乔木与木质藤本的水力与光合性状的差异：以热带森林崖豆藤属和买麻藤属为例

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摘要 木质藤本是热带森林的重要组成部分, 显著影响森林的结构和功能。已有研究发现木质藤本与乔木的水力结构存在显著差异: 木质藤本的缠绕或攀缘茎细小, 但其木质部具有粗大的长导管, 输水效率高, 抗栓塞能力低。为降低基因型差异对比较结果的影响, 该研究选取热带崖豆藤属(*Millettia*)和买麻藤属(*Gnetum*)的乔木和木质藤本, 比较同属内不同生长型植物的水力和光合性状的差异, 分析水分传导效率与抗栓塞能力之间以及水力与光合性状之间的相关关系。结果发现: (1)崖豆藤属植物水力性状的种间差异大, 与生活型和需光性有关。耐阴的木质藤本反而具有较低的水分传导效率和较高的抗栓塞能力。(2)买麻藤属植物是裸子植物较为进化的类群(具有导管和阔叶), 其乔木的水分传导效率很低, 但是其木质藤本的水分传导效率高于其他阳生性的被子植物。(3)不论乔木还是木质藤本, 水分传导的有效性与安全性在枝条和叶片水平上均没有显著的权衡关系。(4)与同属乔木相比, 木质藤本的叶片较枝条的抗栓塞能力更强, 在旱季具有更高的最大净光合速率和气孔导度, 支持了木质藤本的“旱季生长优势假说”。该研究揭示了热带木质藤本水力性状的多样性和重要性, 为阐明环境变化对这一重要植物类群的影响, 需要它们的水力特征进行更广泛的研究。

关键词 水力结构; 抗栓塞能力; 权衡关系; 脆弱性分段; 光合速率

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Hydraulic and photosynthetic characteristics differ between co-generic tree and liana species: a case study of *Millettia* and *Gnetum* in tropical forest

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Abstract

Aims Liana is an important component of tropical forest, and exert a significant impact on community structure and function. Previous studies have found significant differences in hydraulic traits between lianas and trees, as indicated that lianas tended to have large and long vessels to compensate hydraulically to their thin stems, resulting in high hydraulic conductivity but low resistant to drought-induced cavitation. In order to reduce the influence of different genotypes on the comparative results, we aimed to compare the differences in hydraulic and photosynthetic characteristics between the two life forms from two genera *Millettia* and *Gnetum*.

Methods We measured branch and leaf hydraulic properties, sapwood density, gas exchange rates in the dry season for nine tree and liana species grown in common garden. We compared the hydraulic and photosynthetic traits between each species using one-way ANOVA. In addition, we analyzed hydraulic efficiency-safety trade-off, and the relationship between dry-season photosynthetic rates and hydraulic traits.

Important findings (1) There was a significant variations in hydraulic traits in genus *Millettia*, which was related to their light requirements and life forms. Compared with trees, the shade-tolerant liana species had lower hydraulic conductivity and higher resistance to cavitation. (2) Despite angiosperm-like characteristics such as vessels and broad pinnate-veined leaves, the *Gnetum* tree species had the lowest hydraulic conductivity among the nine species. However, the *Gnetum* liana species had higher hydraulic conductivity, comparable to light-demanding

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angiosperm species in this study. (3) There was no significant trade-off between hydraulic conductivity efficiency and hydraulic safety in both branch- and leaf-level across all the species, or within each plant group. (4) Compared to co-generic tree species, liana species' leaves were more resistant to cavitation than branches, as indicated by higher maximum net photosynthetic rates and stomatal conductance during the dry season. These results support the hypothesis of "growth advantages at dry season" for liana species. This study reveals the high diversity and significance of hydraulic functioning in tropical lianas. Extensive measurements of hydraulic properties are needed to promote understanding of tropical species response to environmental change.

Key words hydraulic function; cavitation resistance; trade-off; vulnerability segmentation; photosynthetic rates

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植物的水力特征是探讨植物生理生态适应的核心内容(Choat *et al.*, 2012)。植物水力学性状主要包括: (1)水力传导能力(有效性), 如边材和叶片比导率(k_s 、 k_l), 它是衡量植物水分传导效率的指标(Sperry *et al.*, 1988)。水分传导效率与叶片的光合能力密切相关(Santiago *et al.*, 2004), 并最终影响植物的生长速率(Brodribb *et al.*, 2010)。(2)抗栓塞能力(安全性), 用植物输导组织损失50%导水能力时的水势值(P_{50})表示, 与植物的干旱适应策略有关。植物水分传导有效性与安全性之间存在权衡关系, 是探讨植物的生长策略以及沿水分梯度分布等方面的重要的生理生态机制(Markestijn *et al.*, 2011)。但是基于全球数据分析发现这种权衡关系较弱(Gleason *et al.*, 2016; Santiago *et al.*, 2018), 在水分胁迫不严重的热带森林中甚至没有权衡(van der Sande *et al.*, 2019)。植物不同器官的水力特征之间的差异或者协同关系是水力学研究的重要内容(Bucci *et al.*, 2012)。经典的脆弱性分段假说认为植物茎的抗栓塞能力要强于末端的叶片, 在水分胁迫状况下, 叶片更容易发生栓塞, 从而减少水分进一步损失, 保证了茎的水力安全(Zimmerman & Brown, 1971; Tyree & Ewers, 1991)。因此, 叶片在植物整个水分运输通路中起到了“安全阀”的作用(McCulloh *et al.*, 2014)。但是, 也有部分研究发现热带亚热带森林的植物并不符合脆弱性分段假说: 叶片的抗栓塞能力与枝条相近(Villagra *et al.*, 2013), 甚至要强于枝条(Zhu *et al.*, 2015), 原因在于枝-叶的脆弱性分段与生境的干旱指数相关, 生长在湿润地区的植物具有稳定的水分来源, 环境选择压力小; 另外, 缺乏枝-叶脆弱性分段的植物具有丰富的水力补偿策略维持叶片的水分供给, 在潜在的干旱胁迫下可能具有生长优势(Zhu *et al.*, 2016)。基于水力性状可以分析植物的水分适应策略, 被广泛地用于解释植物一系列的生态

