Vegetation in karst terrain of southwestern China allocates more biomass to roots

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Abstract

In mountainous areas of southwestern China, especially Guizhou Province, continuous, broadly distributed karst landscapes with harsh and fragile habitats often lead to land degradation. Research indicates that vegetation located in karst terrains has low aboveground biomass, and land degradation reduces vegetation biomass, but belowground biomass measurements are rarely reported. Using the soil pit method, we investigated the root biomass of karst vegetation in five degraded (successional) stages: grassland, grass-scrub tussock, thorn-scrub shrubland, scrub-tree forest, and mixed evergreen and deciduous forest in Maolan, southern Guizhou Province, growing in two different soil-rich and rock-dominated habitats. The results show that roots in karst vegetation, especially the coarse roots, and roots in rocky habitats, are mostly distributed in the topsoil layers (89 % on the surface up to 20 cm depth). The total root biomass in all habitats of all vegetation degradation periods is 18.77 Mgha\(^{-1}\), in which roots in rocky habitat have higher biomass than in earthy habitat, and coarse root biomass is larger than medium and fine root biomass. The root biomass of mixed evergreen and deciduous forest in karst habitat (35.83 Mgha\(^{-1}\)) is not greater than that of most typical, non-karst evergreen broad-leaved forests in subtropical regions of China, but the ratio of root to aboveground biomass in karst forest (0.37) is significantly greater than the mean ratio (0.26 ± 0.07) of subtropical evergreen forests. Vegetation restoration in degraded karst terrain will significantly increase the belowground carbon stock, forming a potential regional carbon sink.

1 Introduction

Karst is a highly special geomorphology mainly consisting of limestone and dolomite. This landscape is scattered in many areas worldwide, but continuously and widely distributed in southern America, the Mediterranean coasts, and China (Sweeting, 1972). China has approximately 3.44 million km\(^2\) of karst areas (buried, covered, and exposed...
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completely modified environment, the rock-covered habitat with less soil, and the lack of seed bank in such poor soil make natural restoration of the degraded forests difficult (e.g., Wang et al., 2004; Huang et al., 2008). To rehabilitate the degraded land, we must explore the factors triggering such degradation in geology, hydrology, ecology and human activities (Jiang et al., 2014), and further the features of restoration processes including changes of aboveground (AGB) and belowground biomass (BGB).

The unique karst morphology produces unique ecosystems in SW China. In subtropical China where the East Asian monsoon brings sufficient rainfall and warm air, forming rich, acidic yellow soils, the representative zonal vegetation is the evergreen broad-leaved forest (ECVC, 1980). In the karst mountainous region of SW China, the typical yet azonal vegetation is the mixed evergreen and deciduous broad-leaved forest growing in alkaline soils. The limestone and dolomite create very harsh habitats, and thin but calcic soils. The rainfall in this region is sufficient for plant growth (ca. 1100 to 1300 mm year\(^{-1}\)), but the leakage of soil water leads to low species growth, low biomass and productivity of community, and vulnerability of the forest to environmental change. The forest becomes thorn shrubland and dry grassland when degraded, like in other karst regions such as in Spain (Cerdà, 1997) and the Dominican Republic (Izzo et al., 2013). This change is typical outside of the core area of Maolan National Natural Reserve in southern Guizhou Province. Studies focus more on changes of community composition and structure in each restoration stage (Yu et al., 2002), but AGB has been rarely measured (Yang and Cheng, 1991; Zhu et al., 1995; Yu et al., 2002) and only one measurement of root biomass (RB) has been reported (Luo et al., 2010).

Roots have important functions in ecosystems worldwide. Roots sustain vegetation, especially forests, and connect the ecological processes of belowground and aboveground through the fluxes of materials and energy (Schenk and Jackson, 2002). RB and productivity are key factors of global and regional carbon cycles (Cairns et al., 1997), especially fine roots (Jackson et al., 1996, 1997; Matamala et al., 2003). Roots can protect soil against erosion. Root architectures (root density, root length density, root diameter, root area ratio, and root distribution) effectively decrease the soil de-
attachment rate, reducing the erodibility of root-permeated saturated top soils in karst mountains (De Baets et al., 2006, 2007a, b).

Roots in karst vegetation, especially in places occupied by rock outcrops, are usually displaced on rock surface and in gaps among rocks where very little soils exist. The harsh habitat in karst terrain makes biomass observations very difficult; only a few biomass measurements in Guizhou Province (in most cases, AGB) have been reported thus far (Yang and Cheng, 1991; Tu and Yang, 1995; Zhu et al., 1995; Yu et al., 2002). A mixed evergreen and deciduous broad-leaved forest with 95% rock outcrop in Maolan of southern Guizhou has an AGB of 89.198 Mg ha\(^{-1}\) in its tree layer, which was measured using the standard tree and harvest method (Yang and Cheng, 1991). Karst forests located in different parts of the mountains have different AGB, but the typical mixed evergreen and deciduous broad-leaved forest has a total AGB of 168.02 Mg ha\(^{-1}\), which is lower than that in other subtropical forests (Zhu et al., 1995). For these two studies, no RB of trees was measured; only those of understory shrubs and herbs (Yang and Cheng, 1991). The RB was measured in degraded karst shrublands in central Guizhou (Tu and Yang, 1995), but only values of total RB have been reported and no detailed sampling method can be found. The roots of shrubs were not separated to coarse, medium, and fine roots (Tu and Yang, 1995). A preliminary RB estimation in the forests, scrub-shrublands, and grasslands of Maolan was recently published (Luo et al., 2010), but the number of root samples was very limited (only four samples in each plot) and the RB was possibly not representative.

