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Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest

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Abstract
Lianas are an important component of most tropical forests, where they vary in abundance from high in seasonal forests to low in aseasonal forests. We tested the hypothesis that the physiological ability of lianas to

fix carbon (and thus grow) during seasonal drought may confer a distinct advantage in seasonal tropical forests, which may explain pan-tropical liana distributions. We compared a range of leaf-level physiological attributes of 18 co-occurring liana and 16 tree species during the wet and dry seasons in a tropical seasonal forest in Xishuangbanna, China. We found that, during the wet season, lianas had significantly higher CO_2 assimilation per unit mass (A_{mass}), nitrogen concentration (N_{mass}), and $\delta^{13}C$ values, and lower leaf mass per unit area (LMA) than trees, indicating that lianas have higher assimilation rates per unit leaf mass and higher integrated water-use efficiency (WUE), but lower leaf structural investments. Seasonal variation in CO_2 assimilation per unit area (A_{area}), phosphorus concentration per unit mass (P_{mass}), and photosynthetic N-use efficiency (PNUE), however, was significantly lower in lianas than in trees. For instance, mean tree A_{area} decreased by 30.1% from wet to dry season, compared with only 12.8% for lianas. In contrast, from the wet to dry season mean liana $\delta^{13}C$ increased four times more than tree $\delta^{13}C$, with no reduction in PNUE, whereas trees had a significant reduction in PNUE. Lianas had higher A_{mass} than trees throughout the year, regardless of season. Collectively, our findings indicate that lianas fix more carbon and use water and nitrogen more efficiently than trees, particularly during seasonal drought, which may confer a competitive advantage to lianas during the dry season, and thus may explain their high relative abundance in seasonal tropical forests.

Introduction

Annual rainfall and the seasonal distribution of rainfall are arguably two of the most important factors responsible for the distribution of plant species within the tropics (Gentry 1982). While some tropical forests have high annual rainfall with relatively little change in the amount of monthly precipitation during the year (e.g., rain forests), most tropical forests experience seasonal drought, where precipitation is greatly reduced for up to 6 months per year (Walsh and Newbery 1999). During periods of seasonal drought, plants may be exposed to considerable water stress, indicated by low leaf water potentials and wilting (Veenendaal et al. 1995), as well as increased mortality and substantially decreased growth rates (Condit et al. 1995; Engelbrecht et al. 2005). Consequently, many plant species in seasonal tropical forests have special adaptations to deal with periods of drought, such as reduced net assimilation rate, reduced stomatal conductance, or deciduousness (Holbrook et al. 1995; Borchert 1998; Slot and Poorter 2007). The presence of one or more of these adaptations may determine the abundance and distribution of a species or functional group in a particular forest (Swaine 1996; Bongers et al. 1999; Schnitzer 2005; Domingues et al. 2007).

Most organisms increase in abundance with increasing mean annual precipitation and decreasing seasonality (Gentry 1982). One plant group that is an exception to this general rule, however, are the lianas (woody vines), which appear to increase in abundance with decreasing mean annual precipitation and increasing seasonality (Schnitzer 2005; DeWalt et al., unpublished; but see van der Heijden et al. 2008). Schnitzer (2005) proposed that lianas exhibit their distinct geographic distribution due to their unique ability to grow during seasonal drought, while their competitors, particularly trees, have greatly reduced physiological activity. This dry season growth advantage may allow lianas to increase in abundance in seasonal forests, whereas the competitive advantage is absent in aseasonal forests, thus explaining pan-tropical patterns of liana abundance (Schnitzer 2005). Lianas are a key component of many tropical forests, where they can influence a number of important forest processes, including tree recruitment, regeneration, fecundity, and mortality (Putz and Mooney 1991; Schnitzer and Bongers 2002; Schnitzer et al. 2000, 2004, 2005; Wright et al. 2005; Kainer et al. 2006). Thus, explaining the mechanisms responsible for the abundance of lianas in tropical forests is critical for understanding tropical forest dynamics, as well as predicting how liana abundance will change with climate and land-use changes.

Currently, the evidence to support the dry season growth advantage hypothesis is limited. For example, in the seasonally deciduous forest of Barro Colorado Island in Panama (BCI), Schnitzer (2005) measured the height growth of liana and tree species throughout consecutive wet and dry seasons and reported that, during the wet

season, lianas grew two times faster than trees, but in the dry season this growth difference increased to seven times, suggesting that lianas benefit during the dry season relative to trees, possibly because lianas suffer less water stress during seasonal drought. This finding is consistent with observations that many liana species retain and even produce new leaves during severe seasonal droughts, whereas most trees do not (Putz and Windsor 1987; Opler et al. 1991; Kalácska et al. 2005). Several characteristics common to lianas may enable them to compete particularly well during seasonal droughts, including: deep and well developed root systems (Tyree and Ewers 1996; Restom and Nepstad 2004), hydraulic activity (Andrade et al. 2005), low leaf construction costs per unit photosynthetic area (Castellanos 1991), and rapid vegetative growth rates (Putz 1984; Schnitzer et al. 2000, 2004), as well as high potential for response to changes in light intensity (Avalos and Mulkey 1999; Salzer et al. 2006) and elevated atmospheric CO_2 concentrations (Granados and Korner 2002; Mohan et al. 2006; Zotz et al. 2006). To date, however, there have been no systematic tests of the dry season growth advantage hypothesis to explain patterns of liana distribution.

In this study, we compared seasonal variability in leaf physiology among co-occurring liana and tree species throughout wet and dry seasons in a tropical seasonal forest in Xishuangbanna, SW China, to determine whether lianas, compared to trees, can fix more carbon, and thus grow more, during seasonal drought (Schnitzer 2005). We predicted that lianas should perform better than trees during the dry season via higher carbon fixation and resource use efficiency. During the wet season, however, lianas and trees should be more similar to each other in each of these attributes.