学表现(de Guzman *et al.*, 2017)。

木质藤本植物是热带森林的重要组成部分(Schnitzer & Bongers, 2011)。木质藤本具有木质化的茎, 但是不能直立生长, 通过攀附或缠绕其他植物(主要是乔木)的茎到达森林冠层, 由于投资到支撑结构的生物量较少, 木质藤本把较多的生物量配置到叶片和根系上(Rodríguez-Ronderos *et al.*, 2016)。木质藤本植物在水力结构和碳经济学方面与乔木显著不同(Angyalossy *et al.*, 2014)。与乔木相比, 木质藤本具有较高的比叶面积和光合速率(Cai *et al.*, 2009), 具有发达且高效的维管系统(高的水力传导效率)为叶片运输水分和营养(Isnard & Feild, 2014), 但该结构导致木质部较低的抗栓塞能力(Isnard & Silk, 2009)。基于木质藤本对季节性干旱的生理生态响应, Schnitzer (2005)提出了木质藤本植物的“旱季生长优势”假说, 即木质藤本在干旱季节的生长速率要显著高于其他直立树木。这可能与木质藤本具备有效的水力适应策略有关, 如发达的根系保证其在旱季获得深层土壤水分, 以及较强的气孔和渗透调节能力维持旱季光合作用并减少过度的水分损失(Maréchaux *et al.*, 2017)等。长期的森林监测数据表明, 随着全球气候日益干热化对森林结构影响加剧(Allen *et al.*, 2010), 木质藤本植物在热带季节性森林中的丰富度在增加, 将显著影响热带森林的群落结构和功能(Campbell *et al.*, 2018), 这一现象印证了“旱季生长优势”假说的同时, 也使木质藤本的生理生态特征受到广泛的关注(Schnitzer & van der Heijden, 2019)。

木质藤本和乔木的生理生态学比较研究加深了对木质藤本这一重要的植物功能类群的认识(Santiago *et al.*, 2014)。但是种间差异可能会影响不同植物类群之间的比较结果, 因此选择同属的木质藤本和乔木进行比较研究能够降低不同物种基因型

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差异所带来的影响。在植物分类系统中大多数属内都有木质藤本,其物种多样性非常高,而且广泛地分布于热带森林的各种生境(Putz, 1984)。而以往研究较多地关注丰富度显著增加的部分木质藤本及其快速生长策略(Collins *et al.*, 2016),但对许多生长在林下荫蔽生境中的木质藤本的生理生态特征研究较少(Santiago & Wright, 2007)。本研究选择生长在热带同质园不同光环境的崖豆藤属(*Millettia*)和买麻藤属(*Gnetum*)的木质藤本与乔木(表1),通过测定它们的枝叶水力结构和旱季气体交换参数,研究以下内容并提出假设:(1)比较同属木质藤本和乔木的水力性状的差异性。假设:与同属的乔木相比,木质藤本不都具有较快水分传导效率和较低的抗栓塞能力。(2)分析植物枝条和叶片水平上水分传导的有效性与安全性之间的权衡关系。假设:乔木表现出显著的权衡关系,而木质藤本不存在权衡关系。(3)分析枝-叶脆弱性分段及其与旱季气体交换速率之间的相关关系。假设:与乔木相比,木质藤本不符合经典的脆弱性分段假说,并具有较高的旱季光合速率和气孔导度。研究结果有助于加深对木质藤本水力性状的了解,为探讨环境变化对木质藤本的影响提供依据。

1 材料和方法

1.1 研究地点与植物材料

本试验在中国科学院西双版纳热带植物园(21.68° N, 101.42° E, 海拔580 m)内进行。研究地点位于热带北缘,年降水量1 550 mm,年平均气温21.7 °C,相对湿度85%。受西南季风的影响,一年中有明显的干季(11月–翌年4月)和雨季(5–10月)之分,雨季降水量占全年的80%以上。

