

# 九种不同材性的温带树种叶水力性状及其权衡关系

金 鹰 王传宽\*

东北林业大学生态研究中心, 哈尔滨 150040

**摘 要** 不同材性树种的解剖、叶脉分布等结构性状差异会影响树木的水分运输效率和水分利用策略, 进而限制树木的生存、生长和分布。然而, 材性对叶导水率、水力脆弱性及其潜在的权衡关系的影响尚不清楚。该研究选择东北温带森林中不同材性的9种树种(散孔材: 山杨(*Populus davidiana*)、紫椴(*Tilia amurensis*)、白桦(*Betula platyphylla*); 环孔材: 蒙古栎(*Quercus mongolica*)、水曲柳(*Fraxinus mandshurica*)、胡桃楸(*Juglans mandshurica*); 无孔材: 红皮云杉(*Picea koraiensis*)、樟子松(*Pinus sylvestris* var. *mongolica*)、红松(*Pinus koraiensis*), 测量其基于叶面积和叶质量的叶导水率( $K_{area}$ 和 $K_{mass}$ )、水力脆弱性( $P_{50}$ )、膨压丧失点水势( $TLP$ )及叶结构性状, 以比较不同材性树种叶水力性状的差异, 并探索叶水力效率与安全的权衡关系。结果表明: 3种材性树种的 $K_{area}$ 、 $K_{mass}$ 和 $P_{50}$ 均差异显著( $p < 0.05$ )。无孔材树种的 $K_{area}$ 和 $K_{mass}$ 最低, 而散孔材和环孔材树种差异不显著; 环孔材树种 $P_{50}$ 最高, 而散孔材和无孔材树种差异不显著。 $K_{area}$ 和 $K_{mass}$ 均与 $P_{50}$ 显著负相关( $p < 0.05$ ), 但散孔材、环孔材和无孔材树种的相关关系分别呈线性、幂函数和指数函数关系。这表明叶水力效率与安全之间存在一定的权衡关系, 但该关系受树木材性的影响。 $K_{mass}$ 与 $TLP$ 显著负相关( $p < 0.01$ ), 其中散孔材和环孔材树种呈线性负相关, 无孔材树种呈负指数函数关系; $P_{50}$ 随 $TLP$ 的增加而增加, 这表明树木在面临水分胁迫时, 其质外体和共质体抗旱阻力共同协调保护叶片活细胞, 防止其水分状况到达临界阈值。 $K_{mass}$ 与叶干物质含量、叶密度、比叶重均显著负相关, 而 $P_{50}$ 与之显著正相关( $p < 0.01$ ,  $P_{50}$ 与比叶重的关系除外), 表明树木叶水力特性的变化受相同叶结构特性驱动, 树木增加对水力失调的容忍需要在叶水力系统构建上增加碳投资。

**关键词** 叶水力性状; 叶导水率; 叶水力脆弱性; 权衡关系; 散孔材; 环孔材; 无孔材

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## Leaf hydraulic traits and their trade-offs for nine Chinese temperate tree species with different wood properties

JIN Ying and WANG Chuan-Kuan\*

Center for Ecological Research, Northeast Forestry University, Harbin 150040, China

### Abstract

**Aims** Trees with different wood properties display variations in xylem anatomy and leaf vein structure, which may influence tree water transport efficiency and water-use strategy, and consequently constrain tree survival, growth and distribution. However, the effects of wood properties on leaf hydraulic conductance and vulnerability and their potential trade-offs at leaf level are not well understood. Our aims were to examine variations in leaf hydraulic traits of trees with different wood properties and explore potential trade-offs between leaf hydraulic efficiency and safety.

**Methods** Nine tree species with different wood properties were selected for measuring the leaf hydraulic traits, including three diffuse-porous species (*Populus davidiana*, *Tilia amurensis*, *Betula platyphylla*), three ring-porous species (*Quercus mongolica*, *Fraxinus mandshurica*, *Juglans mandshurica*), and three non-porous species (*Picea koraiensis*, *Pinus sylvestris* var. *mongolica*, *Pinus koraiensis*). Four dominant and healthy trees per species were randomly selected. The hydraulic traits measured included leaf hydraulic conductance on leaf area ( $K_{area}$ ) and dry mass ( $K_{mass}$ ) basis, leaf hydraulic vulnerability ( $P_{50}$ ), and leaf water potential at turgor loss point ( $TLP$ ), while the leaf structural traits were leaf dry mass content ( $LDMC$ ), leaf density ( $LD$ ) and leaf mass per unit area ( $LMA$ ).

