the fine roots ($\text{Mg}\cdot\text{ha}^{-1}$), $B_{\text{fine root}}$ is the dry biomass of the fine roots per hectare ($\text{Mg}\cdot\text{ha}^{-1}$), and $C_{\text{conc fine root}}$ is the C concentration of the fine roots.

The C stocks of the litter layer were calculated as follows:

$$CS_{\text{litter}}(\text{Mg}\cdot\text{ha}^{-1}) = B_{\text{litter}} \times C_{\text{conc litter}} \quad (5)$$

where CS_{litter} is the C stock of the litter layer ($\text{Mg}\cdot\text{ha}^{-1}$), B_{litter} is the dry biomass of the litter per hectare ($\text{Mg}\cdot\text{ha}^{-1}$), and $C_{\text{conc litter}}$ is the C concentration of the litter.

The C stocks of the CWD were calculated as follows:

$$CS_{\text{CWD}}(\text{Mg}\cdot\text{ha}^{-1}) = \sum_{i=1}^n V_i \times D_i \times C_{\text{conc}_i} \quad (6)$$

where CS_{CWD} is the C stock of the CWD ($\text{Mg}\cdot\text{ha}^{-1}$), i represents decay classes I, II, III, IV, and V, V_i is the volume of CWD decay class i per hectare ($\text{m}^3\cdot\text{ha}^{-1}$), D_i is the density of CWD decay class i ($\text{Mg}\cdot\text{m}^{-3}$), and C_{conc_i} is the C concentration of CWD decay class i .

The soil C stocks were calculated by the following formula:

$$CS_{\text{soil}}(\text{Mg}\cdot\text{ha}^{-1}) = \sum_{i=1}^n BD_i \times C_{\text{conc}_i} \times T_i \times 10 \times (1 - \eta_i) \quad (7)$$

where CS_{soil} is the C stock of the soil ($\text{Mg}\cdot\text{ha}^{-1}$), i represents the 0–10, 10–20, 20–30, 30–50, and 50–100 cm soil layers, BD_i is the soil bulk density of layer i ($\text{g}\cdot\text{cm}^{-3}$), C_{conc_i} is the soil organic C concentration of layer i ($\text{g}\cdot\text{kg}^{-1}$), T_i is the soil thickness of layer i (cm), and η_i is the volumetric percentage of the coarse soil fraction (i.e., >2 mm) of layer i . This item (η_i) was assigned a value of 0 in each soil layer because there were no more than 0.2 mm soil fractions in all the samples.

2.6. Statistical Analysis

All data were tested for normality by the Kolmogorov-Smirnov (K-S) method before analysis. One-way ANOVA was used to compare the differences in the biomass C stocks of the trees, shrubs, herbs, fine roots, litter and CWD in the different forest succession stages. The significance of the effects of the forest succession stages and soil depths on the soil C stocks was tested by multiple comparisons using Duncan's test. Values were considered significantly different at $p < 0.05$. All statistical tests were conducted in SPSS 22.0 for Windows (SPSS Inc., 2018, Chicago, IL, USA).

3. Results

3.1. Vegetation Biomass Carbon Stocks

The tree biomass carbon stock (including the stems, branches, foliage and roots) in the QBF ($108.38 \text{ Mg}\cdot\text{ha}^{-1}$) was significantly greater than that in the PBF ($86.18 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($62.27 \text{ Mg}\cdot\text{ha}^{-1}$) (Figure 2A). In contrast, the shrub biomass carbon stock in the QBF ($0.35 \text{ Mg}\cdot\text{ha}^{-1}$) was significantly lower than that in the PBF ($0.51 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($0.76 \text{ Mg}\cdot\text{ha}^{-1}$) (Figure 2B). The herb biomass carbon stocks in the QBF ($0.01 \text{ Mg}\cdot\text{ha}^{-1}$) and PBF ($0.01 \text{ Mg}\cdot\text{ha}^{-1}$) were significantly lower than that in the PF ($0.02 \text{ Mg}\cdot\text{ha}^{-1}$) (Figure 2C). The increases in the tree C stocks were much greater than the decreases in the shrub and herbaceous C stocks, resulting in a significant increase (from 63.05, 86.70 and $108.73 \text{ Mg}\cdot\text{ha}^{-1}$ in the PF, PBF and QBF, respectively) in the vegetation carbon stocks throughout the development of the forests (Figure 2D).