Research shows that in karst habitat, the AGB of mixed evergreen and deciduous forest is lower than that of zonal subtropical evergreen forest because the rocky and less soil habitat impedes plant growth (Zhu et al., 1995). Preliminary research with very limited root samples indicated that karst vegetation has higher RB than non-karst vegetation in the same bioclimatic zone (Luo et al., 2010). We hypothesize that more biomass allocates to the roots in karst vegetation, but more systematically established plots and samples are needed to prove this hypothesis. Therefore, we intensively re-sampled and re-estimated the RB of karst vegetation in Maolan. We considered three
aspects of the differences of RB: at various restoration stages, at different root diameter classes, and in different edaphic and rocky habitats. The aims of this study are to investigate the RB and its distribution in soil layers in the mountainous karst forest of SW China, in order to reveal the roles of RB in specific karst vegetation restoration and in potential carbon stock increment of degraded subtropical China.

2 Materials and methods

2.1 The study area

The study was conducted in Maolan National Natural Reserve (25°09′–25°21′ N, 107°52′–108°05′ E), located in Libo County of southern Guizhou Province, southern subtropical SW China (Fig. 1). The summer monsoon system brings rich rainfall and warm air. The average annual precipitation is 1148 mm in Libo city (25°25′ E, 107°53′ N, 428.7 m) and mainly falls from April to October (86%). The mean annual temperature is 18.3°C, with the temperature in January at 8.5°C and in July at 26.5°C. The air is humid (relative humidity is 79%) and the sky is very cloudy (sunshine percentage is only 24%).

The reserve is a typical peak-clump karst depression landscape (a cluster of small peaks with a common base) in a mountainous area covered by limestone and dolomite bedrock and with an altitude ranging from 430 to 1078 m a.s.l. (Fig. 1). The exposed rocks are distributed everywhere. The black limestone soil is very shallow and discontinuous, but rich in nutrition and calcium. However, soil water easily leaks out through the rock lacunas, resulting in a specific drought if sufficient rainfall is absent.

The karst topography, humid and warm monsoon climate, and specific edaphic and rocky microhabitats make the vegetation in this area different from other non-karst subtropical regions. Evergreen trees (accounting for ca. 65% of total species) mixed with a proportion of deciduous trees (35%) in the canopy and sub-canopy layers comprise the typical karst forest, a non-zonal soil climax that is widely distributed in subtropical
SW China. Abundant biodiversity and rich rare species can be found in this karst forest (Zhang et al., 2012).

Artificial fire for agriculture and fern picking, goat and cow grazing, and firewood are three major human disturbances in this region, although vegetation within the natural reserve is well protected. The restoration of degraded karst forest can be naturally performed. Such restoration usually passes through five periods, starting from the grassland, to grass-scrub tussock, thorn-scrub shrubland, scrub-tree forest, and finally to the mixed evergreen and deciduous broad-leaved forest (Yu et al., 2002).

2.2 Root biomass measurements

Five typical vegetation types representing five restoration stages mentioned above were chosen around the Laqiao and Yaogu villages found outside but close to the core area of the Maolan Reserve. Each vegetation type grows in two different soil-rich and rock-dominated habitats. Vegetation was intensively investigated in 10 plots, with a total area of 30 m × 30 m for forest, 20 m × 20 m for shrubland, 10 m × 10 m for scrub tussock, and 5 m × 5 m for grassland, respectively. Species name, height, diameter at breast height (the basal diameter for small shrubs), and crown range were recorded for woody plants. Species name, height, and coverage were surveyed only for herbaceous plants. The rock outcrop percentage was visually counted and the human disturbance was enquired (Table 1). Normally the grassland is built due to the artificial fire for collecting ferns (as a kind of vegetable) every year. The grass-scrub tussock is subject to heavy or light grazing by goats and cows. The thorn-scrub shrubland is exposed to the light cut-off for firewood. The scrub-tree forest and the mixed evergreen-deciduous broad-leaved forest are faced with light cow grazing.

