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Variations of the biodiversity and carbon functions of karst forests in two morphologically different sites in southwestern China

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Abstract Knowledge of the biodiversity and carbon (C) functions of karst forests is scarce. This study comprehensively compared the species diversity and floristic characteristics, biomass and its allocation, leaf and soil C and nitrogen (N) concentrations, and photosynthetic capacity of dominant tree species between peak clump depression (PCD)-type and plateau surface (PS)-type karst forests on the basis of two large plots (i.e., 1 and 2 ha, respectively) in southwestern China. Results showed that PCD-type karst forest exhibits higher biodiversity and more tropical family and genus types than PS-type karst forest. These two types of karst forest presented similar total biomass, but PCD-type karst forest allocated more biomass to supporting roots and less biomass to absorbing roots. PS-type karst forest had higher C/N ratios in leaves and soils than PCD-type karst forest. Deciduous tree species in PS-type karst forest had low net photosynthetic rates, resulting in lower net photosynthetic rate in PS-type karst forest than in PCD-type karst forest. Species richness and C storage in the karst morphologies would be considerably enhanced if degraded vegetation in different types of karst area could be successfully restored to forests according to respective morphological and vegetation features. A comprehensive understanding of the biodiversity and C functions of karst vegetation is essential to biodiversity conservation, regional C storage estimation, vegetation management and restoration, and potential global change mitigation.

Keywords biodiversity; biomass; C/N ratio; net photosynthetic rate; karst morphology

Introduction

Biodiversity loss and global warming are two key issues of global environmental change. Forest approximately accounts for one-third of the global land area and is one of the dominant gene and carbon (C) pools on Earth. Thus, it contributes considerably to global biodiversity conservation and C sequestration (Dixon et al., 1994; Schimel et al., 2001; Pan et al., 2013; Anderson-Teixeira et al., 2015; Köhl et al., 2015). Species diversity, floristic characteristics, and C functions, such as biomass, carbon-to-nitrogen (C/N) ratio, and photosynthesis, of forests worldwide have been intensively investigated in the past several decades (de Vires et al., 2006; Luyssaert et al., 2007; Pereira et al., 2013; Zhu et al., 2013; IPCC, 2014; Liu et al., 2016a; Wheeler et al., 2016). However, given the difficulties in conducting field measurements or the lack of sufficient attention, the biodiversity and C functions of several types of forest have not been comprehensively inventoried. An example of such forest type is the mixed evergreen and deciduous broad-leaved forest developed in karst morphologies, which are largely, continuously distributed in subtropical and northern tropical climate zones. Significantly different from the typical evergreen broad-leaved forests (i.e., southeastern China) or deserts (i.e., northern Africa and central Asia) in non-karst regions in the same latitudinal zone, karst forests often grow on remote and steep mountains with special features of high vegetation fragmentation, high rate of rock exposure, high habitat heterogeneity, low water-holding and retarding capacities, and shallow and discrete soils. Such special features directly lead to the difficulties in field experiment implementation, particularly for vegetation root and soil sampling, and further limit studies on the biodiversity and C functions of karst forests.

Southwestern China (particularly Guizhou Province, Yunnan Province, and Guangxi Autonomous Region) has the largest, continuous distribution of karst morphologies worldwide. Peak clump depression (PCD)-type and plateau surface (PS)-type are two typical karst morphologies with the largest distribution areas and are the main obstacles to karst rock desertification, a desert-like landscape with exposed rock (Wang et al., 2013; Jiang et al., 2014). Geotectonically, PCD-type karst morphology is located in the mid-Yangtze Platform, and PS-type karst morphology is located in the South China Caledonian Geosyncline and its north platform subsidence belt. Topographically, PCD-type karst morphology lies in the steep slope transition zone of Yunnan–Guizhou Plateau and Guangxi plain