Materials and methods

Study site

The study was conducted in a tropical seasonal forest in Xishuangbanna (21°09′–22°33′N, 99°58′–101°50′E), SW China. The forest of Xishuangbanna is on the northern edge of tropical SE Asia, and it differs from lowland rain forests located close to the equator mostly by having fewer epiphytes and megaphanerophytes. Liana abundance and diversity in this region, however, is relatively high, especially in seasonal forests (Cai et al. 2009), which is the most common and dominant forest type of the region (Zhu et al. 2006).

Lying in the East Asian Monsoon Region, Xishuangbanna is dominated by warm-wet air masses from the Indian Ocean in summer and continental air masses from the sub-tropical regions in winter, resulting in a highly seasonal environment. The forest used in this study receives approximately 1,550 mm of rainfall annually, of which 85% occurs in the 6-month rainy season (May–October). During the study period, rainfall varied from 3 mm in February 2004 to 297 mm in August 2004. Mean monthly temperature in this area is 21.4°C and ranges from 14.5 to 25.7°C (Fig. 1a). Surface soil (0–20 cm) was drier in the dry season compared to the wet season, while deep soil water content (100 cm) was similar (Fig. 1b).
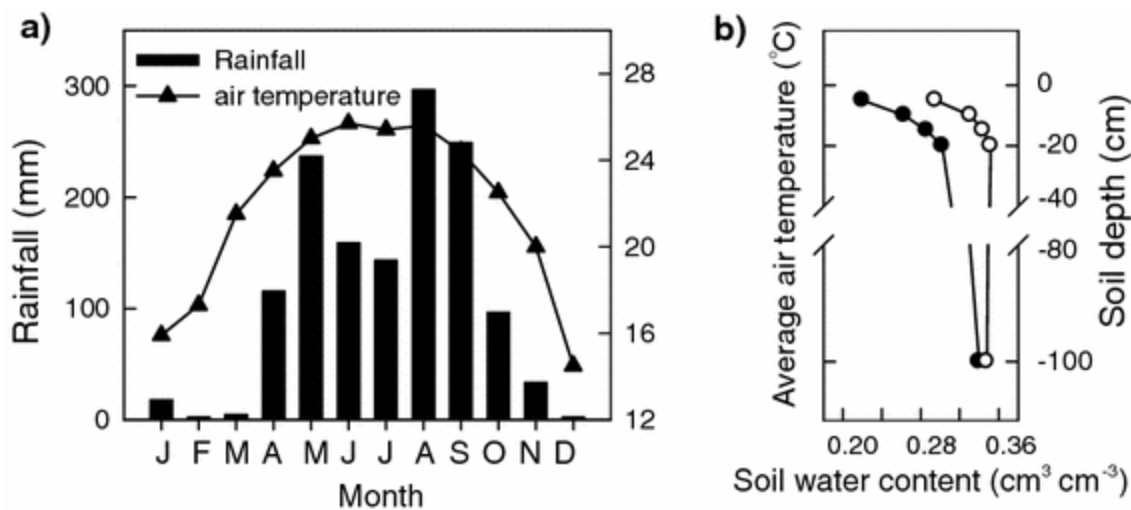
Fig. 1
Seasonal changes in monthly rainfall and average air temperature (**a**) and volumetric water content (**b**) in 2004 (*open circle* dry season in March, *black circle* wet season in September). Weather data was from the nearby Meteorological Station of Xishuangbanna Tropical Botanical Garden, The Chinese Academy of Sciences

Study species and measurements

We studied 18 evergreen liana species and 16 evergreen tree species (all species utilize C_3 photosynthesis; Table 1). To determine photosynthetic parameters, including photosynthetic rate and dark respiration, we collected branches from the upper canopy using a tree pruner attached to a long handle. For each tree and liana species, we sampled 4–6 leaves from the same individual (2–3 individuals per species) at the end of each season. We use leaf functional trait measurements because leaves provide valuable insights into whole-plant performance (Wright et al. 2004a, b; Poorter and Bongers 2006). All individuals had comparable stem diameters (dbh) and were growing in the same general area on similar soil types. The trees were approximately 20 m tall, and the branches and leaves of the liana species were located on top of the tree crowns. All branches were collected during the wet (September) and dry (March–April) seasons between 9:30 and 11:00 a.m., when maximum photosynthetic rates occurred (Foster and Brooks 2005; Domingues et al. 2007). Within 10 min of collection, we cut the branches under water, immersed the stems in de-ionized water to maintain the xylem water column, and measured photosynthesis. Photosynthetic parameters were measured on fully expanded, recently matured sun canopy leaves (methods follow Foster and Brooks 2005; Salzer et al. 2006; Santiago and Wright 2007). We measured the rate of CO_2 assimilation per unit area (A_{area}) under a light-saturating irradiance (Photon flux density > 1,500 µmol m^{-2} s^{-1}, provided by an internal red/blue LED light source; LI6400-02B) under ambient CO_2 concentration (~380 ppm) with a portable photosynthetic system (Li-6400; LiCor, Lincoln, NE, USA). Leaf temperature and vapor pressure deficit (VPD) in the cuvette were kept at 25–26°C and less than 1 kPa, respectively. We also measured dark respiration (R_d) in the leaf chamber, allowing several minutes for the leaves to stabilize before recording data.

