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散孔材与环孔材树种枝干、叶水力学特性的比较研究

左力翔[1,2],李俊辉[3],李秧秧[2,3,*],赵丽敏[1,2]

(1. 西北农林科技大学资环学院,杨凌　712100;
2. 西北农林科技大学黄土高原土壤侵蚀与旱地农业国家重点实验室,杨凌　712100;
3. 中国科学院水利部水土保持研究所,杨凌　712100)

摘要:为揭示散孔材与环孔材树种树木水分生理特性的差异,选取了常见的 3 种散孔材落叶树种(毛白杨、法国梧桐和樱花)和 3 种环孔材落叶树种(刺槐、合欢和白蜡),研究了其枝干与叶水力学性质的差异及其协调性。结果表明:3 种环孔材树种枝干横截面积基础上的最大比导水率($K_{\text{s-max}}$)大于 3 种散孔材树种,但其木质部对空穴化的脆弱性($P50_{\text{branch}}$)高于散孔材树种,6 种树木枝干的水分传输能力和抵抗空穴化能力之间存在一种相互制约的权衡关系。3 种散孔材与 3 种环孔材树种的叶最大水力导度($K_{\text{l-max}}$)和水力脆弱性($P50_{\text{leaf}}$)并无显著差异;对于 3 种散孔材树种,叶的水力脆弱性要高于枝干,但对 3 种环孔材树种而言,枝干的水力脆弱性要高于叶。6 种树木枝干和叶的水力学性质($K_{\max}$、$P50$)之间并无相关关系。这些结果表明:散孔材与环孔材树种的枝干水力学特性有明显差异,但叶水力学特性无差异;枝干与叶水力学性质之间是相互独立的。

关键词:散孔材;环孔材;枝干和叶;水力学性质

Comparison of hydraulic traits in branches and leaves of diffuse-and ring-porous species

ZUO Lixiang[1,2], LI Junhui[3], LI Yangyang[2,3,*], ZHAO Limin[1,2]

1 *College of Resources and Environment, Northwest Agriculture and Forestry University, Yangling* 712100, *China*

2 *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest Agriculture and Forestry University, Yangling* 712100, *China*

3 *Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling* 712100, *China*

Abstract: Angiosperm tree species in temperate regions are broadly divided into diffuse-porous and ring-porous species based on their xylem anatomy. Diffuse-porous species show very little distinction between the diameter of vessel elements in early versus late wood, while ring-porous species have a bimodal distribution of vessel diameters associated with large, early season vessels and small late season vessels. These anatomical differences result in differences between these two kinds of tree species in stem water transport capacity and in the vulnerability to drought-induced cavitation. However, it is not clear if diffuse-porous and ring-porous species show differences in leaf hydraulic traits. Water transport resistance in leaves accounts for 30%—80% of the total hydraulic resistance of the whole-plant water transport pathway, and relatively few studies have focused on leaf hydraulics owing to methodological barriers; hence, elucidating the differences between diffuse-porous versus ring-porous species in leaf hydraulics and in leaf hydraulic trait coordination with stem hydraulic traits can be helpful in demonstrating the differences between diffuse-porous and ring-porous tree species in plant water use, geological distribution, leaf phenology and ecological adaptation.

We compared hydraulic traits of branches and leaves in three diffuse-porous deciduous tree species (*Populus*

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* **通讯作者** Corresponding author. E-mail: yyli@ms.iswc.ac.cn

tomentosa, *Platanus hispanica*, *Prunus serrulata*) and three ring-porous deciduous tree species (*Robinia pseudoacacia*, *Albizia julibrissin*, *Fraxinus chinensis*) growing in northwestern China. Branch and leaf water transport capacity was evaluated by their maximum hydraulic conductivities (K_{max}), and the hydraulic vulnerability was evaluated with $P50$, which corresponds to the branch or leaf water potential at 50% loss of maximum hydraulic conductivities. For stems, $P50$ was inferred from the vulnerability curves generated by air injection or bench dehydration method. For leaves, the curves were constructed by measuring hydraulic conductance (K_{leaf}) in leaves rehydrated from a range of water potentials (ψ_{leaf}). K_{leaf} was measured by assessing kinetics of ψ_{leaf} relaxation upon leaf rehydration.

The results showed that branch cross-sectional area-based maximum specific conductivities ($K_{s\text{-}max}$) of the ring-porous species were greater than those of the diffuse-porous species. Ring-porous species were more vulnerable to cavitation ($P50_{branch}$) than diffuse-porous species and a tradeoff relationship was evident between $K_{s\text{-}max}$ and $P50_{branch}$ in branches. No differences were found between leaf water transport capacities ($K_{l\text{-}max}$) or the vulnerability to hydraulic dysfunction ($P50_{leaf}$) in the two species types, and there was no tradeoff relationship between $K_{l\text{-}max}$ and $P50_{leaf}$. In the three diffuse-porous species, leaves were more vulnerable than branches to water stress-induced dysfunction, but in the ring-porous species, branches were more vulnerable than leaves. Pearson correlation analysis indicated that there was no correlation between branch and leaf hydraulic traits (K_{max} and $P50$) in the six investigated woody species. These results suggest that in our study: (1) diffuse-porous and ring-porous species diverged mainly in branch but not in leaf hydraulics, so that leaf hydraulics alone cannot be used to explain the differences between these two tree types in ecological function and adaptation. (2) Branch and leaf hydraulic traits were relatively independent and may be correlated with branch and leaf structure, respectively.

