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Leaf and Stem Traits are Linked to Liana Growth Rate in a Subtropical Cloud Forest

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Abstract: There is accumulating evidence that the abundance and biomass of lianas are increasing with global climate change in the Neotropics. However, our knowledge of growth–trait relationships among lianas is surprisingly rare. Here, we monitored the relative growth rate of 2860 individuals from seven deciduous and four evergreen liana species in a 20 ha subtropical cloud forest dynamics plot at high elevation (2472–2628 m a.s.l.) in southwest China. We linked the relative growth rate of lianas with nine leaf traits associated with leaf morphology, nutrient concentrations, and water hydraulic capacity as indicated by leaf vein density, and five stem wood traits related to stem water transport capacity and wood density. Our results showed that deciduous lianas have higher relative growth rates than their evergreen counterparts. Across all lianas studied, the relative growth rate was positively correlated with the leaf area and specific leaf area, but negatively correlated with leaf dry matter content. The relative growth rate of lianas was strongly correlated with nitrogen concentration after excluding the legume liana species. The relative growth rate was decoupled from leaf phosphorus and potassium concentrations, leaf vein density, and stem vessel traits across all lianas investigated. For four evergreen lianas, there were positive associations of the relative growth rate with the leaf thickness and diameter of the largest vessels. This study is the first to illustrate the relationships of liana growth with leaf and stem traits in the high-elevation subtropical cloud forest. More studies from diverse forest ecosystems are needed to comprehensively understand the mechanism underlying liana growth patterns.

Keywords: functional traits; nutrient concentrations; stem hydraulic conductivity; subtropical forest; vein density; woody climbers

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1. Introduction

Plant traits are morphological, physiological, and reproductive properties that potentially determine plant fitness via direct or indirect effects on individual growth, reproduction, and survival [1]. Over the last two decades, trait-based studies on plant performance (e.g., growth) have received particular attention. To date, it is still an open question as to whether plant traits are strongly linked with their growth rate [2–5]. The majority of previous studies about plant trait–growth patterns have focused on trees [2–4,6–8], with fewer reports concerning lianas [9,10]. It is, therefore, of importance to unveil how the growth rate of lianas is driven by their interspecific variation in plant traits.

A number of previous studies have shown that plant growth rate is positively related to leaf morphological and physiological traits associated with resource acquisition [2,3,5,6,11–13]. For example, it has been acknowledged that leaf area influences light capture, thereby influencing photosynthesis [14,15]. Lianas generally develop most of their leaves on the top of the forest canopy [16]. The leaf area is, therefore, of particular importance to photosynthesis, and hence the growth rate. The specific leaf area (SLA), representing the leaf area per unit leaf dry mass, is a key trait governing the growth rate because it enables plants to expose a large leaf area to light and CO_2 per given biomass invested in leaves [17]. In addition, leaf nutrients, such as nitrogen (N), phosphorus (P), and potassium (K), involve many physiological aspects of photosynthesis [18], thus influencing plant growth. Specifically, N is the essential component of Rubisco [19]; P is an important component of nucleic acids, lipid membranes, and bioenergetic molecules such as ATP [17,20]; and K is involved in the maintenance of membrane potentials and controls stomatal movement [21]. High SLA, N, P, and K concentrations are usually positively related to a high photosynthetic rate [22–24] and ultimately high growth rate [4,5]. However, some traits, such as leaf dry matter content due to support tissues, are negatively associated with growth rate.

Stem hydraulic properties have been shown to be strongly linked with plant growth rate. For instance, the growth rate of tropical trees is positively associated with the stem vessel diameter and theoretical hydraulic conductivity [4,7]. Stem wood density is considered to be a key functional trait that represents the biomass investment [25,26]. Species with high wood density usually possess small vessels, high vessel density, and low stem water transport capacity [7,27,28], ultimately low photosynthetic and potential growth rates [29,30]. Indeed, many previous studies have shown that plant growth rate is negatively correlated with wood density in tropical trees [2,5,11,31]. It is unclear whether the association of plant growth rate with stem traits reported on trees holds for lianas.

Lianas are responsible for a proportion of biodiversity and biomass in tropical and subtropical forest ecosystems [32–36]. However, studies on the associations of liana growth rate with leaf and stem traits are extremely lacking or controversial. For instance, Putz (1990) reported that the correlation between the rate of diameter increment and wood density was non-significant across 15 liana species on Barro Colorado Island, Panama [9]. However, a significantly negative correlation was found between the relative growth rate and wood density among lianas in a montane forest in southwest (SW) China [10]. It is imperative to include more studies from diverse forest ecosystems to unveil the liana growth–trait patterns.