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and hilly land, and PS-type karst morphology lies in the Yunnan–Guizhou Plateau. As determined by geotectonics and topography, mountains in PCD-type karst morphology (approximately 45°) are steeper than those in PS-type karst morphology (approximately 30°), and slope further influences water balance, soil coverage, depth, and nutrients (Luyssaert et al., 2007; Zhang et al., 2012a; Wang et al., 2013; 2015; Liu et al., 2016b). Both karst morphologies are controlled by subtropical Asian monsoon climate systems. For low latitude and elevation, PCD-type karst morphology exhibits a relatively warm climate condition. Forests in both karst morphologies are largely fragile to anthropogenic disturbances, such as deforestation, overgrazing, and land degradation; once destroyed, rocky desertification occurs (Jiang et al., 2014). Thus, understanding the biodiversity and C functions of karst forests and further protecting these karst forests are necessary.

A PCD-type karst forest in southern Guizhou Province showed more heterogeneous habitats and higher woody species diversity than non-karst forests in the same climate zone (Guizhou Forestry Department, 1987; Zhu et al., 1993; Zhang et al., 2012a). Different succession stages of PS-type karst vegetation also exhibited a rich diversity of species (Liu et al., 2011). PCD-type and PS-type karst forests in Guizhou Province and Guangxi Autonomous Region presented lower biomass than non-karst forests in subtropical China, and PCD-type karst forests in southern Guizhou allocated more biomass to roots (Zhu et al., 1995; Yu et al., 2002; Zeng et al., 2007; Liu et al., 2009; Luo et al., 2010; Liu et al., 2013; Ni et al., 2015; Liu et al., 2016b). Soil organic carbon (OC) concentrations in PCD-type karst morphologies decreased with the increase in land use intensity; and forests showed higher soil OC concentrations than degraded vegetation, cropland, and bare land (Li et al., 2006; Yuan et al., 2007; Wu et al., 2009; 2012; Zhang and Pan, 2012; Huang et al., 2013).

However, most of the previously mentioned studies focused on certain biodiversity and C functions (sporadic and uncomprehensive) and were based on small plots (400 or 900 m^2) and limited soil pits (four soil pits), which could not represent all the features of the considerably heterogeneous karst habitats. Only OC concentrations of surface soils were analyzed in most studies. Some C function, like photosynthesis, has rarely been measured. Thus, a comprehensive inventory of biodiversity and C functions of karst vegetation based on large plots and a large number of soil samples should be performed. Furthermore, all previous studies focused on one morphological type of karst vegetation, and no comparison study among different morphological types of karst vegetation was conducted. On the basis of a 1 ha plot in a PCD-type karst forest in southern Guizhou and a 2 ha plot in a PS-type karst forest in central Guizhou (both plots are sufficiently large to cover all typical vegetation types and soils), this study aims to provide a comprehensive report on biodiversity and C function differences between two morphological types of karst forest, including species diversity and floristic characteristics, biomass and its allocation strategy, leaf and soil C and nitrogen (N) concentrations, and net photosynthetic rates of dominant tree species. This study will provide basic data for plant biodiversity and regional C budget estimation in karst morphologies in southwestern China. Moreover, it will contribute to the improvement of regional forest restoration and management and the reparameterization of global and regional vegetations and C models.

Materials and methods

Study areas

The data presented were collected from Dongge site in Maolan National Nature Reserve, Libo County, southern Guizhou, southwestern China (representative area of PCD-type karst morphology) and Tianlongshan site in Houzhaihe River watershed, Puding County, central Guizhou, southwestern China (representative area of PS-type karst morphology) (Fig. 1). Both areas are controlled by subtropical humid monsoon climates. According to records from local weather stations from 1961–2014, Libo and Puding counties had sufficient precipitation and inadequate illumination (low sunshine percentage), but Libo County had a higher temperature condition than Puding County (Table 1). Limestone and dolomite outcrops (particularly the former) are distributed everywhere in both areas. Forests are only distributed in hill tops with less anthropogenic disturbances; degraded vegetation and artificial cultivation occupy other places.