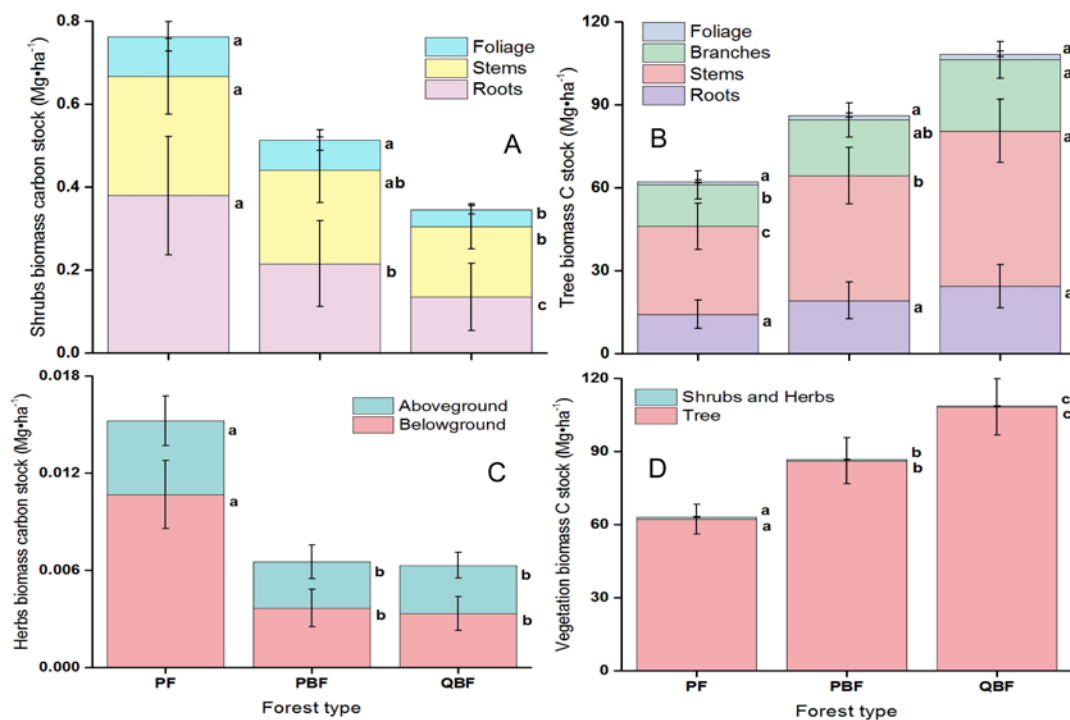


Figure 2. The vegetation biomass carbon stocks of the various components in the pure *Pinus tabuliformis* forest (PF), pine-broadleaved mixed forest (PBF) and *Quercus*-broadleaved mixed forest (QBF) in the central Loess Plateau of China. (A–D) illustrate the tree, shrub, herb, and vegetation carbon stocks, respectively. a, b, and c indicate significant differences in the carbon stocks of the same components at different succession stages at $p = 0.05$.

3.2. Fine Roots, Litter and CWD Carbon Stocks

The fine root biomass carbon stock in the QBF ($6.82 \text{ Mg}\cdot\text{ha}^{-1}$) was significantly greater than that in the PBF ($4.92 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($4.53 \text{ Mg}\cdot\text{ha}^{-1}$) (Figure 3). The litter carbon stocks in the QBF ($8.18 \text{ Mg}\cdot\text{ha}^{-1}$) was significantly greater than that in the PBF ($6.67 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($6.15 \text{ Mg}\cdot\text{ha}^{-1}$). In contrast, the CWD carbon stocks in the QBF ($0.34 \text{ Mg}\cdot\text{ha}^{-1}$) and the PBF ($0.47 \text{ Mg}\cdot\text{ha}^{-1}$) were significantly lower than that in the PF ($1.14 \text{ Mg}\cdot\text{ha}^{-1}$). The increase in the fine root and litter carbon stocks was greater than the decrease in the CWD carbon stock with secondary succession, resulting in more intermediate matter (sum of fine roots, litter and CWD) carbon stocks in the QBF ($15.34 \text{ Mg}\cdot\text{ha}^{-1}$) than in the PBF ($12.06 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($11.82 \text{ Mg}\cdot\text{ha}^{-1}$).

