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PATTERNS AND RELATIONSHIPS OF PLANT TRAITS, COMMUNITY STRUCTURAL ATTRIBUTES, AND ECO-HYDROLOGICAL FUNCTIONS DURING A SUBTROPICAL SECONDARY SUCCESSION IN CENTRAL YUNNAN (SOUTHWEST CHINA)

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Abstract —Human-induced changes in land use lead to major changes in plant community composition and structure which have strong effects on eco-hydrological processes and functions. We here tested the hypothesis that changes in traits of living plants have resulted in changes in structural attributes of the community that influenced eco-hydrological functions by altering eco-hydrological processes. This was done in the context of a subtropical secondary forest succession following land abandonment in Central Yunnan (Southwest China). During the succession, species with high specific leaf area (SLA), high leaf nitrogen concentration (LNC), high specific root length (SRL), and low leaf dry matter content (LDMC) were progressively replaced by species with the opposite characteristics. The obtained results of correlation analyses were as follows: (1) Correlations were significant between community-aggregated SLA, LNC, and the leaf area index (LAI). Significant correlations were detected between LAI, canopy interception and stemflow, and surface runoff and soil erosion. (2) Significant correlations were also found between community-aggregated SLA, LNC, LDMC, and accumulated litter biomass. High accumulated litter biomass strongly increases the maximum water-retaining capacity of litter. However, significant correlations were not found between the maximum water-retaining capacity of litter and surface runoff and soil erosion. (3) Correlations were significant between community-aggregated SLA, LNC, and fine root biomass. Fine root biomass was not significantly related to the maximum water-retaining capacity of the soil, but was significantly related to surface runoff and soil erosion. These results suggest that canopy characteristics play a more important role in control of runoff and soil erosion at the studied site. It follows that plant functional traits are closely linked with canopy characteristics, which should be used as a standard for selecting species in restoration and revegetation for water and soil conservation.

Key words: Plant functional traits, forest ecological hydrology, community structure, water and soil conservation

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INTRODUCTION

The changes of land-use and climate induced by human activities lead to the changes in plant community composition, which subsequently influence the processing and functioning of ecosystems and eco-hydrology (Houghton, 1994; Vitousek et al., 1997; Chapin et al., 2000; Díaz and Cabido, 2001; Ahearn et al., 2005; Cortez et al., 2007; Podwojewski et al., 2008). Soil and water conservation is a key strategy in efforts to maintain ecosystem functions. However, alternations in land use and land management impose great pressures on watershed management due to their influence on soil erosion, hydrology, and water quality (Ahearn et al., 2005; Podwojewski et al., 2008). On the basis of these considerations, it is necessary to understand how changes in land use affect community properties and eco-hydrological functions, and how this relates to changes in the functional characteristics of living vegetation (Chapin et al., 1997, 2000; Díaz et al., 2007; Quétier et al., 2007).

Previous studies have demonstrated that eco-hydrological processes and functions mainly depend on the soil, vegetation properties, and features of living plants. For example, canopy cover, the leaf area index (LAI), mean tree height, forest floor, and forest root-bearing soil are thought to be the key factors affecting canopy and floor interception, runoff, and erosion control (Gash et al., 1995; Van Dijk and Bruijnzeel, 2001; Hartanto et al., 2003; Liu et al., 2003). Similarly, properties of the soil such as its organic matter, porosity, and cohesion, are also important in the control of surface runoff and erosion (Angers and Caron, 1998). In addition, certain plant traits can be used as mediators if they affect both ecosystem properties and functions. By using these traits, it should be possible to predict the ecosystem-level consequences of land use/cover changes for plant communities (Lavorel and Garnier, 2002; Gross et al., 2008; Suding et al., 2008).

There is evidence to support this hypothesis at both the species and community levels. At the species level, some leaf traits, e.g., specific leaf area (SLA), leaf dry matter content (LDMC), and leaf nitrogen content (LNC), affect litter decomposability and above-ground accumulated litter biomass (Cornelissen et al., 1999; Quétier et al., 2007). The same relationship can be extended to the community level. For example, community-aggregated traits (e.g., SLA, LDMC, and LNC) affect ecosystem properties and functions such as nutrient cycling, productivity, and invasiveness (Garnier et al., 2004; Xu et al., 2004; Cortez et al., 2007; Quétier et al., 2007). However, little information has been obtained about the relationships between plant traits, community structure, and eco-hydrological processes and functions.