As an important component of evergreen broadleaved forests in subtropical climate zones of China [37], cloud forest covers the mid-Ailao Mountains, Yunnan Province, SW China. This cloud forest hosts relatively high liana diversity, with both evergreen and deciduous lianas co-occurring in the primary forest [38]. In this study, we monitored the relative growth rate of 2860 individuals from seven deciduous and four evergreen liana species in a 20 ha forest dynamics plot. We also measured nine leaf traits associated with light capture, nutrient status, and hydraulic capacity as indicated by leaf vein density, as well as five stem wood xylem traits associated with stem hydraulic conductivity. A range of previous studies showed that deciduous species have high SLA, leaf nutrient concentrations, and photosynthetic capacity [39,40]; it is, therefore, expected that deciduous species may grow more rapidly than evergreen species. We first hypothesized that deciduous lianas have a higher relative growth rate than their evergreen counterparts. Light is a major limitation on plant photosynthesis, especially in the rainy season, due to a lower proportion of sunny days occurring in the Ailao Mountains [41] (Table 1). We then hypothesized that the relative growth rate of lianas is positively correlated with leaf area, an indicator of light harvesting area. In addition, soil N instead of P and K is limited at high elevation [42,43]. We also hypothesized that the association of the relative growth rate with leaf N across lianas is stronger than those with P and K. We finally hypothesized that the relative growth rate of lianas is positively correlated with leaf and stem resource acquisition traits, such as SLA, leaf vein density, stem hydraulic conductivity, and vessel diameter, but negatively correlated with resource conservation traits, such as leaf dry matter content, leaf thickness, and vessel and wood densities.

Table 1. The average number of sunny, cloudy, foggy, and rainy days; average rainfall; and average temperature during 2016-2018 in Ailao Mountains, SW China.

Parameter	Sunny Days (d)	Cloudy Days (d)	Foggy Days (d)	Rainy Days (d)	Rainfall (mm)	Temperature (°C)
Mean annual	82.7	282	230.7	162.7	2053.4	11.7
Rainy season mean (May–October)	11.0	172.3	150.7	125.3	1873.4	14.8
Dry season mean (November–April)	71.7	109.7	80.0	37.3	166.2	8.7

2. Materials and Methods

2.1. Study Site

In 2014, the present study was carried out in a 20 ha forest dynamics plot (500 × 400 m, consisting of 500 20 × 20 m quadrats) in a national nature reserve in Ailao Mountains, Yunnan Province, SW China (101.03°–101.03° E, 24.53°–24.54° N; 2472–2628 m a.s.l.) [44]. This permanent plot was constructed based on the standard protocols proposed by the Center for Tropical Forest Science (CTFS). The mean annual precipitation is ca. 1778 mm, 86% of which is concentrated in the rainy season (from May to October, 2002–2011) [44]. The mean annual temperature is 11.3 °C, with the mean monthly temperature being 5.7 °C in January and 15.6 °C in July. The type of soil is yellow-brown, which contains 129.1 g kg^{-1} organic matter, 5.2 g kg^{-1} N, 0.6 g kg^{-1} P, 9.46 g kg^{-1} K at 0–20 cm depth. The available N, P, and K concentrations are 45.66, 11.10, and 185.39 mg kg^{-1}, respectively; the pH value is 4.24. The 20 ha plot is dominated by evergreen broadleaved tree species [44].

2.2. Relative Growth Rate of Lianas

During October 2015 to January 2016, all rooted individuals of 11 liana species with diameters ≥ 1 cm (Table 2) were tagged, measured, and identified at the species level according to a standardized census method [45–47]. Based on this method, we measured liana diameters 130 cm from the last rooting point at the ground surface. When lianas branched below 130 cm (but above 40 cm from the soil), we measured the liana diameter 20 cm below the branching point. We re-measured the diameters of all liana stems at the same point marked in the first census time during May to July 2018. We monitored liana species with individuals ≥ 50 to reduce the measurement error due to small samples. In total, 2860 liana individuals from 11 species of eight families (seven deciduous and four evergreen liana species) were monitored in the present study (Table 2).

Liana growth is strongly correlated with the diameter increment [48–50]. We, therefore, used the increment rate of the diameter to estimate the relative growth rate of lianas. The relative stem diameter growth rate (RGR) was calculated as ($\log[D_2]–\log[D_1]$)/time (yr) [2], where D_1 and D_2 represent the diameters of lianas at the first (2015–2016) and second (2018) census times, respectively. We excluded lianas with diameter growth rates that were negative and anomalous (≥4 cm), assuming such growth data were caused by measurement error.

Table 2. Liana species with details of family and leaf habits in a 20 ha forest dynamics plot, SW China.

Species	Family	Code	*n*	Phenology
Rubus paniculatus Smith	Rosaceae	Rp	309	D
Actinidia callosa Lindl.	Actinidiaceae	Ac	308	D
Celastrus hookeri Prain	Celastraceae	Cho	303	D
Parthenocissus semicordata (Wall.) Planch.	Vitaceae	Ps	236	D #
Celastrus hirsutus Comber	Celastraceae	Chi	235	D
Sabia yunnanensis Franch.	Sabiaceae	Sy	115	D
Actinidia glaucocallosa C. Y. Wu	Actinidiaceae	Ag	88	D
Rosa longicuspis Bertol.	Rosaceae	Rl	870	E #
Holboellia latifolia Wall.	Lardizabalaceae	Hl	253	E #
Kadsura heteroclita (Roxb.) Craib	Schisandraceae	Kh	79	E
Callerya dielsiana (Harms) P. K. Loc ex Z. Wei and Pedley	Leguminosae	Cd	64	E #
Total			2860	

Note: *n* is the number of liana individuals used for growth monitoring. D, deciduous; E, evergreen. #, liana species with compound leaves. Nomenclature follows Flora of China (http://www.iplant.cn/foc/).