**Important findings** The  $K_{area}$ ,  $K_{mass}$ , and  $P_{50}$  differed significantly among the tree species with different woody properties ( $p < 0.05$ ). Both  $K_{area}$  and  $K_{mass}$  were the lowest for the non-porous trees, and did not differ significantly between the diffuse-porous and ring-porous trees. The ring-porous trees had the highest  $P_{50}$  values, while the

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\* 通信作者Author for correspondence (E-mail: wangck@nefu.edu.cn)

diffuse-porous and non-porous trees showed no significant differences in  $P_{50}$ . Both  $K_{\text{area}}$  and  $K_{\text{mass}}$  were negatively correlated with  $P_{50}$  ( $p < 0.05$ ) for all the trees, and the relationships for the diffuse-porous, ring-porous, and non-porous trees were fitted into linear, power, exponential functions, respectively. This indicates that significant trade-offs exist between leaf hydraulic efficiency and safety. The  $K_{\text{mass}}$  was correlated ( $p < 0.01$ ) with  $TLP$  in a negative linear function for the diffuse- and ring-porous trees and in a negative exponential function for the non-porous trees. The  $P_{50}$  increased with increasing  $TLP$ . These results suggest that apoplastic and symplastic drought resistance are strictly coordinated in order to protect living cells from approaching their critical water status under water stresses. The  $K_{\text{mass}}$  was negatively correlated ( $p < 0.01$ ) with  $LDMC$ ,  $LD$ , or  $LMA$ , while the  $P_{50}$  was positively correlated with  $LDMC$  and  $LD$ ; this suggests that variations in  $K_{\text{mass}}$  and  $P_{50}$  are driven by similar changes in structural traits regardless of wood traits. We conclude that the tree tolerance to hydraulic dysfunction increases with increasing carbon investment in the leaf hydraulic system.

**Key words** leaf hydraulic trait; leaf hydraulic conductance; leaf hydraulic vulnerability; trade-off; diffuse-porous; ring-porous; non-porous

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叶片既是植物进行光合作用的主要场所,也是植物进行气体交换、水分蒸腾和运输的门户,其形态结构特征直接影响植物的生理活动和生态功能(潘昕等, 2015; Zhu *et al.*, 2015)。叶片在进行光合作用的同时不可避免地丧失水分,高水分传导率能够保证更有效的水分运输,补充植物蒸腾散失的水分,以保持叶片较高的气孔导度,从而维持高光合速率(Zhang *et al.*, 2015; 张树斌等, 2016)。因此,叶片水力在限制树木生长、竞争和分布中起着关键的作用(Brodribb *et al.*, 2005; Hao *et al.*, 2008; Villagra *et al.*, 2013)。叶导水率(基于叶面积( $K_{\text{area}}$ )或基于叶质量( $K_{\text{mass}}$ ))是指单位时间、单位水势压力梯度下流经叶的水流量(Sack & Holbrook, 2006),表征叶的水分运输阻力。虽然叶水分运输路径在整个植株中占的比例较小,但其水分运输阻力占整株的比例高达60%。叶水力脆弱性( $P_{50}$ )是指叶导水率降低50%时所对应的叶水势,反映叶的栓塞阻力或水力安全。一般而言,在枝水平上抗栓塞能力的增加常伴随水力效率的降低或碳消耗的增加(Bucci *et al.*, 2006; Jacobsen *et al.*, 2007),但在叶水平上是否存在雷同的权衡关系尚不清楚(Nardini *et al.*, 2012a; Villagra *et al.*, 2013; Nardini & Luglio, 2014)。以往研究报道叶水平的 $P_{50}$ 与 $K_{\text{area}}$ 缺乏相关性,因此,人们常认为在叶水平上不存在水力效率与水力安全的权衡(Blackman *et al.*, 2010; Scoffoni *et al.*, 2011, 2012; Bucci *et al.* 2012; Nardini *et al.*, 2012a)。然而,近期一些研究发现, $K_{\text{mass}}$ 与 $P_{50}$ 之间存在显著的相关关系(Nardini *et al.*, 2012a; Nardini & Luglio, 2014)。这引

发人们思考:考虑到叶肉组织中的水分运输和碳投资,叶水力效率与水力安全之间是否存在一种更为普适的权衡关系?对这个问题的回答,可深入理解叶生物物理结构构建与生理代谢的关系。

不同材性树种叶片的木质部结构和叶脉分布模式不同,从而导致水分运输效率和水分利用策略的差异(Brodribb *et al.*, 2005; McCulloh *et al.*, 2010; Scholz *et al.*, 2014)。无孔材树种依靠结构简单的单一主脉和直径较小的管胞输导水分;散孔材和环孔材树种则依靠结构复杂的网状叶脉系统和直径较大的导管进行水分运输,其中散孔材和环孔材树种叶脉木质部导管直径、导管密度和叶肉细胞结构可能也存在差异(Brodribb *et al.*, 2005; 左力翔等, 2012)。这些内部结构特性的差异使3种不同材性的树种在应对水分胁迫时采取躲避或忍受对策(李吉跃和翟洪波, 2000; Gomez-Aparicio *et al.*, 2011; Carnicer *et al.*, 2013; Coll *et al.*, 2013)。近年来关于叶水力学特性的研究已经成为植物生理生态的研究热点(潘莹萍和陈亚鹏, 2014; 张志亮等, 2014; 龚容和高琼, 2015; 金鹰和王传宽, 2015),但国内对叶水力特性的报道不多。左力翔等(2012)报道我国西北干旱地区的散孔材和环孔材树种的叶导水率和水力脆弱性均无显著差异。我国东北森林地处水热同步的温带地区,生长季树木受干旱胁迫的情况不多,不同材性树种叶水力特性是否存在差异、叶水力效率与水力安全是否存在权衡尚不清楚。为此,本研究在东北温带森林中选择了9种常见树种,分别代表无孔材、散孔材和环孔材树种,比较不同材性的树种叶

