

DOI: 10.20103/j.stxb.202305201065

程莉,李玉霖,宁志英,杨红玲,詹瑾,姚博.木本植物应对干旱胁迫的响应机制:基于水力学性状视角.生态学报,2024,44(7):2688-2705.

Cheng L, Li Y L, Ning Z Y, Yang H L, Zhan J, Yao B. Response mechanisms of woody plants to drought stress: a review based on plant hydraulic traits. Acta Ecologica Sinica, 2024, 44(7): 2688-2705.

# 木本植物应对干旱胁迫的响应机制:基于水力学性状视角

程 莉<sup>1,2</sup>, 李玉霖<sup>1,2,3,\*</sup>, 宁志英<sup>1,2</sup>, 杨红玲<sup>1,2</sup>, 詹 瑾<sup>1,2</sup>, 姚 博<sup>1,2</sup>

1 中国科学院西北生态环境资源研究院,兰州 730000

2 中国科学院大学,北京 100049

3 中国科学院西北生态环境资源研究院奈曼沙漠化研究站,通辽 028300

**摘要:**干旱最显著的影响表现在区域尺度的森林死亡事件中,可以在短时间内杀死数百万棵树木。鉴于未来极端干旱事件的频率和强度可能随温度的升高而增加,迫切需要明确树木对于干旱胁迫的响应对策以及衰退死亡机理,揭示木本植物在干旱环境中存活和死亡的生理机制,了解树木在未来气候下的适应机制,提高预测树木对于干旱反应的准确性。在常用植物功能性状的基础上,重点纳入与植物水分运输能力及耐旱性相关的水力学性状,系统总结了:1)植物木质部水分运输的物理机制;2)植物应对干旱胁迫的水力响应过程;3)干旱胁迫下木本植物水分利用对策;以及4)干旱胁迫下木本植物衰退/死亡机理。最后,提出3个尚待解决的主要问题:1)加强纳入水力性状阐明植物对于干旱胁迫的响应和调节机制;2)加强从全株植物的角度考虑植物不同组织性状间的关系;3)深入探究树木干旱致死机理。

**关键词:**木本植物;干旱胁迫;水力性状;水分运输策略;干旱致死机理

## Response mechanisms of woody plants to drought stress: a review based on plant hydraulic traits

CHENG Li<sup>1,2</sup>, LI Yulin<sup>1,2,3,\*</sup>, NING Zhiying<sup>1,2</sup>, YANG Hongling<sup>1,2</sup>, ZHAN Jin<sup>1,2</sup>, YAO Bo<sup>1,2</sup>

1 Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

2 University of Chinese Academy of Sciences, Beijing 100049, China

3 Naiman Desertification Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Tongliao 028300, China

**Abstract:** The most notable effects of drought are manifested in regional-scale forest mortality events, which can kill millions of trees in a short time, further affecting regional climate and ecosystem structure and function. Given that the frequency and intensity of extreme drought events in the future may increase with increasing temperature, it is urgent to clarify the response strategies of trees to drought stress and the mechanisms of their survival and death, reveal the physiological mechanism of woody plants in arid environment, understand the adaptation mechanism of trees in future climates, and improve the accuracy of predicting the response of trees to drought stress. Plant functional traits refer to the morphological, physiological, or phenological characteristics of plants at the individual level, which indirectly affect the performance of plants by directly affecting the growth, survival or reproduction of plants, and at the same time reflect the long-term adaptation of plants to the growth environment. Plant functional traits and their variation regulations can be used to explain the adaptive mechanism and functional optimization mechanism of plants to the environment, and help to predict the

