



# Aboveground carbon stock, allocation and sequestration potential during vegetation recovery in the karst region of southwestern China: A case study at a watershed scale



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## ABSTRACT

Karst landscape in southwestern China is one of the most typical landscapes developed on carbonate bedrock and has the largest area in the world. Carbon sequestration potentials during secondary karst vegetation recovery remain uncertain. Based on the vegetation map and 87 sampling plots at five stages of natural vegetation succession, this study estimated aboveground (AG) vegetation carbon stocks and dynamics at a watershed scale. AG carbon density of grasslands, shrublands, shrub forests, secondary forests and primary forests was 1.70, 4.15, 22.3, 70.3, 142.2 Mg ha<sup>-1</sup>, respectively. The ten most important species stored 71.6–96.1% of total AG carbon stock, indicating that carbon pool in karst vegetation was determined by a few dominant species. Main contributors to AG carbon stock shifted from individuals in small diameter classes in shrublands to individuals in large diameter classes in primary forests, indicating that carbon increases in the early vegetation succession resulted from high recruitment of woody plants, while carbon accumulations in the later forests were mainly due to tree growth. The long time required for secondary forests to recover carbon density to the level of primary forests could be explained by the slow speed of large evergreen trees reaching a high level of dominance during secondary succession on the harsh habitats. The total AG carbon stock of the studied watershed (7.50 × 10<sup>3</sup> ha) was 85.9 × 10<sup>3</sup> Mg, of which paddy fields, dry lands, grasslands, shrublands, shrub forests and secondary forests accounted for 22.6%, 3.49%, 0.34%, 5.97%, 12.3% and 55.3%, respectively. The AG carbon stock in this watershed would increase by 92.5% in 50–100 years and by 4.40 times in 140–200 years if the degraded vegetation types could continue to develop into mature forests. Although carbon density of karst forests was significantly lower than that of the forests on non-karst habitats in the same latitudinal zone, the degraded karst vegetation showed a great carbon sequestration potential due to the large distribution area in southwestern China.

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## 1. Introduction

The dynamic of carbon storages in terrestrial ecosystems plays an important role in regulating the global carbon cycle and atmospheric CO<sub>2</sub> concentration (Dixon et al., 1994; Houghton et al.,

2000). Quantifying carbon stocks and assessing carbon sequestration potentials of different ecosystem types is one of the key issues of global carbon cycle study (Houghton et al., 2000; Fang et al., 2007; Yu et al., 2010a). Many forestry-developed countries or continents, such as America (Pacala et al., 2001), Brazil (Houghton et al., 2000) and Europe (Janssens et al., 2003; Nabuurs et al., 2003), have comprehensively assessed their national vegetation carbon stocks, especially carbon stocks in forests. In China, previous studies have assessed the carbon stocks in grasslands

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(Ni, 2002; Piao et al., 2007; Fan et al., 2008), shrublands (Hu et al., 2006; Yu et al., 2010a), forests (Zhou et al., 2000; Fang et al., 2001; Wang et al., 2001; Zhao and Zhou, 2006) and terrestrial ecosystems (Fang et al., 2007; Piao et al., 2009; Yu et al., 2010a).

Both biotic and abiotic factors, such as climate, site condition, species composition, community structure and human disturbance, largely influence vegetation carbon stocks. The different understanding of how these factors affect carbon cycle process, different estimating methods, and the spatial and temporal variability and complexity of ecosystem carbon stocks result in large uncertainties in estimating Chinese vegetation carbon stocks (Zhou et al., 2000; Wang et al., 2001; Zhao and Zhou, 2006). For example, the estimates of carbon storage in Chinese grasslands ranged between 1.05 Pg C (Piao et al., 2007) and 3.32 Pg C (Fan et al., 2008), while the estimates for Chinese forest carbon stock varied from 3.26 Pg C (Wang et al., 2001) to 7.47 Pg C (Yu et al., 2010a). China, with a vast territory, has a variety of climates, topographies and ecosystem types. Therefore, based on the local ecological and environmental conditions, the detailed study on carbon stocks and cycles at small regional and/or ecosystem scales is urgently needed for explaining and assessing these uncertainties and improving the accuracy of estimating carbon storages in Chinese terrestrial ecosystems (Yu et al., 2010a).

Karst topography is widespread throughout the world and covers about 12% of the world's land area (Liu, 2009). China has approximately 3.44 million km<sup>2</sup> of karst areas (buried, covered, and exposed carbonate rock areas), about 36% of its total land and 15.6% of all karst areas in the world (Jiang et al., 2014). The karst landscape of southwestern China is one of the most typical landscapes developed on carbonate bedrock in the world and is characterized by extremely slow soil formation from the underlying limestone and very shallow and patchy soil with a low water retention capacity (Zhu, 1997; Liu, 2009). The dominant vegetation in the subtropical karst region is a mixed evergreen and deciduous broad-leaved forest, which is remarkably different from the typical vegetation types in non-karst regions of China (i.e., evergreen broad-leaved forest) and in other regions of the world (e.g., deserts in Northern Africa and Central Asia) at the same latitudinal zone (Guo et al., 2011). Quantifying vegetation carbon storages in this unique region is very important for improving the accuracy of estimating Chinese vegetation carbon storages and evaluating the

role of Chinese terrestrial ecosystems in global carbon cycle. However, due to the high habitat heterogeneity, high vegetation fragmentation, and complex and irregular plant growth forms, biomass and carbon stocks of different vegetation types in the region are difficult to be measured and have seldom been studied (Liu et al., 2009; Tan et al., 2014). Only a few studies have reported the biomass of karst forests (Yang and Cheng, 1991; Zhu et al., 1995; Liu et al., 2009; Yu et al., 2010b) and shrublands (Tu and Yang, 1995).

Land-use and land-cover change plays an important role in CO<sub>2</sub> exchange between terrestrial biosphere and atmosphere (IPCC, 2001). Secondary forests have the potential to capture large amounts of C released during vegetation degradation and can play an important role in sequestering atmospheric CO<sub>2</sub> and regulating regional carbon cycle (Orihuela-Belmonte et al., 2013). In the past decades, many karst forests have experienced varying degrees of degradation due to human disturbances, such as deforestation, agricultural expansion, livestock overgrazing and fire (Liu, 2009). Rocky desertification is the most serious ecological and environmental problem in this region. The desertification area is about 12 million ha, which is up to 26.5% of the whole karst area of southwestern China (The State Forestry Administration of China, 2012). Many protection measures and re-vegetation programs have been carried out to counteract this trend, leading to widespread secondary vegetation succession in this region. Dramatic changes in species composition and vegetation structure occur during the process of secondary succession (Liu et al., 2011b), which largely influence carbon stocks and dynamics (Culmsee et al., 2010; Mascaro et al., 2012; Orihuela-Belmonte et al., 2013). However, carbon dynamics during secondary karst vegetation recovery have seldom been addressed. Only a few studies reported significant carbon accumulations during natural karst vegetation recovery (Liu et al., 2013; Tan et al., 2014) and in an age-sequence of *Zanthoxylum bungeanum* plantations (Cheng et al., 2015). Moreover, regional carbon sequestration potential during vegetation recovery in this area is still unclear, which is important for assessing its contribution to global carbon cycle and providing new insights into reforestation programs and carbon sink managements in this region (Cheng et al., 2015).