本研究以热带森林两个常见的属为研究对象:(1)崖豆藤属,豆科,广泛分布在非洲、亚洲和大洋洲的热带和亚热带森林中(中国科学院中国植物志编辑委员会, 1993; 李延辉等, 1996)。崖豆藤属选取3种木质藤本——厚果崖豆藤(*Millettia pachycarpa*)、香花崖豆藤(*Millettia dielsiana*)、海南崖豆藤(*Millettia pachyloba*)与3种乔木——思茅崖豆(*Millettia leptobotrya*)、红河崖豆(*Millettia cubittii*)、变色鸡血藤(*Millettia versicolor*);(2)买麻藤属,买麻藤科,广泛分布于纬度较低地区的热带亚热带森林(中国科学院中国植物志编辑委员会, 1993; 李延辉等,

1996)。买麻藤属植物是裸子植物中发展到高级阶段的类群,具有一系列较为进化的与被子植物相似的特征,如:叶片呈交叉状、具有木质部导管和宽羽状脉叶片(Doyle & Donoghue, 1986; Tomlinson & Fisher, 2005)。买麻藤属选取两种乔木——灌状买麻藤(*Gnetum gnemon*)、少苞买麻藤(*Gnetum brunonianum*)与一种木质藤本——小叶买麻藤(*Gnetum parvifolium*)。

选取的两个属共9种木本植物基本信息见表1。所有木质藤本均从野(国)外引种并栽种在西双版纳热带植物园的藤本园内,乔木栽种在同一植物园内的各个分类园,生长的土壤和气候条件一致(同质园)。所有物种个体成熟,生长状况良好,乔木均无藤本攀爬。乔木红河崖豆植株较为高大,处于分类园植物群落的上层;思茅崖豆、变色鸡血藤、灌状买麻藤和少苞买麻藤分布于分类园植物群落下层。木质藤本通过攀缘和缠绕附近的乔木(高度5–7 m)向上生长,厚果崖豆藤、香花崖豆藤以及小叶买麻藤均为阳生木质藤本,叶片分布在树冠;而海南崖豆藤大部分叶片则分布在树冠下相对荫蔽环境。根据每种植物材料情况选取3–5株个体进行测定。海南崖豆藤个体较少,样本量不够,故叶片水力性状指标没有测定。

1.2 测定方法

1.2.1 枝条导水率的测量

在5:00–7:00从每个物种的3–5株个体上采集6–10段较长且分枝少的阳生小枝条(直径5–10 mm),放在有湿润毛巾的黑色塑料袋中,迅速带回实验室。首先用充气法确定植物的最大导管长度(Brodribb & Feild, 2000; 表1),由于样本量原因,变色鸡血藤、海南崖豆藤和灌状买麻藤没有测定最大导管长度,本研究参考了同属同生活型最大值。在水下剪取一段枝条用于导水率的测定,茎段长度要大于该树种的最大导管长度;但是对于厚果崖豆藤和小叶买麻藤(最大导管长度太长),尽量选取适合直径范围内最长的茎段。在水中将两端切口修剪齐平后,在0.1 MPa的水压下用过滤且除气后的0.02 mol·L⁻¹ KCl溶液冲洗茎段(Sperry *et al.*, 1988),冲洗时间以导水率稳定不再增加为准。用水分传导测定装置(Sperry *et al.*, 1988)测定其导水率(k_h),该指标定义为通过一个离体茎段的水流量(F , kg·s⁻¹)与该茎段引起水流动的压力梯度(dp/dx , MPa·m⁻¹)

表1 9种植物的生活型、名称缩写、最大导管长度以及生态学特性描述

Table 1 Life form, species abbreviations, maximum vessel length and ecological descriptions for the nine woody species

物种 Species	生活型 Life form	缩写 Abbreviation	最大导管长度 Maximum vessel length (m)	原生境分布 Native habitat of adult in the forest
崖豆藤属(豆科) <i>Millettia</i> (Fabaceae)				
思茅崖豆 <i>Millettia leptobotrya</i>	乔木 Tree	<i>M. lep</i>	0.69	山坡疏林或常绿阔叶林中, 海拔300–1 000 m Open forest on slopes or evergreen broad-leaved forest; 300–1 000 m a.s.l.
红河崖豆 <i>Millettia cubittii</i>	乔木 Tree	<i>M. cub</i>	0.49	河边的林地或路边, 海拔300–1 000 m Riparian forest or roadside; 300–1 000 m a.s.l.
变色鸡血藤 <i>Millettia versicolor</i>	乔木 Tree	<i>M. ver</i>		引种于非洲南部热带次生林、稀树草原 Tropical secondary forests and savannas of southern Africa
厚果崖豆藤 <i>Millettia pachycarpa</i>	藤本 Liana	<i>M. pac</i>	1.50	山坡疏林、阔叶林内或路边, 海拔100–2 000 m Open forest on slopes, broad-leaved forest or roadside; 100–2 000 m a.s.l.
香花崖豆藤 <i>Millettia dielsiana</i>	藤本 Liana	<i>M. die</i>	0.82	山坡杂木林与灌丛中, 海拔300–2 500 m Tree-shrub mixed forest on slopes; 300–2 500 m a.s.l.
海南崖豆藤 <i>Millettia pachyloba</i>	藤本 Liana	<i>M. pab</i>		沟谷常绿阔叶林中, 海拔1 500 m以下 Evergreen broad-leaved forests in valleys; below 1 500 m a.s.l.
买麻藤属(买麻藤科) <i>Gnetum</i> (Gnetaceae)				
灌状买麻藤 <i>Gnetum gnemon</i>	乔木 Tree	<i>G. gne</i>		湿润的常绿次生森林下, 海拔1 600–2 000 m Moist evergreen secondary forests; 1 600–2 000 m a.s.l.
少苞买麻藤 <i>Gnetum brunonianum</i>	乔木 Tree	<i>G. bru</i>	1.14	海拔350 m的阔叶林下 Broad-leaved forest; below 350 m a.s.l.
小叶买麻藤 <i>Gnetum parvifolium</i>	藤本 Liana	<i>G. par</i>	2.00	海拔较低的干燥平地或湿润谷地的森林, 海拔100–1 000 m Dry flat or moist valleys forests at lower altitude; 100–1 000 m a.s.l.