**基金项目:**国家自然科学基金项目(32071845);甘肃省科技计划资助(23JRRA572);内蒙古自治区科技重大专项(2021ZD0015);甘肃省科技计划资助(23JRRA671)

**收稿日期:**2023-05-20; **网络出版日期:**2024-01-12

\* 通讯作者 Corresponding author. E-mail: liyl@lzb.ac.cn

response of trees to drought. Compared with commonly used plant functional traits, hydraulic traits may better describe the response of trees to drought stress. On the basis of common plant functional traits, we increased the hydraulic traits which are related to water transport capacity and drought tolerance and systematically summarized: 1) the physical mechanism of long-distance water transport in xylem; 2) phases of drought stress and the response of plants; 3) plasticity in plant functional traits and water regulation strategies: Isohydic regulation strategy and anisohydic regulation strategy, xylem efficiency-safety trade-off strategy, conservative water use strategy and risk-taking water use strategy; and 4) mechanisms of drought-related mortality: hydraulic failure hypothesis, carbon starvation hypothesis and biotic agents hypothesis. Finally, three main problems were put forward to be solved: 1) strengthening the inclusion of hydraulic traits to clarify the response and regulation mechanism of plants to drought stress, understanding and predicting plant survival, growth, distribution and death in the context of global change. 2) strengthening the consideration of the relationship between different plant tissue traits from the perspective of the whole plant, revealing the distribution characteristics of plants in the ecosystem, and predicting community composition; 3) the precise physiological mechanism behind tree death is still unclear, future studies need to further explore the mechanisms of drought-related mortality.

**Key Words:** woody plants; drought stress; hydraulic traits; water regulation strategies; drought-related mortality mechanisms

自工业革命以来,不断增强的人类活动导致了全球变暖<sup>[1-2]</sup>。联合国政府间气候变化专门委员会(IPCC)评估报告表明,2011—2020年 全球地表温度比 1850—1900 年高出 1.1℃,预计在 2021—2040 年全球升温或将达到 1.5℃。随着气温上升,未来干旱肯定会恶化(当自然干旱发生时,它们会来的更快,强度更大)<sup>[3]</sup>。较高的温度通常会导致更大的蒸散,与温度较低时相比,土壤和植物会更快的干燥<sup>[4]</sup>。这种“全球变化型干旱”已经对生态系统产生了严重影响,比如大量树木死亡<sup>[5-6]</sup>。区域尺度上的树木死亡事件改变了地表反照率以及地表-大气能量和潜热交换,对区域气候产生反馈<sup>[7]</sup>;广泛的树木死亡事件有能力在十年以下的时间尺度内从根本上改变区域尺度的景观,对生态系统结构和功能产生重大影响<sup>[8]</sup>。在此背景下,我们必须提高预测树木对干旱反应的准确性,以了解树木在未来气候制度下的适应能力<sup>[9]</sup>。

植物功能性状是指植物在个体水平上的形态、生理或物候特征,它们通过直接影响植物的生长、存活或繁殖,从而间接影响植物的性能<sup>[10-11]</sup>,同时反映植物对生长环境的长期适应<sup>[12]</sup>。植物功能性状有助于预测树木对干旱的响应<sup>[12-13]</sup>。近 30 多年来,科研人员常使用植物功能性状及其变异规律来解释植物对环境的适应机制和功能优化机制。然而,随着研究的深入,人们逐步发现自然界生长的植物均是通过多个功能性状共同来完成其适应或功能优化,或者说任何一种功能均是通过多种功能性状来协同实现。准确量化这些多性状间的权衡和依赖关系,有助于我们更好地揭示植物的生境适应策略。然而,研究发现:1) 常用植物功能性状的变异性与降水梯度并不一致,例如平均年降水量(Mean annual precipitation, MAP)对全球尺度上自然生物群系比叶面积(Specific leaf area, SLA)变异的解释率不到 1%;2) 常用植物功能性状与干旱引起的树木死亡率的跨物种模式仅存在微弱的相关性,例如纳入 SLA 和木材密度(Wood density, WD)时,模型对物种死亡率的解释率从只考虑干旱的 30%增加到 37%<sup>[14]</sup>。相比之下,水力性状可能更好地描述树木对干旱胁迫的响应。近年来发现反映植物水分运输能力或植物耐旱性的水力性状如叶片的最大导水率( $K_{max}$ )、膨压消失点叶水势( $\Psi_{ip}$ )、水力安全边际(Hydraulic safety margin, HSM)等与降水梯度高度吻合<sup>[15-17]</sup>。因此纳入水力性状阐明植物对干旱的响应和调节机制,对于理解和预测全球变化背景下植物生存、生长、分布以及死亡有着重要意义。

鉴于未来极端干旱事件的频率和强度可能随温度的升高而增加,迫切需要更好地了解植物对干旱胁迫的应对和调节机制以及不同植物的干旱致死机制,本文重点阐述了:1) 植物木质部水分运输的物理机制;2) 干旱胁迫下植物的水力响应过程;3) 植物水分利用策略的多样性;以及 4) 植物干旱致死机理。