After complete vegetation surveys, a 1 ha plot at Dongge site in Maolan National Nature Reserve and a 2 ha plot at Tianlongshan site in Houzhaihe River catchment were established (Fig. 1). Dongge PCD-type karst forest was in the succession stage of climax with old stand age. The height of the tree layer reached 15–18 m. However, Tianlongshan PS-type karst forest was in the succession stage of subclimax, with high stand density, relatively small diameter at breast height (DBH), and short height of the tree layer (only 6–10 m). The two forests also presented different species compositions. Soils in the two forests were classified as limestone soil. Meanwhile, Dongge PCD-type forest had lower soil coverage and shallower soil depth than Tianlongshan PS-type forest (Table 1).

Stand investigation and biomass estimation

The living vegetation in the two large plots was fully investigated based on the field survey protocol of global forest dynamics permanent plots (Condit, 1995). For convenience, the plots were divided into small quadrats (each with an area of 10 m × 10 m). Slope and coverage of soil and vegetation of all quadrats were recorded. Then, every woody plant with DBH ≥ 1 cm was labeled and located (relative coordinates), and its species, DBH, height (or length), and crown length were recorded.

Vegetation root investigation was conducted in the plot (Dongge PCD-type karst forest) or beside the plot but with a similar habitat (Tianlongshan PS-type karst forest). A total of 10 and 25 soil pits (each with an area of 50 cm × 50 cm)

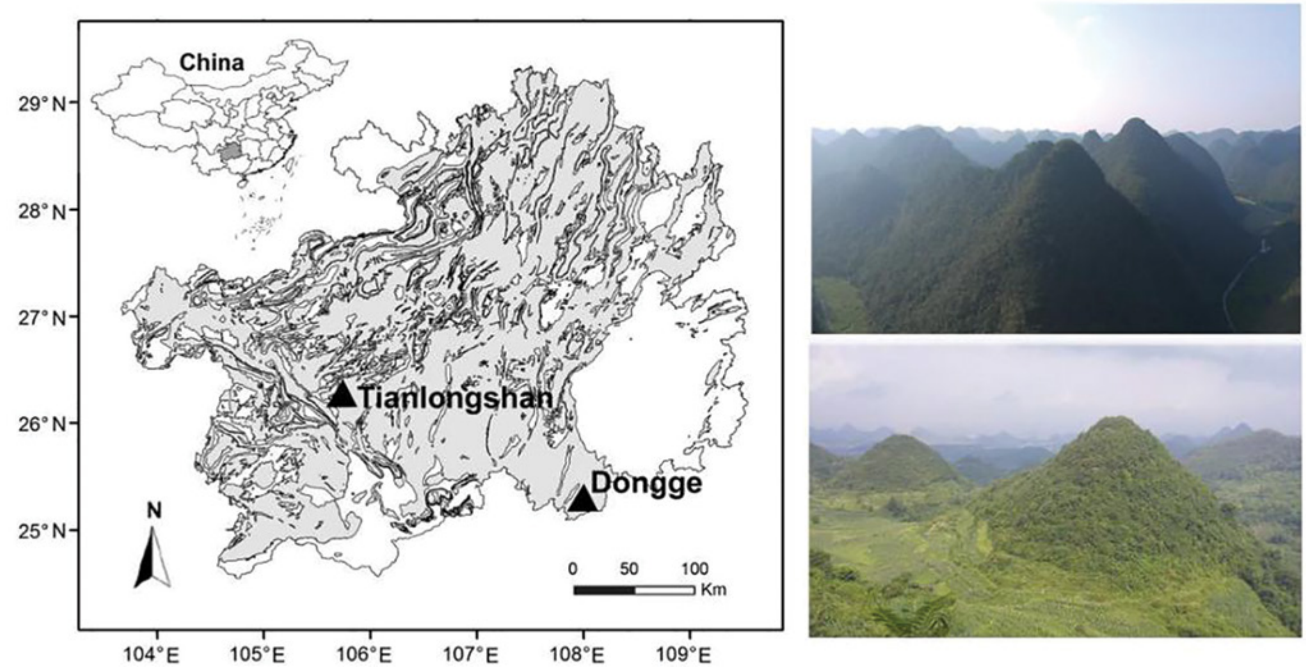

Figure 1. Location and physiognomy of Dongge peak clump depression-type karst forest in Maolan National Nature Reserve (top right) and Tianlongshan plateau surface-type karst forest in Houzhaihe River watershed (bottom right) in the distribution map of the karst area (in gray) in Guizhou Province, southwestern China.