水力性状的差异,并探索叶水力效率与水力安全的权衡关系,以便深入理解不同树种在群落中的共存机制。

## 1 试验材料和方法

### 1.1 研究地概况和试验设计

研究地位于黑龙江帽儿山森林生态站(45.40° N, 127.67° E)。平均海拔400 m,平均坡度10°–15°。地带性土壤为暗棕色森林土。气候属大陆性温带季风气候,四季分明,夏季湿热,冬季干冷,年降水量629 mm,约50%的降水量集中在6–8月,年蒸发量864 mm,年平均气温3.1 °C。1月份平均气温–18.5 °C,7月份平均气温22.0 °C。无霜期120–140天。现有植被是原地带性植被——阔叶红松林屡遭人为干扰后演替成的天然次生林和人工林,代表了东北东部山区典型的森林类型(Wang *et al.*, 2013)。

本研究选择9种树种,分别代表3种不同的材性(表1)。为了消除林分中林木分化效应,我们选择了胸径相近的健康优势木作为样木,每个树种随机选取4株样木,于2015年的生长季中期(7月)进行叶水力和结构性状的相关测定。

### 1.2 压力-容积(PV)曲线测定

黎明前在每株样木上随机选取1个阳生带叶小枝,迅速放入水桶内,在水中剪掉切口端约10 cm,并在水下水化约1 h后取出,吸干表面的水分后,立即用电子天平(0.000 1 g)称量其饱和鲜质量,测定饱和状态下对应的叶水势( $\Psi_l$ , MPa),  $\Psi_l \geq -0.1$  MPa即为饱和状态,实验继续。之后,将叶放置在室温条件下自然失水一定时间(失水2–5 mg),再测定叶鲜质量和相对应的水势;如此周期性测定叶鲜质

量和水势,直至叶水势不明显下降(Nardini *et al.*, 2012a)。将测定完的叶置于75 °C下烘干48 h,称得其干质量。根据Tyree和Hammel (1972)方法确定膨压丧失点水势( $TLP$ , MPa)。

以相对含水量( $RWC$ , %)和 $\Psi_l$ 作图,求得膨压丧失点前后线性部分的斜率 $\Delta RWC/\Delta \Psi_l$ ,用以计算膨压丧失点前后的叶水容( $C_{leaf}$ ,  $\text{mmol} \cdot \text{m}^{-2} \cdot \text{MPa}^{-1}$ ),计算公式如下:

$$C_{leaf} = \frac{\Delta RWC}{\Delta \Psi_l} \times \left( \frac{DW}{LA} \right) \times \left( \frac{WW}{DW} \right) / M \quad (1)$$

式中:  $DW$ 为叶干质量(g);  $LA$ 为叶面积( $\text{m}^2$ );  $WW$ 为饱和时叶的含水量(g);  $M$ 为水的摩尔质量( $\text{g} \cdot \text{mol}^{-1}$ )。

### 1.3 叶导水率及脆弱性曲线测定

用再水化动力学法(rehydration kinetic technique)确定叶导水率和水力脆弱性曲线(Brodribb & Holbrook, 2003)。黎明前在每株样木上随机采集若干带叶枝条,在水下剪去10 cm后,用塑料袋套住带回实验室;然后,若干个小枝条在自然状态下失水不同时间以形成不同的叶水势梯度,达到不同水势的小枝条分别放入黑色塑料袋中密封,并保存黑暗处至少1 h使其稳定(枝条上的所有叶片水势相同)。每个枝条上选取两个叶片用压力室测定初始叶水势( $\Psi_0$ , MPa),取平均值;然后在水下切断相邻叶,并使之复水一定时间( $t$ , s)(复水时间根据叶片初始水势而定,即高水势复水时间短、低水势复水时间加长),水化后立即取出测定水化后叶水势( $\Psi_t$ , MPa)。基于电容再补充的原理类推出叶导水率( $K_{leaf}$ ),计算如下:

$$K_{leaf} = C_{leaf} \ln (\Psi_0 / \Psi_t) / t \quad (2)$$

式中:  $C_{leaf}$ 分别用叶面积和叶质量标准化,可得到基

表1 9种不同材性的温带树种样木的基本特性(平均值±标准误差,  $n = 4$ )

Table 1 Basic characteristics of the sampled trees for the nine temperate tree species with different wood properties (mean ± SE,  $n = 4$ )