Table 1
Leaf traits of evergreen liana and tree species measured during the wet season in a seasonal forest in Xishuangbanna, China

Species	Family	LA	LMA	Aarea	Amass	Rd area	Rd mass	A/Rd	Nmass	Pmass	A/Chl	Car/Chl	δ13C	PNUE	PPUE
Liana species															
Iodes covalis	Icacinaceae	144.5	79.2	9.17	115.8	1.13	14.3	8.12	4.99	2.73	30.1	0.23	−31.02	32.5	1.31
Fissistigma polyanthoides	Annonaceae	77.5	69.8	11.45	164	1.67	23.9	6.86	4.19	2.38	46.5	0.18	−29.08	54.8	2.13
Bauhinia glauca	Caesalpiniaceae	15	55.8	6.62	118.6	0.67	12	9.87	2.43	1.76	33.4	0.22	−30.57	68.3	2.09
Ziziphus attopensis	Rhamnaceae	22.1	65.2	10.69	163.9	1.01	15.5	10.58	2.51	2.15	40.2	0.22	−30.1	91.3	2.37
Gnetum parvifolium	Gnetaceae	110.5	72.7	10.23	140.7	1.14	15.7	8.97	3.55	1.54	35.2	0.25	−31.18	55.5	2.84
Tetrastigma planicaulum	Vitaceae	58.5	72.8	11.45	157.2	1.34	18.4	8.54	2.65	1.97	61.6	0.23	−29.02	83.2	2.47
Byttneria aspera	Sterculiaceae	81.8	46	11.95	259.6	1.41	30.6	8.48	3.12	2.18	63.1	0.22	−29.92	116.6	3.70
Uncaria macrophylla	Rubiaceae	101.4	111.1	9.08	81.7	0.78	7.0	11.64	2.13	1.31	30.8	0.28	−30.09	53.7	1.93
Bauhinia yunnanensis	Caesalpiniaceae	8.1	61.8	8.67	140.4	0.65	10.5	13.34	3.61	2.98	27.9	0.2	−	54.4	1.46
Tinomiscium tokinensis	Menispermaceae	228	59.7	9.95	166.6	0.87	14.6	11.43	2.86	2.04	64.5	0.23	−31.41	81.6	2.53
Ficus subulata	Moraceae	71.1	68.7	7.72	112.3	0.56	8.2	13.78	2.54	1.46	27	0.23	−30.64	61.9	2.38
Uncaria rhynchophylla	Rubiaceae	42.8	115	8.46	73.5	0.82	7.1	10.31	1.47	0.82	25.6	0.24	−28.96	70.3	2.79
Ventilago calyculata	Rhamnaceae	47.8	63.3	10	158	1.14	18	8.77	3.17	1.46	36.6	0.23	−30.24	69.7	3.35
Millettia dielsiana	Leguminosae	41.1	63.6	10.45	164.3	1.65	25.9	6.33	3.37	1.23	29.1	0.21	−29.46	68.2	4.14
Fissistigma polyanthum	Annonaceae	28.5	55.9	10.4	186.1	1.11	19.9	9.37	2.3	1.26	32.1	0.2	−31.49	113.4	4.57

Millettia oosperma	Leguminosae	37	107.3	12.65	117.9	1.54	14.3	8.21	2.45	1.62	25	0.24	−29	67.5	2.26
Celastrus paniculatus	Celastraceae	33	92.6	11.13	120.1	1.5	16.2	7.42	2.25	2.07	52.1	0.24	−28.65	74.8	1.80
Securidaca inappendiculata	Polygalaceae	32.3	84.2	9.44	112.2	0.78	9.3	12.11	3.13	1.83	40.2	0.25	−30.39	50.3	1.90
Tree species															
Ficus cyrtophylla	Moraceae	71.5	50.2	9.69	193.1	0.89	17.7	10.89	3.34	1.88	45.2	0.24	−30.48	81	3.19
Combretum latifolium	Combretaceae	135.9	134.6	12.12	90.1	1.76	13.1	6.89	1.65	1.04	24.1	0.23	−29.09	76.2	2.68
Ficus hirta	Moraceae	149.2	84	11.88	141.4	1.18	14	10.06	3.17	3.52	45.4	0.24	−30.69	62.4	1.25
Baccaurea ramiflora	Euphorbiaceae	116	88.1	9.87	112.1	1.06	12	9.31	1.95	1.42	38.3	0.22	−32.12	80.7	2.45
Carallia lanceaefolia	Rhizophoraceae	69.2	101.2	6.58	65	0.58	5.7	11.34	2.12	1.5	27.5	0.25	−32.06	43	1.34
Ficus auriculata	Moraceae	516.9	76.3	7.89	103.4	0.72	9.4	10.96	1.37	1.96	43.1	0.2	−32.17	105.8	1.64
Lepisanthes senegalensis	Sapindaceae	107.3	61.2	6.05	98.8	0.48	7.8	12.6	2.97	1.28	17.9	0.23	−34.15	46.6	2.39
Barringtonia macrostachya	Lecythidaceae	238.9	129	10.56	81.9	1.06	8.2	9.96	2.48	1.75	15.1	0.24	−32.71	46.3	1.45
Shorea chinensis	Dipterocarpaceae	92.7	73.3	9.07	123.7	0.96	13.1	9.45	2.32	1.62	25.6	0.24	−33.72	74.6	2.37
Ficus callosa	Moraceae	191.5	104.1	17.5	168.1	1.89	18.2	9.26	2.45	1.88	45.5	0.25	−30.2	95.9	2.78
Castanopsis indica	Fagaceae	136.9	95.5	11.34	118.8	1.65	17.3	6.87	2.14	1.21	33.1	0.21	−31.31	77.9	3.04
Mayodendron igneum	Bignoniaceae	36.8	78.6	8.08	102.8	0.82	10.4	9.85	2.7	1.59	21.7	0.24	−29.39	53.3	2.00
Litsea panamonja	Lauraceae	115.2	92.5	9.58	103.6	1.06	11.5	9.04	2.58	2.71	54.4	0.23	−30.46	56.1	1.19