The roots were sampled from July to September 2009. Measuring RB is time-consuming and prone to sampling error, especially in rocky soil (Park et al., 2007). By comparing three different methods of measuring RB (root coring, soil pit, and allometric equation) in six forest stands, Park et al. (2007) found that if the depth and diameter distribution of roots are required, soil pits are the only method allowing characterization
of root distribution by depth in rocky soil and can accurately characterize roots up to about 2 cm. Many roots extend for long distances into rock lacuna where few soils exist in the karst terrain (Fig. 1). Some roots can be seen in deep caves, and their lengths are unknown. The huge rock outcrops and steep slopes (normally 30–45°) make the access to a right sampling place very difficult. A normal root sampling strategy by marking five points an equal distance apart along two diagonals in a quadrat is therefore not possible here. Luo et al. (2010) dug four soil pits around an averaged standard tree in a quadrat to sample the roots, but the spatial representative of root samples is not sufficient. An “S” route was roughly setup in this study from the left corner in the lower elevation to the right corner of the upper elevation within each plot. Ten randomly selected soil pits in an area of 50 cm × 50 cm each were excavated using a shovel along the “S” route. Every soil pit was dug at soil layers of 10 cm interval until no roots were found. If rocks were encountered in multi-ways, we attempted to obtain the soils and roots around rocks and/or in rock gaps, gouges, and troughs. Roots on the rock surface were directly cut down. Roots in any gap among rocks were obtained as completely as possible using different digging, grabbing, and hollowing techniques. All soils and roots were stored in plastic bags and moved to the house in Laqiao village nearby.

Small rocks were removed from the soil samples, and then the soil samples were carefully washed, avoiding the loss of fine roots. All washed roots were air-dried in the room overnight. Roots were classified into three categories based on the root diameter: fine root (< 2 mm), medium root (2 to 10 mm), and coarse root (> 10 mm). The roots were stored in envelopes, oven-dried at 80 °C for 48 h, and weighed. Roots that were too large to be stored in envelopes, their total dry weight was calculated based on the ratio of fresh to dry materials of small pieces. RB in each plot was averaged according to the measurements of 10 soil pits.

Statistical test is performed using the F test (SPSS Inc., 2010).
3 Results

3.1 Root distribution

Roots in vegetation on karst terrain are mostly \( (p < 0.01) \) distributed in the top soil layers (Fig. 2). The first top layer (surface to 10 cm depth) accounts for 65\% and the second layer (10 to 20 cm) for 24\% roots. Roots in rocky habitats are more distributed in top layers (90.7 to 95\%) than those in earthy habitat (86.8 to 90\%), but this is not significant \( (p > 0.1) \). Coarse roots occur more slightly \( (p < 0.1) \) in the two top layers (92.5\%) than medium roots (89.2\%) and fine roots (88.8\%). This result is true in both rocky and earthy habitats. However, in rocky habitats, the roots of the three diameter classes in soil depth below 10 cm are all less than those in earthy habitat. No roots in soil depth between 50 and 60 cm in rocky habitat were detected and no coarse roots in soil depth between 40 and 60 cm were observed in both rocky and earthy habitats. The distribution of roots exhibits a similar pattern in different restoration stages as the general aforementioned pattern, but all roots in the stages of grassland, shrubby grassland, and scrub shrubland are only distributed in soil depth less than 30 cm (<20 cm in shrubby grassland). The scrub-tree forest has fine and medium roots in all layers from soil surface to 60 cm and coarse roots in soil depths less than 40 cm. The mixed evergreen-deciduous broad-leaved forest only has roots at depths less than 40 cm.

3.2 Root biomass

The total RB in all habitats of all vegetation types is 18.77 Mgha\(^{-1}\). The coarse roots have the largest biomass compared with those of medium and fine roots (all \( p < 0.01 \)). The total RB in rocky habitat is slightly higher than that in earthy habitat \( (p > 0.1) \). The coarse and medium roots have the same trend as the total, but the fine roots have a slightly higher biomass \( (p > 0.1) \) in earthy habitats than in rocky habitats (Table 2). During the vegetation restoration from grassland to mixed evergreen-deciduous broad-leaved forest, the total RB significantly increases by ca. sevenfold \( (p < 0.01) \).
coarse roots largely increase their biomass from grassland to grass-scrub and shrub-land (16-fold, \( p < 0.01 \)), and then increase again to shrub-forest and forest (2.5-fold, \( p < 0.1 \) to 3.4-fold, \( p < 0.05 \)). The medium and fine roots have changeable biomass in different restoration stages. Although the climax (mixed evergreen-deciduous broad-leaved forest) has the highest values among all stages, the pioneer stage (grassland) does not have the lowest values of fine and medium roots (Table 2). The climax forest in rocky habitat has the total RB of 39.55 Mg ha\(^{-1}\), whereas it in earthy habitat has a lower RB of 32.10 Mg ha\(^{-1}\).