Key Words: diffuse-porous species; ring-porous species; branch and leaf; hydraulic traits

植物不同器官(根、茎和叶)的水力学特性是整株植物水力结构的重要组成部分,对这方面的研究大多集中在茎上,根次之,对叶的水力学特性由于研究方法的限制相对开展较少。近来研究表明:叶中的水分传输阻力可占整株植物水分传输阻力的30%—80%,是植物水分传输的主要瓶颈之一,并直接制约着叶片的生理功能如光合和蒸腾[1]。和茎相比,叶水力特征可能处于更强的选择压力下,因而对空穴化可能更敏感[2-3]。研究叶的水力学特性对于了解植物整体水分关系和其它生理功能都有十分重要的意义。

植物的木质部是其水分运输的主要通道,按照茎木质部的孔性特征,温带被子植物可粗分为散孔材和环孔材两类。散孔材树种导管在一个年轮里分布均匀,导管数目较多、孔径较小、导管较短,且在从水滨边到干旱地区均广泛分布;而环孔材树种在一个年轮里早材管孔比晚材管孔大,早材中导管稀少、导管较长,环孔材是在散孔材基础上进化而来,主要分布在北温带[4]。环孔材和散孔材茎木质部的结构特征导致其水分传输特性存在显著差异。环孔材树种茎干水分传输能力和存贮能力明显高于散孔材树种[5],但其更容易遭受栓塞的威胁[4,6-8]。叶的水力学特性是否也表现如此,尚不清楚。为此,本研究选择了3种散孔材和3种环孔材落叶树种,对其枝干与叶的水力学特性同时进行了研究,以揭示散孔材与环孔材树种水力结构的差异,为阐释散孔材与环孔材树种在水分利用能力、物候、地理分布等方面的差异[7-9]提供理论依据。

1 材料与方法

1.1 材料

选取陕西杨凌常见的6种绿化植物,包括3种散孔材树种:毛白杨(*Populus tomentosa*)、法国梧桐(*Platanus hispanica*)、樱花(*Prunus serrulata*)和3种环孔材树种:刺槐(*Robinia pseudoacacia*)、合欢(*Albizia julibrissin*)、白蜡树(*Fraxinus chinensis*)为研究对象。所选树种均为落叶树种,树龄均在20a左右。其中合欢、樱花、白蜡的胸径为20—25 cm,树高为7—10 m,毛白杨、梧桐和刺槐的胸径为35—40 cm,树高为12—15 m。选取树冠上部光照条件好、无病虫害的生长健康的叶和2—3年生枝干为研究对象。实验在2011年8月

进行。

1.2　测定项目与方法

1.2.1　枝干脆弱性曲线

枝干脆弱性曲线用两种方法测定,其中毛白杨、樱花、刺槐、合欢和白蜡的枝干用空气注入法测定[10],梧桐的枝干用自然风干的方法测定[11],所用枝干长度均为 25—30 cm。

空气注入法是把一定长度的茎段先用 10 kPa 压力的冲洗液(20 mmol/L KCl+1 mmol/L $CaCl_2$) 冲洗以消除原位栓塞,然后将茎段放入特制的压力腔中且两端露出,压力腔上连接一压力表,茎段近轴端与有一定静水压的水头和气泡排出管连接,在茎段远轴端用已称重的装有吸水纸的离心管每隔一定时间来收集单位时间的出流量,稳定后的出流量即为水流通量 Q(g/min) ,用以计算导水率($K_h = Q/\Delta P/L$,ΔP 为所用静水压水头,L 为茎段长度) 和比导水率($K_s = K_h/S$,S 为茎干横截面积) 。测定导水率的溶液和冲洗液相同。初始的最大导水率($K_{h\text{-}max}$) 测定后,在第一设定压力下加压 10 min 以诱导栓塞的形成,停止加压至压力充分释放后,然后测定相应导水率(K_{hi}) ,依此类推,直至导水率损失($PLC = (1 - K_{hi}/K_{h\text{-}max}) \times 100$) 达 80% 以上。所用压力和相应的 PLC 之间关系的曲线即为枝干的脆弱性曲线。

自然风干的方法是将样品采集后,充分饱和,然后在室内逐渐失水,在每一水分梯度下测定枝干上包裹的叶水势来替代枝干木质部水势,完后测定原位枝干的导水率(K_{hi}) ,再用 10 kPa 压力的冲洗液冲洗枝干后,测定相应枝干的最大导水率($K_{h\text{-}max}$) ,导水率损失 PLC(%) 计算同上。导水率测定溶液和冲洗液均为 20 mmol/L KCl+1 mmol/L $CaCl_2$。