材性(代码)	树种(代码)	叶习性	生境	胸径
Wood property (code)	Species (code)	Leaf habit	Habitat	DBH (cm)
散孔材	白桦 <i>Betula platyphylla</i> (BH)	落叶阔叶 Deciduous-broadleaved	山坡中部 Mid slope	24.46 ± 1.05
Diffuse-porous (DP)	山杨 <i>Populus davidiana</i> (SY)	落叶阔叶 Deciduous-broadleaved	山坡上部 Upper slope	31.15 ± 0.55
	紫椴 <i>Tilia amurensis</i> (ZD)	落叶阔叶 Deciduous-broadleaved	山坡上部 Upper slope	25.75 ± 1.30
环孔材	水曲柳 <i>Fraxinus mandshurica</i> (SQL)	落叶阔叶 Deciduous-broadleaved	山坡下部 Toe slope	34.30 ± 0.45
Ring-porous (RP)	蒙古栎 <i>Quercus mongolica</i> (MGL)	落叶阔叶 Deciduous-broadleaved	山坡上部 Upper slope	27.86 ± 1.19
	胡桃楸 <i>Juglans mandshurica</i> (HTQ)	落叶阔叶 Deciduous-broadleaved	山谷 Valley bottom	34.60 ± 1.38
无孔材	红松 <i>Pinus koraiensis</i> (HS)	常绿针叶 Evergreen-coniferous	山坡中部 Mid slope	28.17 ± 0.91
Non-porous (NP)	云杉 <i>Picea koraiensis</i> (YS)	常绿针叶 Evergreen-coniferous	山谷 Valley bottom	30.05 ± 0.65
	樟子松 <i>Pinus sylvestris</i> var. <i>mongolica</i> (ZZS)	常绿针叶 Evergreen-coniferous	山坡中部 Mid slope	26.32 ± 1.15

DBH, diameter at breast height.

于叶面积( $K_{\text{area}}$ )和叶质量( $K_{\text{mass}}$ )的叶导水率(Nardini *et al.*, 2012a)。

叶水力脆弱性曲线是用 $K_{\text{leaf}}$ 与 $\Psi_0$ 建立关系。当叶导水率为最大导水率的50%时所对应的叶水势即为 $P_{50}$ , 代表叶水力脆弱性。

#### 1.4 叶结构性状测定

黎明前采集的枝条在水下泡至饱和后, 每株样木选取10–20个健康叶, 首先用电子天平(0.000 1 g)称量叶饱和质量, 再用排水法测定其叶体积, 然后, 用扫描仪扫描叶面积, 最后在75 °C下烘干48 h确定叶干质量。比叶重( $LMA$ )是叶面积与叶干质量的比值; 叶密度( $LD$ )是叶干质量与叶体积的比值; 叶干物质含量( $LDMC$ )是叶干质量与叶饱和质量的比值。

#### 1.5 数据分析

统计分析用SPSS 19.0统计软件完成。采用一般线性模型(GLM)把材性作为固定因子、把样木作为随机因子, 比较不同材性之间 $K_{\text{area}}$ 、 $K_{\text{mass}}$ 及 $P_{50}$ 的差异。采用回归分析建立叶水力性状之间及其与叶结构性状之间的关系。

## 2 结果

### 2.1 不同材性树种叶水力性状比较

9个树种 $K_{\text{area}}$ 和 $K_{\text{mass}}$ 变化范围分别为16.88 (水曲柳*Fraxinus mandshurica*)–40.49 (胡桃楸*Juglans mandshurica*)  $\text{mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$ 和69.03 (云杉*Picea koraiensis*)–458.95 (胡桃楸)  $\text{mmol}\cdot\text{kg}^{-1}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$ , 平均值分别为 $(25.31 \pm 3.19) \text{ mmol}\cdot\text{m}^{-2}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$ 和 $(229.82 \pm 42.10) \text{ mmol}\cdot\text{kg}^{-1}\cdot\text{MPa}^{-1}\cdot\text{s}^{-1}$  (图1)。不同材性树种之间的 $K_{\text{area}}$ 和 $K_{\text{mass}}$ 差异显著( $p < 0.05$ ), 均表现为: 散孔材>环孔材>无孔材, 而环孔材与散孔材树种差异不显著(图1A, 1B)。

9个树种 $P_{50}$ 变化范围–2.02 (山杨*Populus davidiana*) – –0.65 (胡桃楸) MPa, 平均值为 $-1.17 \pm 0.13$  MPa, 其中, 山杨是胡桃楸的3倍左右(图1)。不同材性树种之间 $P_{50}$ 差异显著( $p < 0.01$ ), 环孔材树种最高( $-0.86 \pm 0.08$  MPa), 而散孔材( $-1.42 \pm 0.16$  MPa)和无孔材( $-1.24 \pm 0.07$  MPa)树种差异不显著(图1C)。

### 2.2 不同材性树种叶水力性状、叶结构性状的关系

叶水力脆弱性( $P_{50}$ )随 $K_{\text{area}}$ 或 $K_{\text{mass}}$ 的增加而下降, 但不同材性的树种表现出的两者关系不同(图2); 其中, 散孔材树种呈负线性关系, 环孔材树种呈负幂函数关系, 无孔材树种呈负指数函数关系。散孔材

和环孔材树种的 $K_{\text{mass}}$ 与 $TLP$ 之间呈负线性关系, 而无孔材树种呈负指数关系(图3A)。散孔材和环孔材树种的 $P_{50}$ 与 $TLP$ 均呈正相关关系, 但无孔材树种两者之间关系不显著(图3B)。