Consistent with the root distribution (Fig. 2), the RB distribution has a similar pattern in different soil layers (Fig. 3). RB mostly concentrates on the surface up to 10 cm soil depth, accounting for 85.6% of total RB in all habitats. In 10 to 20 cm soil depth, only 12.6% of total RB is distributed; very few total RB occurs in soil layer > 20 cm. The coarse roots have the highest biomass (\( p < 0.01 \)) in each soil layer above 40 cm, following the medium and fine roots (Fig. 3a). This pattern also exists in rocky (Fig. 3b) and earthy habitats (Fig. 3c), except that coarse roots at 20 to 40 cm depth in rocky habitat have less biomass than medium roots (Fig. 4b). The biomass of coarse and medium roots in rocky habitat is higher (all \( p > 0.1 \)) than that in earthy habitat at soil depth < 10 cm, but the fine roots have slightly less biomass (\( p > 0.1 \)) in rocky habitats than in earthy habitats (Fig. 3b and c). At 10 to 20 cm soil depth, coarse roots have less biomass (\( p > 0.1 \)) in rocky habitats than in earthy habitats, but other roots have the opposite trend (all \( p > 0.1 \)). At depth of 20 to 40 cm, all roots (except for fine roots at 30 to 40 cm) in rocky habitat have less biomass (\( p < 0.05 \) for coarse root, and all \( p > 0.1 \) for medium and fine roots) than in earthy habitat (Fig. 3b and c).

On average, the total RB at soil surface to 10 cm increases from grassland to forest climax (\( p < 0.01 \)), but the difference between grass-scrub and scrub shrublands is not significant (\( p > 0.1 \), Fig. 4a). At 10 to 20 cm, the total RB in grassland is higher than in grass-scrub shrubland (\( p < 0.1 \)) and slightly higher than in scrub shrubland (\( p > 0.1 \)). At other depths, the scrub-tree forest always has higher total RB (\( p < 0.05 \)) than the mixed forest (Fig. 4a). However, roots in different diameter classes have very different
biomasses in each restoration stage (Fig. 4b–d). Forest climax has the highest RB in any diameter class from the surface up to 20 cm soil depth compared with other restoration stages ($p < 0.05$ only for forest climax to grassland comparison), except for medium root in grassland at 10 to 20 cm depth. Scrub-tree forest, scrub, and grass-scrub shrublands have intermediate RB at each layer, but their trends are changeable for different diameter classes. However, grassland shows higher fine RB (all $p > 0.1$) at soil depth $< 10$ cm than scrub-tree forest and shrubland (Fig. 4b). Grassland has higher medium RB at the first soil layer than grass-scrub shrubland and scrub-tree forest, and the highest medium RB ($p < 0.05$ for grass-scrub shrubland and $p < 0.1$ for scrub shrubland; $p > 0.1$ for others) at depth of 10 to 20 cm among all stages (Fig. 4c). Coarse RB in grassland is the lowest (all $p < 0.01$, Fig. 4d). The scrub-tree forest has the highest RB (in all diameters) in other soil layers less than 20 cm (Fig. 4b–d).

4 Discussion

4.1 Uncertainties of root biomass measurements on karst terrain

As mentioned above, accessing to a right place to sample roots in karst terrain is quite difficult because of the very steep slope, sharp and large extended outcrops, and extremely high heterogeneity of soil distribution (very few in some places and often distributed among outcrop gaps). The commonly used root sampling methods, namely, root coring and soil pit sampling, have to be modified in rocky soils (Park et al., 2007). The random selection of sampling sites is impossible on karst terrain. A site with general characteristics of the common habitat in a plot has to be subjectively chosen. Roots on outcrop surfaces are easily cut, but obtaining all of the roots on the surface is difficult because some roots extend to long distances or to very deep soils or both. Roots distributed in very deep soil and rock gaps are very hard to obtain, possibly underestimating the RB in karst vegetation. Distinguishing the root and root sprout of several shrubs and small trees is also difficult. Both roots and root sprouts were
harvested in this study, likely resulting in overestimated RB. Furthermore, coarser roots are encountered too rarely to be estimated by the method of soil pits (Park et al., 2007), resulting in an underestimate of coarse roots. In addition, the difficulty of sampling leads to insufficient root plot areas and inadequate duplicates for statistics. Although RB in this region was sampled using a similar method (Luo et al., 2010), the number of root samples was highly limited (only four soil columns in each vegetation type). Thus, this study is the first to comprehensively measure RB in karst vegetation of SW China.

Soils in karst terrain have extraordinary heterogenetic distribution, both vertically and horizontally (e.g. Wang et al., 2007). This distribution is ascribed to rock outcrops that are distributed everywhere and huge rocks that are embedded in deep underground. Soils are very shallow and tiny on the surface ground and unevenly, discontinuously distributed in deep underground. Therefore, root distribution is vertically and horizontally chaotic. Some roots are distributed on the surface ground and rock surface, some in long-distance rock gaps, and some in very deep rock gaps, even chiseling in deep belowground caves. Such heterogeneities of soil and root distributions result in a need of more soil and root samples to represent sufficiently the root distribution and to fulfill the statistical requirements. Ten soil pits with highly limited volume are insufficient, i.e., the RB in Maolan in this study is possibly underestimated. A greater number and larger-sized supplementary soil pits obtained via sampling using soil drilling equipment are needed. A better way is to set up grid points in 2–5 m intervals among grids.