The Central Yunnan Plateau is the keystone area for soil and water conservation in the Yangtze River basin. On the plateau, a continuous decrease of human activities during the twentieth century has dramatically altered patterns of vegetation type and cover in the course of successions. Previous studies conducted in the context of land abandonment have focused on two aspects: (1) vegetation composition and structure; and (2) eco-hydrological processes and functions. But there have been few attempts to integrate these aspects using plant functional traits in the context of successions. Many studies have shown that changes in vegetation properties and functions corresponded to a process whereby species with high SLA and LNC but low LDMC in the first stages following abandonment were successively replaced by species with the opposite characteristics as the succession proceeded (Garnier et al., 2004; Cortez et al., 2007). These traits have been identified as key factors, both for individual plants and for ecosystem functioning (Lavorel and Garnier, 2002; Eviner and Chapin, 2003; Garnier et al., 2004; Cortez et al., 2007; Suding et al., 2008) in keeping with the "mass-ratio" hypothesis (Grime, 1998), i.e., that species traits are weighted by the relative abundance of species (Garnier et al., 2004; Vile et al., 2006).

The aim of the present study was to clarify how changes in community structure and eco-hydrological functions are related to changes in vegetation functions with the context of a successional series in the Central Yunnan (China). In addressing the above question, we propose three hypotheses that focus on four functional traits important for soil and water conservation: SLA, LNC, LDMC, and specific root length (SRL). Our first hypothesis refers to the canopy. We expect that vegetation with low SLA and LNC but high LDMC has high LAI (Jouven et al., 2006) because of the trade-off between accumulation of foliage biomass in low-SLA species and the competitive advantage of high-SLA leaves (Read et al., 2006). During rainfall, canopies with a high LAI can intercept more rainfall and reduce surface runoff and soil erosion (Aston, 1979; Fleischbein et al., 2005).

Our second hypothesis concerns the litter layer. We expect that leaf traits [e.g., SLA, LNC, and LDMC (Wright et al., 2004)] can serve as markers of aboveground litter accumulation. Lower SLA and LNC but higher LDMC are related to lower decomposition and higher litter accumulation (Cortez et al., 2007; Quétier et al., 2007). We therefore expect that vegetation with lower SLA and LNC but higher LDMC, which has higher litter accumulation, will intercept more rainfall and slow and trap runoff and sediments.

The third hypothesis focuses on the forest's root-bearing soil. We expect that the trait SRL can serve as a marker of underground root structure and fine root biomass of vegetation (Berntson et al., 1995; Pregitzer et al., 2002). In root-bearing soil, the continuous 'root net' weaved by numerous fine roots plays an important role in increase of soil water storage capacity and decrease surface runoff and soil erosion.

MATERIALS AND METHODS

Study site

Field work was carried out at the ecological observation station of Mouding County (25°24'09''N; 101°28'18''E), approximately 200 km west of Kunming, capital of Yunnan Province in China. The average annual rainfall in the area is 846 mm (mid-subtropical climate zone), and the rainy season lasts from May to October each year. The average annual temperature is 16°C. The soil of the area is red earth. The original vegetation was a subtropical ever-green broad-leaved forest, which has now been almost completely destroyed. Within this area, four main categories of lands were selected and defined as follows: (1) Referencing abandoned land: the land has been closed at least seven years since the last domestic livestock grazing. (2) *Pinus yunnanensis* forest with a history of aerial planting on abandoned lands, followed by closing of the land for reforestation. (3) Needle-type broad-leaved mixed forest dominated by *Pinus yunnanensis* and *Keteleerla evekyniana*, with a history of clear cutting, followed by a period of about 35 years of forest reservation. (4) Natural secondary forest dominated by *Cyclobalanopsis glaucoldes* and *Keteleerla evekyniana*, with a history of clear cutting, followed by a period of about 45 years of forest reservation without any interruptions. For each community type, three non-contiguous duplicate plots (10×40 m permanent plots) were established. All 12 plots have similar climatic conditions, soil type, and slope gradient. Community composition data, species traits, community structural attributes, and ecosystem processes and functions were monitored for each plot (see below).