原生境信息来源于《中国植物志》(中国科学院中国植物志编辑委员会, 1993)和《引种植物名录》(李延辉等, 1996)。

Native habitat descriptions of these species were extracted from Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China, Chinese Academy of Sciences, 1993) and Li *et al.* (1996).

的比值(Cruiziat *et al.*, 2002):

$$k_h = F/(dp/dx) \quad (1)$$

测定导水率后的枝条, 用甲基兰溶液染色确定两端边材面积, 其平均值为该茎段边材面积(A_s , m^2)。该茎段边材比导率(k_s)定义为单位茎段边材横截面积的导水率:

$$k_s = k_h/A_s \quad (2)$$

叶比导率(k_l)反映单位叶片的水分供应, 用 k_h 除以该茎段形态学末端的总叶面积(A_l , m^2)可得:

$$k_l = k_h/A_l \quad (3)$$

叶面积/边材面积比(A_l/A_s)为茎段末端总叶面积与所测茎段边材面积的比值, 反映单位边材横截面积可供水分的茎末端叶片面积。

1.2.2 枝条的脆弱性曲线的测定

本研究使用注气法测定枝条的脆弱性曲线(Cochard *et al.*, 1992; Sperry & Saliendra, 1994; En-najeh *et al.*, 2011)。取样方法和使用的茎段长度同枝条导水率测定, 将枝条(避免节)中间的一部分放置于气穴室(PMS, 1505D-EXP; 气穴室长度为12 cm)中。在0.1 MPa的压力下用过滤且除气后的0.02 mol·L⁻¹ KCl溶液冲洗20–40 min后测定其最大导水率(k_{max} ; 以导水率数值稳定不再增加为准)。随

后连接压力室水势仪(PMS, Corvallis, Oregon, USA), 向气穴室依次加压至0.3、0.5、1.0、1.5、2.0、2.5 Mpa……直至该段枝条的导水率丧失百分比(PLC, %)达到80%以上。在每个压力下, 加压时间保持5–10 min, 然后降低至一个较低的压力水平(0.1 MPa左右), 并且保持5–20 min (压力越大, 时间越长), 最后完全释放压力测定该段枝条的水分传导速率(k_l), 并计算该压力下的PLC:

$$PLC = 100 \times (1 - k_l)/k_{max} \quad (4)$$

在SigmaPlot 12.5中使用Sigmoid模型拟合PLC与所对应的压力值之间的关系(Pammenter & van der Willigen, 1998), 并计算PLC为50%时的木质部水势值($P_{50branch}$)用于表征枝条木质部的抗栓塞能力。

1.2.3 边材密度的测定

测定水力传导速率的枝条样品可用于测定边材密度, 选取一小段无分枝枝条(长度约5 cm), 利用甲基蓝染色区分并用小刀分离出边材, 在水中充分饱和后利用排水法确定边材体积(V , cm^3), 然后在60 °C的烘箱中烘干72 h后测定干质量(DW , g)。边材密度(WD , $g \cdot cm^{-3}$)为:

$$WD = DW/V \quad (5)$$

1.2.4 叶片脆弱性曲线的测定

在凌晨采集带叶的阳生小枝条(此时叶片水分状况接近饱和), 放在有湿润毛巾的黑色塑料袋中, 迅速带回实验室。将带叶枝条放在实验室内让其自然干燥不同时间(0–48 h), 以达到不同的水势, 期间始终保持枝条上下两端的叶片被包裹。使用两点复水法测定叶片的导水率和脆弱性曲线(Brodribb & Holbrook, 2003)。在每个水势下, 在测定叶片导水率(K_{leaf})前, 将带叶枝条放在黑色塑料袋平衡至少1 h, 然后选取枝条两端的包裹叶片分别测定水势, 若差值小于0.1 MPa, 则视为水势平衡。测量初始叶片水势(Ψ_0)后, 在蒸馏水中再剪下同一枝条的两片相邻的叶片, 使叶片重新复水10–120 s (初始水势越负, 复水时间越长), 然后把叶片放入放有湿纸中的自封袋里平衡10–60 min, 最后测量复水后的水势(Ψ_t), 通过下列公式计算 K_{leaf} :