Plant size needs to be considered when comparing the interspecific growth rate if plant growth is size-dependent and if size distribution patterns significantly differ among species [2]. We evaluated this potential influence for our growth data by comparing liana absolute growth rates standardized to 2.5 cm diameter with an average RGR for the 2860 individuals, as Poorter et al. (2008) suggested [2]. The logarithm of the absolute growth rates of lianas was fitted to the logarithm of the initial diameter for the liana species studied. We then used this equation to estimate the absolute growth rate of lianas at 2.5 cm diameter. We found that the estimated absolute growth rate and the average RGR observed for all liana species were strongly correlated (Figure 1), indicating that the size effect on the liana growth rate in the present study can be neglected in the subsequent analysis [2].

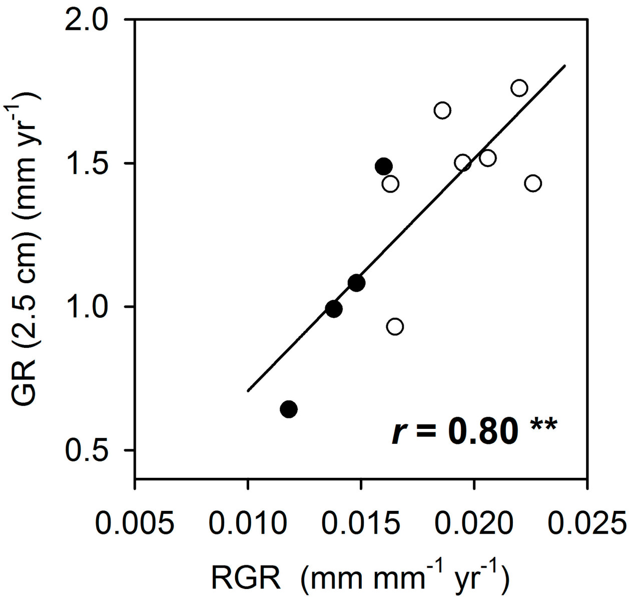

Figure 1. Relationship between the estimated growth rate (GR) standardized to 2.5 cm diameter and the average relative growth rate (RGR) values observed for seven deciduous (open circle) and four evergreen (filled circle) liana species. Note: ** $p < 0.01$.

2.3. Leaf and Stem Traits

We measured 14 key leaf and stem traits of 11 liana species in the rainy season (July to September) in 2016. Briefly, we collected 3–6 individuals with diameters of 2–6 cm per liana species and 3–5 stems per individual with intact, mature, healthy, and sun-exposed leaves. We used a HP Scanjet G3110 scanner and ImageJ software (https://imagej.en.softonic.com/) to measure the areas (LA) of simple leaves or leaflets of compound leaves. Leaflets were considered to be functionally equivalent to simple leaves [51]. We measured leaf fresh weights and then leaf samples were oven-dried at 70 °C for at least 48 h. The specific leaf area (SLA) was calculated as the leaf area divided by leaf dry mass, while the leaf dry matter content (LDMC) was calculated as leaf dry mass per unit leaf fresh weight. Cross-section images of each of five to seven leaves or leaflets were taken with a Binocular Biological microscope (Leica DM2500, Wetzlar, Germany) and leaf thickness (LT) values were measured using ImageJ. An additional three to five leaf segments were immersed in a 5% NaOH solution until leaf veins became clear. Images were then taken using the Binocular Biological microscope and the total vein lengths in whole images were determined using ImageJ. Leaf vein density (D_{vein}), an indication of leaf hydraulic capacity, was calculated as the total vein length divided by leaf area. Leaf thickness, total vein length, and vessel diameter were measured using the measurement tool in ImageJ software (https://imagej.en.softonic.com/).

Leaf samples of each of three to five individuals per liana species were oven dried at 70 °C for 48 h and ground to pass through a 60-mesh sieve. We measured the leaf N concentration with a Dumas-type combustion C-N elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Hanau, Germany). We determined leaf P and K concentrations with an inductively coupled plasma atomic emission spectrometer (iCAP 7400, Thermo Fisher Scientific, Bremen, Germany). The N/P ratio was calculated as a proxy of nutrient limitation [52].

Stem wood traits were measured on a 5-cm-long stem segment with a diameter of ca. 1 cm. The volume of fresh wood with the pith and bark removed was first measured using the water displacement method. Wood samples were then oven-dried at 70 °C for 72 h for dry weight. Wood density (WD) was calculated as the wood dry mass per unit fresh volume. Another stem segment of ca. 2 cm in length was used to determine the vessel diameter (D_V) and density (VD). At least ten images were taken at 100–1000× magnification per individual using a microscope (Smartzoom 5, Carl Zeiss, Germany) and then D_v was determined for all vessels with ImageJ. Due to the elliptical shape of most vessels, D_v was calculated as [53]:

$$D_v = \left[32(ab)^3/\left(a^2+b^2\right)\right]^{1/4} \tag{1}$$

where a and b indicate the radii of vessel major and minor axes, respectively. Vessel density was defined as the vessel number per area. For each species, we also selected 6–10 images of each of 3–6 individuals and measured the diameters of the ten biggest vessels ($D_{\max}$), which are strongly correlated with stem hydraulic conductivity [54]. Stem theoretical hydraulic conductivity (K_t) was determined as:

$$K_t = (\pi\rho/128\eta A)\left[\sum_{i=1}^{n}\left(D_{V_i}^4\right)\right] \tag{2}$$

where π is a constant of 3.14, ρ is the water density (997.05 kg m^{-3}) and η is the water viscosity (0.89×10^{-9} MPa s^{-1}) at 25 °C, A is the image area, and i = 1 to n vessels in the image [55].