## 1 植物体内的水分传输

与所有维管植物一样,木本植物通过一个复杂的中空死亡细胞(导管或管胞)管道系统,即木质部,将水分从土壤输送到叶片来防止干燥损伤<sup>[9]</sup>。植物木质部长距离水分运输是保证植物体内水分平衡、叶片气孔运动、光合作用以及其它各种代谢活动的主要纽带,被称为“植物生理学的支柱”<sup>[18]</sup>。综述植物体内木质部长距离水分运输过程,特别是了解防止植物蒸腾速率( $E$ )超过临界速率( $E_{crit}$ )的结构和生理机制,有助于理解植物发生水力失败和碳饥饿的风险;1) 临界蒸腾速率会导致与水力失败和共质体失败相关的木质部水势阈值( $\Psi_{crit}$ )的发生;2) 此外,避免 $E_{crit}$ (关闭气孔)对光合作用的影响以及随后对碳水化合物储备的影响对理解碳饥饿至关重要<sup>[19-20]</sup>。

为了维持组织的水合和光合作用,植物必须补充蒸腾作用损失的水分<sup>[8]</sup>。内聚力-张力假说(C-T理论)认为,蒸腾拉力是水分沿木质部上升的主要驱动力,叶面的蒸腾拉力将土壤中的水分通过植物木质部长距离运输提升到冠层并扩散到大气中<sup>[8, 21-22]</sup>,这样从根系到叶片的水就能补充蒸腾作用损失的水分<sup>[23]</sup>。其中,蒸腾拉力( $E$ )可以通过土壤-植物-大气水力连续体的稳态公式明确描述<sup>[8]</sup>:

$$E = K_1(\Psi_s - \Psi_{leaf} - h\rho_w g)$$

式中, $E$ 为叶片蒸腾拉力, $K_1$ 为叶片水力导度, $\Psi_s$ 是土壤水势, $\Psi_{leaf}$ 是叶水势, $h\rho_w g$ 是高度为 $h$ ,密度为 $\rho_w$ 的水柱的重力拉力。当 $E$ 为0时, $\Psi_{leaf} = \Psi_s$ (图1A, a点)。随着 $E$ 的增加,当 $K_1$ 保持不变时,导管并未发生空穴化,植物体内的张力差( $\Psi_s - \Psi_{leaf}$ )与 $E$ 成正比, $\Psi_{leaf}$ 逐渐下降(图1左,虚线a—b)。然而气种假说表明:木质部导管中的水柱在张力作用下处于亚稳定状态,导管中的亚稳态液流所承受的张力随 $E$ 的增加而增加,此时空气经由木质部导管壁上的纹孔膜进入导管,导管开始发生空穴化,空穴化的发展逐渐加重木质部导管栓塞程度, $K_1$ 逐渐下降。当 $E$ 每增加一个单位时,由于 $K_1$ 的下降,会导致 $\Psi_{leaf}$ 的下降逐渐增大(图1左,实线a—c)。当 $E$ 超过 $E_{crit}$ 时,木质部水势( $\Psi$ )超过 $\Psi_{crit}$ ,则会发生水力失败。在干旱胁迫发生时,干旱降低了根区的 $\Psi_s$ ,植物在 $E$ 较低时便会发生水力失败(图1右,将实线a—c和实线d—e进行比较)。在昼夜尺度上,植物通过关闭气孔保持 $E$ 低于 $E_{crit}$ (植物通过降低气孔导度( $G_s$ )来响应增加的 $E$ <sup>[24]</sup>,气孔闭合程度与导致栓塞的 $\Psi_{crit}$ 有关<sup>[25]</sup>)。减少 $G_s$ 的好处是减少水分损失,但他的代价是减少二氧化碳( $CO_2$ )从大气扩散到羧基化位点,从而限制光合作用对 $CO_2$ 的吸收<sup>[20]</sup>,这种水分流失和 $CO_2$ 吸收之间的平衡可能会在干旱期间导致植物出现生存、水力衰竭和碳饥饿三种结果。