Species traits

Species accounting for at least 80% of the maximum standing live biomass of the community were identified and selected for trait measurement. Two types of data were collected. (1) The first type pertains to species composition, determined as described in a previous paper (Tang et al., 2007). It should be noted that the dominant species of abandoned land, *Keteleeria evekyniana*, has been replaced by *Eupatorium adenophorum* because of its extreme invasiveness. (2) The second type pertains to plant traits. In keeping with the floristic inventory and the hypotheses we posed, we measured four traits of 34 species selected in the four community types. These traits were: SLA, LDMC, LNC, and SRL. Plant traits were measured on 5-10 individual plants per species. These individuals were distributed evenly across the plots where they were present. Leaf traits were measured following standardized protocols (Cornelissen et al., 2003). Finally, for each plot, a community-aggregated plant trait value was calculated using the trait's value for each species in the corresponding community weighted by relative abundance of the species in the plot (Grime, 1998; Garnier et al., 2004).

Community structural attributes and eco-hydrological processes and functions

Community structural attributes were assessed using three main indices: LAI, aboveground accumulated litter biomass, and underground fine root biomass. Hemispherical photographs were taken vertically upward with a digital camera mounted on a leveling device. In each plot, photos were taken at a height of 1.5 m above the ground. The images of all plots were analyzed for LAI (WinScanopy, 2004a; Régent Instruments Inc., Sainte-Foy, Canada). Aboveground accumulated litter biomass in May was represented by the weight on 1 m^2 area after drying in a fan oven for 48 h at 60°C. In order to measure underground fine root biomass, three cores (7.6 cm in diameter) of the soil layer (0-30 cm) were taken randomly in each plot. Samples were soaked overnight to facilitate the separation of soil from roots. The roots were then carefully separated from the soil and washed under running tap water. After the roots were dried at 80°C for 48 h, we classified them into two diameter classes: fine (<2 mm) and coarse (>2 mm). The fine roots were weighed and the biomass data were converted to g/m^2.

During the rainy season from May to October of 2005, each day's precipitation was recorded by two automatic rain gauges and two standard rain gauges in an open area of the experimental station. Also, 10 sample trees were chosen in each forest. Under the canopy of each sample tree, a global collector was installed to collect the throughfall. In this study, we combined canopy interception and stemflow because the percent of stemflow is very low, using the formula:

$$I_c + S_f = P - T_f \quad (1)$$

where I_c = canopy interception; S_f = stemflow; P = precipitation; and T_f = throughfall. On the basis of the data taken on the 10 sample trees, we calculated canopy interception and stemflow for the forest as a whole. Maximum water-retaining capacity of litter was calculated as the difference between dry mass (80°C, 12 h) and wet mass (dipped in water for 24 h). The maximum water-retaining capacity of soil was calculated using the formula:

$$W_t = 10000\ P_t\ h \quad (2)$$

where W_t = the maximum water-retaining capacity of soil; P_t = total porosity of soil; and h = soil depth.

Runoff plots were laid out for the 12 plots selected for the investigation at the experimental station. Surface runoff was collected and its volume measured on every rainy day with an auto-fluviograph from May to October over four years (2004-2007). We also monitored soil erosion. A sample of about 500 ml was taken from the tank after thorough mixing to bring all the sediments into suspension. In the laboratory, a sub-sample of 100 ml was oven-dried at 105°C and weighed. The soil erosion data were then converted to $t/hm^2 \cdot a$. Finally, the data on surface runoff and soil erosion for four years were averaged to produce a new average volume characterizing each of the 12 plots.

Statistical analyses

The Pearson correlation coefficient was used to reveal correlations between field ages, plant traits for both species and community levels, community structural attributes, and eco-hydrological processes (canopy interception and stemflow, maximum water-retaining capacity of litter and soil) and functions (surface runoff and soil erosion). Correlation analyses were carried out using SPSS software (SPSS, Chicago, Illinois, USA).