$$K_{\text{leaf}} = C \times \ln(\Psi_0/\Psi_t)/t \quad (6)$$

式中, t 是复水时间(s), 叶片水容 C 的计算公式为:

$$C = \Delta RWC/\Delta \Psi_1 \times (DW/LA) \times (WW/DW)/M \quad (7)$$

式中, DW 为叶片干质量(g), LA 为叶片面积(m^2), WW 为叶片相对含水量为100%时的水分质量(g), M 为水分摩尔质量($\text{g} \cdot \text{mol}^{-1}$)。叶片的相对含水量(RWC)与叶片水势的关系($\Delta RWC/\Delta \Psi_1$)可从叶片的压力-容积曲线计算。本研究用自然失水法测定叶片的压力-容积曲线(Brodribb & Holbrook, 2003), 即让水分饱和的叶片自然干燥失水, 在此期间不断测定叶片鲜质量和水势, 测定完成后测其干质量。通过叶片压力-容积曲线计算程序拟合曲线(Schulte & Hinckley, 1985), 并计算膨压丧失点水势前后的 $\Delta RWC/\Delta \Psi_1$ 。通过测定不同水势梯度下的叶片水力导度, 使用直线或sigmoid方程拟合 K_{leaf} 与 Ψ_0 的相关关系。计算水势为0的叶片导水率, 即为叶片最大水力导度($K_{\text{leaf-max}}$), 并计算叶片最大导水率损失50%的叶片水势值($P_{50\text{leaf}}$)用于表征叶片的抗栓塞能力。

枝-叶脆弱性分段($P_{50\text{leaf-branch}}$)为叶片水力导度损失50%的叶片水势值($P_{50\text{leaf}}$)减去枝条木质部导水率损失50%时的水势值($P_{50\text{branch}}$), 即:

$$P_{50\text{leaf-branch}} = P_{50\text{leaf}} - P_{50\text{branch}} \quad (8)$$

1.2.5 旱季最大净光合速率和气孔导度

使用LI-6400便携式光合作用测定仪(LI-COR, Lincoln, USA)在旱季的连续晴朗天气测定成熟健康

叶片的光合作用。根据以往的测定经验(Ma *et al.*, 2015), 阳生树种饱和光强设定为 $1\,500\, \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, 阴生树种的饱和光强设定为 $1\,000\, \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, CO_2 浓度设置为 $390\, \mu\text{mol} \cdot \text{mol}^{-1}$, 叶片温度根据外界环境值, 保持在25–35 °C范围内。每个物种选择3–5株个体, 每个个体选取3片叶片进行测定, 具体测定时间为8:00–11:30, 先使用LED光源(LI-6400-2B)诱导, 待气体交换参数稳定后记录测量结果, 获得光饱和时的最大净光合速率(A_{max})和最大气孔导度($g_{\text{s-max}}$)。部分乔木或木质藤本上部的叶片较高, 则借助建筑和梯子或者利用绳子拉下枝条进行活体测定。

1.3 数据分析

为满足方差分析的同质性检验, 对所有指标数据进行了对数转换, 用单因素方差分析比较不同树种的水力性状的差异显著性($p < 0.05$)。用直线回归方程分析水分效率指标之间与光合效率指标之间的Pearson相关性(F -test; $p < 0.05$)。利用SPSS 20.0软件进行数据分析, 利用SigmaPlot 12.5软件绘图。

2 结果

2.1 乔木与木质藤本的水力性状

崖豆藤属中, 木质藤本香花崖豆藤的枝条抗栓塞能力最低, 为–0.67 MPa, 但是木质藤本海南崖豆藤与乔木变色鸡血藤和思茅崖豆的枝条抗栓塞能力相近, 分别为–1.39、–1.42和–1.40 MPa; 木质藤本厚果崖豆藤与乔木红河崖豆的枝条抗栓塞能力也相差不大。在叶片水平, 除乔木红河崖豆的抗栓塞能力最低(–2.18 MPa)外, 其余种的抗栓塞能力相当(图1)。

买麻藤属中, 木质藤本小叶买麻藤的枝条抗栓塞能力要低于其余两种乔木, 但是它们的叶片抗栓塞能力相当(图1)。

将所研究的9种木本植物划分为乔木和木质藤本两个类群进行比较, 它们的枝条和叶片的抗栓塞能力均没有显著差异($p > 0.05$; 附录I)。

崖豆藤属内木质藤本和乔木作为两个类群进行比较, 它们的导水率、叶面积/边材面积和边材密度均没有显著差异($p > 0.05$; 附录I)。从种间水平来看, 木质藤本厚果崖豆藤的边材比导率最大

图1 崖豆藤属(左)与买麻藤属(右)木本植物的枝条和叶片脆弱性曲线。实心和空心圆分别代表乔木和木质藤本。树种名称缩写见表1。垂直虚线表示枝条与叶片导水率损失50%时的水势值($P_{50branch}$ 和 P_{50leaf})。

Fig. 1 Branch and leaf vulnerability curves of the woody species in *Millettia* (left) and *Gnetum* (right). Filled and open circles indicate tree and liana species, respectively. Species abbreviations are shown in Table 1. Water potential at 50% loss of branch hydraulic conductivity ($P_{50branch}$) and leaf hydraulic conductance (P_{50leaf}) are indicated by vertical dashed lines. K_{leaf} , leaf hydraulic conductivity.