Table 1. Environmental and stand characteristics of peak clump depression (PCD)-type and plateau surface (PS)-type karst forests. Density, average diameter at breast height, and average height were focused on woody plants with DBH ≥ 1 cm.

Items	PCD-type karst forest	PS-type karst forest
Location	107°57′ E, 25°19′ N	105°45′ E, 26°14′ N
Elevation (m)	860	1,450
Aspect	ES	S
Slope (°)	45	31
Annual temperature (°C)	18.3	15.2
Annual precipitation (mm)	1,269	1,367
Sunshine percentage (%)	26	26
Soil coverage (%)	15	55
Soil depth (cm)	25.9	44.8
Stand age (years)	More than 100	54
Density (individuals/ha)	5,993	8,410.5
Average diameter at breast height (cm)	5.7 ± 5.0	5.0 ± 4.2
Average height (m)	6.2 ± 4.4	5.4 ± 2.4
Dominant tree species	*Cyclobalanopsis myrsinifolia* (Blume) Oersted, *Platycarya strobilacea* Sieb. Et Zucc., *Celtis biondii* Pamp., *Clausena dunniana* Levl., *Castanopsis carlesii* (Hemsl.) Hay.	*Lithocarpus confinis* Huang, *Platycarya strobilacea*, *Itea yunnanensis* Franch., *Machilus cavaleriei* Levl., *Carpinus pubescens* Burk.

were dug into the bedrock in PCD-type and PS-type karst forests, respectively. Roots were sampled at every 10 cm layer, separated into coarse (root diameter ≥ 10 mm), medium (root diameter = 2–10 mm), and fine (root diameter ≤ 2 mm) roots, and finally oven-dried.

Biomass allometric functions in Zhu et al. (1995) and Liu et al. (2016b) were used to estimate aboveground biomass of each woody plant in PCD-type and PS-type karst forests, respectively. The average root biomass of the 10 and 25 soil pits in each forest was used to represent its total root biomass.

The species diversity and aboveground biomass in the present study were only focused on woody plants with DBH ≥ 1 cm.

Samples for determining C and N concentrations

Of 10 common tree species in each forest (i.e., *Acer wangchii* Fang, *Carpinus pubescens* Burk., *Rhododendron latoucheae* Franch., *Distylium myricoides* Hemsl., and *Swida parviflora* (Chien) Holub in Dongge PCD-type karst forest and *Pittosporum brevicalyx* (Oliv.) Gagnep., *Rhamnella franguloides* (Maxim.) Weberb., *Celtis sinensis* Pers., *Lindera communis* Hemsl., and *Fraxinus chinensis* Roxb. in Tianlongshan PS-type karst forest were additional species, except those mentioned in Table 1), 5 individuals with different DBHs were selected. Leaf samples were taken from the upper, middle, and lower layers. Mineral soil samples for determining the soil OC and N concentrations were collected while sampling root biomass. According to average soil depths of 25.9 and 44.8 cm, these soil samples were taken at two (Dongge; 0–10 and >10 cm) or four (Tianlongshan; 0–10, 10–20, 20–30, and >30 cm) depth ranges in each soil pit. Rocks and gravels were carefully wiped out of all soil samples.

Photosynthesis measurements

The net photosynthetic rates of dominant tree species were tested using LICOR-6400. As mentioned in the section "Samples for determining C and N concentrations" above, a total of 10 tree species (i.e., 5 evergreen species and 5 deciduous species) in each karst forest were tested. Five mature individuals were selected for each species. Sun-exposed branches were cut, instantly immersed in water, and tested.