The peak-clump depression is only one of the eight karst morphological types in SW China. The RB measurement is only a representative of vegetation in this kind of karst landscape. Other karst morphological types, such as the plateau surface type in central Guizhou Province, the gorge type in the west, the trough valley type in the north, the fault basin in northeastern Yunnan Province, and the peak-forest and plain type in northeastern Guangxi Autonomous Region, all need their own RB measurements to characterize their belowground features of local and regional vegetation.
4.2 Comparison with subtropical forests

The globally averaged root distribution for temperate and tropical forest ecosystems was approximately 60% of roots in the top 30 cm, estimated based on a soil depth of 2 m (Jackson et al., 1996). However in karst ecosystems the soil depth is mostly 50–60 cm only and ca. 95% of roots are distributed in the top 30 cm. A key reason is that most of roots, especially the coarse roots, must be allocated in the top soils to support the shoot to be firmly fixed in the harsh karst habitat. Similarly, ca. 98% of RB is in the top 20 cm soils in karst ecosystem, whereas ca. 50–70% of RB is allocated in the top 30 cm soils in world's temperate and tropical forests (Jackson et al., 1996).

Studies of mixed evergreen-deciduous forests at different habitats in Maolan (Yang and Cheng, 1991; Zhu et al., 1995) and of scrubs in central Guizhou Province (Tu and Yang, 1995) show that karst vegetation has lower ABG than other typical evergreen broad-leaved forests in subtropical China. A preliminary study indicated that RB in karst vegetation is not less than that of either broad-leaved or needle-leaved forests in subtropical China (Luo et al., 2010). The present study with more number of root samples further confirmed this finding, showing that our hypothesis of more biomass in karst vegetation being allocated to roots is true. However, it is not the RB in karst forest always significantly greater than that of typical evergreen forests, whereas it is the ratio of RB to AGB.

The RB of mixed evergreen and deciduous broad-leaved forest in Maolan is only greater than half of measurements of typical evergreen broad-leaved forests in subtropical regions (Table 3). The average RB in eastern (49.09 Mgha$^{-1}$) and western (59.37 Mgha$^{-1}$) subtropical regions are both higher than that of karst forest based on Luo et al. (2010) and this study (46.99 Mgha$^{-1}$). However the ratio of root to shoot in karst forest (0.37) is similar to and almost greater than the ratio of evergreen forests in the east (0.16–0.34) and in the west (0.24–0.37). In the world's boreal, temperate and tropical forest ecosystems the averaged root/shoot ratio (Jackson et al., 1996) is 0.25 (0.18–0.34). This difference is due to the suitable non-karst habitat favoring AGB.
accumulation and the harsh karst habitat favoring BGB. Plants growing in tiny, shallow soils and rocky habitats tend to allocate more resources to roots to maintain and physically support the ecosystem. On the other hand, dominant canopy tree species in karst forests have low net photosynthetic rate and low light photosynthetic productivity (Yang, 2011), but changes of hydraulic conductivity of deep tree roots may help the trees maintain the use of reliable water resources from depth (McElrone et al., 2007). Such eco-physiological evidences imply that karst forests have lower growth rate and lower biomass and productivity, but in such a shallow-water lacking environment more roots are developed to elevate deeper groundwater.

4.3 Implications for land rehabilitation and carbon increment

The harsh karst habitat is fragile. The root is the only physical support of woody plants in the tiny soil, rocky, and heterogenetic habitat, and is the only tissue that can absorb deep underground (river) water. The degradation or destruction of karst forest results in restoration difficulty of the original vegetation. After the disturbances of firewood cutting, fire, and grazing in Maolan area, karst vegetation can be more rapidly restored to scrub shrubland and woodland in 5 to 10 years because of its better natural environment and less interference of human activities. However, in Guanling area of central Guizhou Province, the cutting of the original karst forest in the late 1950s completely modified the local habitat, making the restoration of the original vegetation impossible for at least 50 years. This effect is ascribed to the extremely strong human-land contradiction in the plateau surface region of central Guizhou Province. Before the 1950s, the karst region of the entire Guizhou Province was mostly covered by forests, but in the 1980s to the 1990s, rocky desertification accelerated after karst forest degradation and heavy soil erosion (Zhang et al., 2006). In the 1990s to the 2000s, large-area and high-intensity afforestation slowly minimized rocky desertification, but complete control of the rocky desertification and improvement of local economy of the poor areas are still very difficult tasks. Therefore, an urgent need exists to protect the current karst forests, to restore the degraded vegetation, and to improve the quality of life of locals.
The area of scrub land (ca. $62.57 \times 10^3 \text{ km}^2$) and tussock and grassland ($29.68 \times 10^3 \text{ km}^2$) accounts for 52.5% of the total vegetation area in Guizhou (ECVMC, 2007). If this degraded land is converted into forested land, which currently only occupies ca. 23.7% of the total vegetation area, the biomass carbon stock in Guizhou Province could increase significantly by 3–4 folds in aboveground and 4–7 folds in belowground. This is a great potential carbon sink for mitigating regional climate warming in the future.