($10.06 \text{ kg} \cdot \text{m}^{-1} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$), 乔木思茅崖豆最小 ($2.38 \text{ kg} \cdot \text{m}^{-1} \cdot \text{s}^{-1} \cdot \text{MPa}^{-1}$), 两者之间差异显著 ($p <$

0.05); 其余种的边材比导率相近。阳生性的乔木 红河崖豆、木质藤本厚果崖豆藤和香花崖豆藤的

图2 崖豆藤属与买麻藤属9种植物的边材比导率(k_s)、叶比导率(k_l)、叶面积/边材面积(A_l/A_s)和边材密度(WD)的比较(平均值+标准误差)。实心和空心柱分别表示乔木和木质藤本。不同字母表示各指标之间有显著性差异($p < 0.05$)。物种名称的缩写见表1。

Fig. 2 Comparison in branch hydraulic traits among the nine woody species in *Millettia* and *Gnetum* (mean + SE). k_s , sapwood specific hydraulic conductivity; k_l , leaf specific hydraulic conductivity; A_l/A_s , leaf area/sapwood area ratio; WD , sapwood density. Filled and open bars indicate tree and liana species, respectively. Different letters indicate significant difference at $p < 0.05$. Species abbreviations are shown in Table 1.

叶比导率相近,且高于其余耐阴树种。红河崖豆的叶面积/边材面积最小($1.38 \text{ m}^2 \cdot \text{cm}^{-2}$),且显著低于其余树种($p < 0.05$)。木质藤本厚果崖豆藤、海南崖豆藤以及乔木红河崖豆的边材密度分别为 0.53 、 0.54 、 $0.53 \text{ g} \cdot \text{cm}^{-3}$,显著低于其余树种(大于 $0.60 \text{ g} \cdot \text{cm}^{-3}$)。

买麻藤属中,木质藤本小叶买麻藤的边材比导率、叶比导率和叶面积/边材面积都显著高于其余两种乔木,但是它的边材密度最小($0.33 \text{ g} \cdot \text{cm}^{-3}$)。

将所研究的9种木本植物划分为乔木和木质藤本两个类群进行比较,它们在4个水力性状(k_s 、 k_l 、 A_l/A_s 、 WD)之间均具有显著差异($p < 0.05$; 附录I)。

2.2 枝条和叶片的抗栓塞能力与导水效率之间的相关性

对于本研究的所有树种,枝条抗栓塞能力与边材比导率之间没有显著的相关关系($p > 0.05$; 图3A);在乔木与木质藤本两个类群内,两者之间也不存在显著的相关关系($p > 0.05$; 附录II)。与枝条类似,不

管从所有树种还是植物类群内(乔木和木质藤本)进行分析,叶片抗栓塞能力与叶片最大水力导度之间也没有显著的相关关系($p > 0.05$; 图3B; 附录II)。说明植物水分传导有效性与安全性之间在枝条和叶片水平均不存在权衡关系。

2.3 水力性状与旱季光合性状指标之间的相关性

对于所有树种来说,旱季最大净光合速率与枝条和叶片的水分传导效率之间没有显著的线性相关关系($p > 0.05$; 图4A、4B),但是与枝条和叶片的抗栓塞能力显著相关,即物种的抗栓塞能力越强,旱季最大净光合速率越高($p < 0.05$; 附录II)。

枝-叶脆弱性分段与旱季最大净光合速率和最大气孔导度之间存在显著的负相关关系($p < 0.05$; 图4C、4D)。物种的枝-叶脆弱性分段的数值越小(负),意味着它们的叶片较枝条的抗栓塞能力越强,在旱季最大净光合速率和气孔导度则越高。与同属的乔木相比,木质藤本倾向于具有更小(负)的枝-叶脆弱性分段和更高的旱季光合能力。

图3 植物水分传导有效性与安全性之间的相关关系。A, 枝条木质部抗栓塞能力($P_{50branch}$)与边材比导率(k_s)之间的相关关系; B, 叶片抗栓塞能力(P_{50leaf})与叶片最大导水率($K_{leaf-max}$)之间的相关关系。误差线为标准误差。

Fig. 3 Relationship between sapwood specific hydraulic conductivity (k_s) and vulnerability to cavitation in branches (A), and relationship between maximum hydraulic leaf conductance ($K_{leaf-max}$) and vulnerability to cavitation in leaves (B). $P_{50branch}$, xylem water potential at 50% loss of branch hydraulic conductivity; P_{50leaf} , leaf water potential at 50% loss of leaf hydraulic conductivity. Error bars are standard errors.

图4 水力性状与旱季叶片气体交换速率之间的相关关系。A、B, 旱季最大净光合速率(A_{max})与叶比导率(k_l)和叶片水力导度($K_{leaf-max}$)之间的相关性; C、D, 枝-叶脆弱性分段($P_{50leaf-branch}$)与旱季最大净光合速率(A_{max})和气孔导度(g_{s-max})之间的相关关系。误差线为标准误差。

Fig. 4 Relationships between maximum net photosynthetic rates during the dry season (A_{max}) and leaf specific hydraulic conductivity (k_l)(A), or maximum leaf hydraulic conductance ($K_{leaf-max}$)(B), and relationships between the difference in P_{50} between leaves and branches ($P_{50leaf-branch}$) and A_{max} (C) or maximum stomatal conductance during the dry season (g_{s-max})(D). Error bars are standard errors.