RESULTS

Changes in plant traits, community structural attributes, and eco-hydrological processes and functions

At the species level, we recorded four functional traits for the four vegetation types. Values of SLA, LNC, and SRL showed a significant decrease with field age, while LDMC showed the opposite trend (Fig. 1). At the community level, community-aggregated traits displayed changes with field age similar to those of traits at the species level (Table 1). Community-aggregated SLA, LNC, and SRL showed a decreasing trend with field age, while LDMC showed the opposite trend (Table 1). Significant increases of community structural attributes (LAI, accumulated litter biomass, and fine root biomass) were detected in the secondary successional series (Table 1). In addition, canopy interception and stemflow also showed significant increase with field age. By contrast, the maximum water-retaining capacities of litter and soil, surface runoff, and soil erosion did not show any significant trend with field age (Table 1).

Relationships among plant traits, community attributes, and eco-hydrological functions

Correlation analyses revealed that community-aggregated SLA and LNC were significantly negatively related to LAI, accumulated litter biomass, and fine root biomass, while community-aggregated LDMC was significantly positively related to accumulated litter biomass (Fig. 2). Significant positive correlations were also found between LAI and canopy interception and stemflow, and between accumulated litter mass and the maximum water-retaining capacity of litter (Fig. 2). The increasing values of canopy interception and stemflow and of the maximum water-retaining capacities of litter and soil reduced surface runoff and soil erosion, but only canopy interception and stemflow had a significant effect (Fig. 2). In addition, significant correlations were also found between LAI and surface runoff and soil erosion, and between fine root biomass and surface runoff and soil erosion (Fig. 2).

Table 1. Field age, community-aggregated traits, community structural attributes, and eco-hydrological processes and functions for 12 plots. Key to abbreviations: SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; SRL, specific root length; LAI, leaf area index. The last line shows the Pearson coefficients between field age and community-aggregated traits, community structural attributes, eco-hydrological processes, and functions calculated with all plots. nd, not determined. Levels of significance: * P < 0.05; ** P < 0.01.

Field age (year)	**Community-aggregated traits**				**Community structural attributes**			**Eco-hydrological processes**			**Eco-hydrological functions**	
	SLA (m^2/kg)	LDMC (mg/g)	LNC (mg/g)	SRL (m/g)	LAI	Accumulated litter mass (g/m^2)	Fine root biomass (t/hm^2)	Interception of canopy and stem-flow (mm)	Maximum water-retaining capacity of litter (t/hm^2)	Maximum water-retaining capacity of soil (t/hm^2)	Surface runoff (m^3/hm^2·a)	Soil erosion (t/hm^2·a)
7	15.32	253.5	24.52	59.18	nd	77.2	1.021	nd	1.85	3813.2	29.28	5.55
7	16.29	247.9	25.43	67.54	nd	71.6	1.125	nd	1.93	4213.1	29.12	6.56
7	17.52	243.4	27.51	55.31	nd	69.6	1.260	nd	1.60	4385.4	113.37	30.00
25	12.86	437.9	25.47	31.56	1.7	212.0	0.735	32.58	7.00	3988.6	505.20	81.63
25	14.15	395.6	22.53	38.42	1.8	270.8	1.425	43.38	8.67	4152.9	52.47	9.79
25	13.65	412.9	26.07	30.68	1.7	181.2	0.853	36.99	6.16	4098.5	531.87	92.98
35	12.84	335.4	16.25	44.05	2.4	209.0	1.307	38.02	6.69	4211.1	186.36	29.78
35	10.24	389.3	19.07	43.91	2.8	233.6	1.847	47.34	8.18	4800.8	0.69	0.13
35	10.47	422.2	19.23	44.98	2.7	225.4	1.903	55.15	8.11	4459.1	2.43	0.42
45	9.25	363.2	18.74	49.12	2.8	302.4	3.586	59.44	11.49	4258.7	0.09	0.00
45	9.64	392.5	19.48	48.73	2.7	262.4	2.978	48.14	8.92	4126.4	3.54	0.20
45	9.18	376.3	18.29	45.41	2.6	200.6	3.047	54.15	6.62	4014.8	4.46	0.57
Pearson	-0.95**	0.69*	-0.83**	-0.43	0.85**	0.86**	0.78**	0.77*	0.87**	0.18	-0.18	-0.24