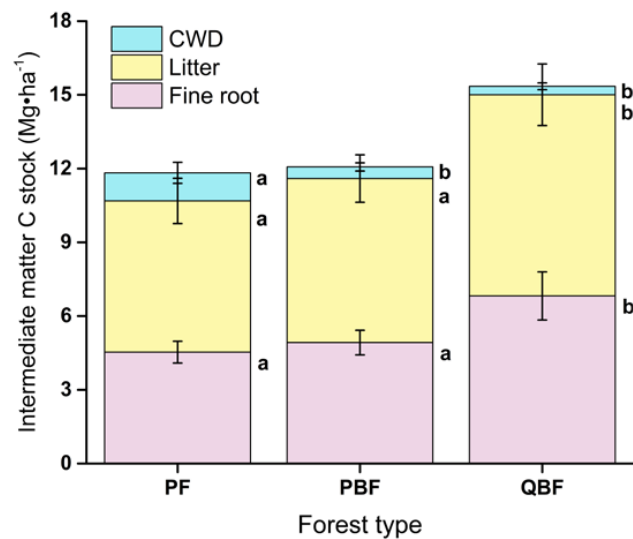


Figure 3. The intermediate matter carbon stocks in the pure *Pinus tabuliformis* forest (PF), pine-broadleaved mixed forest (PBF) and *Quercus*-broadleaved mixed forest (QBF) in the central Loess Plateau of China. a and b indicate significant differences in the carbon stocks of the same components at different succession stages at $p = 0.05$.

3.3. Soil Carbon Stocks

The soil C stock in the QBF (113.88 Mg·ha⁻¹) was significantly greater than that in the PBF (97.15 Mg·ha⁻¹) and the PF (90.38 Mg·ha⁻¹), but there was no significant difference between the PBF and the PF (Figure 4). The soil C stocks at depths of 0–10, 10–20, 20–30 and 30–50 cm varied significantly but showed no variation at depths of 50–100 cm. The soil C stocks at a depth of 0–50 cm accounted for 59.85%, 63.44% and 68.06% of the total C stocks in the top 1 m of the soils in the PF, PBF and QBF, respectively.

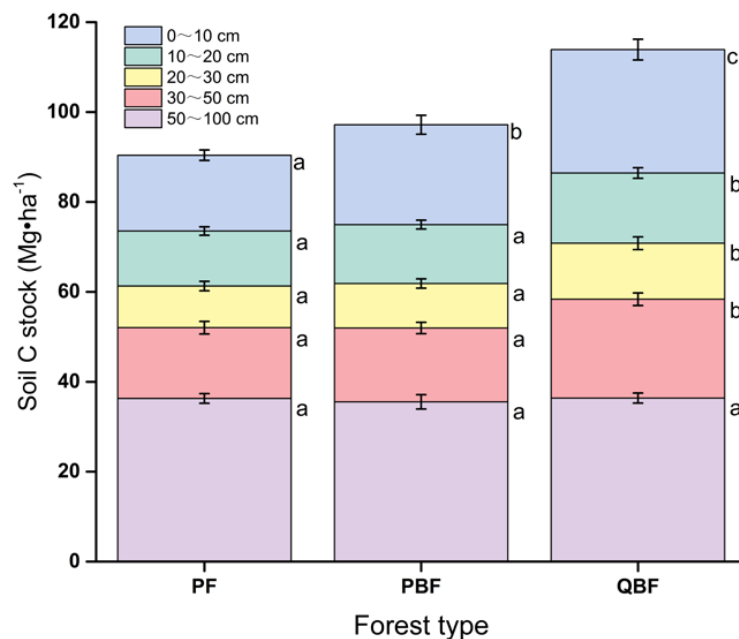


Figure 4. The soil carbon stocks of the various soil layers in the pure *Pinus tabuliformis* forest (PF), pine-broadleaved mixed forest (PBF) and *Quercus*-broadleaved mixed forest (QBF) in the central Loess Plateau of China. a, b, and c indicate significant differences in the carbon stocks of the same components at different succession stages at $p = 0.05$.

3.4. Ecosystem Carbon Stocks

The ecosystem C stock in the QBF ($237.96 \text{ Mg}\cdot\text{ha}^{-1}$) was significantly greater than that in the PBF ($195.91 \text{ Mg}\cdot\text{ha}^{-1}$) and the PF ($165.25 \text{ Mg}\cdot\text{ha}^{-1}$) (Figure 5A). Soil and vegetation biomass were the two largest contributors to the ecosystem C pool. The soil carbon stocks contributed 54.69%, 49.59% and 47.86% of the ecosystem C stocks in the PF, PBF and QBF, respectively, and showed a declining trend with forest secondary succession (Figure 5B). The vegetation biomass carbon stock contributed 38.15%, 44.25% and 45.70% of the ecosystem C stock to the PF, PBF and QBF, respectively, and showed an increasing trend with forest growth. As shown in Figure 5B, the contribution of soil and vegetation to the ecosystem C stocks seem to be gradually coming into balance (46.78% each in the QBF) with the forest secondary succession. The fine root, litter and CWD carbon stocks contributed a small portion (average 6.59%) to the ecosystem, and there was no significant variation in their contributions in the PF, PBF and QBF.