所有枝干脆弱性曲线测定重复 3 次,且用 Weibull 分布函数 $PLC/100 = 1 - \exp(-(-x/b)^c)$ 来拟合[12],其中 b 为最大导水率下降 63.2% 时所对应的木质部压力的绝对值,c 为在 b 时曲线的陡度,b 值越大,曲线越陡。通过拟合求得导水率损失 50% 时所对应的木质部水势 $P50_{branch}$ 来代表枝干抵抗空穴化能力的大小。

1.2.2　叶脆弱性曲线

叶脆弱性曲线采用 Brodribb 等提出的叶水势松弛法[13]测定。清晨在不同树上采集带叶的枝条,塑料袋包裹后迅速带回实验室,然后在实验室下失水不同时间,以形成不同的叶水势梯度。3 种散孔材树种均用单叶,而 3 种环孔材树种叶较小,均用复叶测定。每一叶水势梯度下用压力室测定叶初始水势 ψ_0,然后在水下切断相邻叶并使之复水不同时间(30—300 s) ,完后立即取出擦干,测定不同复水时间后的相应叶水势 ψ_f。由于干燥叶的复水过程与通过单个电阻的单个电容的充电过程相类似,因而叶水力导度 $K_{leaf} = C_{leaf}\ln(\psi_0/\psi_f)/t$,其中 C_{leaf} 为叶水容,t 为复水时间。

叶水容(C_{leaf},mmol·m^{-2}·MPa^{-1}) 通过 PV 曲线的斜率来确定。利用 Tyree 等提出的自然风干法制作 PV 曲线[14],利用美国加州大学 Schulte 等编制的 PV 曲线分析程序拟合[15],求得膨压损失点 ψ_{tlp}。然后以叶相对含水量(RWC) 对叶水势(ψ_l) 作图,求得膨压损失点 ψ_{tlp} 之前和之后线性部分的斜率 $\partial RWC/\partial\psi_l$(MPa^{-1}) 用以计算膨压损失点之前和之后的叶水容。叶水容计算如下:

$$C_{leaf} = \frac{\partial RWC}{\partial \psi_l} \times \frac{DW}{LA} \times \frac{WW}{DW} \times \frac{1}{M}$$

式中,DW 为叶片干重(g) ,LA 为叶面积(m^2) ,WW 为饱和时叶片中的水量(=叶饱和重-叶干重,g) ,M 为水的摩尔质量(g/mol) 。叶面积通过照相后,用图像分析软件求得。

叶水势(ψ_l) 和水力导度 K_{leaf} 之间关系的曲线即为叶的脆弱性曲线。叶的脆弱性曲线用一个 3 参数的 Sigmoid 函数拟合[16],

$$y = \frac{a}{1 + e^{-\left(\frac{x - x_0}{b}\right)}}$$

当叶水势为 0 时,即可求得叶最大水力导度 $K_{leaf\text{-}max}$。当叶水力导度为最大水力导度的 50% 时所对应的叶水势即为 $P50_{leaf}$,代表了叶水分传输功能对干旱胁迫的脆弱性。

2 结果

2.1 散孔材与环孔材树种枝干的水力学特性

图1为6种树木枝干的脆弱性曲线。从中可看出，3种散孔材树种毛白杨、梧桐和樱花枝干的脆弱性曲线均为S型曲线，而3种环孔材树种导水率在−1 MPa前下降很快，在−1 MPa时，3种环孔材树种的导水率已损失75%以上。Weibull函数较好地模拟了6个树种枝干的脆弱性曲线。3种散孔材树种的 $P50_{\mathrm{branch}}$ 为 −1.80— −3.49 MPa，平均为−2.55 MPa，而3种环孔材树种的 $P50_{\mathrm{branch}}$ 为−0.07— −0.65 MPa，平均为−0.27 MPa。环孔材树种的 $P50_{\mathrm{branch}}$ 显著高于散孔材树种(独立样品 t 检验，$P<0.05$)，表明环孔材树种枝干抵抗空穴化的能力明显弱于散孔材树种。

3种环孔材树种枝干的最大比导水率 $K_{\mathrm{s\text{-}max}}$ 显著高于3种散孔材树种(独立样品 t 检验，$P<0.05$)(图1)。