3 讨论

3.1 与乔木相比, 木质藤本不都具有较快水分传导效率和较低的抗栓塞能力

与第一个研究假设相符, 与乔木相比, 木质藤本的枝条木质部并非都表现出高的水分传导效率和低的抗栓塞能力。比如, 崖豆藤属树种水力性状的种间差异除了受生活型的影响外, 还可能与它们的需光性有关。崖豆藤属阳生木质藤本厚果崖豆藤和香花崖豆藤具有相对较高的水分传导效率(k_s 、 k_l)和较低的抗栓塞能力($P_{50branch}$), 但是与阳生乔木红河崖豆相比并没有显著的差异; 而生长在林下的阴生乔木思茅崖豆和变色鸡血藤与阴生木质藤本海南崖豆藤都表现出较低的水分传导效率和较强的抗栓塞能力。Schnitzer等(2000)的研究发现人为干扰导致热带次生林木质藤本的丰富度显著增加, 但是同时伴随着阴生乔木多样性的降低和阳生乔木多样性的增加。原因可能在于阳生性乔木和木质藤本都具有较高的水分传导效率和光合能力, 在干扰的生境下比阴生乔木具有生长优势。另外, 由于阴生木质藤本与阴生树种具有相似的水力和光合性状, 人为干扰和全球变化可能也会导致这类木质藤本多样性的降低, 这需要进一步研究。

买麻藤属植物是特殊的植物类群, 其生理生态适应机制引起广泛的关注(Kotowska *et al.*, 2015)。Feild和Balun (2008)对几种买麻藤植物的水力和光合相关性状进行了测定, 结果发现它们的水分传导效率和光合速率都很低。虽然买麻藤植物进化出与被子植物相似的导管系统和阔叶, 但是还没有进化出类似热带雨林需光种的典型特征, 如: 高繁殖速率与高光合速率, 因此常分布于热带森林林下阴生湿润生境中(Feild & Balun, 2008; Celis & Avalos, 2013)。本研究中买麻藤属乔木树种灌状买麻藤与少苞买麻藤的测定结果符合这一结论。但是, 买麻藤属木质藤本小叶买麻藤则表现出很高的水分传导效率, 与阳生性的被子植物相当。这可能与其已进化出粗大的导管有关, 其平均水力导管直径为171 μm (未发表数据), 远高于热带森林植物的平均值(100 μm ; Zhu *et al.*, 2017)。但其光合速率仍无法与阳生性的被子植物相比, 这可能与其进化史有关, 因为多功能基因的缺失导致的低光合速率可能是买麻藤属固有的特性(Deng *et al.*, 2019)。

本研究使用注气法测定木质部脆弱性曲线, 但是该方法的准确性受到质疑。在测量过程中, 当使用的茎段长度小于最大导管长度时产生的导管开口现象, 以及加压过程中形成的气泡效应, 会导致PLC被高估(抗栓塞能力被低估; Choat *et al.*, 2010; Yin & Cai, 2018)。另外, 加压的时间以及压力套的长度都会对曲线造成影响(Yin & Cai, 2018)。由于本试验物种(部分为引种)可破坏性采集的样本量少, 无法选择较为精确但是枝条样本量需求较多的自然干燥法(Sperry *et al.*, 1988)。另外, 本研究尽量使用足够长的枝条以防止开口导管产生的影响(Ennajeh *et al.*, 2011)。已有研究利用自然干燥法测定了部分物种的 $P_{50branch}$, 如红河崖豆(Fu *et al.*, 2012)、厚果崖豆藤(Zhu & Cao, 2009)和小叶买麻藤(Chen *et al.*, 2015), 本研究测定的结果与之相似。

在叶片水平上, 木质藤本与乔木两个类群的 P_{50leaf} 值没有显著差异(附录I)。但是崖豆藤属和买麻藤属植物的叶片栓塞脆弱性曲线显著不同(图1)。崖豆藤属植物叶片的抗栓塞能力强且脆弱性曲线呈“S”形: 在受到干旱胁迫影响的初期, K_{leaf} 对水势的下降不敏感, 叶片继续失水到达一定阈值之后, 导水率迅速下降直至完全失水。而买麻藤属植物的叶片栓塞脆弱性曲线趋于“直线”形: 干旱胁迫导致叶片水势降低过程中, K_{leaf} 随即响应开始下降。被子植物与裸子植物对于干旱胁迫的水力响应的差异可能与它们的气孔调控能力不同有关(Brodribb & Holbrook, 2006)。与裸子植物相比, 被子植物具有较强气孔控制能力, 在一定水势范围内, 维持水分平衡的同时还能保证光合作用不受影响从而最大限度提高碳收益, 这也是被子植物在陆地生态系统占据优势的一个重要生理机制(Brodribb & Holbrook, 2004)。