In this paper, based on the vegetation map and data collected from 87 plots at different stages of karst vegetation succession, we

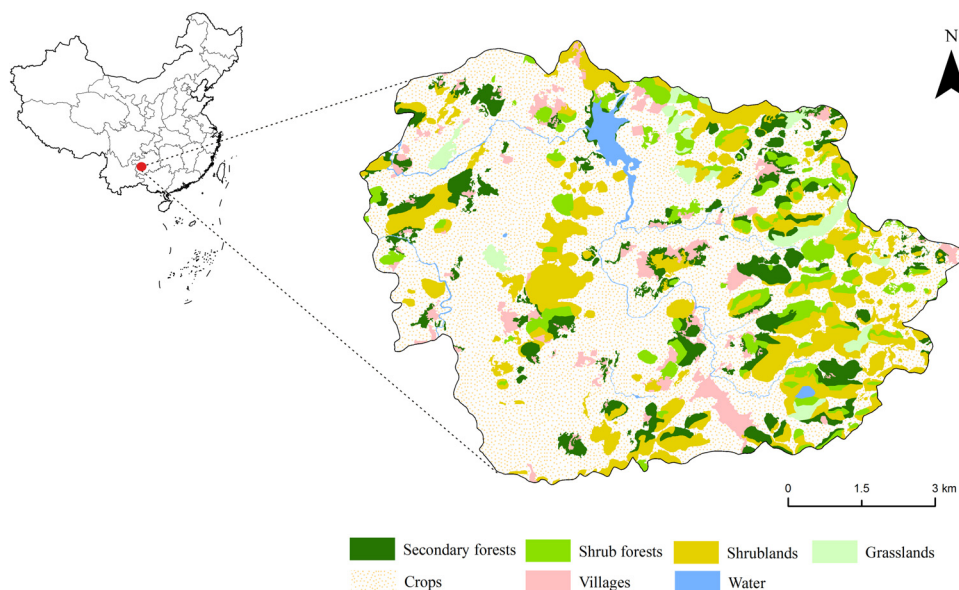


Fig. 1. Vegetation map of the Houzhai watershed, SW China.

estimated the aboveground (AG) vegetation carbon stocks and allocations at a watershed scale and assessed regional carbon sequestration potentials during vegetation recovery.

## 2. Materials and methods

### 2.1. Study region

The research was carried out in Houzhai watershed, Puding Karst Ecosystem Research Station, the Chinese Academy of Sciences in Guizhou Province, China (26°12'–26°18'N, 105°40'–105°49'E; Fig. 1). The altitude varies from 1300 to 1600 m. The total area of Houzhai watershed is  $7.50 \times 10^3$  ha, of which 34.1% is covered by karst natural vegetation and 59.8% by croplands (paddy fields and dry lands). The main cultivations include rice-rape rotation in paddy fields ( $3.58 \times 10^3$  ha) and corn-rape rotation in dry lands ( $0.91 \times 10^3$  ha). The mean annual precipitation and temperature of this region are 1390 mm and 15.1 °C, respectively. The main soil types are limestone soil and yellow soil, and the topsoil in this region is extremely shallow and patchy, in the range of 0–30 cm deep. The original vegetation is subtropical mixed evergreen and deciduous broad-leaved forest. However, most of the primary forests (PF) were clear-cut in the 1950s, and only a few forests nearby villages and temples were preserved but subjected to different degrees of human disturbance. After re-vegetation programs, secondary vegetation succession widely occurs and there are four main successional vegetation types in this watershed: secondary forests (F), shrub forests (SF), shrublands (S), and grasslands (G). The vegetation map of this watershed was derived from the high-resolution Google Earth and Spot images, combined with extensive field investigations (i.e. investigating vegetation types of all the hills in the watershed). We used ArcGIS 9.3 to process the data and estimate the total area by different vegetation types (Fig. 1).

F is dominated by *Platycarya longipes*, *Carpinus pubescens*, *Lithocarpus confinis*, *Itea yunnanensis* and *Cyclobalanopsis glauca*. The mean height of canopy trees is about 10–15 m and the mean

canopy coverage is about 90%. SF is dominated by *P. longipes*, *I. yunnanensis*, *Cladrastis platycarpa*, *Rhamnella martinii* accompanied by many thorny shrubs such as *Rosa cymosa* and *Rhamnus heterophylla*. The mean height of the canopy trees in SF is about 5 m. S is dominated by many thorny shrub species (2 m height), such as *R. cymosa*, *R. heterophylla*, *Zanthoxylum armatum* and *Pyracantha fortuneana*. G is dominated by *Themeda japonica*, *Heteropogon contortus* and *Carex lanceolata* and contains some dwarf shrubs. More details about the four vegetation types were described in the report of Liu et al. (2011b). Fortunately, we found some remnants of primary karst forests, with a distance of about 100 km to Houzhai watershed, which are almost not subjected to human disturbance. The primary forests are dominated by *Photinia bodinieri*, *Photinia glabra*, *Quercus fabri*, *Celtis sinensis* and *P. longipes*. The maximum diameter at breast height (DBH) of the canopy trees is 76 cm and the mean height of canopy trees is about 16 m. The main differences among vegetation types are the consequences of human induced vegetation degradation. PF is considered as a reference to the natural vegetation with little disturbance, while S and G are the results of intensive disturbances.

### 2.2. Vegetation survey

The vegetation survey was conducted in June–July, 2010 and in June–August, 2013. According to the vegetation map and previous field investigations, there are 22 main community types belonging to the four vegetation successional stages in Houzhai watershed (Table 1). We investigated 3–4 plots for each community type. In total, we investigated 84 plots of the 22 community types within and around the border of the watershed. Of these, 10 plots were grasslands (including three community types), 15 plots were shrublands (four community types), 19 plots were shrub forests (five community types), and 40 plots were secondary forests (ten community types). In addition, 3 plots of primary karst forests were also investigated for comparative study. In primary and secondary forests, all woody plants with a height > 1.5 m were measured inside each sampling plot (400–600 m<sup>2</sup>). Height, DBH,

**Table 1**

Description of the vegetation types in this study. Data are mean ± SE. Values in parenthesis show ranges. Different lowercase letters indicate significant differences among vegetation types at  $P < 0.05$ .