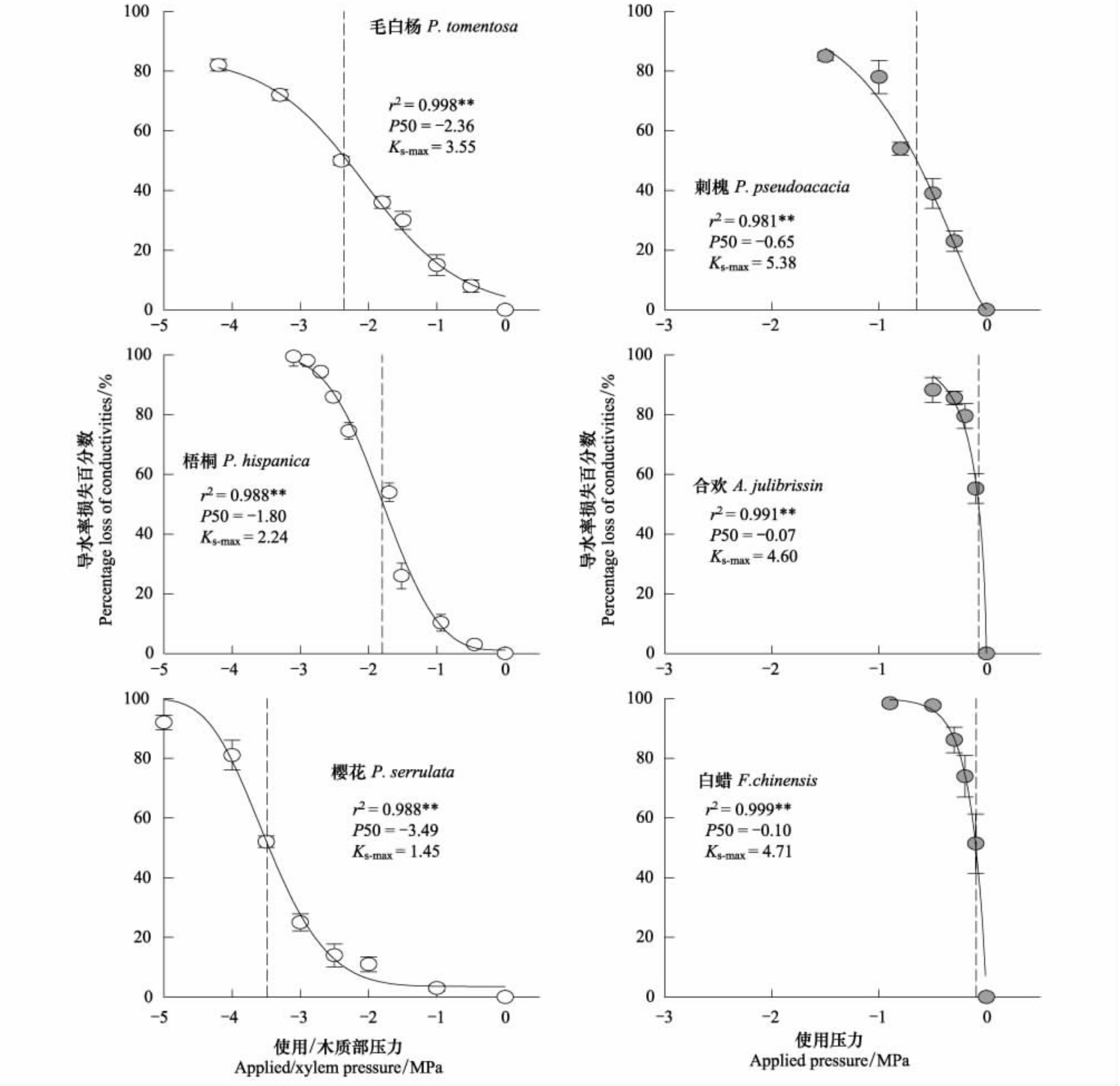

图1 3种散孔材和3种环孔材树种枝干的脆弱性曲线

Fig. 1 Branch vulnerability curves for three diffuse-and three ring-porous species

图中竖线表示 $P50$; $P50$ 和 $K_{\mathrm{s\text{-}max}}$ 的单位分别为 MPa 和 $\mathrm{kg \cdot MPa^{-1} \cdot s^{-1} \cdot m^{-1}}$

6 种树木枝干的最大比导水率 $K_{\text{s-max}}$ 和 $P50_{\text{branch}}$ 之间呈显著的负相关关系(表 1),表明不同树种间枝干的水分传输能力和抵抗空穴化能力之间存在着一种相互制约的权衡关系。

表 1　6 种树木枝干与叶水力学特性的相关性分析($n=6$)

Table 1　Pearson correlations between branch and leaf hydraulic traits of six woody species

	枝干最大比导水率 Maximum specific hydraulic conductivity of branch ($K_{\text{s-max}}$)	枝干 $P50$ Branch water potential at 50% loss of $K_{\text{s-max}}$	叶最大水力导度 Leaf maximum hydraulic conductance ($K_{\text{l-max}}$)	叶 $P50$ Leaf water potential at 50% of $K_{\text{l-max}}$
枝干最大比导水率 Maximum specific hydraulic conductivity of branch ($K_{\text{s-max}}$)	1			
枝干 $P50$ Branch water potential at 50% loss of $K_{\text{s-max}}$	0.868^{*}	1		
叶最大水力导度 Leaf maximum hydraulic conductance ($K_{\text{l-max}}$)	-0.576^{ns}	-0.497^{ns}	1	
叶 $P50$ Leaf water potential at 50% of $K_{\text{l-max}}$	0.339^{ns}	0.451^{ns}	-0.767^{ns}	1