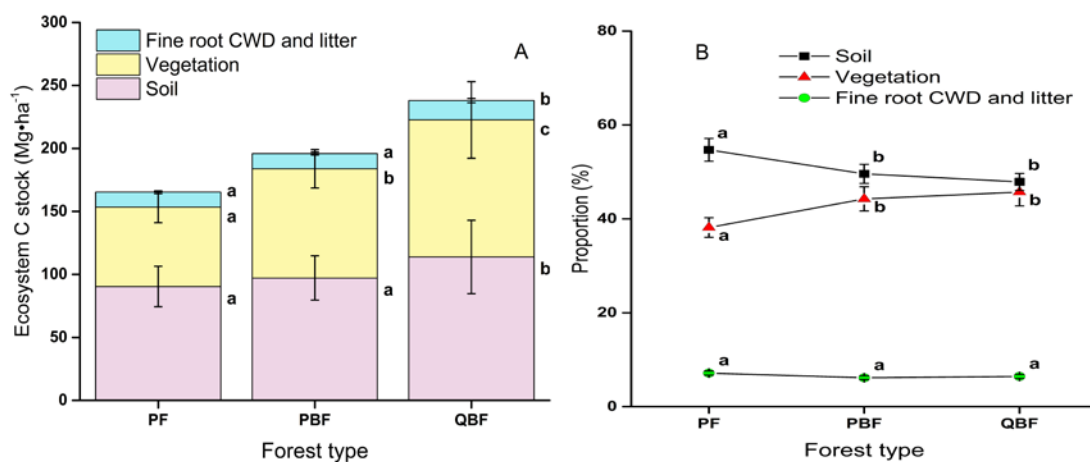


Figure 5. Ecosystem carbon stocks (A) and contribution proportions (B) of the various components in the pure *Pinus tabuliformis* forest (PF), pine-broadleaved mixed forest (PBF) and *Quercus*-broadleaved mixed forest (QBF) in the central Loess Plateau of China. a, b, and c indicate significant differences in the carbon stocks of the same components at different succession stages at $p = 0.05$.

4. Discussion

In the current study, a gradual increase in the vegetation biomass carbon stocks was observed throughout forest succession in the central Loess Plateau of China. Previous researchers found similar results that forest restoration favours biomass carbon accumulation. Risch et al. [42] reported that long-term secondary forest succession of mountain pine would lead to a mean increase in C stocks of $120 \text{ Mg C}\cdot\text{ha}^{-1}$ and a mean yearly C sequestration rate of $0.76 \text{ Mg C}\cdot\text{ha}^{-1}$. Furthermore, Wang and Epstein [43] proposed that successional ecosystems are carbon sources at the beginning of secondary succession and then become carbon sinks, and the switching point is approximately between 5 and 19 years following agricultural abandonment.

The tree biomass C stocks accounting for a considerable proportion (>98.77%) of the vegetation biomass C stocks in our study and directly determined the changes in vegetation biomass C stocks. The tree biomass C stocks ranged from 62.27 to $108.38 \text{ Mg}\cdot\text{ha}^{-1}$, which is well within the tree biomass C stock ranges (26 – $286 \text{ Mg}\cdot\text{ha}^{-1}$) reported for subtropical forests [44–46] and much higher than the average C stocks ($57.07 \text{ Mg}\cdot\text{ha}^{-1}$) of forest vegetation in China [47,48]. However, the mean tree biomass C stocks ($85.61 \text{ Mg}\cdot\text{ha}^{-1}$) was at a very low carbon stock level for subtropical evergreen broadleaved forest (84 – $128 \text{ Mg}\cdot\text{ha}^{-1}$) [49]. This indicates that the forest in our study region still has great carbon sink potential.

Understorey play a very important role in nutrient cycling and biodiversity, and their nutrient turnover efficiency is much faster than that of trees, although they contribute a very small proportion to

ecosystem C stocks. This contribution is particularly important in early stages of secondary succession forest with relatively simple structures. Consistent with this, we found the highest carbon stock in PF and their C stocks declined with forest succession. There are three possible reasons for this downward trend. First, the increased tree canopy and tree density with forest succession constrains the standing crop of understory plants [50]. Second, canopy closure prevents sunlight from reaching understory plants [51,52] and the photosynthesis of understory plants is suppressed, and the biomass C accumulation decreases. Third, canopy closure contributes to lower ambient temperatures that cause a relatively high metabolic rate of understory plants, resulting in lower biomass C accumulation [53].