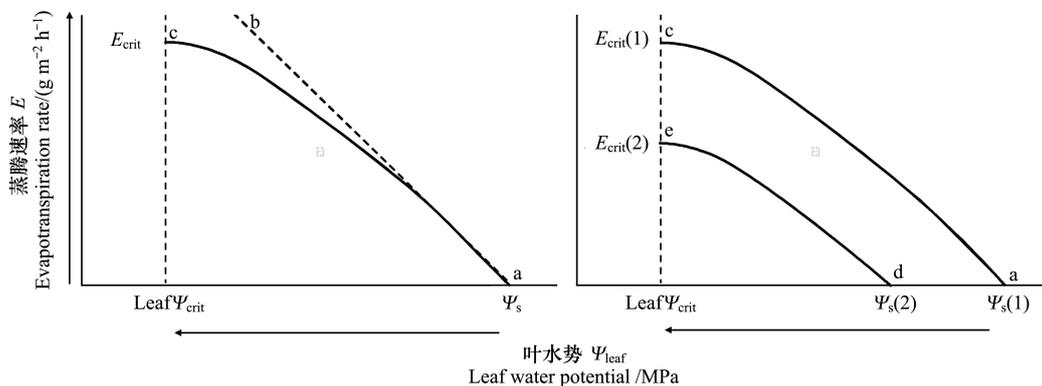


图1 基于达西定律模型求解的蒸腾拉力( $E$ )与叶水势( $\Psi_{leaf}$ )的变化

Fig.1 The transpiration rate ( $E$ ) versus leaf water potential ( $\Psi_{leaf}$ ) is based on the model solution of Darcy's law  
 $\Psi_s$  是土壤水势;  $E_{crit}$  是最大蒸腾速率, 取决于  $\Psi_s$ ;  $\Psi_{crit}$  是  $E_{crit}$  处的  $\Psi_{leaf}$ , 也是允许水分吸收的最低  $\Psi_s$

## 2 植物应对干旱胁迫的水力响应过程

植物应对干旱胁迫的响应过程主要分为两个阶段:1) 干旱胁迫开始到气孔闭合期间;2) 气孔闭合到木质

部完全栓塞期间<sup>[26]</sup>。在干旱期间,降水减少导致土壤湿度下降,这往往伴随着更高的温度和增加的大气蒸发需求,这些因素结合在一起引起植物的水分胁迫,导致植物  $\Psi_x$  下降(木质部水柱所受张力增加),因此植物关闭气孔以限制水分流失和延缓  $\Psi_x$  的下降。最近研究表明,尽管气孔关闭会造成一系列负面影响,但气孔仍旧会在木质部水势达到明显的气穴化形成阈值(气孔导度损失 88% 对应的水势值, the water potential at 88% loss of stomatal conductance,  $P_{gs88}$ )之前关闭<sup>[26-28]</sup>。气孔关闭后,  $\Psi_x$  随着水分通过气孔渗漏<sup>[29]</sup>以及表皮和树皮等其他组织损失而继续缓慢下降,植物通过释放内部储存水来缓冲  $\Psi_x$  的下降<sup>[30]</sup>。与此同时,植物整个水力途径的水力导度通过一系列生物物理和生理机制而下降,比如叶脉的可逆塌缩<sup>[31]</sup>、细胞膜水通道蛋白调节<sup>[32]</sup>和细根皮层腔隙的形成<sup>[33]</sup>等。这一阶段的失水速率通常比气孔完全打开时低 100—1000 倍<sup>[29]</sup>。如果持续干旱,水势持续下降最终达到一个临界阈值(水力导度损失 50% 对应的水势值, the water potential at 50% loss of hydraulic conductance,  $P_{50}$ )时,栓塞开始在木质部中扩散<sup>[34-35]</sup>,这一过程发生在包括植物根茎叶在内的整个水力系统中<sup>[36-37]</sup>。由于栓塞大大减少了向冠层的水分输送,这种水力功能障碍导致了分支斑块性死亡和冠层叶面积显著减少<sup>[38]</sup>。随着栓塞逐渐遍布整个输水网络,造成植物水力系统不可逆的损伤(水力导度损失 80% 对应的水势值, the water potential at 88% loss of hydraulic conductance,  $P_{88}$ ),最终导致整株植株死亡。