Laboratory analyses

Leaf and soil samples were all oven-dried, comminuted, and sieved through a 0.2 mm sieve before chemical analyses. The C and N concentrations of leaves were determined using the iCAP 6300 ICP-OES Spectrometer Analyzer (Thermo Fisher Scientific, Waltham, MA, USA). The OC and N concentrations of soils were determined by the oil bath $K_2Cr_2O_7$ titration and Kjeldahl methods, respectively (Liu, 1996).

Statistical analyses

All statistical analyses were conducted using SPSS version 19. One-way analysis of variance and independent-sample *t* test were used to analyze the C and N concentrations and C/N ratio differences among (Tianlongshan) or between (Dongge) soil layers. Independent-sample *t* test was used to determine the climate differences between Libo and Puding counties, as well as the leaf C and N concentrations and C/N ratio differences between evergreen and deciduous tree species and between Dongge PCD-type and Tianlongshan PS-type karst forests. One-sample *t* test was used to show the fine root biomass/root biomass ratio differences among Dongge PCD-type karst forest, Tianlongshan PS-type karst forest, and other forests in the world.

Results

Species diversity and floristic characteristics

Dongge PCD-type karst forest had much richer species than Tianlongshan PS-type karst forest at the species (i.e., 204 to 66), genus, and family scales (Table 2). The Simpson index, Shannon–Weiner index, and Pielou's evenness index values in Dongge PCD-type karst forest (i.e., 0.97, 4.13, and 0.78, respectively) were all greater than those in Tianlongshan PS-type karst forest (i.e., 0.86, 2.43, and 0.58, respectively).

Dongge PCD-type karst forest had more tropical family and genus types than Tianlongshan PS-type karst forest. When cosmopolitan-type areas were not considered, the proportions of tropical to temperate family types of Dongge PCD-type and Tianlongshan PS-type karst forests were 71.70% to 28.30% and 61.54% to 38.46%, respectively, and the proportions of tropical to temperate genus types were 68.08% to 29.08% and 42.31% to 55.77%, respectively (Table 2).

Biomass

The total biomass of Dongge PCD-type and Tianlongshan PS-type karst forests were 161.7 Mg/ha and 155.8 Mg/ha, respectively. Dongge PCD-type karst forest showed a slightly higher total biomass than Tianlongshan PS-type karst forest. Dongge PCD-type karst forest allocated more

Table 2. Areal types of families and genera of woody plants with DBH ≥ 1 cm in peak clump depression (PCD)-type and plateau surface (PS)-type karst forests.

Area types	PCD-type karst forest				PS-type karst forest			
	No. of families	% of families	No. of genera	% of genera	No. of families	% of families	No. of genera	% of genera
1 Cosmopolitan	12	/	3	/	10	/	3	/
2 Pantropic	28	52.8	37	26.2	13	50.0	9	17.3
3 Tropical and Subtropical East Asia, (South) Tropical America disjuncted	6	11.3	6	4.26	2	7.7	1	1.9
4 Old World Tropic	2	3.8	13	9.2	1	3.8	3	5.8
5 Tropical Asia to Tropical Australasia Oceania	0	0	7	5.0	0	0	3	5.8
6 Tropical Asia to Tropical Africa	1	1.9	5	3.5	0	0	2	3.8
7 Tropical Asia	1	1.9	28	19.9	0	0	4	7.7
Subtotal of Tropical (2–7)	38	71.7	96	68.1	16	61.5	22	42.3
8 North Temperate	12	22.6	14	9.9	8	30.8	9	17.3
9 East Asia and North America disjuncted	1	1.9	11	7.8	1	3.8	9	17.3
10 Old World Temperate	0	0	4	2.8	0	0	4	7.7
11 Temperate Asia	0	0	0	0	0	0	1	1.9
12 Mediterranean, West to Central Asia	0	0	1	0.7	0	0	0	0
14 East Asia	2	3.8	11	7.8	1	3.8	6	11.5
Subtotal of Temperate (8–14)	15	28.3	41	29.1	10	38.5	29	55.8
15 Endemic to China	0	0	4	2.8	0	0	1	1.9
Total	65	100	144	100	36	100	55	100