5 Conclusions

Forests on fragile karst habitat are easily degraded due to human disturbances in southwestern China, leading to significant rocky desertification. Root biomass of vegetation is reduced in different degraded stages from forest to scrub shrubland and tussock grassland. The ratio of root to aboveground biomass in karst forest is greater than that of evergreen forests in the subtropical China. This confirmed that plants growing in tiny, shallow soils and rocky habitat of karst terrain tend to allocate more resources to roots in order to maintain and physically support the ecosystem. However due to the extraordinary heterogenetic distributions of soils and roots in karst terrain, and the difficulty in access to every root in deep underground, root biomass might be underestimated in this study. More and larger-area soil and root samples are needed in future study.

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Table 1. Key features of 10 plots for root biomass sampling in Maolan National Natural Reserve, Guizhou Province, SW China.

<table>
<thead>
<tr>
<th>No.</th>
<th>Habitat</th>
<th>Restoration stages</th>
<th>Long/Lat</th>
<th>Altitude (m)</th>
<th>Slope (°)</th>
<th>Aspect</th>
<th>Dominant species</th>
<th>Coverage (%)</th>
<th>DBH (cm)</th>
<th>Height (m)</th>
<th>Density (No ha⁻¹)</th>
<th>Stand age (yr)</th>
<th>Human disturbance</th>
<th>Rock outcrop (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ML-23 Rock</td>
<td>Grassland</td>
<td>107°54.290′</td>
<td>25°23.634′</td>
<td>678</td>
<td>/</td>
<td>/</td>
<td>Pteridium revolutum, grass</td>
<td>/</td>
<td>/</td>
<td>1.0</td>
<td>/</td>
<td>10</td>
<td>heavy</td>
<td>40</td>
</tr>
<tr>
<td>ML-02 Rock</td>
<td>Grass-scrub tussock</td>
<td>107°55.559′</td>
<td>25°19.480′</td>
<td>907</td>
<td>35</td>
<td>SE40</td>
<td>Lindera communis, Triptiza sinensis</td>
<td>45</td>
<td>1.6 (BD)</td>
<td>1.4</td>
<td>2020</td>
<td>8–12</td>
<td>light</td>
<td>50</td>
</tr>
<tr>
<td>ML-06 Rock</td>
<td>Thorn-scrub shrubland</td>
<td>107°55.815′</td>
<td>25°18.598′</td>
<td>842</td>
<td>35</td>
<td>SE10</td>
<td>Lindera communis, Platycarya longipes</td>
<td>55</td>
<td>3.8</td>
<td>4.0</td>
<td>5600</td>
<td>12–18</td>
<td>very light</td>
<td>80</td>
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<tr>
<td>ML-13 Rock</td>
<td>Scrub-tree forest</td>
<td>107°57.263′</td>
<td>25°18.592′</td>
<td>851</td>
<td>40</td>
<td>WS14</td>
<td>Swida austroisinsisi, Clausena dunniana, Platycarya longipes</td>
<td>65</td>
<td>7.8</td>
<td>6.8</td>
<td>2775</td>
<td>60–133</td>
<td>no</td>
<td>80</td>
</tr>
<tr>
<td>ML-Q1 Rock</td>
<td>Mixed evergreen-deciduous broad-leaved forest</td>
<td>107°57.483′</td>
<td>25°18.653′</td>
<td>860</td>
<td>45</td>
<td>ES</td>
<td>Clausena dunniana, Platycarya longipes</td>
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<tr>
<td>ML-24 Soil</td>
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<td>107°53.777′</td>
<td>25°23.680′</td>
<td>647</td>
<td>/</td>
<td>/</td>
<td>Pogonatherum crinitum</td>
<td>/</td>
<td>/</td>
<td>0.2</td>
<td>/</td>
<td>0.5</td>
<td>heavy</td>
<td>5</td>
</tr>
<tr>
<td>ML-04 Soil</td>
<td>Grass-scrub tussock</td>
<td>107°58.018′</td>
<td>25°18.180′</td>
<td>743</td>
<td>20</td>
<td>SE30</td>
<td>Liquidambar formosana, Rhamnus crenata</td>
<td>85</td>
<td>1.5</td>
<td>1.0</td>
<td>1800</td>
<td>8–12</td>
<td>light</td>
<td>5</td>
</tr>
<tr>
<td>ML-08 Soil</td>
<td>Thorn-scrub shrubland</td>
<td>107°55.800′</td>
<td>25°18.610′</td>
<td>863</td>
<td>40</td>
<td>NW40</td>
<td>Lindera communis, Pyracantha atalantoides</td>
<td>50</td>
<td>3.9</td>
<td>4.1</td>
<td>4875</td>
<td>13–18</td>
<td>very light</td>
<td>10</td>
</tr>
<tr>
<td>ML-12 Soil</td>
<td>Scrub-tree forest</td>
<td>107°57.263′</td>
<td>25°18.211′</td>
<td>711</td>
<td>30</td>
<td>N</td>
<td>Swida parviflora, Lindera communis</td>
<td>75</td>
<td>8.6</td>
<td>6.9</td>
<td>1956</td>
<td>25–54</td>
<td>no</td>
<td>10</td>
</tr>
<tr>
<td>ML-Q2 Soil</td>
<td>Mixed evergreen-deciduous broad-leaved forest</td>
<td>107°57.350′</td>
<td>25°18.117′</td>
<td>925</td>
<td>30</td>
<td>ES, EN</td>
<td>Ilex ficoidea, Castanopsis carlesi var. spinulosa</td>
<td>75</td>
<td>9.6</td>
<td>8.2</td>
<td>2833</td>
<td>60–135</td>
<td>no</td>
<td>20</td>
</tr>
</tbody>
</table>