Leea crispa	Leeaceae	98.1	123.3	7.76	62.9	0.85	6.9	9.13	3.36	2.28	16.1	0.23	−30.72	26.2	0.86
Ficus superba	Moraceae	115.2	81.5	10.32	126.7	1.07	13.1	9.64	2.62	1.62	33.5	0.22	−31.15	67.8	2.43
Syzygium latilimbum	Myrtaceae	147.4	115.5	11.65	100.9	1.65	14.3	7.06	1.21	0.87	41.8	0.24	−28.87	116.9	3.58
Liana mean		65.6	74.7	9.97	141.8	1.10	15.63	9.67	2.93	1.82	38.94	0.23	−30.07	70.4	2.6
Tree mean		146.2	93.1	10.00	112.1	1.11	12.04	9.52	2.40	1.76	33.02	0.23	−31.21	69.4	2.2

Nomenclature follows Li et al. 1996

Measurements and units: *LA* leaf area (cm^2), *LMA* leaf mass ratio (g cm^{-2}), A_{area} area-based CO_2 assimilation (mmol m^{-2} s^{-1}), A_{mass} mass-based CO_2 assimilation (nmol g^{-1} s^{-1}), $R_{d\ area}$ area-based dark respiration (μmol m^{-2} s^{-1}), $R_{d\ mass}$ mass-based dark respiration (μmol g^{-1} s^{-1}), N_{mass} nitrogen per mass (%), P_{mass} phosphorus per mass (mg g^{-1}), *A/Chl* photosynthesis rate to chlorophyll ratio, *Car/Chl* cartenoid to chlorophyll ratio, $\delta^{13}C$ carbon isotope (‰), *PNUE* photosynthetic N-use efficiency (μmolC mol^{-1} N s^{-1}), *PPUE* photosynthetic P-use efficiency (mmolC mol^{-1}P s^{-1})

Following field measurements, we immediately placed each leaf (excluding the petiole) in a sealed plastic bag containing a damp paper towel. In the laboratory, we extracted the chlorophyll and total carotenoid contents from the leaves with 80% (v/v) acetone in the dark and measured pigments (Lichtenthaler and Wellburn 1983) with a spectrophotometer (UV-B 2501; Shimadzu, Japan). We measured the area of each leaf with a leaf area meter (Li-3000A; Li-Cor). We then oven-dried the leaves at a minimum of 48 h at 70°C and calculated leaf dry mass and leaf mass area (LMA, g cm^{-2}). For each plant, we ground three to five leaves into a fine powder for elemental analyses in the Biogeochemical Laboratory of the Kunming Division of the Xishuangbanna Tropical Botanical Garden, The Chinese Academy of Sciences. The total N concentration per unit leaf dry mass (N_{mass}, %) was determined using semi-micro Kjeldahl, a commonly used wet digestion procedure. Phosphorus concentration (P_{mass}, mg g^{-1}) was measured by atomic absorption spectrum-photometry (AAS, Type 932GBC; Scientific Equipment, Australia). Instantaneous photosynthetic nitrogen- and phosphorus-use efficiency (PNUE, μmolC mol^{-1} N s^{-1}; PPUE, mmolC mol^{-1} P s^{-1}) were calculated as CO_2 assimilation rate per unit mass (A_{mass}) per leaf N_{mass} and P_{mass}, respectively.

We measured the $\delta^{13}C$ (in parts per thousand) of all species on 2 mg ground subsamples of leaves using a Thermo Finnigan MAT stable isotope mass spectrometer (Bremen, Germany) at the Stable Isotope Laboratory in Institute of Botany, The Chinese Academy of Sciences. $\delta^{13}C$ provides an integrated estimate of the ratio of photosynthesis to conductance, and therefore can be used as an index of intrinsic water-use efficiency (Farquhar and Richards 1984). Because we collected young (but fully expanded) leaves near the end of the wet and dry seasons, and because leaf development and expansion occurs rapidly in tropical forests (Kursar and Coley 1991), our $\delta^{13}C$ measurements likely reflect the season in which they were taken.

Statistical analysis

We used two-way repeated-measures ANOVA to compare morphological and physiological leaf traits between growth-form (liana and tree), season (wet and dry) and growth-form × season interactions. We then used LSD contrasts to examine whether each trait differed between growth-forms within and between the seasons. Data were tested for normality and homogeneity of variance and, when necessary, were log$_{10}$-transformed before analysis. Rather than focus on a phylogenetically controlled sampling strategy (e.g., Cai et al. 2008), we intentionally selected species from multiple families in order to generalize as much as possible about lianas and trees. Because *Ficus* is a particularly speciose genus, with more than 40 species in Xishuangbanna (Xu 1994), we included five *Ficus* species in this study. To control for a potential phylogenetic bias, we used the average response of the five *Ficus* species (Schnitzer 2005). Because the results did not differ whether we used the mean of the *Ficus* species or all five *Ficus* species as replicates, we present the results from the larger dataset of 16 tree species (Table 1). Correlations amongst leaf traits were analyzed with a Pearson's correlation; all reported correlations were significant at an alpha level of $P < 0.05$. All statistical analyses were conducted using SPSS version 11.0 (SPSS, Chicago, IL, USA).

Results

During the wet season, species' mean LMA varied from 46 to 134.6 g m^{-2}, with the smallest value for the liana *Byttneria aspera* and the largest one for the tree *Combretum latifolium*. The rate of CO_2 assimilation per unit area (A_{area}) and unit mass (A_{mass}) ranged from 6.05 to 17.5 µmol m^{-2} s^{-1} and from 65 to 259.6 nmol g^{-1} s^{-1} for the trees *Lepianthes senegalensis* and *Ficus cyrtophylla*, respectively (Table 1). The tree *Syzygium latilimbum* had the lowest N_{mass}(1.21%) and the liana *Iodes covalis* had the highest (4.99%). Variation in Car/Chl among the 34 species was small, while the differences in values of PNUE were quite large, ranging from 26.2 to 116.9 µmolC mol^{-1} N s^{-1}. Water-use efficiency, measured by δ^{13}C, ranged from −28.65 to −34.15‰.