biomass to roots (39.5 Mg/ha, 24.4% of the total biomass) than to aboveground components compared with Tianlongshan PS-type karst forest (20.3 Mg/ha, 13.0% of the total biomass). Among root biomass, Tianlongshan PS-type karst forest had 3.3 Mg/ha fine root biomass, which accounted for 16.3% of the total root biomass. By contrast, Dongge PCD-type karst forest had 2.2 Mg/ha fine root biomass, which only accounted for 5.5% of the total root biomass.

The aboveground biomass of Tianlongshan PS-type karst forest was more highly concentrated on a few species. Ten dominant woody plants in Dongge PCD-type karst forests only accounted for 56.0% of the total aboveground biomass. The corresponding biomass percentage of Tianlongshan PS-type karst forest was 97.3%. Only the two most dominant species (i.e., *L. confinis* and *P. strobilacea*) accounted for approximately 70% of the total aboveground biomass.

C and N concentrations in leaf and soil

Evergreen species had higher leaf C and N concentrations than deciduous species. This finding was true for Dongge PCD-type and Tianlongshan PS-type karst forests (Table 3). Dongge PCD-type karst forest presented significantly ($p < 0.01$) higher leaf C and N concentrations but significantly ($p < 0.01$) lower C/N ratios than their counterparts (evergreen and deciduous species) in Tianlongshan PS-type karst forest (Table 3).

Soil OC and N concentrations decreased with soil depth in both karst forests. The top soil layers (surface to 10 cm depth) had significantly ($p < 0.05$) higher soil OC and N concentrations. However, the soil C/N ratio showed a positive relationship with the soil depth (Table 3). Tianlongshan PS-type karst forest had a higher C/N ratio at same soil depth than Dongge PCD-type karst forest (Table 3).

Net photosynthetic rate

In general, the average net photosynthetic rate of all species in Dongge PCD-type karst forest was higher than that in Tianlongshan PS-type karst forest (Table 4), where the net photosynthetic rate difference of deciduous species was the main determining factor. That is, the net photosynthetic rate of deciduous species in Dongge PCD-type karst forest was significantly ($p < 0.01$) higher than that in Tianlongshan PS-type karst forest (Table 4). Deciduous species had significantly ($p < 0.01$) higher photosynthetic rate than evergreen species in Dongge PCD-type karst forest. However, Tianlongshan PS-type karst forest exhibited opposite results (Table 4).

Table 4. Net photosynthetic rate (μmol/m^2/s) of dominant tree species in peak clump depression (PCD)-type and plateau surface (PS)-type karst forests.

Items	PCD-type karst forest	PS-type karst forest
Evergreen species	6.8 ± 2.9	7.5 ± 1.8
Deciduous species	10.9 ± 5.3	4.8 ± 1.8
Average	8.9 ± 4.1	6.2 ± 1.8

Discussion

At the global scale, climate-related factors, such as latitude, elevation, temperature, and precipitation, primarily control the biodiversity of potential natural vegetation. However, at the local, landscape, and regional scales, other environmental factors, including floristic and stand characteristics, topography, slope, rock coverage, parent materials, soil depth and nutrients, habitat heterogeneity, and natural and anthropogenic disturbances, all affect vegetation biodiversity patterns (Grubb, 1977; Currie and Paquin, 1987; Su, 1996; Gaston, 2000; Long, 2007; Zhang et al., 2011). In the present study, Dongge PCD-type karst forest in Maolan National Nature Reserve had lower latitude and elevation and higher mean annual temperature than Tianlongshan PS-type karst forest in Puding County. These reasons explain why Dongge PCD-type karst forest had more species, higher diversity indices, and more tropical family and genus types than Tianlongshan PS-type karst forest. Precipitation does not seem to be a limiting factor that controls the vegetation biodiversity of the two karst forests when it exceeds 1,100 mm (Gaston, 2000). Biodiversity increases with the progressive succession of natural vegetation (Zhu, 1987; Liu et al., 2011), which is another major reason Dongge climax karst forest presented higher species diversity than Tianlongshan subclimax karst forest. Moreover, high habitat fragmentation creates diverse local niches for species appearance, particularly for rare species (≤1 individual/ha) (Zhang et al., 2012a). The number of rare species in Dongge PCD-type karst forest with high heterogeneous habitats (high coefficient of variation of soil coverage and depth) and Tianlongshan