* $P<0.05$, ns 不显著

2.2　散孔材和环孔材树种叶的水力学特性

图 2 为 6 种树木叶的脆弱性曲线。3 种散孔材树种的叶最大水力导度 $K_{\text{l-max}}$ 为 9.08—30.44 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$,平均为 20.41 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$;3 种环孔材树种的 $K_{\text{l-max}}$ 为 5.62—20.45 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$,平均为 10.61 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$,3 种散孔材树种的 $K_{\text{l-max}}$ 与 3 种环孔材树种相比并无显著差异(独立样品 t 检验,$P>0.05$)。3 种散孔材树种叶的 $P50_{\text{leaf}}$ 为 -1.40— -1.76 MPa,平均为 -1.62 MPa;3 种环孔材树种的 $P50_{\text{leaf}}$ 为 -0.74— -1.86 MPa,平均为 -1.34 MPa,二者亦无显著差异(独立样品 t 检验,$P>0.05$)。6 个树种叶的 $K_{\text{l-max}}$ 和 $P50_{\text{leaf}}$ 之间并无显著的相关关系(表 1)。

2.3　散孔材与环孔材树种枝干和叶的相对水力脆弱性

Perason 相关分析表明:6 个树种的枝干和叶的 K_{max} 之间并无显著的相关关系,枝干和叶的 $P50$ 之间亦无无显著的相关关系(表 1),表明 6 个树种枝干与叶的水力性质是相互独立的。3 个散孔材树种叶的 $P50$ 要高于枝干,表明对散孔材而言叶比茎更脆弱;而 3 个环孔材树种叶的 $P50$ 要小于枝干,表明环孔材树种茎比叶更脆弱(图 3)。

3　讨论

前人研究表明:环孔材树种最大水分传输能力强于散孔材树种,但抵抗空穴化化的能力弱于散孔材树种[4-8],本研究也证实如此。不同树种枝干水分传输能力和抵抗空穴化的能力主要与其木质部结构有关。水分传输能力主要决定于木质部导管数目、大小,锥度、纹孔膜的阻力和木质部汁液组成成分等,而抵抗空穴化能力主要与木质部导管大小和长度,导管纹孔膜的尺寸,纹孔膜的弹性及木材密度等有关[17]。环孔材树种导管直径大于散孔材树种,但导管数目少于散孔材树种,按照 Hagen-Poiseuille 方程,导水率与导管直径的 4 次方成正比,与导管数目为累加关系,因而环孔材树种导水率应大于散孔材树种。按照“气种学说”,栓塞形成主要决定于导管之间纹孔膜上的微孔,微孔直径越大,越容易形成栓塞。环孔材上大的导管直径一方面增加了纹孔膜上大微孔的几率,另外也可能降低了导管管壁的机械强度,从而使其比散孔材抵抗空穴化的能力弱。散孔材和环孔材树种水力性质的差异反映了其不同的水分利用策略,环孔材树种在无栓塞发生时通过高的水分传输能力来充分获取水分,而散孔材树种则通过低水分传输能力来获取水分以延缓栓塞的发生。

本研究中 6 种树木叶的最大水力导度 $K_{\text{leaf-max}}$ 为 5.62—30.44 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$,平均为 15.51 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$,与 Brodribb 等报道被子植物的叶最大水力导度介于 3.9—36 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ 之