Vegetation types	Secondary vegetation types in Houzhai watershed						
	Paddy fields	Dry lands	Grasslands	Shrublands	Shrub forests	Secondary forests	Primary forests
Total area (ha)	3577.6	911.2	173.8	1235.5	473.7	675.5	–
Plot area (m <sup>2</sup> )	–	–	4	100–200	100–200	400–600	400
Numbers of plots	–	–	10	15	19	40	3
Community height (m)	–	–	<1	24	5	10–15	16
Woody plant density ( $\times 10^3$ No. ha <sup>-1</sup> )	–	–	–	32.7 ± 4.03b	29.6 ± 4.92b	9.70 ± 1.17a	8.52 ± 1.04a
DBH of the largest tree (cm)	–	–	–	4.79 ± 0.37a (3.2–8.6)	12.3 ± 1.44b (4.4–26)	32.4 ± 1.44c (18.1–52.8)	65.4 ± 5.76d (56.2–76.0)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	–	–	–	6.04 ± 1.13a (2.82–17.4)	15.7 ± 0.97b (7.48–21.6)	25.4 ± 0.81c (14.1–37.8)	58.5 ± 1.99d (56.4–62.4)
AG carbon density (Mg ha <sup>-1</sup> )	5.42*	3.29*	1.70 ± 0.13a (1.34–2.61)	4.15 ± 0.97a (1.09–14.4)	22.3 ± 2.13b (9.79–42.7)	70.3 ± 2.81c (31.0–117.9)	142.2 ± 3.42d (135.5–144.3)
AG carbon stock ( $\times 10^3$ Mg)	19.4	3.00	0.30	5.13	10.6	47.5	–

AG: aboveground, DBH: diameter at breast height. Basal diameter (BD) instead of DBH was used in shrublands. \* Data are from Luo (2008).

Grasslands include three community types indicated by the dominant species: *Themeda japonica* (n=4), *Heteropogon contortus* + *Themeda japonica* (3), and *Themeda japonica* + *Bothriochloa bladhii* (3).

Shrublands include four community types: *Rosa cymosa* + *Pyracantha fortuneana* (4), *Rhamnus heterophylla* (4), *Pterolobium punctatum* + *Pyracantha fortuneana* (4), and *Coriaria nepalensis* (3).

Shrub forests include five community types: *Platycarya longipes* (4), *Itea yunnanensis* (4), *Rhamnella martinii* + *Rhamnus heterophylla* (4), *Cladrastis platycarpa* + *Celtis bungeana* (4), and *Quercus fabri* + *Quercus acutissima* (3).

Secondary forests include ten community types: *Platycarya longipes* (4), *Itea yunnanensis* (4), *Platycarya longipes* + *Lithocarpus confinis* (4), *Carpinus pubescens* + *Lithocarpus confinis* (4), *Cyclobalanopsis glauca* (4), *Quercus variabilis* (4), *Cladrastis platycarpa* + *Carpinus pubescens* (4), *Quercus fabri* (4), *Carpinus pubescens* + *Itea yunnanensis* (4), and *Platycarya longipes* + *Itea yunnanensis* (4).

Primary forests include three plots: *Photinia bodinieri*, *Photinia glabra*, and *Photinia bodinieri* + *Celtis sinensis*.

basal diameter (BD) (only for shrubs) were recorded for each plant. Woody plants with a height <1.5 m were measured in 4 subplots of 25 m<sup>2</sup> size (5 m × 5 m). BD and height were recorded for all individuals in the subplots. In shrub forests and shrublands, BD and height were measured for all individuals in each plot (100–200 m<sup>2</sup>). DBH was also recorded for individuals with a height >1.5 m in shrub forests. Four herbaceous subplots of 4 m<sup>2</sup> size (2 m × 2 m) were set up in each plot of primary and secondary forests, shrub forests and shrublands. Height, coverage and abundance were recorded for each plant species. The same method of herbaceous survey was applied to the 4 m<sup>2</sup> sampling plots of grasslands.

### 2.3. Biomass and carbon determination

The AG biomass of the woody plants in all plots was estimated from DBH or BD and height of individuals, using the allometric regression equations for woody and foliar parts of 15 dominant and common species in this region. The method of establishing these equations was introduced in detail in our previous studies (Liu et al., 2009, 2013). In grasslands, all plants were harvested in 4 m<sup>2</sup> plots. Fresh weights were determined in the field. Oven-dried weights were determined in the laboratory. AG carbon stocks were calculated using the species-specific carbon concentrations reported by our previous study. Carbon concentrations of foliage and wood of the 15 common species varied from 43.6 to 53.0% and from 44.5 to 50.7%, respectively (Liu et al., 2013). According to our previous study, the herbaceous carbon stocks of secondary forests and shrub forests only accounted for 0.1–0.2% of the total AG carbon stocks (Liu et al., 2013). Therefore, the herbaceous carbon component in primary and secondary forests, shrub forests and shrublands was not taken into consideration in this study. AG carbon density (Mg ha<sup>-1</sup>) of each sampling plot was calculated by dividing AG carbon stock of each plot by the plot area.

### 2.4. Data analysis

Basal area (BA) of each plot was calculated using the following equation:  $BA (m^2 ha^{-1}) = 0.00007854 \times DBH^2$  (BD was used in shrublands). Data on woody plant density, diameter of the largest tree, basal area and AG carbon density were subjected to general linear models (GLM, type III: unbalanced ANOVA) to determine differences among vegetation types. The relationships of AG carbon density with basal area, diameter of the largest tree and carbon density of the largest trees were explored by Pearson's correlation analysis and linear regression. All the plots of the same vegetation types were pooled together to determine carbon allocations among DBH classes and plant species for each vegetation type. The mean AG carbon density of each vegetation type was multiplied by its area to obtain its AG carbon stock in this watershed, and the total vegetation carbon stock of this watershed was the sum of carbon stocks of all vegetation types. According to Luo (2008), mean AG carbon density in paddy fields and dry lands with the same cultivations in the karst region was 5.42 and 3.29 Mg ha<sup>-1</sup>, respectively, which was used to calculate AG carbon stock in croplands. Carbon increase after the degraded natural vegetation developing into the next stage or mature forests was considered as the recent carbon sequestration potential or the maximum carbon sequestration potential. Since 1999, owing to the Grain for Green Program (GGP) in the China, many croplands have been converting into natural vegetation types in the karst areas to prevent further soil erosion and improve the natural environment (Cheng et al., 2015). Carbon change after croplands being changed into grasslands or shrub forests was considered as the recent or maximum carbon sequestration potential of croplands. When necessary, data were log<sub>10</sub>-transformed to improve normality.

Statistical tests were performed with R statistical platform (R Development Core Team, 2012) and SPSS 15.0 (SPSS, Chicago, USA).