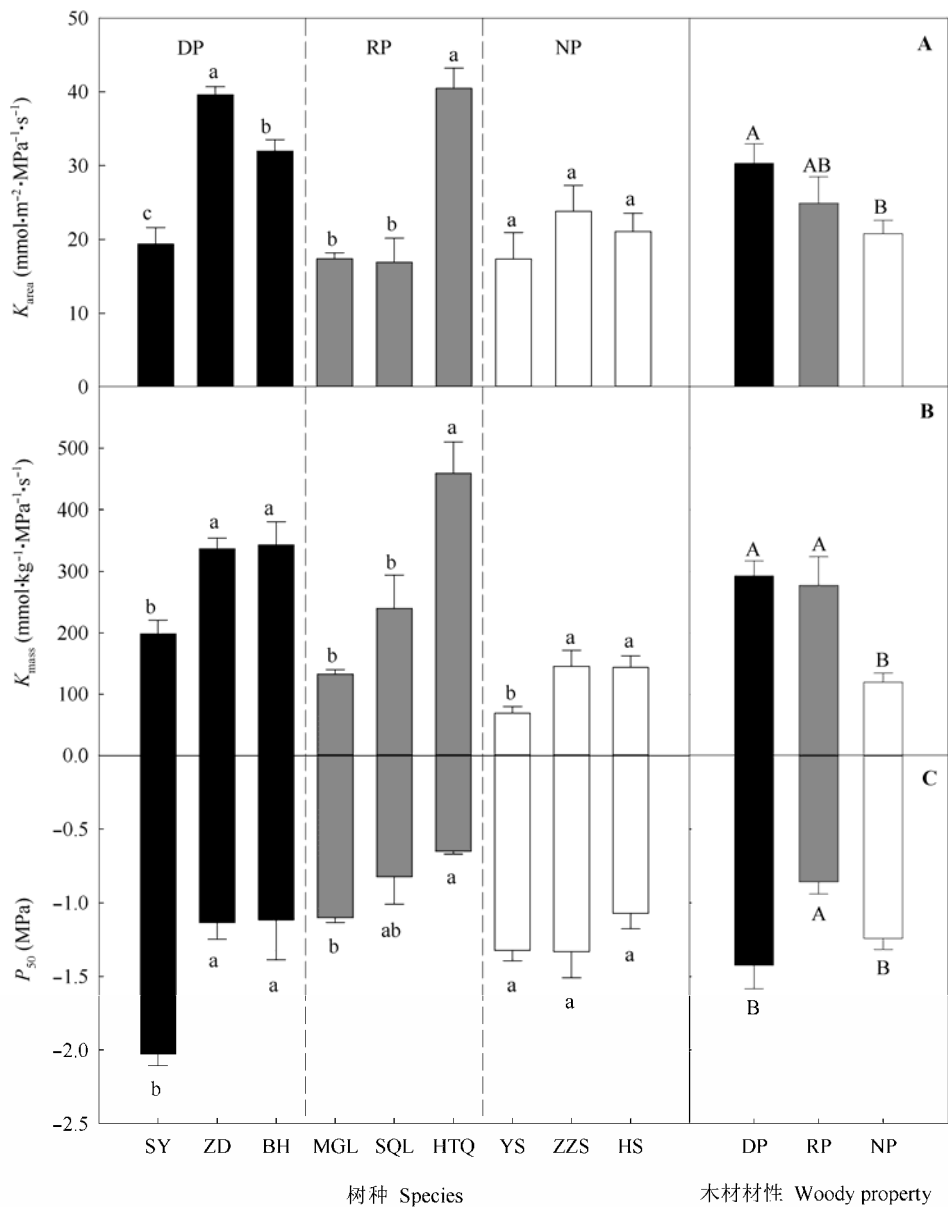
将不同材性的9个树种综合分析显示:  $K_{\text{mass}}$ 与 $LDMC$ 、 $LD$ 和 $LMA$ 均显著负相关( $p < 0.01$ , 图4A–4C);  $P_{50}$ 与 $LDMC$ 和 $LD$ 显著正相关( $p < 0.01$ ), 而与 $LMA$ 的关系不显著(图4D–4F)。

## 3 讨论

### 3.1 不同材性树种叶导水率和水力脆弱性差异

不同材性树木的叶导水率差异显著, 以无孔材树种的 $K_{\text{leaf}}$ 最低、而散孔材和环孔材树种的 $K_{\text{leaf}}$ 差异不显著(图1)。左力翔等(2012)在我国西北干旱地区的测定结果也显示散孔材和环孔材树种的叶导水率无显著差异。这可能是由于散孔材和环孔材树种的 $K_{\text{leaf}}$ 变异性较大导致的(图1)。从解剖结构看: 尽管环孔材导管直径可能大于散孔材, 可以承载的水分运输较强, 但由于导管密度与导管直径负相关, 因此其较低的导管密度抵消了其较大直径导致的高导水率(Giordano *et al.*, 1978; Nardini *et al.*, 2012a)。无孔材树种的 $K_{\text{leaf}}$ 最低, 是由于其叶的水分运输依赖于由单一主脉组成的输水结构, 且输水单元为直径较窄的管胞, 因此, 其导水能力较差; 而散孔材和环孔材树种的叶水分运输依赖于高度分支的叶脉网络把水分输送到蒸发表面, 且输水单元为直径较大的导管(Brodribb *et al.*, 2005; Sperry *et al.*, 2006, 2008)。此外, 本研究中的无孔材树种均为常绿针叶树种(表1), 其叶导水率和 $P_{50}$ 均较低(图1), 这说明它们具有较强的栓塞阻力, 为此其叶水力系统的构建需要有较大的碳投资(Simonin *et al.*, 2012), 这也可能是避免冬季冻融栓塞的一种对策(Feild & Brodribb, 2001)。