DBH: diameter at breast height; BD: basal diameter.
Table 2. Root biomass of karst vegetation in Maolan, southern Guizhou Province, SW China.

<table>
<thead>
<tr>
<th>Root biomass (Mgha(^{-1}))</th>
<th>All habitat</th>
<th>Rocky</th>
<th>Earthy</th>
<th>G</th>
<th>GS</th>
<th>S</th>
<th>SF</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fine root</td>
<td>1.72 ± 0.42</td>
<td>1.61 ± 0.43</td>
<td>1.84 ± 0.37</td>
<td>1.68 ± 0.03</td>
<td>1.58 ± 0.75</td>
<td>1.56 ± 0.11</td>
<td>1.60 ± 0.08</td>
<td>2.20 ± 0.04</td>
</tr>
<tr>
<td>Medium root</td>
<td>3.54 ± 1.39</td>
<td>3.87 ± 1.24</td>
<td>3.22 ± 1.45</td>
<td>3.40 ± 2.16</td>
<td>2.18 ± 0.26</td>
<td>3.68 ± 0.46</td>
<td>3.37 ± 0.17</td>
<td>5.09 ± 0.57</td>
</tr>
<tr>
<td>Coarse root</td>
<td>13.50 ± 10.34</td>
<td>13.77 ± 11.38</td>
<td>13.24 ± 9.19</td>
<td>0.57 ± 0.08</td>
<td>8.23 ± 0.30</td>
<td>8.53 ± 1.00</td>
<td>21.64 ± 1.77</td>
<td>28.54 ± 4.33</td>
</tr>
<tr>
<td>Total</td>
<td>18.77 ± 11.14</td>
<td>19.25 ± 11.66</td>
<td>18.29 ± 4.79</td>
<td>5.65 ± 2.28</td>
<td>11.99 ± 1.32</td>
<td>13.77 ± 0.43</td>
<td>26.62 ± 1.85</td>
<td>35.83 ± 3.72</td>
</tr>
</tbody>
</table>

G: Grassland; GS: Grass-scrub tussock; S: Thorn-scrub shrubland; SF: Scrub-tree forest; F: Mixed evergreen and deciduous forest.
Table 3. Root biomass (RB) and the ratio of RB to aboveground biomass (AGB) of typical evergreen broad-leaved forests in subtropical China.