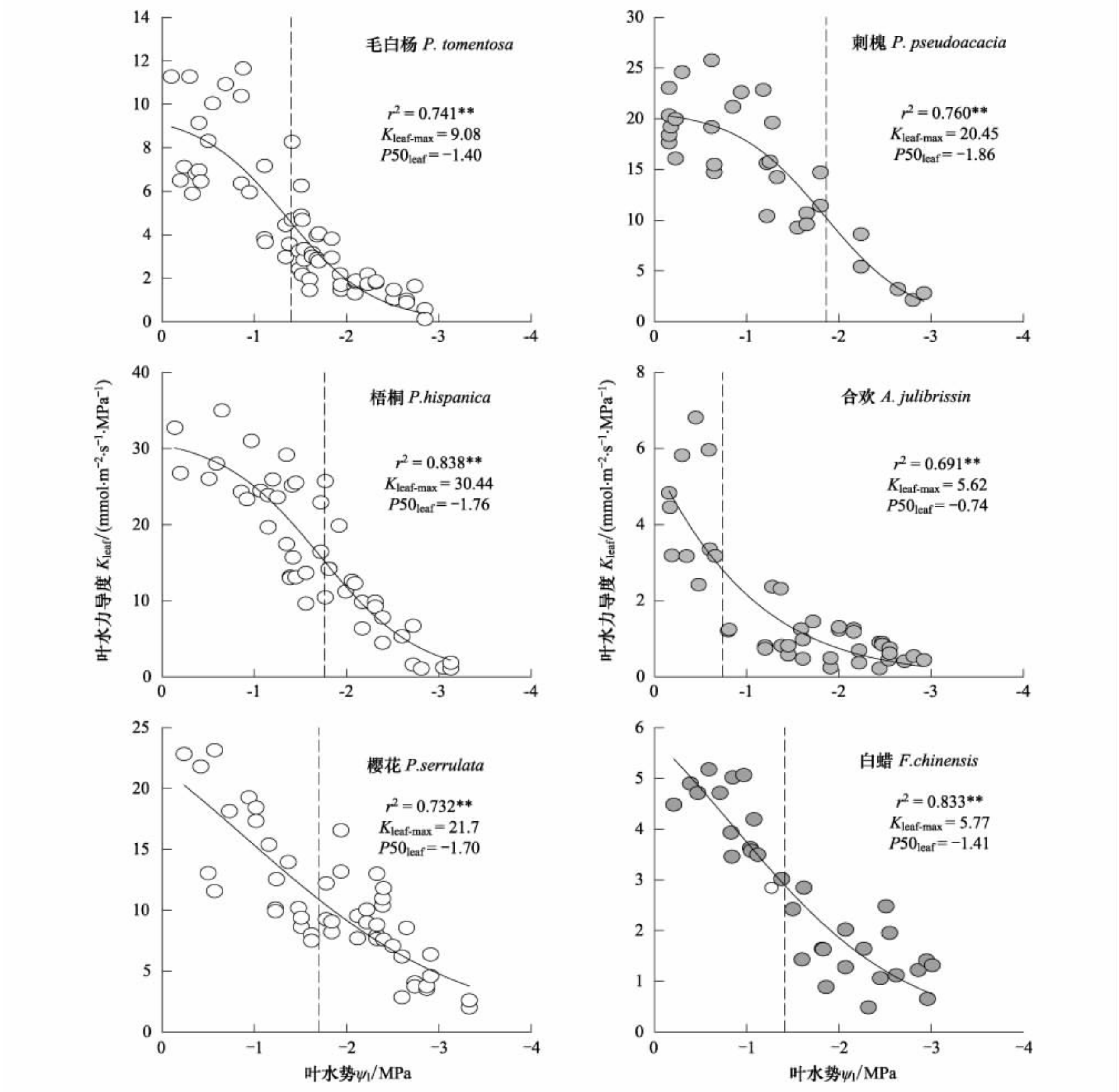

图2　3种散孔材与3种环孔材树种的叶脆弱性曲线

Fig. 2　Leaf hydraulic vulnerability curves for three diffuse- and three ring-porous species

图中竖线为$P50_{leaf}$，$P50_{leaf}$和$K_{leaf\text{-}max}$的单位分别为MPa和mmol·m^{-2}·s^{-1}·MPa^{-1}

间[18]一致。叶最大水力导度主要决定于叶中脉的木质部导管直径、叶脉分枝结构[1,19]及叶肉细胞结构，如叶上表皮的厚度、栅栏组织的厚度和叶片厚度、栅栏/海绵组织相对比例、叶水容等[20-21]，6种植物的叶最大水力导度的差异反映了其结构的差异。3种散孔材树种和3种环孔材树种的叶最大水力导度并无显著差异，且6种树木上叶最大水力导度和枝干的最大比导水率之间并无显著相关性(表1)，表明叶水分传输效率并不受茎水分传输能力的影响。茎与叶水分传输能力的解耦联可能与茎与叶的水分传输能力决定于各自的木质部解剖结构;叶中水分传输受气孔调节的影响，而茎中水分传输主要受水凝胶的调控;叶中水势与气孔导度存在生理反馈关系等原因有关。

干旱时叶水力导度会下降，其原因主要与叶木质部空穴化[22]、细叶脉中木质部导管的变形或塌陷[23]和木质部以外叶肉细胞中膜透性和水孔蛋白表达下降[24]等有关。本研究中6种树种的$P50_{leaf}$为-0.74—