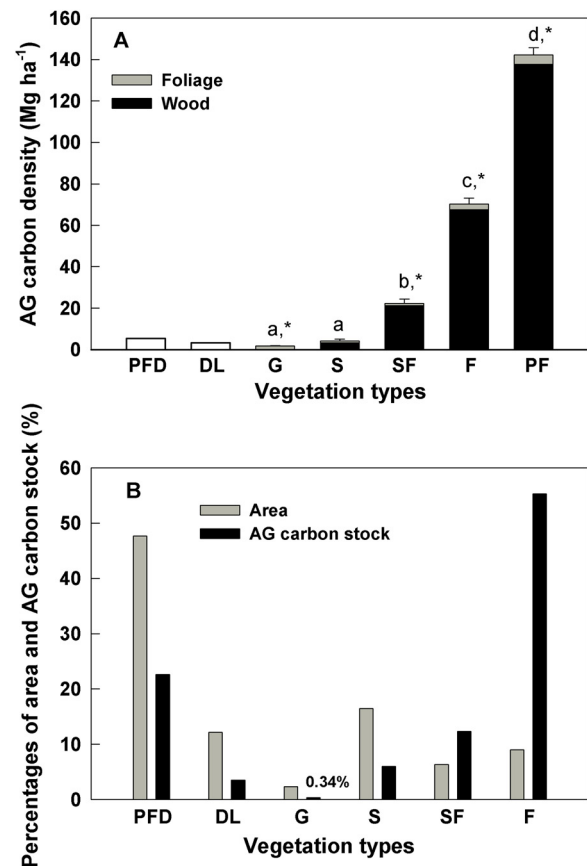
## 3. Results

### 3.1. Vegetation structure and AG carbon density

The community structural parameters were significantly different among vegetation types (Table 1). Community height, DBH of the largest tree and basal area significantly increased and plant individual density decreased during the process of vegetation succession. Mean AG carbon density varied greatly among different vegetation types, ranging from 1.70 Mg ha<sup>-1</sup> in grasslands to 142.2 Mg ha<sup>-1</sup> in primary forests (Table 1 and Fig. 2A). At the beginning of succession, AG carbon density of grasslands was significantly lower than those of paddy fields and dry lands, while AG carbon increased largely at the stage of shrub forests. The foliar pool contributed 87.5% to the total AG carbon stock of grasslands, while woody pool contributed 79.4–96.9% to the AG carbon stocks of the other four natural vegetation types (Fig. 2A).

### 3.2. AG carbon allocations among species and DBH classes

During karst vegetation succession, most of AG carbon was concentrated in fewer dominant species. The ten most important species were responsible for 51.9%, 45.8%, 29.9% and 17.6% of total



**Fig. 2.** The dynamic of aboveground (AG) carbon density during the process of vegetation succession (A) and the percentages of distribution area and AG carbon stock of different vegetation types in Houzhai watershed (B). PFD: paddy fields, DL: dry lands, G: grasslands, S: shrublands, SF: shrub forests, F: secondary forests, PF: primary forests. AG carbon densities of PFD and DL were obtained from Luo (2008). Different lowercase letters indicate significant differences among natural vegetation types at  $P < 0.05$ . \*AG carbon density of natural vegetation types is significantly different from those of and PFD and DL (by  $t$ -test).



number of individuals but 85.5% (2.75 Mg ha<sup>-1</sup>), 78.5% (18.2 Mg ha<sup>-1</sup>), 71.6% (49.7 Mg ha<sup>-1</sup>) and 96.1% (136.6 Mg ha<sup>-1</sup>) of the total AG carbon stock of shrublands, shrub forests, secondary forests and primary forests, respectively (Table 2). The five most important species accounted for 71.3% (2.30 Mg ha<sup>-1</sup>), 62.5% (14.5 Mg ha<sup>-1</sup>), 53.7% (37.2 Mg ha<sup>-1</sup>) and 92.4% (131.3 Mg ha<sup>-1</sup>) of the total carbon stock in each vegetation type, respectively.

Although most of total individuals were concentrated in the smallest DBH class in all the natural vegetation types (71.9–91.1%), the majority of AG carbon stock distributed in smaller trees in the early succession stages and gradually changed to larger trees in the later stages (Fig. 3). Plant individuals with BD classes of < 2 and 2–4 cm contributed 36.2% (1.17 Mg ha<sup>-1</sup>) and 43.9% (1.42 Mg ha<sup>-1</sup>) to the total AG carbon stock of shrublands, while individuals with DBH classes of 2–5 and 5–10 cm accumulated 40.7% (9.44 Mg ha<sup>-1</sup>) and 32.3% (7.48 Mg ha<sup>-1</sup>) of the total AG stock of shrub forests. However, in secondary forests, 39.4% (27.4 Mg ha<sup>-1</sup>) and 27.8%

(19.3 Mg ha<sup>-1</sup>) of the total carbon stock were concentrated in individuals with DBH classes of 10–20 and 20–30 cm, whereas 24.4% (34.8 Mg ha<sup>-1</sup>) and 54.3% (77.2 Mg ha<sup>-1</sup>) of the carbon stock of primary forests were stored in trees with DBH classes of 30–40 and > 40 cm. The distribution of basal area showed the similar pattern of AG carbon in each vegetation type (Fig. 3).

The values of AG carbon density at plot level were significantly and positively correlated with the DBH of the largest tree (R<sup>2</sup>=0.83), basal area (R<sup>2</sup>=0.88) and AG carbon density of the largest tree (R<sup>2</sup>=0.79) and of the five largest trees (R<sup>2</sup>=0.87) (Fig. 4). The AG carbon stock of the largest tree contributed to 5.43 ± 0.71%, 8.73 ± 2.23%, 9.56 ± 0.66% and 15.4 ± 3.17% of the total AG carbon stock of shrublands, shrub forests, secondary forests and primary forests, respectively, while the five largest trees accounted for 17.5 ± 1.90%, 23.8 ± 3.92%, 31.8 ± 2.00% and 54.2 ± 7.69% of the total AG carbon stock of the above vegetation types, respectively.