2.4. Data Analyses

All variables were $\log_{10}$-transformed to improve the normality of distribution before analysis. The differences in RGR and other traits between seven deciduous and four evergreen liana species were compared using independent sample t-tests. Pearson's correlation and principal component analysis (PCA) were used to evaluate trait associations. PCA was performed based on $\log_{10}$-transformed data and varimax rotation was chosen to simplify the axes. All analyses were conducted in SPSS (version 22.0; SPSS, Inc., Chicago, IL, USA).

3. Results

Deciduous lianas had significantly higher RGR values than evergreen lianas ($p < 0.01$; Figure 2). Across liana species, RGR was positively significantly correlated with leaf area (Figure 3a). However, the positive association of RGR with leaf area only existed in deciduous lianas (Figure 3a). RGR was positively related to SLA (Figure 3b), but negatively related to LDMC (Figure 3c) across all lianas. Surprisingly, RGR was positively associated with leaf thickness in evergreen lianas, but negatively associated with leaf thickness in deciduous lianas (Figure 3d).

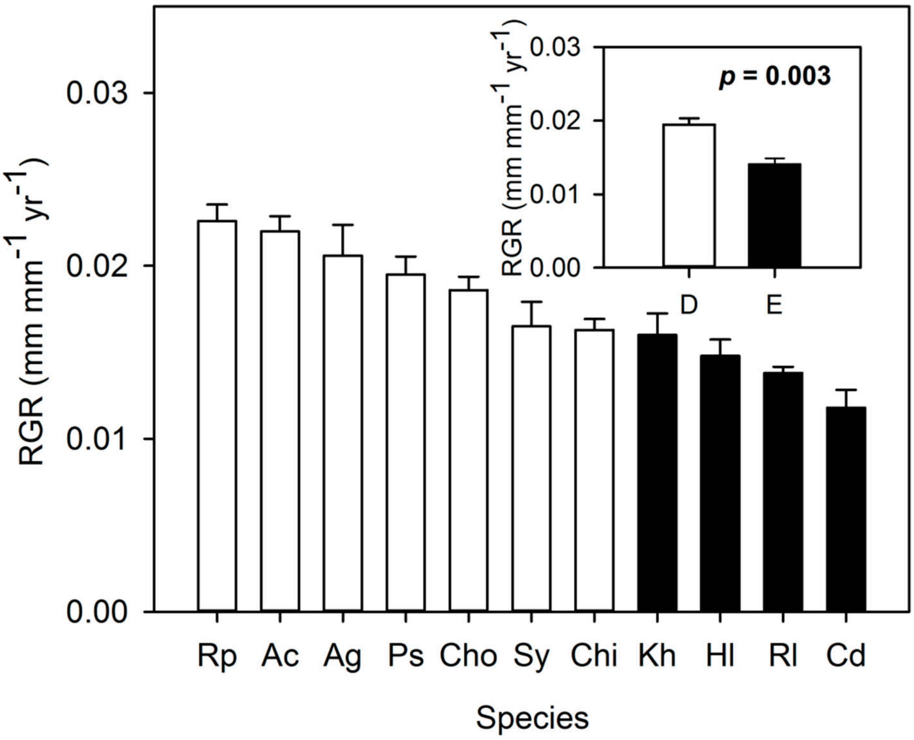

Figure 2. Relative growth rate (RGR) values in deciduous (open bar) and evergreen (filled bar) liana species. The insert indicates the difference in RGR between deciduous (D) and evergreen (E) lianas. See Table 2 for species codes. Data were means ± SE.

There were no significant correlations of RGR with P, K concentrations, and N/P ratios (Figure 4) across deciduous, evergreen, or pooled lianas. When the legume liana (*Callerya dielsiana* (Harms) P. K. Loc ex Z. Wei & Pedley) was excluded, RGR was positively correlated with N concentration across the remaining ten liana species (Figure 4a). As for the associations of RGR with leaf vein and stem xylem properties (Figure 5), we only found that RGR was positively related to diameter for the biggest vessels in evergreen lianas (Figure 5a).

The results of principal component analysis based on RGR and 14 traits of 11 liana species showed that the first and second components accounted for 34.3% and 27.6% of the total variance, respectively (Figure 6). The first axis was positively correlated with traits representative of RGR and stem xylem vessel parameters (e.g., $D_{\max}$, D_V, K_t). At the opposite end were species with high LDMC, vessel density, and vein density (Figure 6a). The second axis correlated positively with N and P concentrations and negatively with the N/P ratio. Deciduous lianas overlapped with evergreen lianas to a large extent in the multivariate trait space (Figure 6b).