During the wet season, lianas and trees had a similar mean A_{area}, $R_{d\,area}$, P_{mass}, PNUE, PPUE, and Car/Chl ratio (Fig. 2). Compared to trees, however, lianas had significantly higher wet season δ^{13}C, A_{mass}, N_{mass}, and A/Chl ratio, as well as significantly lower LMA and leaf area (Fig. 2).
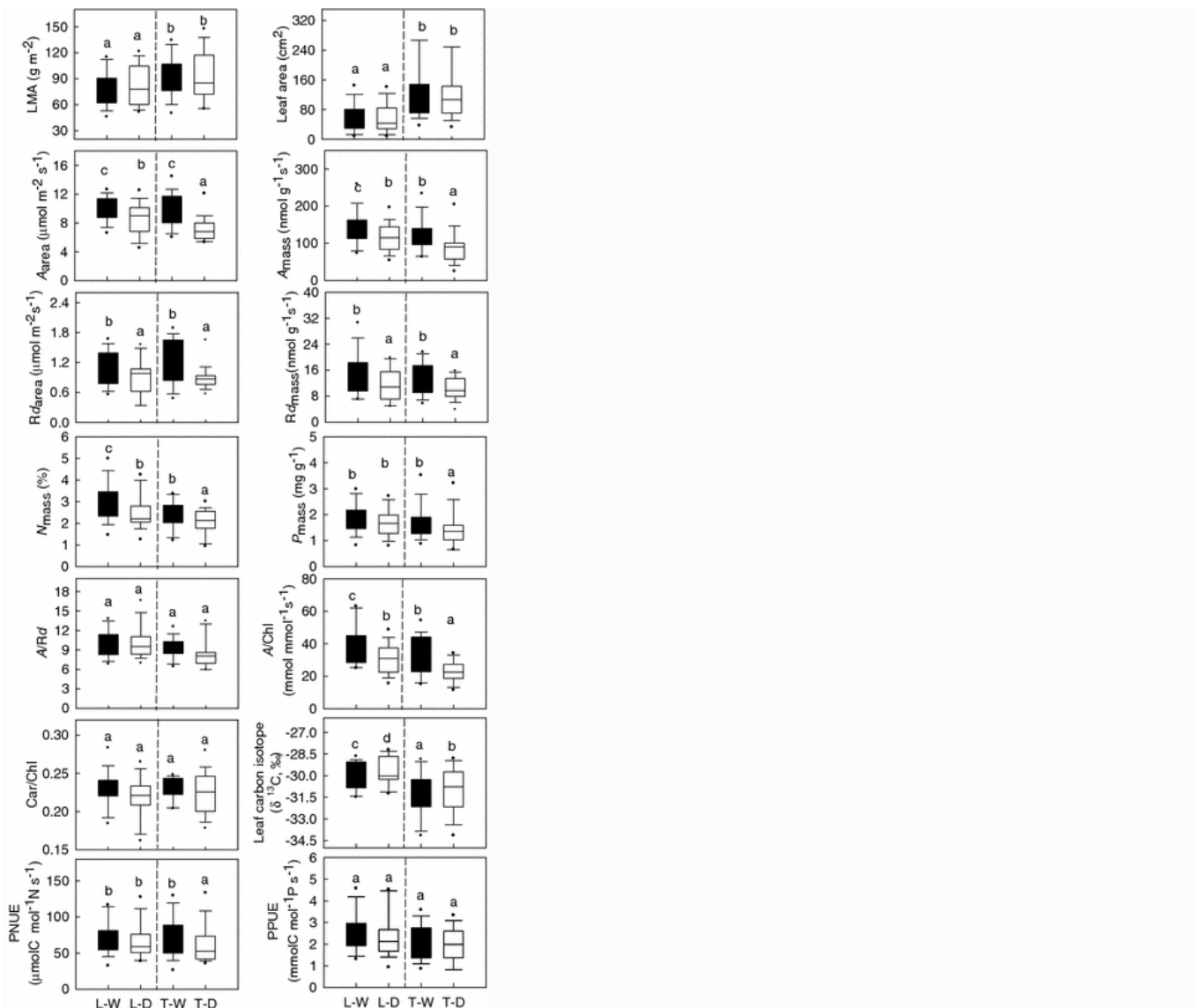

Fig. 2
Box plots of leaf attributes of woody species in the seasonal forest at Xishuangbanna, China. Liana and trees are represented by *L* and *T*, and wet and dry seasons are represented by *-W* and *-D*, respectively. *Boxes* indicate

median, 25th and 75th percentile values, with *error bars* showed 10th and 90th percentile values, and *solid circles*indicating outliers. We compared growth-form, season, and the growth-form × season interaction using a repeated-measured ANOVA with post-hoc least significant difference contrasts to compare the mean leaf traits between the growth forms during each season and between the seasons for each growth form. Different *letters* indicate significant differences at $P \leq 0.05$. Trait abbreviations are defined in Table 1