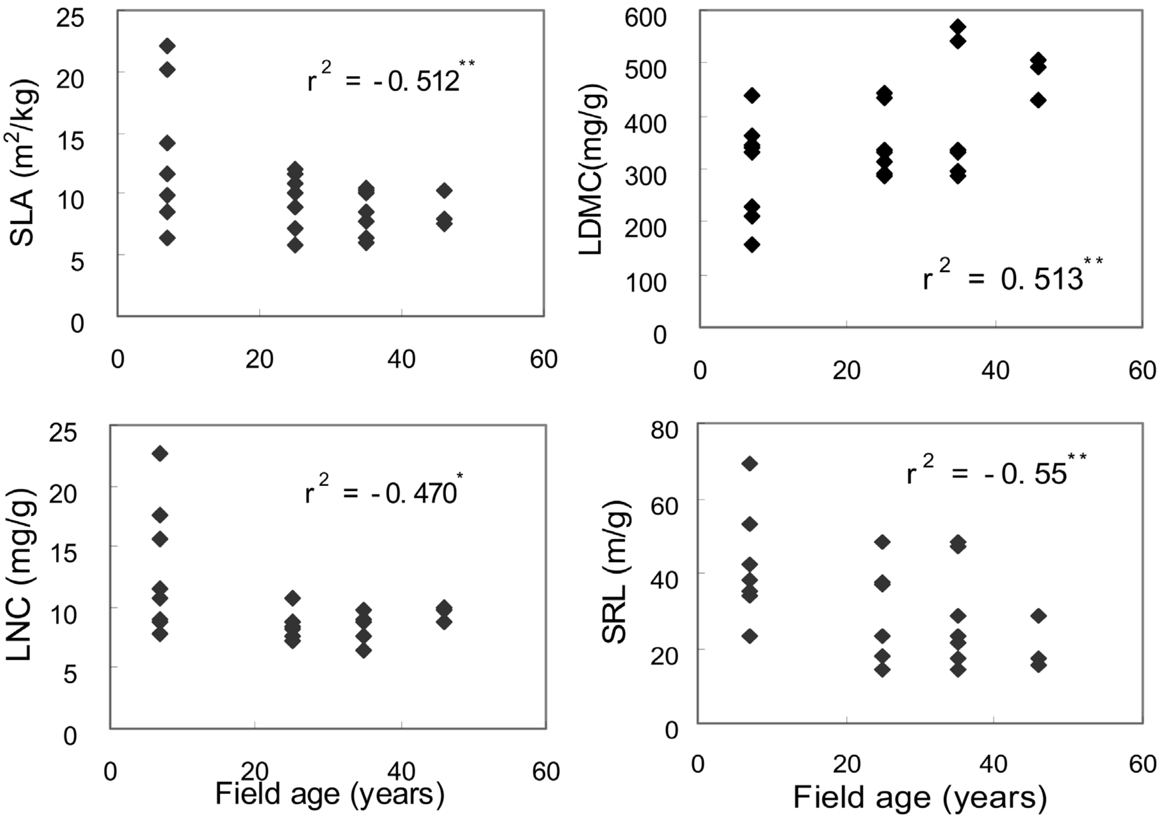

Fig. 1. Relationships between field age and leaf traits of the most abundant species of the communities. SLA, specific leaf area; LNMC, leaf dry matter content; LNC, leaf nitrogen concentration; SRL, specific root length. Pearson correlation coefficients are given in the figures. Levels of significance: * P < 0.05; ** P < 0.01.