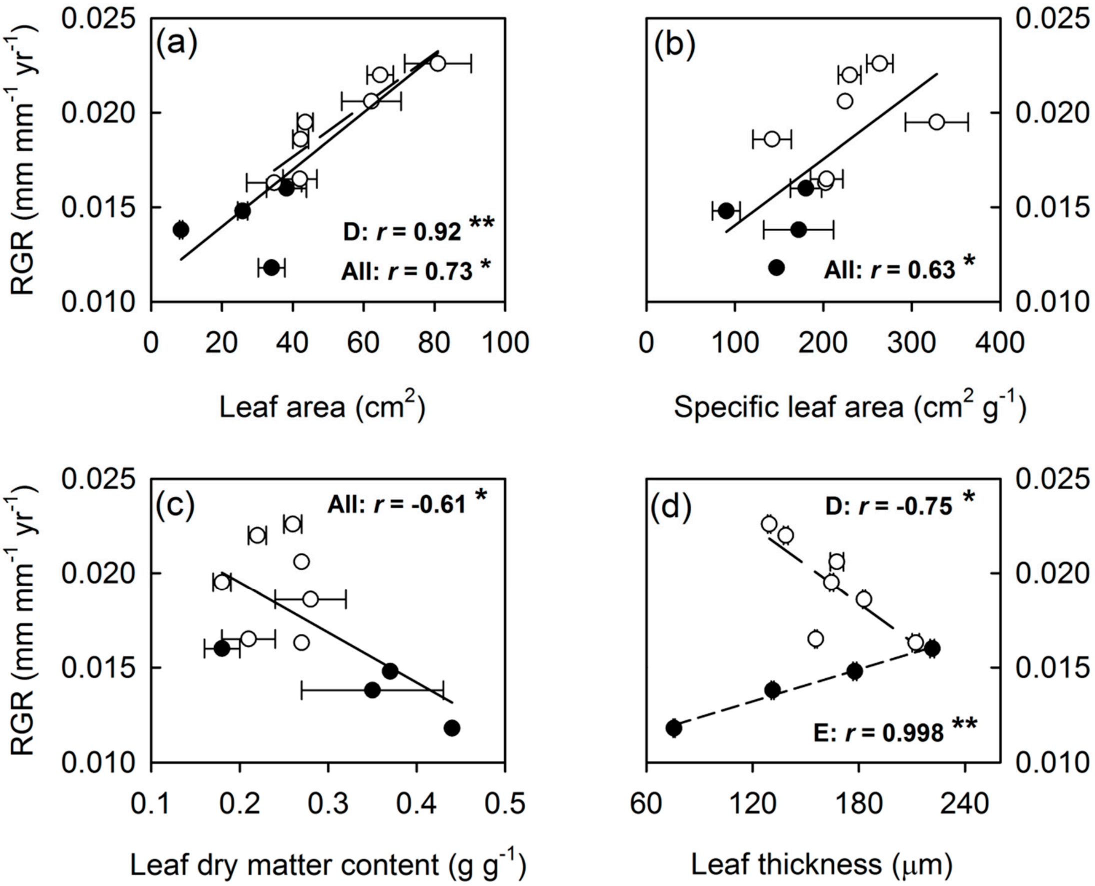

Figure 3. Relationships of relative growth rate (RGR) values with (**a**) leaf area, (**b**) specific leaf area, (**c**) leaf dry matter content, and (**d**) leaf thickness across seven deciduous (D, open circle, long dashed line) and four evergreen (E, filled circle, short dashed line) lianas. Solid lines indicate significant correlations between RGR and leaf traits across 11 liana species. The horizontal error bars indicate the standard error of leaf traits. Note: * $p < 0.05$; ** $p < 0.01$.