Lianas and trees responded differently to seasonal drought, as indicated by significant growth-form by season interactions for A_{area}, P_{mass}, $\delta^{13}C$ and PNUE (Table 2). For example, the similar A_{area} of liana and tree species in the wet season was not maintained throughout the dry season, with tree A_{area} becoming significantly lower than that of lianas (growth-form × season interaction, $F_{1,13} = 8.08$, $P = 0.01$; Fig. 2; Table 2). Although there was large variation in A_{area} in the dry season (4.56–12.53 µmol m^{-2} s^{-1}), mean liana A_{area} remained relatively high (8.7 µmol m^{-2} s^{-1}, 87.2% of that of the wet season), whereas mean dry season tree A_{area} declined to 60.9% of that of the wet season (6.1 µmol m^{-2} s^{-1}; Fig. 2). The rate of CO_2 assimilation per unit mass (A_{mass}) also decreased slightly more during the dry season for trees (77.5% of the wet season) than for lianas (81.8% of the wet season), although the growth-form by season interaction for A_{mass} was not significant (Table 2). For tree species, both P_{mass} and PNUE decreased significantly from wet to dry season ($P = 0.048$ and $P = 0.042$, respectively), whereas neither factor changed for lianas ($P = 0.12$ and $P = 0.23$, respectively), resulting in a significant growth-form × season interaction (Table 2; Fig. 2). N_{mass} decreased significantly from wet to dry season for trees ($P = 0.000$) and only marginally for lianas ($P = 0.052$), but the growth-form by season interaction was not significant (Table 2). The $\delta^{13}C$ values of both lianas and trees increased significantly from wet to dry season (lianas: 1.06%; $P = 0.002$; trees: 0.25%; $P = 0.009$), but the significant growth-form × season interaction indicated that $\delta^{13}C$ increased significantly more during the dry season for lianas than for trees (Table 2). Collectively, these results support the hypothesis that lianas fix more carbon and use water and nitrogen more efficiently than trees during seasonal drought.

Table 2
Two-way repeated-measures ANOVA comparing morphological and physiological leaf traits between growth-form (liana vs tree), season (wet vs dry), and the growth-form × season interaction

Response variable	Growth-form		Season		Growth-form × Season	
	F-ratio	*P*	*F*-ratio	*P*	*F*-ratio	*P*
A_{area}	2.189	0.1630	70.795	**0.000**	8.079	**0.0140**
A_{mass}	6.809	**0.022**	40.760	**0.000**	0.202	0.660
N_{mass}	3.855	0.071	63.012	**0.000**	2.491	0.139
P_{mass}	0.548	0.472	189.224	**0.000**	10.544	**0.006**
$R_{d\,mass}$	2.476	0.140	12.871	**0.003**	0.687	0.422
$R_{d\,area}$	0.071	0.794	6.851	**0.021**	0.169	0.688
A/R_d	3.642	0.079	0.733	0.407	3.071	0.103
A/Chl	2.315	0.152	53.521	**0.000**	1.477	0.246
$\delta^{13}C$	7.333	**0.017**	18.723	**0.001**	10.807	**0.005**
PNUE	0.440	0.519	20.229	**0.001**	5.575	**0.034**
LMA	5.106	**0.040**	2.337	0.149	1.797	0.201
Car/Chl	0.424	0.524	1.160	0.297	0.024	0.879
PPUE	1.633	0.222	7.708	**0.015**	1.044	0.324
LA	6.518	**0.024**	2.645	0.128	3.904	0.070

Bold *P* values indicate significant differences

Numerator degrees of freedom (*df*) = 1 and denominator *df* = 13 for all response variables except δ^{13}C, LMA, and PPUE, which had denominator *df* = 14, and Car/Chl, which had a denominator *df* = 17

Leaf mass area (LMA) was strongly negatively correlated with A_{mass} for lianas and trees during the wet season (Fig. 3a), but only for lianas during the dry season (Fig. 3b). This finding suggests that, compared to trees, lianas realized relatively high carbon assimilation at low leaf construction cost, particularly during the dry season. Water-use efficiency (WUE, indicated by δ^{13}C values) was significantly negatively correlated with PNUE in both wet and dry seasons for trees, but not for lianas (Fig. 4). Thus, lianas appear to maintain relatively high PNUE even in periods of high WUE, whereas trees do not.
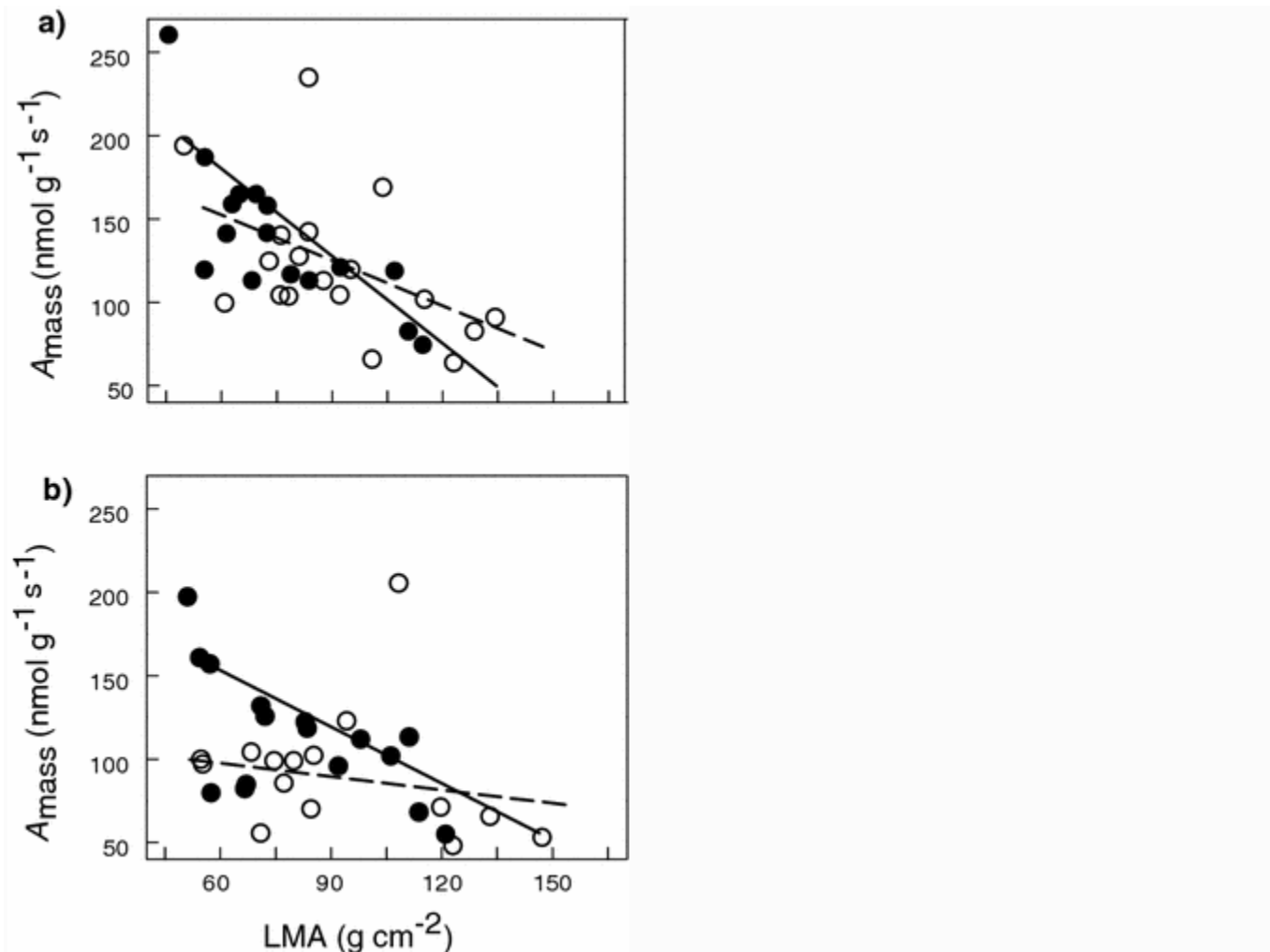