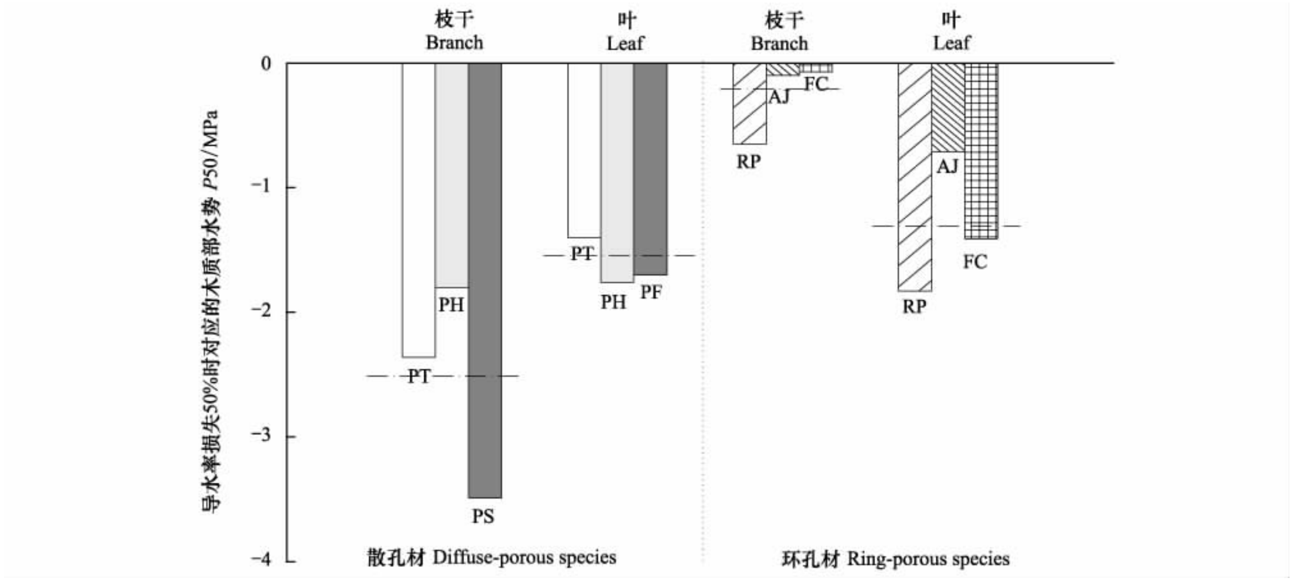

图 3　散孔材和环孔材树种的枝干和叶的水力脆弱性比较

Fig. 3　Comparison of hydraulic vulnerability of branches and leaves in diffuse-and ring-porous species

PT. 毛白杨 *P. tomentosa*; PH. 法国梧桐 *P. hispanica*; PS. 樱花 *P. serrulata*; RP. 刺槐 *R. pseudoacacia*; AJ. 合欢 *A. julibrissin*; FC. 白蜡树 *F. chinensis*. 横线为各组平均值

-1.86 MPa，Blackman 等报道 20 种不同抗旱性的被子植物中，大多数植物的 $P50_{\mathrm{leaf}}$ 介于-1— -3 MPa 之间[23]，本研究中除合欢外的 5 种植物的 $P50_{\mathrm{leaf}}$ 均在这一范围内。少数植物的 $P50_{\mathrm{leaf}}$ 可能低于-1 MPa，如荒漠生境中马鞭草科的一种植物 *Aegiphila Lhotzkiana* Cham 和大戟科的一种落叶树木 *Bischofia javanica* 的 $P50_{\mathrm{leaf}}$ 为-0.8 MPa[2,20]。本研究表明散孔材树种与散孔材树种的 $P50_{\mathrm{leaf}}$ 并无显著差异，且 6 个树种枝干与叶的 P50 之间并无必然联系，表明茎与叶的水力脆弱性是相对独立的。在散孔材落叶树种上，叶比枝干对栓塞更敏感；而在环孔材树种上，枝干比叶对栓塞更敏感。Hao 等发现对于高土壤蒸发需求和潜在低土壤水分有效性的荒漠和临近的森林生境而言，由于叶比茎处于更强的选择压力下，导致叶比茎干对干旱诱导的水力功能失调更敏感[2]。Johnson 等也发现美国东部 2 种落叶散孔材树种 *Acer rubrum*，*Liriodendron tulipifera* 叶的 P50 要高于茎，表明叶的水力脆弱性要高于茎[3]。从植物整体水力结构看，叶比茎更脆弱有利于水分胁迫下植物先损失建造成本低的叶，从而保证茎干的存活，起到安全阀的作用。相比于茎干，叶木质部临近活组织，因而比茎干中的栓塞更易于修复[25]。但本研究发现对 3 种环孔材落叶树种并非如此。Chen 等在大戟科 3 种落叶树种上发现，叶与茎干的水力脆弱性相当[20]。Johnson 等在环孔材落叶树种美国红橡（*Quercus rubra*）上发现叶和枝干的 P50 分别为-1.7 和-0.5 MPa[26]，表明茎比叶更脆弱。由于茎与叶水力脆弱性决定于各自的解剖结构，因而导致环孔材枝干的水力脆弱性比叶高。环孔材树种一般叶水势高，茎干水容大[8]，因而可能通过枝干的高水力脆弱性把茎干中贮存的水分提供给叶，特别是在土壤水分胁迫时。同时，环孔材树种气孔的调节能力也比散孔材树种强[4]，因而可有效降低栓塞的威胁。一些环孔材树种即使在导水率损失 80% 以上仍能正常生长，其高的最大导水率保证茎干即使在严重空穴化时叶也有良好的水分供应[27]。

本研究表明：用脆弱性曲线测定的散孔材树种与环孔材树种的叶最大水力导度和 P50 无显著差异，但由于叶中经常发生栓塞的修复[25]，因而本研究用脆弱性曲线测定的水力导度损失程度和田间原位的是否一致尚不清楚。此外，关于散孔材与环孔材树种叶水力学性质与气孔调节和水分利用等的关系如何，亦需要进行进一步研究。

References:

[1]　Sack L, Holbrook N M. Leaf hydraulics. Annual Review of Plant Biology, 2006, 57(1): 361-381.

[2] Hao G Y, Hoffmann W A, Scholz F G, Bucci S J, Meinzer F C, Franco A C, Cao K F, Goldstein G. Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. Oecologia, 2008, 155(3): 405-415.