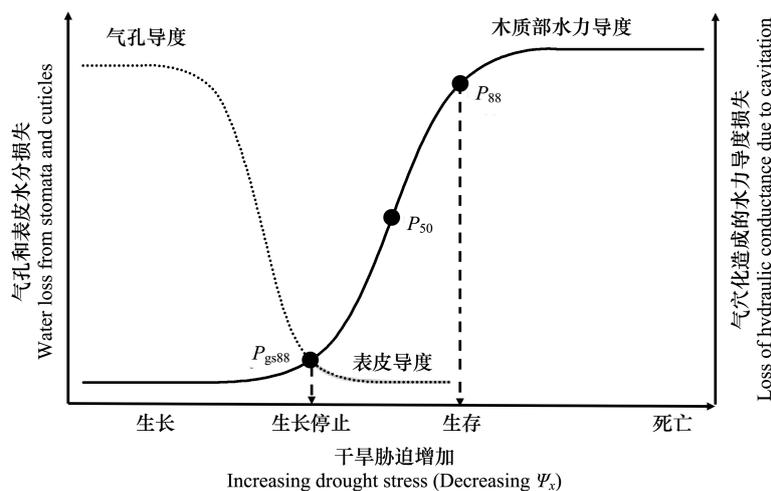


图 2 植物对干旱胁迫的水力响应过程

Fig.2 Phase of drought response to drought stress in plants

随干旱胁迫增加,虚线代表气孔和表皮导度变化趋势,实线代表木质部水力导度损失率; $P_{gs88}$ 代表气孔关闭时的水势; $P_{50}$ 和 $P_{88}$ 分别代表水力导度下降 50%和 88%的水势

### 3 植物水分运输策略的多样性

植物功能性状对植物的建立、存活、生长和繁殖有很大影响,可以很好地表征植物的生长策略<sup>[39]</sup>。然而,在哪些性状可以用来评估生态耐旱性方面,我们的知识仍然有限。

#### 3.1 衡量植物抗旱性的性状

##### 3.1.1 压力-容积曲线(Pressure-volume curve, 简称 P-V 曲线)

基于 P-V 曲线计算得到的参数(如膨压消失点叶水势( $\Psi_{ip}$ )、质壁分离时的相对含水量(RWC<sub>ip</sub>)、饱和含水时的叶渗透势( $\pi_0$ )和细胞体积弹性模量( $\varepsilon$ ))在机制上均与耐旱性有关<sup>[40-41]</sup>。其中, $\Psi_{ip}$ 代表了引起萎蔫的叶片和土壤的干燥程度<sup>[40]</sup>,被认为是最直接量化植物耐旱性的“更高级别”的性状<sup>[42-43]</sup>。植物会改变其他 P-V 参数:1)渗透调节:积累溶质(减少  $\pi_0$ );2)质外体调节:通过将更多的水重新分配到细胞壁外部来减少共质体水分(增加  $a_f$ );3)弹性调节:增加细胞壁的弹性(减少  $\varepsilon$ )以达到足够负的  $\Psi_{ip}$ 值<sup>[41-43]</sup>,提高他们的耐

旱性。然而,由于这些参数通常是同时调整的,因此他们在影响 $\Psi_{\text{tp}}$ 方面的相对重要性仍然存在争议。前人的研究表明, $\Psi_{\text{tp}}$ 与干旱指数呈显著正相关,湿润地区的生物群系比干旱区的生物群系具有更小的负值,这支持了膨压消失点叶水势在木本生物群系尺度上反映耐旱性的观点。尽管大多数人认为负值较大的 $\Psi_{\text{tp}}$ 有利于耐旱性,但也有人提出了相反的观点,认为负值较小的 $\Psi_{\text{tp}}$ 是有益的。当 $\Psi_{\text{leaf}}$ 下降时,负值较小的 $\Psi_{\text{tp}}$ 使叶片迅速失去膨压并关闭气孔,从而保持较高的 $\text{RWC}_{\text{tp}}$ 。 $\text{RWC}_{\text{tp}}$ 也被认为是植物耐旱性的重要衡量标准。尽管大多数研究认为更负的 $\Psi_{\text{tp}}$ 有利于耐旱,一些研究则认为维持细胞水合比维持膨压更重要,因为脱水会导致细胞收缩,细胞壁结构损伤以及由于高离子浓度而产生的潜在渗透压,最终破坏代谢过程。除此之外,细胞总相对含水量低于75%时会严重抑制ATP, RUBP和蛋白质的产生<sup>[44]</sup>。 $\Psi_{\text{tp}}$ 和 $\text{RWC}_{\text{tp}}$ 作为耐旱性预测因子的重要性经常受到争议,但没有得到解决。一个最近的meta分析表明 $\Psi_{\text{tp}}$ 而不是 $\text{RWC}_{\text{tp}}$ 驱动物种与栖息地水分供应的关系<sup>[41]</sup>。

### 3.1.2 木质部栓塞脆弱性曲线(Vulnerability curves, 简称VCs)

木质部栓塞抗性是决定植物抗旱性的最重要性状之一,也是解释近年来干旱导致植物死亡的重要性状之一<sup>[45]</sup>。木质部栓塞抗性通常由VCs决定,该曲线描述了当 $\Psi_x$ 降低时,水力导度丧失百分比(Precent loss of conductivity, PLC)如何增加。VCs可以提供有关特定植物干旱响应的有价值的信息,并已被用于量化植物抗旱性和生态适应性。例如, $P_{50}$ 或 $P_{88}$ 以及水力安全范围被广泛用于量化抗旱性和水力失败的风险<sup>[46]</sup>。