Fig. 3
Relationships between LMA and photosynthetic rates (A_{mass}) of lianas (*black circles*, *straight lines*) and trees (*open circles*, *broken lines*) in wet (**a**) and dry (**b**) seasons. Significant correlations were found during the wet season for both lianas and trees: liana A_{mass} = −1.65 LMA + 264.7, r^2 = 0.59, *P* < 0.001; tree A_{mass} = −0.93 LMA + 205.2, r^2 = 0.24, *P* = 0.039. During the dry season, however, this relationship was significant for lianas (A_{mass} = −0.98 LMA + 192.2, r^2 = 0.37, *P* = 0.013), but not for trees (A_{mass} = −0.27 LMA + 111.2, r^2 = 0.24, *P* = 0.066)
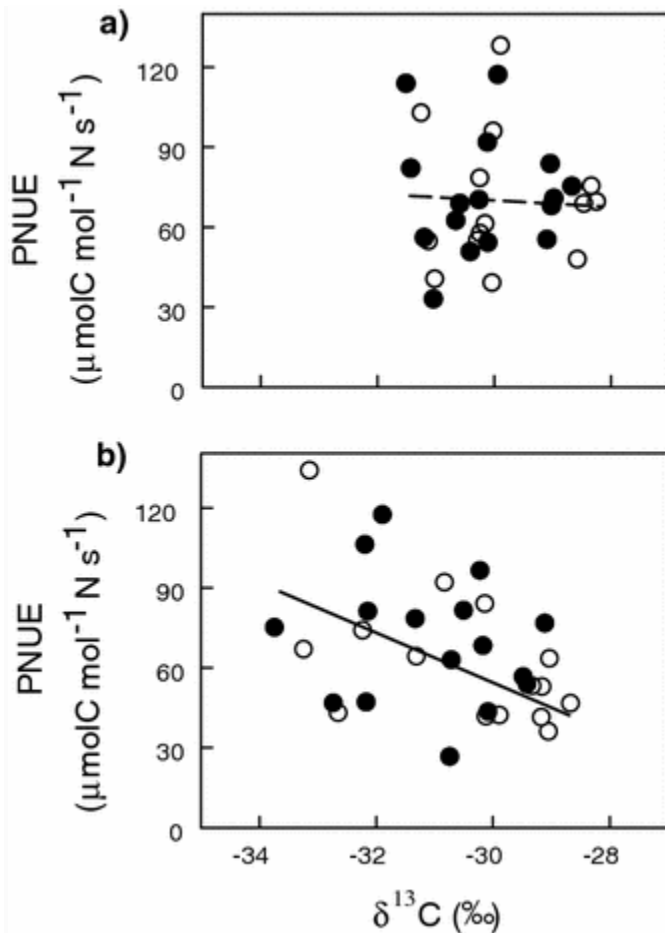
Fig. 4
Relationships between carbon isotope ratio (δ^{13}C) and photosynthetic N-use efficiency (PNUE) for lianas (**a**) and trees (**b**) in the wet (*black circles*) and dry season (*open circles*). Significant correlations during both wet and dry seasons were found for trees ($r^2 = 0.16$, $P = 0.024$), but not for lianas ($r^2 = 0.01$, $P > 0.05$)

Discussion

Testing the dry season growth advantage hypothesis

Our findings demonstrate that, compared to trees, lianas fixed more carbon per unit leaf area and exhibited less water stress during the dry season relative to the wet season. The ability to fix carbon during the dry season when trees are less active may give lianas a competitive advantage over trees in seasonal forests, which may help explain their high abundance in seasonal dry forests and lower abundance in aseasonal wet forests (Schnitzer 2005; Swaine and Grace 2007; DeWalt et al., unpublished). While A_{area}, A_{mass}, N_{mass}, and P_{mass} for lianas and trees in this study were within a wide range of values consistent with other studies (e.g., Reich et al. 1997; Wright et al. 2004a, b), lianas exhibited less of a decrease in these variables during seasonal drought (Fig. 2). The relatively high photosynthetic capacity of lianas over the dry season may enable them to fix more carbon over this period, and thus have more available carbon to allocate to growth and reproduction. Indeed, in the seasonal moist forest of BCI, lianas grew proportionally more than trees during the dry season compared to the wet season (Schnitzer 2005). Zotz and Winter (1996) reported constant photosynthetic rates for the liana *Uncaria tomentosa* between wet and dry seasons on BCI, suggesting that this liana did not suffer from seasonal drought.