叶导水率也能在一定程度上反映树木对不同生境适应能力。一般来说, 生长在水分条件较好的立地上的树木的叶导水率和栓塞阻力较高, 而生长在水分条件较差的立地上的树木的叶导水率和栓塞阻力较低(Bucci *et al.*, 2003; Nardini *et al.*, 2003, 2012a)。本研究中的环孔材胡桃楸, 生长在湿润的沟谷地带(表1), 其叶导水率和 $P_{50}$ 在9个树种中最高(图1); 相反, 环孔材蒙古栎生长在干旱的山脊地带、散孔材山杨常生长在较干旱的山坡上部(表1; Zhang *et al.*, 2014), 其叶导水率和 $P_{50}$ 较低。由此可



**图1** 不同材性树种叶水力性状的比较(平均值±标准误差)。不同大、小写字母分别代表不同材性之间和同一材性不同树种之间差异显著( $p < 0.05$ )。 $K_{area}$ 和 $K_{mass}$ 分别表示基于叶面积和叶质量的叶导水率; $P_{50}$ 表示叶水力脆弱性。材性和树种代码同表1。  
**Fig. 1** Comparisons of leaf hydraulic traits among the tree species with different wood properties (mean  $\pm$  SE). Different uppercase and lowercase letters above columns indicate significant differences among different wood properties and among different tree species with the same wood property, respectively ( $p < 0.05$ ).  $K_{area}$  and  $K_{mass}$ , leaf hydraulic conductance per leaf area and dry mass, respectively;  $P_{50}$ , leaf hydraulic vulnerability. See Table 1 for the codes of tree species and wood properties.

见, 在小尺度范围内, 叶导水率和 $P_{50}$ 可影响树木的分布。叶导水率高的树种, 适宜生长在湿润的立地上, 对光和养分的竞争能力较强, 具有较高的光合和生长速率。相反, 叶导水率低的树种, 常有较高的栓塞阻力, 可在干旱条件下生存, 但同时也降低了其在资源丰富地区的竞争能力(Nardini *et al.*, 2012a)。

以往研究通常用叶面积来标准化叶导水率( $K_{area}$ ), 但近期用叶质量来标准化叶导水率( $K_{mass}$ )的研究越

来越多(Nardini *et al.*, 2012b; Scoffoni *et al.*, 2012; Simonin *et al.*, 2012; Nardini & Luglio, 2014)。近期研究认为,  $K_{area}$ 侧重于叶片-大气界面上的表面生理过程, 忽略了叶肉组织中的水分运输, 只能衡量叶水力系统给叶片蒸发表面提供水分的效率。对于叶片较薄或叶脉末端距离叶蒸发表面较近、水分在叶肉组织中运输距离较短的树种而言, 用 $K_{area}$ 可很好地衡量叶水分运输效率(Nardini *et al.*, 2012a)。但如果

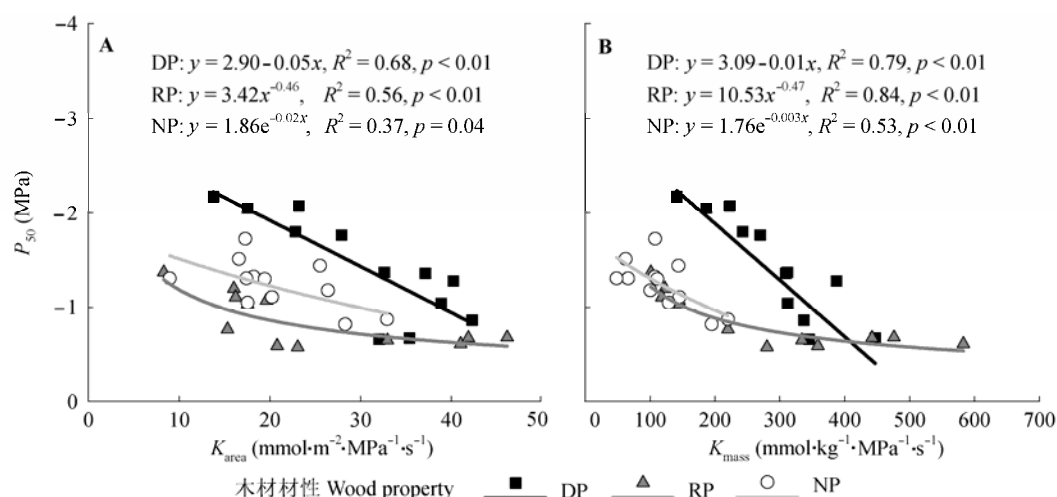


图2 3种材性树种叶水力效率与水力脆弱性( $P_{50}$ )的关系。 $K_{area}$ 和 $K_{mass}$ 分别表示基于叶面积和叶质量的叶导水率。材性代码同表1。  
**Fig. 2** Relationships between leaf hydraulic efficiency and hydraulic vulnerability ( $P_{50}$ ) of the trees with wood properties.  $K_{area}$  and  $K_{mass}$ , leaf hydraulic conductance per leaf area and dry mass, respectively. The codes of wood properties are listed in Table 1.