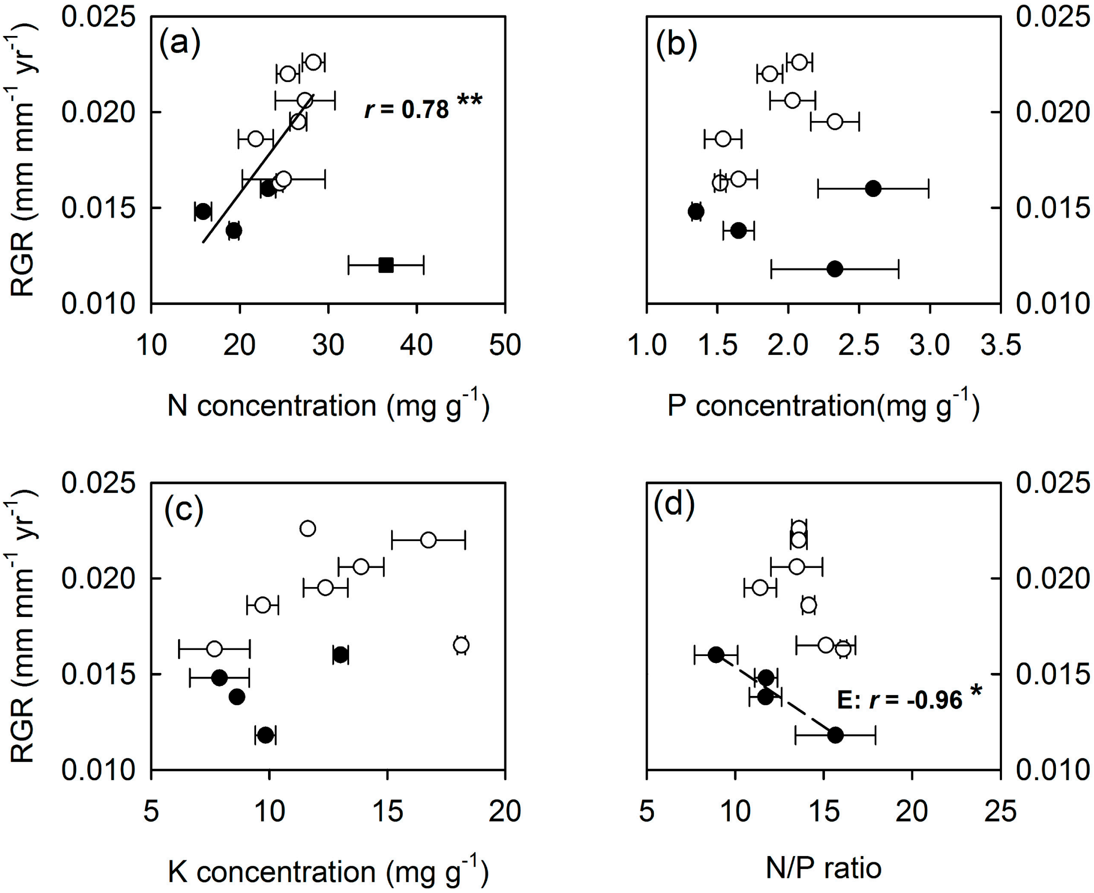

Figure 4. Relationships of relative growth rate (RGR) values with (**a**) N, (**b**) P, (**c**) K, and (**d**) N/P ratios across seven deciduous (open circle) and four evergreen (E, filled circle) lianas. Solid lines indicate significant correlations between RGR and N concentrations across ten liana species, excluding the legume liana species (*Callerya dielsiana* (Harms) P. K. Loc ex Z. Wei & Pedley), which is an outlier (black square). The horizontal error bars indicate the standard error of leaf nutrients. Note: * $p < 0.05$; ** $p < 0.01$.