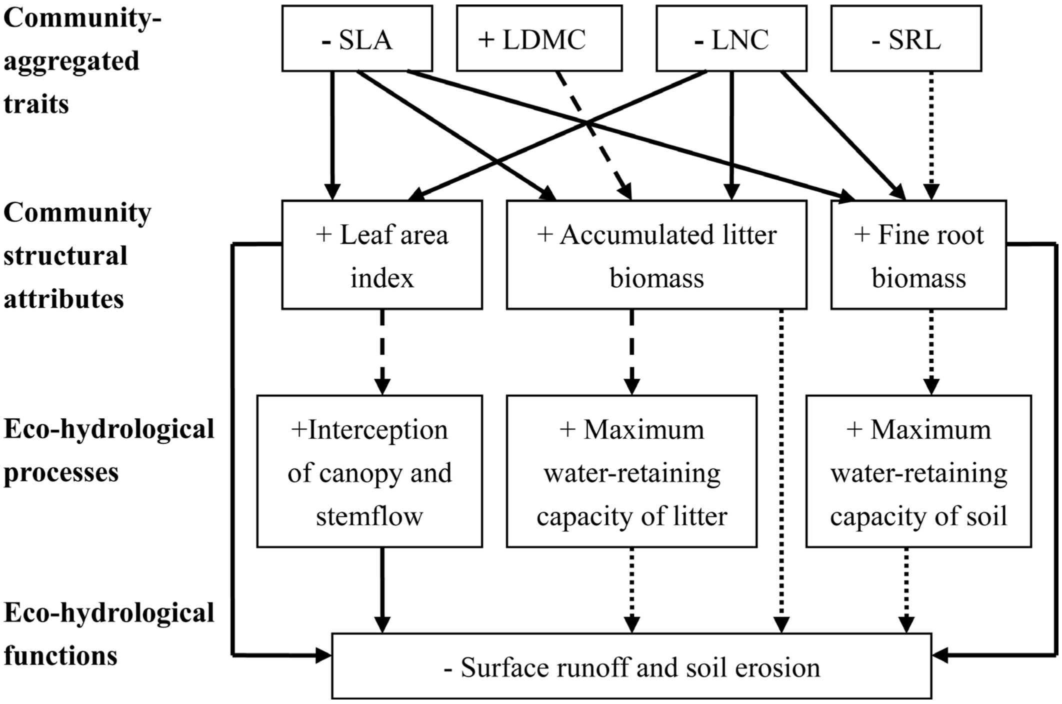

Fig. 2. Relationships between community-aggregated traits, community structural attributes, and eco-hydrological processes and functions. The arrows indicate significant negative correlations between two variables. The dashed arrows indicate significant positive correlations between two variables. The dotted arrows represent no significant correlation between two variables. Plus (+) and minus (-) signs indicate the direction of the variable's response to field age during secondary succession. SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; SRL, specific root length.

DISCUSSION

Succession, plant traits, and vegetation structure

For any given forest structure, changes in plant traits at species and community levels (Fig.1, Table 1) have been observed in different types of successions. At the species level, fast-growing species with high SLA and LNC but low LDMC in early stages of succession were progressively replaced by slow-growing species with low SLA and LNC but high LDMC (Huston and Smith, 1987; Bazzaz, 1996; Garnier et al., 2004). This pattern is consistent with other research results (Ellsworth and Reich, 1996; Garnier et al., 2004; Yan et al., 2006). At the community level, the values of community-aggregated traits displayed the trends similar to changes at the species level. The reason for this may be replacement of species with different trait values (interspecific variation), changes in trait values within a species (intraspecific variation), or a combination of the two (Garnier et al., 2004). However, intraspecific variability in trait values of dominant species was much lower than interspecific variability, as shown elsewhere for some traits (Ellsworth and Reich, 1996; Garnier et al., 2001, 2004). It follows that changes in community-aggregated trait values may be due to replacement of species with different trait values.

In eco-hydrology, LAI, litter biomass, and fine root biomass are very important indices in predicting and controlling rainfall interception, runoff, or soil erosion (Granier et al., 1999). Our results showed that LAI, accumulated litter biomass, and fine root biomass displayed increasing trends in the secondary succession. This is mainly caused by the increase in standing biomass of the communities. The first decade of forest succession after site abandonment is characterized by vegetation dominated by grasses, shrubs, and forbs. After this period, the canopy is dominated by long-lived, taller-statured, but nevertheless light-demanding tree species, concurrent with rapid increase in above- and underground biomass. Eventually, the canopies of these secondary stands may be replaced by other shade-tolerant species. In old-growth forest, the total standing biomass may be positioned at a peak.