Similar to understory plants, fine roots, litter and CWD contribute more to the C turnover than to C accumulation. In this study, the litter and CWD carbon stocks in our study ranged from 7.14 to 8.52 Mg·ha⁻¹, which were much higher than the values reported for subtropical forests (2.7–4.7 Mg·ha⁻¹) in China [46]. The litter C stocks increased with the secondary succession, which mainly attributed to deciduous tree species usually have a higher annual production of litter than coniferous tree species [15,54]. The CWD carbon stocks showed a decreasing trend, which results from the decomposition and a lower production of CWD at the climax stages than early succession stages of intense competition. Fine roots are major contributors of C inputs to soil, directly determining the carbon turnover rate [46]. Moreover, we found that the fine root and litter C stocks increased significantly only in the climax community (the QBF), and the ecosystem carbon turnover rate was also highest at this time. Therefore, if the top-level community cannot succeed, the carbon sink function of the forest ecosystem will be low-efficiency. So we can take forest management measures to accelerate secondary succession to achieve their efficient carbon sink function.

In our study, the soil C stock ranged from 90.38 to 113.88 Mg·ha⁻¹, which was lower than the average value (158.10 Mg·ha⁻¹) of local broadleaf forest soil [55]. Therefore, the soil in the central Loess Plateau still has a great carbon sink potential under secondary succession. Our study demonstrated the C sink effect of forest soil in secondary succession, which was also found in other studies [14,56]. Continuous carbon input from the fine roots and litter is the main factor causing soil C sequestration [57]. Generally, the soil depth is fixed, meaning that C stocks are determined by soil organic carbon (SOC) and soil BD. On the Loess Plateau, Deng et al. [14] reported that the soil BD did not significantly vary and the SOC became the only factor affecting the soil C stocks. Moreover, the SOC was positively correlated with long-term vegetation restoration due to its ability to reduce soil erosion [18]. This explains why soil carbon stocks increase with secondary succession. Moreover, an improved soil environment can induce the colonization and establishment of plant species [55]. In addition, we found that the soil C stocks were higher in the upper (0–50 cm) than in the lower (50–100 cm) layer, and the increments most obviously occurred in the 0–10 cm layer. This was attributed to significant amounts of organic matter added to the topsoil by the decomposition of the microbial community in the litter layer.

The mean ecosystem C stocks in the succession sequence of the central Loess Plateau is about 201.61 Mg·ha⁻¹, which is lower than the average value for China of 258.83 Mg·ha⁻¹ [48]. Ecosystem C stocks significantly increase with the secondary succession. Tang and Li [58] believe that ecosystem C stocks are largely influenced by tree species composition. Deciduous tree species can accumulate more C than coniferous tree species due to their higher wood density [59]. Moreover, deciduous tree species usually have a higher litter production and a faster litter decomposition rate than conifer species, whose leaf contains lower concentrations of soluble carbohydrates and higher concentrations of lignin [60]. In addition, deciduous tree species with the high light transmission can provide a favourable soil temperature for decomposers to speed up carbon turnover [61]. The ecosystem C stocks are mainly determined by the magnitude of vegetation and the soil carbon pool. The C contribution to ecosystem of the two tends to reach equilibrium at the climax stages of succession, due to regulation by fine roots and litter [50]. Consequently, forest succession to the climax stage, mainly deciduous tree species composition in the central Loess Plateau, can maximize the ecosystem C stocks and C turnover rate. Therefore, it is necessary to continue to strengthen forest protection and expand the period and scope of forest protection in the Loess Plateau.

5. Conclusions

We obtained comprehensive carbon stocks results of secondary forests at different succession stages in the central Loess Plateau of China. These results provide evidence that the secondary forests succession of the Loess Plateau reduce atmospheric CO₂. According to the 8th National Forest Inventory, the total carbon stocks of forest in China were 8.43 billion tons [32], and the contribution of secondary forests on the Loess Plateau to the national forest carbon stocks is approximately 1.5%. In addition, we identified the carbon stocks contribution of each component of the forest ecosystem, which provide important information for the implementation of secondary forest restoration management and carbon emission reduction measures on the Loess Plateau.

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