Table 3. C and N concentrations (g/kg) in leaf and soil in peak clump depression (PCD)-type and plateau surface (PS)-type karst forests.

Items	PCD-type karst forest			PS-type karst forest		
	C	N	C/N	C	N	C/N
Leaf						
Evergreen species	478.9±18.8	22.3±6.3	21.5	456.4±18.7	14.1±3.0	32.4
Deciduous species	449.5±29.1	25.3±7.0	17.8	412.5±29.9	17.4±3.1	23.7
Mineral soil						
0–10 cm	77.1 ± 47.5	6.7 ± 4.7	11.5	69.0 ± 21.1	5.0 ± 0.8	13.9
>10/10–20 cm	26.1 ± 6.4	2.2 ± 0.7	11.7	53.7 ± 19.5	2.3 ± 1.0	23.2
20–30 cm	/	/	/	47.9 ± 29.1	1.5 ± 1.1	31.5
>30 cm	/	/	/	27.1 ± 14.0	0.8 ± 0.6	33.3

PS-type karst forest with low heterogeneous habitats (low coefficient of variation of soil coverage and depth) were 52 and 21, respectively.

Forest biomass and its allocation strategy in karst morphologies are jointly controlled by climate, soil, and topography. Dongge PCD-type and Tianlongshan PS-type karst forests presented a similar total biomass but showed completely different biomass allocation status. The aboveground biomass in Tianlongshan PS-type karst forest was highly concentrated in several dominant species compared with that in Dongge PCD-type karst forest. This finding can be attributed to the fact that Dongge PCD-type karst forest is located close to the tropical zone, i.e., warm climate conditions caused Dongge PCD-type karst forest to present many co-dominant tree species and further presented an even biomass allocation among species (Lv et al., 2007). Dongge PCD-type karst forest allocated more biomass to roots than Tianlongshan PS-type karst forest and non-karst forests in subtropical China (Ni et al., 2015). Moreover, among root biomass, the fine root biomass/total root biomass ratio of Dongge PCD-type karst forest was significantly ($p < 0.01$) lower than that of Tianlongshan PS-type karst forest and other types of forests in the world (Table 5). This finding indicated that Dongge PCD-type karst forest allocated more resources to support the plants to be firmly fixed rather than grow (absorption of nutrients and moisture) under adverse (steep slope and small amount of soil) habitats. The total biomass of climax forests in karst morphologies is determined by the soil amount rather than the climate (Yang and Cheng, 1991; Zhu et al., 1995). Dongge PCD-type karst forest exhibited a slightly higher total biomass than Tianlongshan PS-type karst forest at that moment; however, it exhibited a lower total biomass than the latter for a relatively smaller soil amount (lower soil coverage and shallower soil depth) after three years (Liu et al., 2018a). Soil amount caused by topography determined the total biomass, but climate determined the biomass allocation strategy in karst forests.