Relationships among plant traits, community structural attributes, and eco-hydrological functions

Community structural attributes were strongly related to community-aggregated traits: those communities with low SLA and LNC have high LAI and fine root biomass. Those communities with low SLA and LNC but high LDMC had high accumulated litter mass. The negative SLA-LAI relationship means that accumulated leaf biomass increases more quickly than SLA because values of LAI depend on SLA and living leaf biomass (Jouven et al., 2006). The negative LNC-LAI relationship may not be a direct relationship. High SLA means that higher photosynthetic rates, light-capture area per gram, and accumulated biomass of foliage in low-SLA species will be higher than in high-SLA species because of the counterbalance between greater accumulation of foliage in low-SLA species and the competitive advantage of high-SLA leaves (Read et al., 2006). Similarly, the same counterbalance led to negative LNC/SLA-fine root biomass relationships. In addition, changes in the accumulated litter mass are probably due to the combination of increase in the rate of litter input per unit of ground area as the standing biomass of the communities increase and decrease in the rate of litter decomposition as fast-growing species are progressively replaced by slow-growing species producing a litter of lower quality (low LNC and SLA but high LDMC) (Garnier et al., 2004; Cortez et al., 2007; Quétier et al., 2007).

The relationships between community structural attributes and eco-hydrological processes and functions showed that high LAI and fine root biomass strongly reduced surface runoff and soil erosion. The maintenance of eco-hydrological functions mainly depends on three things: (1) The forest canopy. The value of LAI is an important index of the forest canopy. High LAI obviously increased canopy interception of rainfall, which significantly reduced surface runoff and soil erosion. (2) The litter layer. The significant relation between litter mass and water-retaining capacity of litter in our study suggests that the greater the accumulated litter mass, the more rainfall was intercepted by the litter layer. However, increase in the maximum water-retaining capacity of litter in our study did not significantly reduce surface runoff and soil erosion during the secondary succession. This result suggests that the litter layer may play a less important role in controlling surface runoff and soil erosion in comparison with the forest canopy. (3) Root-bearing soil. The continuous root net composed of lateral roots plays an important role in increasing the maximum water-retaining capacity of soil and reducing surface runoff and soil erosion. Our results showed that increase of fine root biomass significantly reduced surface runoff and soil erosion. However, in this process, changes in the maximum water-retaining capacity of soil led by root mass did not have too many effects in controlling surface runoff and soil erosion. These results suggest that canopy characteristics are of great importance in controlling runoff and soil erosion. It follows that plant functional traits tightly linked to canopy characteristics can be used as a basis for species selection in the restoration of water and soil resources and revegetation of forests in Central Yunnan.

Implications for forest management and restoration

The Central Yunnan Plateau is the keystone area for soil and water conservation in the Yangtze River basin. The most important issue for forest managers and ecologists is to achieve effective water and soil conservation in forests on the plateau. Often the first step in restoration is to maintain the local species pool by active planting (Palmer et al., 1997; Parker, 1997). However, the success of community restoration in Central Yunnan is at high risk due to stressful ecological conditions. On the one hand, drought and infertile soils threaten the survival of seedlings and saplings; on the other hand, the restored community can effectively reduce surface runoff and soil erosion. To reconcile these two contrasting aspects, our study suggests selection of mid-successional species for restoration projects, especially trees and large shrubs. This strategy is derived from the tradeoffs between plant responses to stressful ecological conditions and the effects of plants on community structural attributes and eco-hydrological processes and functions. In the early stages of succession, although fast-growing species with high SLA, LNC, and SRL but low LDMC can quicken nutrient turnover time through a high litter decomposition rate, the obtained decreases in accumulated standing biomass, litter biomass, and fine root biomass do not effectively control surface runoff and soil erosion. In later stages of succession, slow-growing species can maintain certain eco-hydrological processes and functions through high LAI, litter biomass, and fine root biomass, but cannot successfully adapt to stressful ecological conditions (e.g., high light, low soil water and nutrient content). Accordingly, we believe that introducing mid-successional, rather than late-successional or early-successional species, may be more desirable for restoration in Central Yunnan for several reasons: (1) Mid-successional species are mostly drought-tolerant and infertile-tolerant forms, ones whose regeneration niches are usually linked to open areas (Valiente-Banuet et al., 2006; Padilla et al., 2009), and their use should help to increase restoration success. (2) They tend to have higher SRL and deeper roots at the seedling stage, which is critical for survival in the dry season (Padilla and Pugnaire, 2007), essential for the establishment of earlier protection against erosion. (3) They facilitate the recruitment of drought-sensitive species under their canopies (Padilla and Pugnaire, 2006), speeding up the succession in a natural way towards a mature community (Padilla et al., 2009).

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