<table>
<thead>
<tr>
<th>Region</th>
<th>Site</th>
<th>Location</th>
<th>Forest type</th>
<th>Age (yr)</th>
<th>RB (Mg ha(^{-1}))</th>
<th>AGB (Mg ha(^{-1}))</th>
<th>RB/AGB</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern-subtropical</td>
<td>Tiantong</td>
<td>121°47’ E, 29°48’ N, 260 m</td>
<td>Schima superba, Castanopsis carlesii</td>
<td>52</td>
<td>49.09</td>
<td>171.33</td>
<td>0.29</td>
<td>Yang et al. (2010)</td>
</tr>
<tr>
<td></td>
<td>Hangzhou</td>
<td>120°10’ E, 30°15’ N</td>
<td>Schima superba, Castanopsis carlesii</td>
<td>32–39</td>
<td>31.97</td>
<td>94.68</td>
<td>0.34</td>
<td>Yu et al. (1993)</td>
</tr>
<tr>
<td>Jiande</td>
<td>119°31’ E, 29°24’ N, 190–230 m</td>
<td>Cyclobalanopsis glauca</td>
<td>30–35</td>
<td>25.50</td>
<td>85.77</td>
<td>0.30</td>
<td>Chen (1993)</td>
<td></td>
</tr>
<tr>
<td>Minging</td>
<td>116°40’ E, 26°15’ N</td>
<td>Cycobalanopsis chungii</td>
<td>35</td>
<td>83.83</td>
<td>303.80</td>
<td>0.28</td>
<td>Huang (2006)</td>
<td></td>
</tr>
<tr>
<td>Wuyi Mt.</td>
<td>117°41’ E, 27°42’ N, 120 m</td>
<td>Castanopsis eyrei</td>
<td>51</td>
<td>56.46</td>
<td>350.82</td>
<td>0.16</td>
<td>Lin et al. (1996)</td>
<td></td>
</tr>
<tr>
<td>Dinghu Mt.</td>
<td>112°35’ E, 23°10’ N, 200 m</td>
<td>Cryptocarya concina, Schima superba, Machilus chinensis</td>
<td>400</td>
<td>38.18</td>
<td>170.20</td>
<td>0.22</td>
<td>Zhang and Ding (1996)</td>
<td></td>
</tr>
<tr>
<td>Dinghu Mt.</td>
<td>112°35’ E, 23°10’ N, 200 m</td>
<td>Castanopsis chinensis, Cryptocarya concina</td>
<td>400</td>
<td>51.77</td>
<td>243.87</td>
<td>0.21</td>
<td>Wen et al. (1997)</td>
<td></td>
</tr>
<tr>
<td>Dinghu Mt.</td>
<td>112°35’ E, 23°10’ N, 200 m</td>
<td>Cryptocarya concina</td>
<td>/</td>
<td>81.50</td>
<td>486.67</td>
<td>0.17</td>
<td>Yi et al. (2000)</td>
<td></td>
</tr>
<tr>
<td>Huitong</td>
<td>109°30’ E, 26°48’ N</td>
<td>Engelhardtia roxburghiana, Schima superba, Cyclobalanopsis glauca</td>
<td>33</td>
<td>23.52</td>
<td>132.90</td>
<td>0.18</td>
<td>Sun (2005)</td>
<td></td>
</tr>
<tr>
<td>Maolan</td>
<td>107°57’ E, 25°18’ N, 860–925 m</td>
<td>Castanopsis carlesii var. spinulosa, Clausena dunniana, Platycarya longipes</td>
<td>60–236</td>
<td>46.99</td>
<td>125.77</td>
<td>0.37</td>
<td>This study, Zhu et al. (1995), Luo et al. (2010)</td>
<td></td>
</tr>
<tr>
<td>Western-subtropical</td>
<td>Fumin</td>
<td>103°33’ E, 25°19’ N, 2300 m</td>
<td>Cyclobalanopsis delavayi</td>
<td>20</td>
<td>34.29</td>
<td>96.28</td>
<td>0.36</td>
<td>Dang et al. (1994)</td>
</tr>
<tr>
<td>Songming</td>
<td>102°45’ E, 25°24’ N, 2300 m</td>
<td>Castanopsis orthacantha</td>
<td>/</td>
<td>60.06</td>
<td>200.75</td>
<td>0.30</td>
<td>Dang and Wu (1994)</td>
<td></td>
</tr>
<tr>
<td>Ailao Mt.</td>
<td>101°25’ E, 24°10’ N, 2400–2600 m</td>
<td>Lithocarpus xylocarpus</td>
<td>166–325</td>
<td>106.67</td>
<td>287.44</td>
<td>0.37</td>
<td>Xie et al. (1996), Liu et al. (2002)</td>
<td></td>
</tr>
<tr>
<td>Puer</td>
<td>100°51’ E, 23°12’ N</td>
<td>Castanopsis echidnoca</td>
<td>12–42</td>
<td>24.34</td>
<td>100.85</td>
<td>0.24</td>
<td>Dang and Wu (1992)</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. Location of study area in the distribution map of karst terrain in China, and the less-human disturbed karst peak-clump depression landscape and well-protected, mixed evergreen and deciduous broad-leaved forest with roots distributed in rock outcrops in Maolan National Natural Reserve, southern Guizhou Province.
Karst vegetation allocates more biomass to roots

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Figure 2. Frequency of root appearance in soil layers. Note that the total number of plots for root biomass sampling is 10 in each vegetation type. A value of 10 indicates that roots occur in this soil layer in all 10 plots. A value of 0 indicates that no roots occurred in this soil layer in all 10 plots. RG: Rock-dominated grassland; SG: Soil-rich grassland; RGS: Rock-dominated grass-scrub tussock; SGS: Soil-rich grass-scrub tussock; RS: Rock-dominated thorn-scrub shrubland; SS: Soil-rich thorn-scrub shrubland; RSF: Rock-dominated scrub-tree forest; SSF: Soil-rich scrub-tree forest; RF: Rock-dominated mixed evergreen and deciduous forest; SF: Soil-rich mixed evergreen and deciduous forest.
Figure 3. Root biomass in different habitats: (a) all habitats; (b) rocky habitat; (c) earthy habitat.
Figure 4. Root biomass in different restoration stages. (a) Total roots; (b) fine roots; (c) medium roots; and (d) coarse roots. F: Mixed evergreen and deciduous forest; SF: Scrub-tree forest; S: Thorn-scrub shrubland; GS: Grass-scrub tussock; G: Grassland.