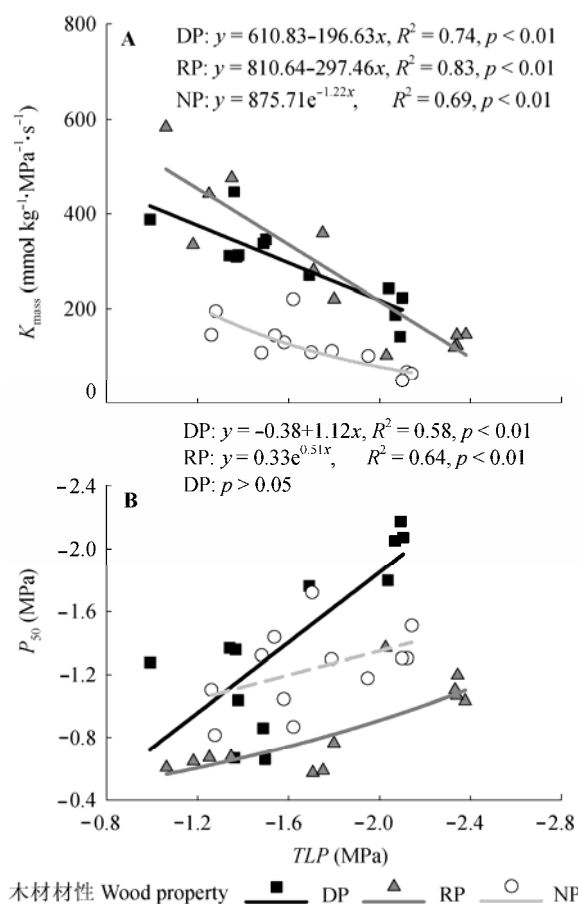


图3 3种材性树种膨压丧失点水势(TLP)与(A)基于叶质量的叶导水率( $K_{mass}$ )和(B)叶水力脆弱性( $P_{50}$ )的关系。虚线表示关系不显著( $p > 0.05$ )。材性代码同表1。

**Fig. 3** Relationships between leaf water potential at turgor loss point (TLP) and (A) leaf-mass-based hydraulic conductance ( $K_{mass}$ ) or (B) leaf hydraulic vulnerability ( $P_{50}$ ) of the trees with wood properties. The dash line denotes non-significant ( $p > 0.05$ ). The codes of wood properties are listed in Table 1.

叶片中的水流从叶脉组织出来后并不是直接到达表皮,而是要在叶肉组织中流经较长的距离(Zwieniecki *et al.*, 2007)时,用 $K_{mass}$ 才能充分地反映出叶水力系统给整个叶组织提供水分的效率。此外, $K_{mass}$ 还可以估计构建叶水力系统的碳投资(Nardini *et al.*, 2012b; Simonin *et al.*, 2012)。本研究同时比较了不同材性 $K_{area}$ 和 $K_{mass}$ 的差异,结果相似,但无孔材 $K_{mass}$ 显著低于散孔材和环孔材;这说明用叶质量标准化的 $K_{mass}$ 估测针叶树种整个叶组织的导水率更恰当。

### 3.2 不同材性树种叶水力效率与安全之间的权衡关系

我们发现,即便有材性效应,但所有树种的 $P_{50}$ 均随 $K_{area}$ 或 $K_{mass}$ 的增大而显著下降(图2),表明这些树种的叶水力效率与水力安全存在不同程度的权衡关系;这与前人基于叶质量标准化叶导水率研究叶片水力效率与安全的权衡关系(Blackman *et al.*, 2010; Scoffoni *et al.*, 2012)一致,说明树木常以降低导水率和提高碳投资为代价来增加栓塞引起的水力失调阻力。

本研究发现, $K_{mass}$ 和 $P_{50}$ 均与质外体的抗旱阻力(TLP)有关(图3),与前人的研究(Blackman *et al.*, 2010; Scoffoni *et al.*, 2012; Villagra *et al.*, 2013)一致。 $TLP$ 低的树种,其叶导水率低,但干旱诱导的质外体抗栓塞阻力高。 $P_{50}$ 和 $TLP$ 的正相关关系表明共质体和质外体抗旱阻力的彼此协调;在树木面临水分胁迫时,膨压损失引起的木质部外水力特性变化与木质部内栓塞抵抗力的共同作用导致气孔关闭、蒸腾降低,从而保护活细胞、防止其接近水分临界值