[3] Johnson D M, McCulloh K A, Meinzer F C, Woodruff D R, Eissenstat D M. Hydraulic patterns and safety margins, from stem to stomata, in three eastern US tree species. Tree Physiology, 2011, 31(6): 659-668.

[4] Bush S E, Pataki D E, Hultine K R, West A G, Sperry J S, Ehleringer J R. Wood anatomy constrains stomatal responses to atmospheric vapor pressure deficit in irrigated, urban trees. Oecologia, 2008, 156(1): 13-20.

[5] Lemeur R, Steppe K. Effects of ring-porous and diffuse-porous stem wood anatomy on the hydraulic parameters used in a water flow and storage model. Tree Physiology, 2007, 27(1): 43-52.

[6] Sperry J S, Sullivan J E M. Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. Plant Physiology, 1992, 100(2): 605-613.

[7] Sperry J S, Nichols K L, Sullivan J E M, Eastlack S E. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology, 1994, 75(6): 1736-1752.

[8] Taneda H, Sperry J S. A case-study of water transport in co-occurring ring-*vs*. diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. Tree Physiology, 2008, 28(11): 1641-1651.

[9] Wang J, Ives N E, Lechowicz M J. The relation of foliar phenology to xylem embolism in trees. Functional Ecology, 1992, 6(4): 469-475.

[10] Sperry J S, Saliendra N Z. Intra-and Inter-plant variation in xylem cavitation in *Betula occidentalis*. Plant, Cell and Environment, 1994, 17(11): 1233-1241.

[11] Sperry J S, Donnelly J R, Tyree M T. A method for measuring hydraulic conductivity and embolism in xylem. Plant, Cell and Environment, 1988, 11(1): 35-40.

[12] Neufeld H S, Grantz D A, Meinzer F C, Goldstein G, Crisosto G M, Crisosto C. Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. Plant Physiology, 1992, 100(2): 1020-1028.

[13] Brodribb T J, Holbrook N M. Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. Plant Physiology, 2003, 132(4): 2166-2173.

[14] Tyree M T, Hammel H T. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. Journal of Experimental Botany, 1972, 23(1): 267-282.

[15] Schulte P J, Hinckley T M. A comparison of pressure-volume curve data analysis techniques. Journal of Experimental Botany, 1985, 36(10): 1590-1602.

[16] Woodruff D R, McCulloh K A, Warren J M, Meinzer F C, Lachenbruch B. Impacts of tree height on leaf hydraulic architecture and stomatal control in Douglas-fir. Plant, Cell and Environment, 2007, 30(5): 559-569.

[17] Fan D Y, Xie Z Q. Several controversial viewpoints in studying the cavitation of xylem vessels. Acta Phytoecologica Sinica, 2004, 28(1): 126-132.

[18] Brodribb T J, Holbrook N M, Zwieniecki M A, Palma B. Leaf hydraulic capacity in ferns, conifers and angiosperms: impacts on photosynthetic maxima. New Phytologist, 2005, 165(3): 839-846.

[19] Sack L, Frole K. Leaf structural diversity is related to hydraulic capacity in tropical rain forest trees. Ecology, 2006, 87(2): 483-491.

[20] Chen J W, Zhang Q, Li X S, Cao K F. Independence of stem and leaf hydraulic traits in six Euphorbiaceae tree species with contrasting leaf phenology. Planta, 2009, 230(3): 459-468.

[21] Sack L, Cowan P D, Jaikumar N, Holbrook N M. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant, Cell and Environment, 2003, 26(8): 1343-1356.

[22] Johnson D M, Meinzer F C, Woodruff D R, McCulloh K A. Leaf xylem embolism, detected acoustically and by cryo-SEM, corresponds to decreases in leaf hydraulic conductance in four evergreen species. Plant, Cell and Environment, 2009, 32(7): 828-836.

[23] Blackman C J, Brodribb T J, Jordan G J. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. New Phytologist, 2010, 188(4): 1113-1123.

[24] Nardini A, Salleo S, Andri S. Circadian regulation of leaf hydraulic conductance in sunflower (*Helianthus annuus* L. cv Margot). Plant, Cell and Environment, 2005, 28(6): 750-759.

[25] Zwieniecki M A, Holbrook N M. Confronting Maxwell's demon: biophysics of xylem embolism repair. Trends in Plant Science, 2009, 14(10): 530-534.

[26] Johnson D M, McCulloh K A, Meinzer F C, Lachencruch B. The terminal portion of the plant hydraulic continuum: branch and leaf vulnerabilities to hydraulic dysfunction//Second International Conference on Forests and Water in a Changing Climate. Raleigh NC, 2009.

[27] Li Y Y, Sperry J S, Taneda H, Bush S E, Hacke U G. Evaluation of centrifugal methods for measuring xylem cavitation in conifers, diffuse-and ring-porous angiosperms. New Phytologist, 2008, 177(2): 558-568.

参考文献:

[17] **樊大勇, 谢宗强. 木质部导管空穴化研究中的几个热点问题. 植物生态学报**, 2004, 28(1): 126-132.