**Table 2**  
Aboveground (AG) carbon allocation among the ten most important species.

Vegetation types	Species	Individual density		Basal area		AG carbon	
		No.ha <sup>-1</sup>	%	m <sup>2</sup> ha <sup>-1</sup>	%	Mg ha <sup>-1</sup>	%
Shrublands	<i>Rosa cymosa</i> <sup>a</sup>	2681	7.61	0.57	11.6	0.68	21.1
	<i>Coriaria nepalensis</i> <sup>a</sup>	810	2.30	0.72	14.8	0.59	18.3
	<i>Pyracantha fortuneana</i> <sup>b</sup>	4129	11.7	0.78	16.0	0.51	15.7
	<i>Rhamnus heterophylla</i> <sup>b</sup>	5633	16.0	0.86	17.7	0.32	9.90
	<i>Pterolobium punctatum</i> <sup>a</sup>	638	1.81	0.30	6.25	0.20	6.33
	<i>Platycarya longipes</i> <sup>a</sup>	252	0.72	0.14	2.77	0.17	5.30
	<i>Zanthoxylum armatum</i> <sup>a</sup>	2343	6.65	0.38	7.78	0.12	3.84
	<i>Rosa rubus</i> <sup>a</sup>	567	1.61	0.10	2.10	0.07	2.21
	<i>Spiraea henryi</i> <sup>a</sup>	1024	2.91	0.11	2.19	0.05	1.62
	<i>Rhus chinensis</i> <sup>a</sup>	210	0.59	0.06	1.27	0.04	1.22
	Total	18287	51.9	4.02	82.5	2.75	85.5
Shrub forests	<i>Platycarya longipes</i> <sup>a</sup>	6422	18.3	4.52	29.8	7.12	30.7
	<i>Itea yunnanensis</i> <sup>b</sup>	2363	6.72	2.45	16.1	3.19	13.8
	<i>Rhamnella martinii</i> <sup>a</sup>	541	1.54	1.07	7.05	1.94	8.37
	<i>Cladrastis platycarpa</i> <sup>a</sup>	115	0.33	0.55	3.63	1.19	5.14
	<i>Carpinus pubescens</i> <sup>a</sup>	548	1.56	0.61	4.02	1.04	4.48
	<i>Machilus cavaleriei</i> <sup>b</sup>	1474	4.19	0.58	3.85	0.86	3.69
	<i>Quercus fabri</i> <sup>a</sup>	119	0.34	0.44	2.90	0.85	3.68
	<i>Celtis bungeana</i> <sup>a</sup>	611	1.74	0.45	2.98	0.70	3.04
	<i>Lithocarpus confinis</i> <sup>b</sup>	226	0.64	0.27	1.79	0.69	2.98
	<i>Rhamnus heterophylla</i> <sup>b</sup>	3652	10.4	0.86	5.68	0.60	2.57
	Total	16071	45.8	11.8	77.8	18.2	78.5
Secondary forests	<i>Platycarya longipes</i> <sup>a</sup>	983	10.1	4.59	18.3	13.7	19.9
	<i>Carpinus pubescens</i> <sup>a</sup>	321	3.29	2.98	11.9	7.90	11.4
	<i>Itea yunnanensis</i> <sup>b</sup>	671	6.87	3.08	12.3	6.88	9.88
	<i>Lithocarpus confinis</i> <sup>b</sup>	515	5.28	1.42	5.64	5.07	7.28
	<i>Quercus fabri</i> <sup>a</sup>	49	0.51	1.10	4.40	3.62	5.20
	<i>Cladrastis platycarpa</i> <sup>a</sup>	58	0.59	0.98	3.91	2.92	4.20
	<i>Quercus variabilis</i> <sup>a</sup>	13	0.13	0.74	2.95	2.51	3.61
	<i>Quercus aliena</i> <sup>a</sup>	35	0.36	0.58	2.32	2.44	3.51
	<i>Cinnamomum bodinieri</i> <sup>b</sup>	43	0.44	0.82	3.25	2.38	3.42
	<i>Cyclobalanopsis glauca</i> <sup>b</sup>	223	2.28	0.96	3.82	2.25	3.23
	Total	2911	29.9	17.3	68.8	49.7	71.6
Primary forests	<i>Photinia bodinieri</i> <sup>b</sup>	317	3.72	26.5	45.2	63.4	44.6
	<i>Photinia glabra</i> <sup>b</sup>	300	3.52	18.6	31.7	44.5	31.3
	<i>Cinnamomum glanduliferum</i> <sup>b</sup>	8	0.10	3.78	6.47	10.2	7.17
	<i>Celtis sinensis</i> <sup>a</sup>	417	4.89	3.00	5.13	8.19	5.76
	<i>Quercus fabri</i> <sup>a</sup>	17	0.20	1.67	2.86	5.05	3.55
	<i>Gleditsia sinensis</i> <sup>a</sup>	25	0.29	0.71	1.21	1.85	1.30
	<i>Pistacia chinensis</i> <sup>a</sup>	58	0.68	0.54	0.92	1.32	0.93
	<i>Carpinus pubescens</i> <sup>a</sup>	75	0.88	0.31	0.54	0.80	0.57
	<i>Platycarya longipes</i> <sup>a</sup>	267	3.13	0.30	0.51	0.67	0.47
	<i>Machilus microcarpa</i> <sup>b</sup>	17	0.20	0.29	0.50	0.62	0.44
	Total	1501	17.6	55.7	95.0	136.6	96.1

<sup>a</sup> Deciduous species.

<sup>b</sup> Evergreen species.

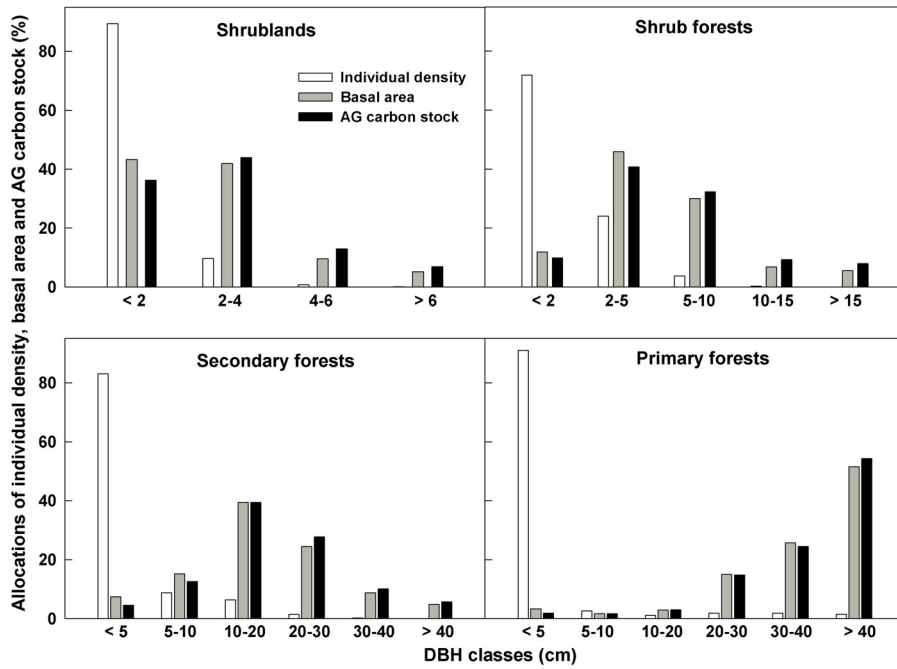


Fig. 3. Allocations of individual density, basal area and aboveground (AG) carbon stock among DBH classes in different vegetation types. DBH: diameter at breast height. Basal diameter (BD) instead of DBH was used in shrublands.

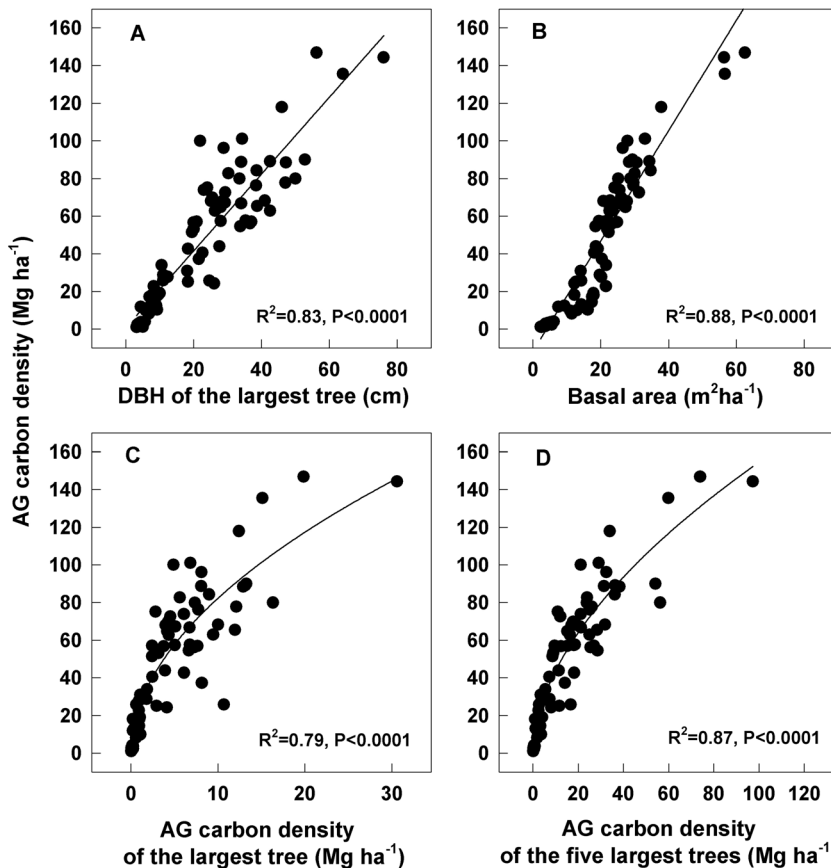


Fig. 4. The relationships between aboveground (AG) carbon density and DBH of the largest tree (A), basal area (B) and AG carbon density of the largest tree (C) and the five largest trees (D) across all sampling plots. DBH: diameter at breast height. Basal diameter (BD) instead of DBH was used in shrublands.