Our findings that lianas had higher WUE than trees, as indicated by the significantly higher $\delta^{13}C$ values in both seasons (Fig. 2), are consistent with findings of Foster and Brooks (2005) and Domingues et al. (2007). In general, high leaf-level WUE is thought to be the result of lower water availability (Lambers et al. 1998). The high specific hydraulic conductivity of liana stems (Tyree and Ewers 1996; Andrade et al. 2005), however, may lead to high stomatal conductance and therefore sustained higher transpiration rates (Restom and Nepstad 2001). Santiago and Wright (2007) suggested that the high sap flow capacity of lianas may be balanced by their relatively high leaf area (Putz 1983; Gerwing and Farias 2000), reducing the amount of water supplied to each leaf and thus increasing the need for greater leaf-level WUE. In addition, lianas typically have a greater ratio of leaf area per cross-sectional area of vascular tissue than do trees (Putz 1983). During periods of high evaporative demand, such allometry might place lianas at a higher risk of xylem embolism (Hacke et al. 2006), and thus high WUE may be a necessary water-use strategy of lianas. Our findings do not imply that lianas will eventually displace trees in highly seasonal tropical forests; rather, they support the hypothesis that lianas abundance is controlled, to a large extent, by mean annual rainfall and seasonality because lianas compete better in forests with these attributes (Schnitzer 2005).

Are lianas superior to trees in resource capture during seasonal drought?

Collectively, our data suggest that lianas and trees differ mostly during the dry season, when lianas become more efficient at capturing resources. We found that lianas and trees were not significantly different in A_{area}, N_{mass}, P_{mass} and PNUE during the wet season, but that the differences in these traits became apparent during the dry season. Our results differ from studies reporting that lianas and trees had similar photosynthetic capacity (Castellanos 1991; Zotz and Winter 1996), or that A_{area} was lower for lianas than for trees (Santiago and Wright 2007). The high levels of $\delta^{13}C$ and PNUE during the dry season indicate that lianas have high water- and nitrogen-use efficiency, suggesting that they capture resources more efficiently than trees, which may be particularly important for dry season growth.

The steep tradeoff between A_{mass} and LMA (Fig. 3) indicates that lianas can attain relatively high carbon assimilation with low leaf construction expenses compared to trees, particularly during the dry season (sensu Field and Mooney 1986; Poorter and Villar 1998). The metabolic efficiency of leaves, however, as measured by the variance of A_{mass} across all ranges of $R_{d mass}$, did not differ between lianas and trees. The Car/Chl ratio for lianas and trees were also similar, indicating that in the high-light canopy conditions lianas and trees have similar strategies for light harvesting and the ability to dissipate excessive light energy via xanthophylls (Demmig-Adams and Adams 1992). Therefore, the differences between lianas and trees appear to lie in the assimilation rate per leaf structural investment (LMA) and the A/Chl ratio: lianas have higher carbon gain per unit leaf area and more photosynthesis per unit chlorophyll. The high N_{mass} and low LMA, which are consistent with previous studies (Kazda and Salzer 2000; Salzer et al. 2006), suggest a higher leaf turnover and a higher decomposition rate (Diaz et al. 2004). Differences between lianas and trees in photosynthetic efficiency over time and leaf life span also affect whole-plant carbon fixation per structural investment, and should be examined to verify whether the conclusions of our short-term study scales temporally and at the whole-plant level. Differences in leaf traits between lianas and trees are likely to have important implications for nutrient cycling in tropical forests if lianas increase substantially in abundance (e.g., Phillips et al. 2002; Wright et al. 2004a, b).

Ecological significance of trade-offs between water-use efficiency and nitrogen efficiency

Prolonged drought restricts the mobility of N through dehydrated soil and thus co-limitation of water and N may be common in seasonal forests. During periods of low water availability, stomata generally close, leading to reduced water loss and thus higher WUE. Typically, however, lower internal leaf CO_2 concentrations result in decreased photosynthesis; while N remains constant, resulting in lower PNUE and a trade-off between WUE and

PNUE in C$_3$plants (Field and Mooney [1986]). In our study, we found a significant WUE–PNUE trade-off for trees, but not for lianas (Fig. [4]). Trees achieved higher PNUE at the expense of decreasing WUE, whereas lianas could simultaneously maintain relative higher WUE and PNUE (Figs. [2], [4]). The differences in the trade-off between PNUE and WUE may partially explain the higher rates of photosynthesis in lianas during periods of drought. Alternatively, the lack of a negative WUE–PNUE trade-off for lianas may be explained by the relatively narrow δ^{13}C range compared to trees, which may have limited our ability to detect this tradeoff (see also Foster and Brooks [2005]; Domingues et al. [2007]).

In conclusion, our findings support the dry season growth advantage hypothesis for lianas, which may help explain the peak in liana abundance in the seasonal tropical forests. Unique root, stem, and leaf-level characteristics appear to allow lianas to achieve relatively high rates of carbon gain per leaf mass, area, and structure cost, as well as high resource use efficiency (water and nitrogen) during seasonal drought. Differences in these physiological attributes may explain the competitive advantage of lianas over trees during seasonal drought.

Notes

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