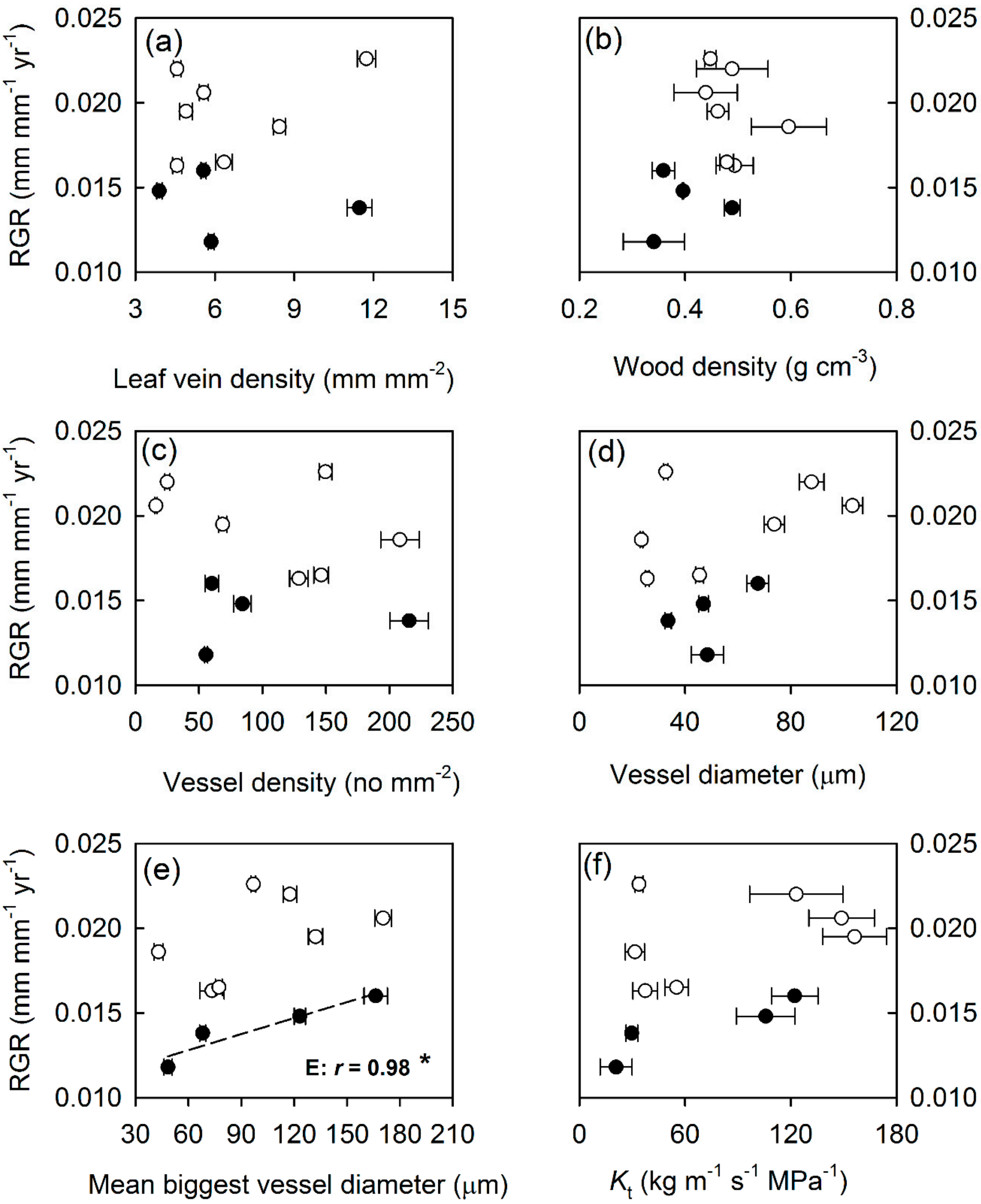

Figure 5. Relationships of relative growth rate (RGR) values with (**a**) leaf vein density, (**b**) wood density, (**c**) vessel density, (**d**) vessel diameter, (**e**) mean biggest vessel diameter, and (**f**) theoretical hydraulic conductivity (K_t) across seven deciduous (open circle) and four evergreen (E, filled circle) lianas. Short dashed lines indicate significant correlations between RGRs and diameters of largest vessels across four evergreen liana species. The horizontal error bars indicate the standard error of leaf vein density and stem traits. Note: * $p < 0.05$.

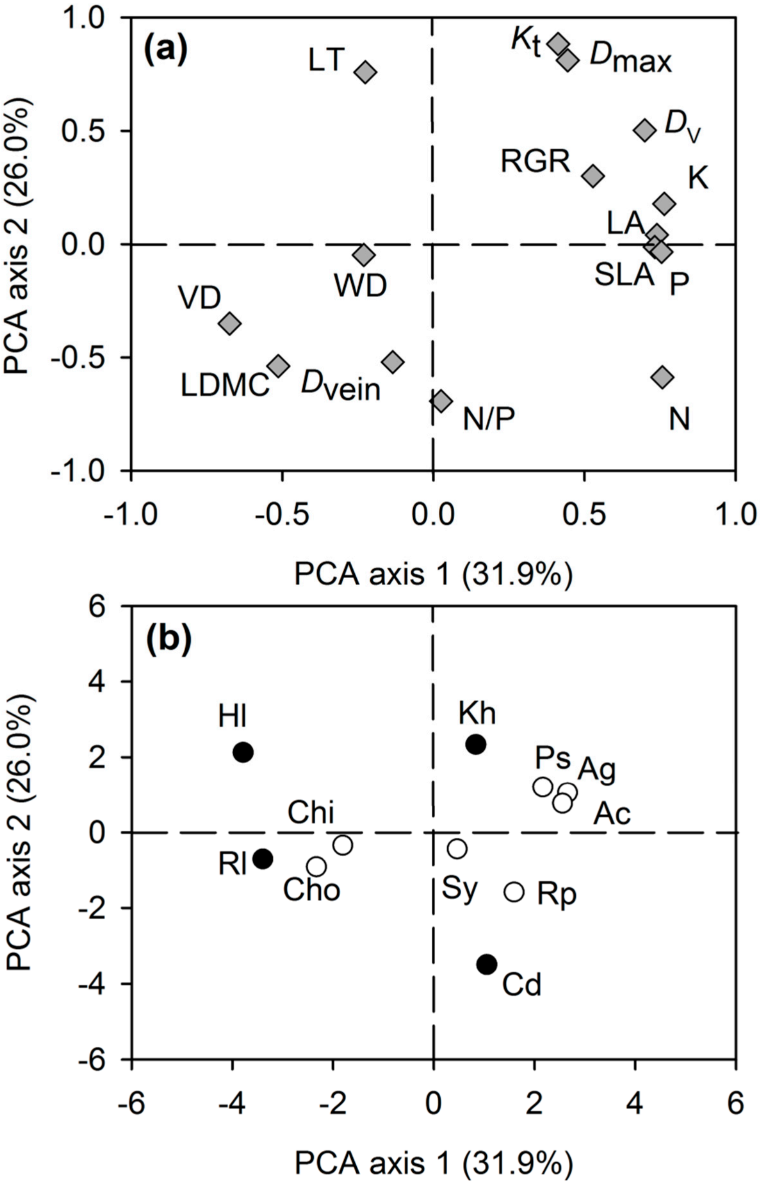

Figure 6. The biplot of the first two axes of the principal component analysis (PCA) for (**a**) the relationships of relative growth rate, leaf, and stem traits and (**b**) the loadings of the seven deciduous (open circle) and four evergreen (filled circle) lianas. See Table 2 for species codes and text for trait abbreviations.