### 3.3. AG carbon stock and sequestration potential in Houzhai watershed

Due to the high habitat heterogeneity and human disturbances, natural vegetation coverage in this karst watershed is very low (Fig. 1). Natural vegetation has an area of  $2.56 \times 10^3$  ha (only 34.1% of the total watershed area) and patchily distributes on the hills, while croplands cover  $4.49 \times 10^3$  ha (59.8% of the total area). The total AG carbon stock of Houzhai watershed was  $85.9 \times 10^3$  Mg (Table 1), of which natural vegetation and croplands accounted for 73.9% ( $63.5 \times 10^3$  Mg) and 26.1% ( $22.4 \times 10^3$  Mg), respectively. Paddy fields cover 47.7% of the total area of this watershed, dry lands 12.1%, grasslands 2.32%, shrublands 16.5%, shrub forests 6.32% and secondary forests 9.01% (Fig. 2B). The AG carbon stock of paddy fields, dry lands, grasslands, shrublands, shrub forests and secondary forests in Houzhai watershed was 19.4, 3.00, 0.30, 5.13, 10.6 and  $47.5 \times 10^3$  Mg, respectively (Table 1), accounting for 22.6%, 3.49%, 0.34%, 5.97%, 12.3% and 55.3% of the total AG carbon stock of this watershed, respectively (Fig. 2B).

During the process of vegetation succession, the AG carbon stock could increase  $0.43 \times 10^3$  Mg (by 1.44 times) in grasslands,  $22.4 \times 10^3$  Mg (4.38 times) in shrublands,  $22.7 \times 10^3$  Mg (2.15 times) in shrub forests and  $48.6 \times 10^3$  Mg (1.02 times) in secondary forests when each natural vegetation type develops into the next stage (Fig. 5). The recent AG carbon sequestration potential of natural vegetation in the Houzhai watershed would be  $94.1 \times 10^3$  Mg, increasing by 1.48 times. The AG carbon stock would increase  $11.9 \times 10^3$  Mg (40.3 times) in grasslands,  $81.7 \times 10^3$  Mg (15.9 times) in shrublands and  $22.7 \times 10^3$  Mg (2.15 times) in shrub forests if these three vegetation types could develop into secondary forests, and the total AG carbon stock of natural vegetation would increase by 1.83 times. In theory, the AG carbon stock would potentially increase  $24.4 \times 10^3$  Mg (82.7 times) in grasslands,  $170.6 \times 10^3$  Mg (33.3 times) in shrublands,  $56.8 \times 10^3$  Mg (5.37 times) in shrub forests and  $48.6 \times 10^3$  Mg (1.02 times) in secondary forests if each vegetation type could grow into mature forests. The maximum AG carbon sequestration potential of natural vegetation in this watershed would be  $300.4 \times 10^3$  Mg, increasing by 4.73 times. The AG carbon stock would decrease  $13.3 \times 10^3$  Mg (by 68.6%) in paddy fields and decrease  $1.45 \times 10^3$  Mg (by 48.3%) in dry lands if the two cropland types were changed into grasslands (Fig. 5). However, the AG carbon stock would increase  $60.4 \times 10^3$  Mg (by 3.11 times) in paddy fields and increase  $17.3 \times 10^3$  Mg (by 5.78 times) in dry lands if the two cropland types could be converted into shrub forests. In this scenario, the maximum AG carbon

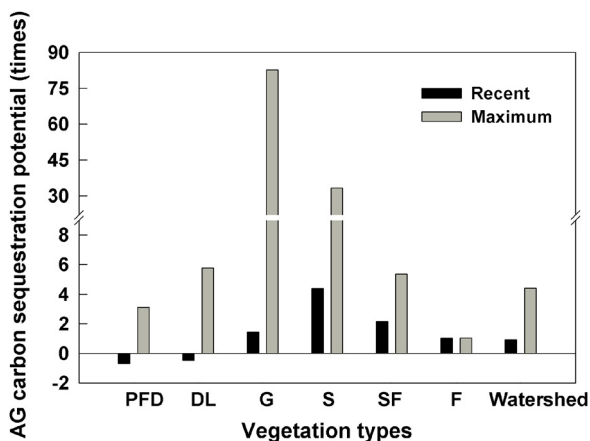


Fig. 5. The recent and maximum aboveground (AG) carbon sequestration potentials during the secondary vegetation succession in Houzhai watershed.

sequestration potential of the whole watershed would be  $378.1 \times 10^3$  Mg, increasing by 4.40 times (Fig. 5).

## 4. Discussion

To the best of our knowledge, this is the first report on the regional AG carbon stocks and sequestration potentials during natural karst vegetation recovery in southwestern China, which could provide important data for assessing the role of karst ecosystems in regional and global carbon cycle. Due to the very low total vegetation coverage and secondary forest coverage, the total AG carbon stock of Houzhai karst watershed was very limited. However, AG carbon density largely increased during the process of vegetation succession. We estimated that AG carbon stock in this watershed would increase by 92.5% in 50–100 years and by 4.40 times in 140–200 years if the degraded vegetation types could continue to develop into mature forests.

### 4.1. The accuracy of carbon estimate in the karst region

Given the large area of karst landscape in southwestern China, precise estimation of vegetation carbon stocks and sequestration potentials in this region is urgently needed for evaluating the role of Chinese terrestrial ecosystems in global carbon cycle. Only a few studies have just reported the biomass and/or carbon stock of karst forests (Yang and Cheng, 1991; Zhu et al., 1995; Xia, 2010; Liu et al., 2013; Tan et al., 2014), most of which used the generalized biomass allometric equations and ignored the differences among species. However, due to the high heterogeneity of karst habitats, karst forests were characterized by high diverse and complex species composition and large variations in allometry, architecture and wood density among plant species (Liu et al., 2009). Therefore, using the generalized biomass allometric equations would result in some errors those could not be neglected. Species-specific equations are very useful in assessing biomass estimates needed for accurate determination of carbon storage (Wang, 2006; N avar, 2009). Besides, karst plant individuals with the similar DBH show large variations in tree height due to high habitat heterogeneity. According to our data, the height of *P. longipes* individuals with a DBH of 15 cm varied from 6 to 15 m and the height of individuals across species with a DBH of 25–26 cm ranged between 7 and 24 m. In our previous study, DBH (or BD) coupled with height has been employed to establish species-specific equations for both woody and foliar parts (Liu et al., 2013), which could significantly improve the applicability of allometric equations to different habitats (Ketterings et al., 2001; Wang, 2006; N avar, 2009). Moreover, large variations in carbon content of wood and foliage among different species (Liu et al., 2013) were also taken into consideration in the current study for improving the accuracy of assessing vegetation carbon stocks (Bert and Danjon, 2006; Zhang et al., 2009). According to carbon allocation among species, the ten most important species were responsible for 85.5%, 78.5% and 71.6% of the total AG carbon stock of shrublands, shrub forests and secondary forests in Houzhai watershed, respectively (Table 2), and 52–58% of the total AG carbon stock were concentrated in the species considered for species-specific allometric models. Therefore, our study could provide more precise vegetation carbon estimates than before in the karst region.