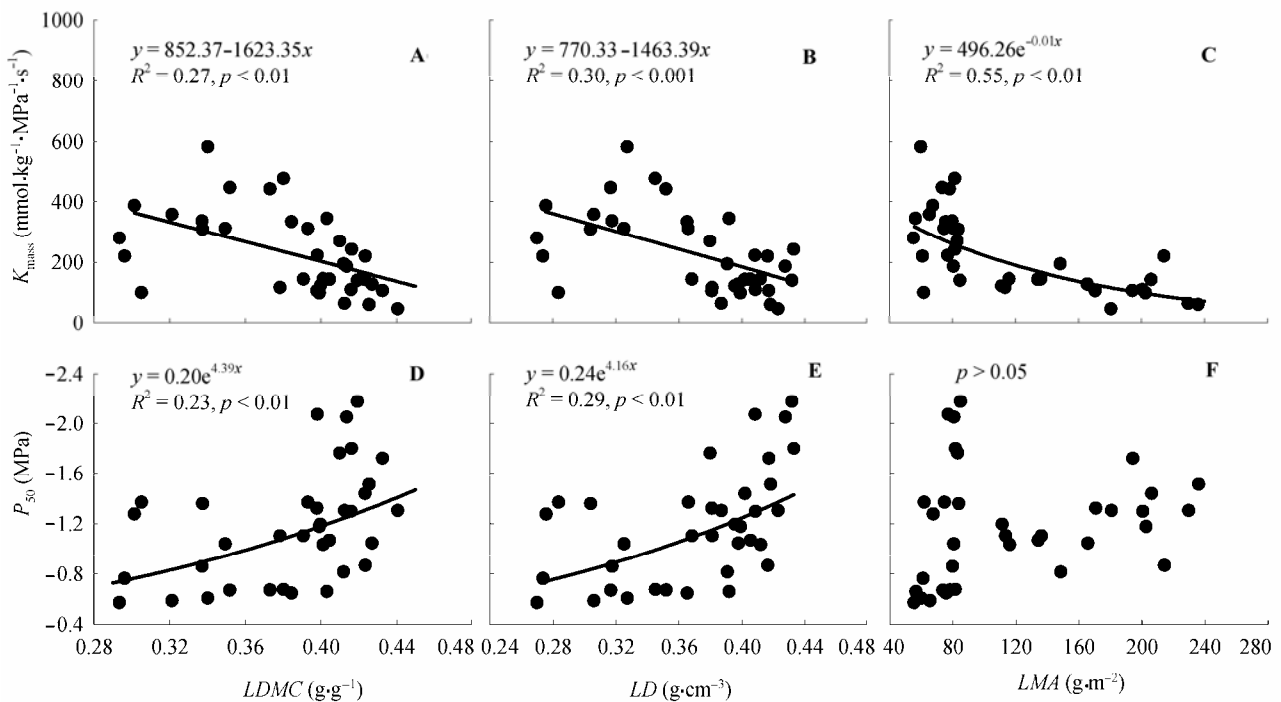


图4 基于所有树种的叶水力性状与叶结构性状的关系。 $K_{\text{mass}}$ ，基于叶质量的叶导水率； $LD$ ，叶密度； $LDMC$ ，叶干物质含量； $LMA$ ，比叶重； $P_{50}$ ，叶水力脆弱性。

**Fig. 4** The relationships between leaf hydraulics and structural traits of all tree species.  $K_{\text{mass}}$ , leaf hydraulic conductance per dry mass;  $LD$ , leaf density;  $LDMC$ , leaf dry mass content;  $LMA$ , leaf mass per unit area;  $P_{50}$ , leaf hydraulic vulnerability.

(Kim & Steudle, 2007; Blackman *et al.*, 2010; Vilagrosa *et al.* 2010; Johnson *et al.*, 2012)。

本研究结果显示， $K_{\text{mass}}$ 与 $LDMC$ 、 $LD$ 、 $LMA$ 显著负相关； $P_{50}$ 与 $LDMC$ 、 $LD$ 显著正相关(图4)。这说明高的栓塞阻力与厚木质部导管壁、高主脉密度或导管密度有关，而这些均与高 $LD$ 和 $LMA$ 有关(Blackman *et al.*, 2010; Scoffoni *et al.*, 2011; Nardini *et al.*, 2012a)。在枝水平上的研究也发现相似的结果，即：高木质部栓塞阻力与高木材密度相关(Meinzer *et al.*, 2009; Hoffmann *et al.*, 2011; Nardini *et al.*, 2013)；而高木材密度意味着厚导管壁或大量的机械组织。因此，为了增加栓塞阻力，树木将大部分碳用于构建木材密度，从而降低了用于生长的碳投资(Nardini & Luglio, 2014)。这些结果表明， $K_{\text{mass}}$ 和 $P_{50}$ 的高低均与叶形态-解剖特性相关。叶导水率低的树种需要构建一个安全的木质部以降低栓塞风险，而构建安全的木质部需要对叶水力系统构建投资较多的碳(即高 $LDMC$ 和 $LD$ )，这就提高了叶的水分供给成本(Wikberg & Ögren, 2004; Simonin *et al.*, 2012; Villagra *et al.*, 2013; Nardini & Luglio, 2014)。

综上所述，不同材性树种叶导水率和水力脆弱

性均差异显著，说明叶水力特性受叶解剖结构和叶脉分布影响。此外，不同材性树种用叶面积和叶质量标准化的叶导水率均与水力安全存在权衡关系，但该关系受树木材性的影响。叶水力脆弱性与叶结构特性的正相关关系表明树木增加对水力失调的容忍需要在叶水力系统构建上增加碳投资。

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