Researchers indicated that forest N concentration and C/N ratio are important indicators of forest C sequestration potential (Akselsson et al., 2005; de Vires et al., 2006; Reich et al., 2006). The present study investigated the N concentrations and C/N ratios in leaves and soils in two karst forests and determined that Dongge PCD-type karst forest showed higher leaf N concentration than the average value (20.1 g/kg) of global forests (Reich and Oleksyn, 2004) and lower soil C/N ratio than the average value (14.3) of global soils (Cleveland and Liptzin, 2007). This outcome indicated that Dongge PCD-type karst forest was a relatively high-N forest. By contrast, Tianlongshan PS-type karst forest showed lower leaf N concentration and higher soil C/N ratio than the average values of global forests and soils. This finding indicated that N was scarce in Tianlongshan PS-type karst forest. Previous research showed that anthropogenic N fertilizer application could increase the C concentrations in leaves and soils in non-karst forests in southwestern China (Du, 2006). Such experiment is recommended to be conducted when restoring forests in PS-type karst areas in the near future to potentially enhance the C sequestration (Liu et al., 2018b).

In general, plants with short leaf longevity usually present high net photosynthetic rates, and vice versa (Wright et al., 2004; Zhang et al., 2012b). However, deciduous trees had lower net photosynthetic rate than evergreen trees in Tianlongshan PS-type karst forest (Table 4). Furthermore, Tianlongshan PS-type karst forest presented lower net photosynthetic rate than Dongge PCD-type karst forest. This finding can be attributed to the fact that Tianlongshan PS-type karst forest is a low-N forest, as mentioned previously, and that leaf N concentration is a crucial influencing factor of photosynthesis (Evans, 1989). Forests with high elevation and low temperature usually have low photosynthetic capacity (Hikosaka et al., 2002), which is also an influencing factor. However, beyond all that, many dominant deciduous tree species in Tianlongshan PS-type karst forest, such as *C. pubescens*, *C. sinensis*, *R. frangu-loides*, and *F. chinensis*, are classified as slow-growing species with dense woody density; thus, these species have low net photosynthetic capacity (Wright et al., 2004, 2005).

With increasing interest in biodiversity conservation and climate change mitigation, degraded vegetations present considerable potential value in restoring forests (Martin et al., 2013; Liu et al., 2016c; Wheeler et al., 2016). In southwestern China, karst forests are particularly fragile to anthropogenic disturbances and intensive land use, resulting in karst primary and even secondary forests being found only in some natural reserves and remote hilltops. Rocky desertification land occupies approximately 22% of the total land area and degraded vegetations occupy approximately 30% of the total vegetation area in this region (ECVMC, 2007; Jiang et al., 2014). Karst primary forest exhibited significantly higher biodiversity and slightly higher C storage than secondary forest, and secondary forest showed significantly higher biodiversity and C storage

Table 5. Root biomass, fine root biomass, and fine root biomass/root biomass ratio in peak clump depression (PCD)-type karst forest, plateau surface (PS)-type karst forest, and other forests in the world.

Forest type	Root biomass (Mg/ha)	Fine root biomass (Mg/ha)	Fine root/total root ratio (%)	References
PCD-type karst forest	39.5	2.2	5.5	This study
PS-type karst forest	20.3	3.3	16.3	This study
Boreal forest	29.0	6.0	20.7	Jackson et al. (1996, 1997)
Temperate coniferous forest	44.0	8.2	18.6	Jackson et al. (1996, 1997)
Temperate deciduous forest	42.0	7.8	18.6	Jackson et al. (1996, 1997)
Tropical deciduous forest	41.0	5.7	13.9	Jackson et al. (1996, 1997)
Tropical evergreen forest	49.0	5.7	11.6	Jackson et al. (1996, 1997)

than degraded vegetations (Liu et al., 2011; Li et al., 2015; Ni et al., 2015). Thus, revealing the variations and determinants of the biodiversity and C functions of different types of karst vegetation and accordingly restoring the vast areas of degraded vegetation in different types of karst area would considerably enhance the biodiversity and C storage in karst morphologies. Therefore, comprehensive biodiversity and C function investigations of karst vegetation would provide basic data not only for regional and global vegetations and C model reparameterization but also for regional species composition and C inventory, vegetation management and restoration, and potential global change mitigation.

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