### 4.2. Low carbon stock in the karst forests

The AG carbon density of grasslands ( $1.70 \text{ Mg ha}^{-1}$ ) in the karst region was significantly higher than the mean value ( $1.19 \text{ Mg ha}^{-1}$ ) of Chinese grasslands and higher than the average ( $1.13 \text{ Mg ha}^{-1}$ ) of grasslands in subtropical area of China (Fan et al., 2008). The AG carbon density of karst shrublands ( $4.15 \text{ Mg ha}^{-1}$ ) in this study was

close to the value ( $4.97 \text{ Mg ha}^{-1}$ ) of the similar community types measured by the harvest method (Tu and Yang, 1995), which was lower than the average of shrublands ( $7.06 \text{ Mg ha}^{-1}$ ) developed on calcareous soils in subtropical and tropical zones of China (Hu et al., 2006). The AG carbon densities of karst secondary forests ( $70.3 \text{ Mg ha}^{-1}$ ) and primary forests ( $142.2 \text{ Mg ha}^{-1}$ ) in our study were higher than the average forest carbon density in China ( $41 \text{ Mg ha}^{-1}$ ; Fang et al., 2007). However, AG carbon densities of secondary and primary karst forests were much lower than those of subtropical evergreen broad-leaved forests on non-karst habitats in the same latitudinal zone, such as secondary *Castanopsis fargesii*+*Machilus pauhoi* forest in Hunan province ( $126.6 \text{ Mg ha}^{-1}$ ; Gong et al., 2011), secondary evergreen broad-leaved forests in Zhejiang province ( $106.3 \text{ Mg ha}^{-1}$ ; Guo et al., 2014) and primary *Castanopsis rufescens*+*Lithocarpus xylocarpus* forest in Yunnan province ( $257.9 \text{ Mg ha}^{-1}$ ; Zhang et al., 2010) of China. Average biomasses of natural and artificial forests were also significantly lower in the karst region than in non-karst regions of China (Yu et al., 2010b; Liu et al., 2013). The low carbon stock in karst forests was mainly due to that ecosystem productivity in this region was largely limited by low water availability and the shortage of soil nutrients resulting from the shallow soil and high porous limestone (Zhang and Wang, 2009; Yu et al., 2010b; Guo et al., 2011). For example, the average depth of topsoil on karst hills was 2–9 cm, which was much lower than soil depths on other non-karst habitats (Zhang and Wang, 2009; Liu et al., 2013). Total nutrient stocks in the topsoil of forests and foliar nutrient concentrations were remarkably low in this region (Liu et al., 2014), and soil water was only sufficient for plant needs for 7–10 days following rainfalls heavy enough to exceed soil field capacity (Zhou and Pan, 2001). Compared with the forests in other karst regions of the world, AG carbon density of secondary and primary forests in our study was higher than that of secondary ( $55.5 \text{ Mg ha}^{-1}$ ) and mature ( $99.6 \text{ Mg ha}^{-1}$ ) forests in Mexico, respectively (Aryal et al., 2014), but lower than that of Mediterranean mature forests ( $172.0 \text{ Mg ha}^{-1}$ ) in Italy (De Simon et al., 2012). This could be explained by that annual precipitation was higher in our study site (1390 mm) than in the Mexican study site (950 mm) and lower than in the Italian study location (1800 mm), and that soil layer in the karst habitats of Italy was thicker and more fertile than that of China.

#### 4.3. Carbon accumulation and community structure during secondary succession

Carbon dynamics during the process of vegetation succession were attributed to the changes in species composition, community structure and environmental conditions (Culmsee et al., 2010; Drake et al., 2011; Hu et al., 2015). The density of woody plants dramatically increased during the initial stage of secondary succession and then gradually decreased in the later stages (Table 1). Main contributors to the total basal area and AG carbon stock shifted from plant individuals in the small diameter classes in shrublands to individuals in the large diameter classes in primary forests (Fig. 3). AG carbon density was also positively correlated with basal area (Fig. 4B), as reported by other authors (Slik et al., 2010; Borah et al., 2015; Hu et al., 2015). The contribution of the five largest trees to total AG carbon stock increased from 17.5% in shrublands to 54.2% in primary forests. These indicated that carbon increases in the early vegetation succession resulted from high recruitment of woody plants, while carbon accumulations in the later forests were mainly due to tree growth, as suggested by other authors (Aryal et al., 2014). At the beginning of the secondary vegetation succession on former grasslands characterized by very patchy and shallow soil and high exposure of carbonate rock, lots of dwarf shrub species (e.g., *R. cymosa*, *P. fortuneana* and *R.*

*heterophylla*) with high tolerance to serious drought and nutrient deficiency invaded and gradually formed the shrublands. However, these shrub species showed a low productivity and accumulated a small amount of AG carbon ( $4.15 \text{ Mg ha}^{-1}$ ). At the stage of shrub forests, many tree species gradually became dominant, species richness increased, and community structure tended to be more complex. Many deciduous trees (e.g., *P. longipes*, *C. platycarpa* and *R. martinii*) with a high growth rate grew quickly, produced a mass of leaves and closed the canopy, which largely improved the ecological and environmental conditions, through reducing transpiration and increasing soil fertility through litter decomposition. AG carbon density at this stage was still limited due to that communities mainly consisted of young trees and saplings. When vegetation grew into secondary forests, AG carbon density increased up to  $70.3 \text{ Mg ha}^{-1}$ , which was remarkably lower than that of undisturbed primary forests ( $142.2 \text{ Mg ha}^{-1}$ ). Secondary forests at the age of 70–90 years just recovered about 50% of AG carbon stock. Similar observations were reported for the secondary karst forests in Maolan National Natural Reserve, which could recover 66% of biomass of primary forests (Xia, 2010). On the karst habitats of Mexico, secondary forests only stored 56–79% of AG carbon stocks of the mature or undisturbed forests (Orihuela-Belmonte et al., 2013; Aryal et al., 2014).