4. Discussion

Our results showed that deciduous lianas grew more quickly than evergreen lianas (Figure 2), supporting our first hypothesis. The reason may lie in the fact that deciduous lianas have higher SLA values than evergreen lianas (227.81 ± 20.18 vs. 147.48 ± 17.62 cm^2 g^{-1}; also see Figure 3b), consistent with similar patterns in trees [56–59], presumably resulting in the conclusion that relatively faster growth is a general feature of deciduous species. Consistent with our second hypothesis, we found that lianas with larger leaf areas had higher growth rates across all lianas studied (Figure 3a). Throughout a given year, the proportion of sunny days in the Ailao Mountains is low, and it is extremely low in the rainy season (Table 1). Increased leaf area will allow lianas to harvest more light for photosynthesis [8,11,22,60], which is possibly an important strategy for lianas to adapt to cloud forest conditions. Interestingly, the positive relationship of RGR with leaf area is existent only in deciduous species (Figure 3a). This is highly important for deciduous lianas because they need to take advantage of the rainy season to grow when their leaves are present.

Partly inconsistent with our third hypothesis, we did not find that RGR was positively correlated with N, P, K, and the N/P ratio across all lianas studied (Figure 4). However, RGR was significantly positively related to N concentration (Figure 4a) when a legume liana species, *Callerya dielsiana*, was excluded. This may suggest that legume lianas employ alternative approaches to fix and use N resources [61]. The N/P ratio has been considered to be an indicator of nutrient limitation, which was divided into three levels: N/P ratio < 14 (N limitation), >16 (P limitation), and 14 ≤ N/P ratio ≤ 16 (limitation of N and P or both not) [52,62,63]. We found that the N/P ratios for eight in 11 lianas were much lower than 14 (Figure 4d), indicating that N is a growth-limiting nutrient for most lianas in subtropical evergreen broadleaved forests in SW China. This does not seem to be true for the legume liana species (*Callerya dielsiana*), because it had the highest N concentration among all lianas measured (Figure 4a).

We found that the relative growth rates for lianas were related to leaf resource acquisition and conservation traits, and were seldom associated with stem hydraulic properties, partly supporting our fourth hypothesis. We found that there were strong correlations of RGR with SLA and LDMC, with deciduous lianas positioned at high SLA or low LDMC ends (Figure 3b,c). A high SLA or low LDMC means low investment in construction but high investment in the photosynthetic apparatus [22,27,64,65], ultimately translating into rapid growth. The positive SLA–growth relationship was also confirmed in seedlings grown under non-limiting conditions [66,67].

Across 11 lianas studied, RGR was not correlated with wood density (Figure 5b), consistent with a report on lianas in Barro Colorado Island, Panama [9]. However, there was a significantly negative correlation between the relative growth rate and wood density among lianas in a montane forest in SW China [10]. Strong leaf and stem water transport capacities are usually positively linked with high growth rates among trees [27]. However, we did not find any significant associations of leaf vessel and stem vessel properties with RGR across lianas (Figure 5), with the exception of a significant correlation between RGR and the mean biggest vessel diameter in evergreen lianas (Figure 5e). These results may suggest that water seems an unlikely limitation on liana growth in the Ailao Mountains, as indicated by high precipitation and a high proportion of foggy days during a year (ca. 63%; Table 1).

Surprisingly, we found some associations of RGR with leaf morphology and stem hydraulic properties only in evergreen lianas, suggesting that deciduous or evergreen lianas may employ some differentiated strategies to adapt to the cloud forest environment. We found that the RGR of evergreen lianas was positively related to leaf thickness (Figure 3d) and the mean biggest vessel diameter (Figure 5e). Thicker leaves usually have longer lifespans [68]. In addition, leaf thickness is positively related to leaf hydraulic conductivity [69]. Evergreen lianas with thicker leaves or larger vessels are able to supply enough water and continuously assimilate in the winter time, during which temperate and sunny weather in the cloud forest (Table 1) is still suitable for photosynthesis [41,70]. Therefore, a strong coordination of RGR with leaf thickness and mean biggest vessel diameter in evergreen lianas could be expected in the cloud forest in the Ailao Mountains.

5. Conclusions

In this study, we attempted to investigate the relationships between liana functional traits and relative growth rate. We found that deciduous lianas possessed higher relative growth rates than evergreen lianas in the subtropical cloud forest. The variation in relative growth rate was mainly driven by leaf area, specific leaf area, leaf dry matter content, instead of leaf nutrient status, leaf hydraulic capacity, and stem hydraulic properties. Interestingly, the relative growth rate for lianas was strongly correlated with N concentration after excluding the legume liana species, suggesting that legume lianas may employ alternative strategies to use N. Deciduous lianas probably perform differently from evergreen lianas, as positive correlations of relative growth rate with leaf thickness and mean biggest vessel diameter exist only in evergreen lianas. These results provide a fundamental understanding of how the liana growth links or decouples from leaf and stem traits in a high-elevation cloud forest. Future investigations must consider liana growth in diverse ecosystems to fully understand the global pattern of liana growth.

Author Contributions: X.-L.B., Y.-B.Z. and J.-L.Z. conceived and designed the experiment. X.-L.B. collected data. X.-L.B., Q.L., Y.-S.-D.W. and D.Y. analyzed the data. X.-L.B., Y.-B.Z. and J.-L.Z. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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