3.2 植物在枝条和叶片水平都不存在水力有效性与安全性之间的权衡关系

植物枝条和叶片的水分传导有效性与安全性之间均没有显著的权衡关系(图3A、3B), 不支持第二个研究假设。对于枝条来说, 部分树种枝条木质部同时具有较低的水分传导效率和抗栓塞能力, 如生长在林下的思茅崖豆。木质部的水分传导效率主要决定于木质部导管特征, 而木质部水力安全是各种水力策略密切协同的结果, 如根系吸水、茎部储水能力和气孔调节(Mencuccini *et al.*, 2015)等, 因此植

物整株水平的水力抗旱机制可能会导致枝条水平上缺乏安全性和有效性的权衡关系(Meinzer *et al.*, 2010)。另外, 由于木质藤本木质部结构的特殊性(Ewers *et al.*, 2015), 它们在木质部支撑和输导组织的分配上受到的限制较少, 在相似的抗栓塞能力的情况下, 可能存在更多的水分传导效率的变化(Bittencourt *et al.*, 2016), 导致木质藤本不受水力权衡关系的约束(Zhu *et al.*, 2017; Zhang *et al.*, 2019)。

叶片水分传导过程分为木质部途径与外木质部途径(Trifiló *et al.*, 2016), 共同影响着叶片水分运输的有效性与安全性(Sack & Frolé, 2006)。叶片细胞特征(如原生质体大小和细胞壁厚度)与外木质部途径密切相关(Scoffoni *et al.*, 2017a)。叶片水容(Pivovarov *et al.*, 2016)与叶片膨压(Scoffoni *et al.*, 2014)影响叶片的渗透调节, 在一定干旱条件下对水势的变化起缓冲作用, 能够影响叶片抗栓塞能力, 也影响了叶片的水分传导效率(Buckley *et al.*, 2015)。在木质部途径中, 叶脉导管壁厚度与导管大小及其比值, 以及叶脉密度(Blackman *et al.*, 2010)等都会影响水分在导管内的传导效率, 同时各指标变化还会伴随着安全性的变化(Scoffoni *et al.*, 2017b)。外木质部途径和木质部途径的作用机制因不同叶片结构而变化(Sack & Holbrook, 2006), 因此影响叶片水分传导有效性与安全性的因素错综复杂, 而它们之间的权衡关系并不能简单地从叶片抗栓塞能力($P_{50\text{leaf}}$)与叶片最大水力导度($K_{\text{leaf-max}}$)两个指标之间的线性关系来探讨, 叶片内各组织结构及其生理过程之间的关系需要更深入的研究。

3.3 木质藤本叶片比枝条的抗栓塞能力更强, 并具有较高的旱季最大净光合速率和气孔导度

与第三个研究假设相符, 两个属的木质藤本植物均不符合传统的枝-叶脆弱性分段假说, 即叶片比枝条具有更强的抗栓塞能力(图4C)。枝-叶脆弱性分段不存在的原因可能与本研究测定脆弱性曲线的方法有关(可能低估了枝条的抗栓塞能力), 但是最近的研究采用相同的方法(光学法)测定枝条和叶片的脆弱性曲线, 同样发现很多树种不符合传统的枝-叶脆弱性分段(Smith-Martin *et al.*, 2020)。另外, 前期研究表明这些植物在增强叶片抗栓塞能力的同时, 拥有有效的水力策略以保证茎的水力安全, 在干旱胁迫的情况下可能会具有生理优势: 能较大限度地推迟关闭气孔, 从而保持光合作用和生长(Zhu

et al., 2016)。本研究发现枝-叶脆弱性分段与旱季最大净光合速率和最大气孔导度呈显著负相关关系, 直接支持Zhu等(2016)的研究论断。另外, 由于木质藤本具有比同属乔木更强的旱季光合能力, 也支持了木质藤本植物的旱季优势生长假说(Zimmerman & Brown, 1971; Tyree & Ewers, 1991; Schnitzer & van der Heijden, 2019)。

4 结论

通过同属木质藤本和乔木水力性状的比较, 研究发现木质藤本的水力性状是复杂多样的, 这与其本身结构特征及其对生境的适应有关。为深入探讨乔木和木质藤本的水分生理生态特征的差异, 需要拓展到更多的属和生境类型, 同时使用更准确的水力指标测量方法, 这将有助于了解人为干扰和气候变化对这一特殊植物类群的影响。

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附录I 本研究崖豆藤属和买麻藤属三个类别下乔木与藤本6个水力性状指标的平均值、标准误差和差异显著性

Supplement I Mean value, standard error and comparisons significance of six hydraulic traits between tree and liana in different groups of *Millettia* and *Gnetum*

<http://www.plant-ecology.com/fileup/1005-264X/PDF/cjpe.2019.0304-S1.pdf>

附录II 本研究崖豆藤属和买麻藤属三个类别不同指标间的相关性分析

Supplement II Trait correlation between function traits across all species, within each genus and within each life in *Millettia* and *Gnetum* of this study

<http://www.plant-ecology.com/fileup/1005-264X/PDF/cjpe.2019.0304-S2.pdf>