The long recovery time required for secondary forests could be explained by the change in species composition from dominance of softwood species to hardwood species during the late stages of succession and the slower growth of these hardwood trees (Aryal et al., 2014). In our study, among the ten most important species, the contribution of deciduous trees to total AG carbon stock decreased from 55.4% in shrub forests, 47.8% in secondary forests to 12.6% in primary forests, while the contribution of evergreen trees increased from 23.0% in shrub forests, 23.8% in secondary forests, to 83.5% in primary forests (Table 2). The typical vegetation in this karst region is the mixed evergreen and deciduous broad-leaved forest. Forest degradation caused serious water and soil erosion (Wang et al., 2004). Deciduous trees are the main dominant species during the secondary succession, largely benefiting from their better adaptive strategies against drought stress than evergreen trees, which usually show a higher growth rate (Liu et al., 2011a) and lower wood density (unpublished data) than evergreen trees. Due to the harsh habitats, the speed of evergreen trees reaching a high level of dominance is extremely slow at the late succession stages. For example, evergreen trees just accounted for 25.0% of the total basal area and 23.8% of AG carbon stock in secondary forests. Moreover, as there are few acid insoluble materials in carbonate bedrock, the soil formation rate is extremely slow in this area (about ten thousand years to form 1 cm of soil; Wei, 1996). With the destruction of primary forests, nutrients lost along with the process of biomass removal and soil erosion and then total amount of soil nutrients reduced sharply. During the secondary vegetation succession, the limited soil nutrients were gradually transferred to vegetation pool and became less and less. Tree growth would be largely limited by the increasing nutrient shortage, especially at the late succession stages. For instance, compared with primary forests, most of AG carbon of secondary forests was stored in individuals in the medium DBH classes.

#### 4.4. Large carbon sequestration potential in the karst region

The sharp increases of AG carbon density during secondary vegetation succession and large areas of degraded vegetation indicated a great carbon sequestration potential in the karst region. The area of croplands in the karst region of southwestern China is extremely limited and is far from meeting the needs of local people (Jiang et al., 2014). Therefore, changing croplands into forests is considered to be very difficult in this region. The practical and



effective approach to improving regional carbon sink is protecting the current natural vegetation and promoting secondary vegetation succession. According to the tree-ring measurements and the regression relationships between the ages and DBHs of dominant trees in karst habitats (Zhu, 1997; Xia, 2010), the growth ages of shrublands, shrub forests, secondary forests and primary forests in our study were estimated to be 8–12, 16–32, 63–94 and 160–215 years, respectively. During secondary vegetation succession, the recent AG carbon stock of natural vegetation in Houzhai watershed will increase  $94.1 \times 10^3$  Mg (1.48 times) when each vegetation type develops into the next stage. In this scenario, it will need 8–20 years for shrublands to grow into shrub forests, about 50 years for shrub forests grow into secondary forests and about 100 years for secondary forests develop into mature forests. In theory, mature secondary forests would occupy 34% of the total watershed area and the maximum AG carbon sequestration potential would be  $300.4 \times 10^3$  Mg (increasing by 4.73 times) if all the degraded vegetation types could grow into mature forests. But this needs a very long recovery time. For example, the time needed for shrublands and shrub forests is roughly estimated to be 140–200 years.

The ten most important species in each vegetation type accounted for 71.6–96.1% of the total AG carbon stock, indicating that carbon pool in karst vegetation was determined by a few dominant species. Therefore, the population dynamics of these species will have significant influences on overall C stocks in this region. Combined with species-specific growth rates and adaptations to the environmental stress, this information is useful for selecting optimal species in long-term reforestation projects to improve regional carbon sink (Kirby and Potvin, 2007; Hu et al., 2015). There are many cultivated lands on the steep slope of karst hills, which show a very low productivity and serious soil erosion. Converting these dry lands into grasslands and/or economic plantations is considered an effective way to prevent soil erosion and increase regional carbon storage (Cheng et al., 2015). For grasslands and scattered shrublands occupying large area and lacking of tree species, to some extent, reforestation could accelerate the process of vegetation recovery. Some species like *P. longipes*, *I. yunnanensis* and *C. platycarpa*, which showed high growth rates and high tolerance to harsh karst habitats and high AG carbon stocks in most stages of secondary succession, could be suitable candidates for reforestation and carbon management programs. For shrub forests and secondary forests, AG carbon stocks were mainly concentrated in trees with small and medium DBH classes. Protecting these forests from wood cutting and fire is very important. Natural recovery would be the best way for carbon accumulation. In addition, total AG carbon largely depended on the large trees (Fig. 4C and D) and the five largest trees stored 23.8 and 31.8% of total AG carbon stocks in shrub forests and secondary forests, indicating that large trees were the main contributors to the carbon storage of karst forests, as reported in other areas (Chave et al., 2003; Culmsee et al., 2010; Lung and Espira, 2015). Therefore, conserving the existing large trees is very important for decreasing carbon release.

The total AG carbon stock of natural vegetation in Houzhai watershed was  $63.5 \times 10^3$  Mg. According to the ratios of belowground to AG biomass of grasslands (0.59), shrublands (0.78), shrub forests (0.57), secondary forests (0.41) and primary forests (0.37) in the karst areas (Luo, 2009; Ni et al., 2015), total natural vegetation carbon stock in Houzhai watershed was estimated to be  $93.1 \times 10^3$  Mg. Total carbon stock could increase by 1.40 times in 50–100 years and by 4.35 times in 140–200 years. Shrublands showed lower carbon density and stock in this watershed but had the largest carbon sink potential due to the largest distribution area. The grasslands and shrublands occupy ca. 52.5% of the total vegetation area in Guizhou province. If this two vegetation types

were converted into forests, the biomass carbon stock in Guizhou could increase by 3–4 fold in aboveground and 4–7 fold in belowground (Ni et al., 2015). In the karst region of southwestern China, the severity of rocky desertification can be mainly classified into potential, light, moderate and severe rocky desertification, with an area of 1331.8, 431.5, 518.9,  $249.7 \times 10^4$  ha, respectively (The State Forestry Administration of China, 2012), which is mainly occupied by shrub forests, shrublands, grasslands and exposed bare rock, respectively (Li et al., 2009; Bai et al., 2013). If these degraded vegetation types gradually recovered to secondary forests, total biomass carbon stock in the karst region of southwestern China could increase about 2.0 Pg, which is 14.6% of the current Chinese vegetation carbon stock (13.71 Pg; Yu et al., 2010a). Therefore, with the increasing success of rocky desertification control and vegetation restoration programs, the karst ecosystems in southwestern China will play an active role in mitigating the increasing CO<sub>2</sub> concentration in atmosphere.

## 5. Conclusions

This study clearly revealed significant aboveground carbon accumulations during secondary vegetation succession at a watershed scale in the karst region of southwestern China. With the changes in species composition and community structure, carbon increases in the early vegetation succession resulted from high recruitment of woody plants, while carbon accumulations in the later forests were mainly due to tree growth. The long time required for secondary forests to recover carbon density to the level of primary forests could be explained by the slow speed of large evergreen trees reaching a high level of dominance during the secondary succession on the harsh habitats. Carbon stock largely depended on a few dominant species and the large individuals. Although carbon density of karst forests was significantly lower than that of the forests on non-karst habitats in the same latitudinal zone, the degraded karst vegetation showed a great carbon sequestration potential due to the large distribution area in southwestern China.

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