大量研究表明,当 $\Psi_x$ 降到 $P_{50}$ 或 $P_{88}$ 以下后, $\Psi_x$ 很小的变化将引起水分传导速率大幅下降,树木也因此面临严重栓塞及死亡风险。 $P_{50}$ 是最常用的栓塞抗性指标。Lamy等对地中海松树的513种基因型的研究发现,气候差异明显的不同种群其 $P_{50}$ 的遗传和表型变异均有限, $P_{50}$ 可能是松树固有特征<sup>[45]</sup>。但是关于栓塞脆弱性的遗传变异和表型可塑性的研究仅限于少数物种,仍需进一步的研究来确定这一结论是否在所有树种中适用。物种水平上,对栓塞抗性在木本种中种间变异的meta分析表明,不同树种木质部栓塞脆弱性存在巨大差异,植物木质部栓塞脆弱性与其生长环境的年平均降水量和干旱程度相关,来自干燥气候的物种比来自湿润气候的物种具有更大的 $P_{50}$ 值,对干旱的忍耐力越强<sup>[47-48]</sup>。然而在群落水平上,在较干燥的栖息地,植物脆弱性的变化往往很大,这表明脆弱性和干旱在某些情况下是解耦的<sup>[49]</sup>。这种解耦是因为一些物种所使用的水分胁迫规避策略,如深根系植物或干旱落叶,这些策略使得它们在干旱时期保持较高的 $\Psi_x$ <sup>[9]</sup>。具有系统发生学差异的植物,其致死的水势临界点(即木质部导水性不能再恢复)与 $P_{50}$ 或 $P_{88}$ 的关系有所差异。裸子植物中的水势临界点与 $P_{50}$ 具有很大正相关性,但被子植物的水势临界点却与 $P_{88}$ 有更高的相关度<sup>[9]</sup>。

水力安全范围有2种计算方式:1)HSM:树种木质部最低水势( $\Psi_{\text{min}}$ )与栓塞抗性( $P_{50}$ 或 $P_{88}$ )的差值(即 $\Psi_{\text{min}} - P_{50}$ 或 $\Psi_{\text{min}} - P_{88}$ ),是预测树木干旱死亡率的关键指标<sup>[50]</sup>。HSM值越小,说明树种面临水力失败的风险越大,反之树种面临水力失败的风险越小<sup>[51]</sup>。然而,Choat等针对全球81个地点226种森林的研究结果发现,70%的森林在应对干旱胁迫时的HSM很窄(约 $<1$  MPa),安全边际在很大程度上与年降水量无关,森林对干旱的脆弱性存在全球趋同:所有森林生物群落无论当前的降雨环境如何,都同样容易遭受水力失败<sup>[48]</sup>。因为 $\Psi_{\text{min}}$ 集成了与环境相关的植物结构(例如,生根深度)和生理(例如,气孔行为)性状的许多重要方面,在不同森林类型中发现的狭窄水力安全边际为植物生态学提供了一个重要视角,这表明植物的水力策略是根据其环境进行微调的,允许最大限度的碳获得,但在干旱期间将植物暴露在水力失败的风险中<sup>[9]</sup>。这也表明了一种普遍存在的“有风险”的策略,即植物对环境的快速变化做出反应的生理潜力有限<sup>[9]</sup>。这加剧了气候变化下极端干旱事件增加所构成的威胁<sup>[9]</sup>。2)气孔安全边际(Stomatal safe margin, SSM):气孔闭合时的水势( $P_{\text{gs}88}$ )与抗栓塞能力( $P_{50}$ 或 $P_{88}$ )的差值(即 $P_{\text{gs}88} - P_{50}$ 或 $P_{\text{gs}88} - P_{88}$ ),用来反映树种的气孔调控策略<sup>[52]</sup>,更直接地将气孔对水势的响应和木质部栓塞抗性结合起来。正的SSM表明气孔关闭发生在茎严重栓塞之前,而负的SSM表明气孔关闭发生在栓塞之后;SSM宽的物种的耐旱时间更长。有明确证据表明,等水和非等水植物的部分死亡和完全死亡与水力失败有关,这进一步凸显了气孔调节和木质部栓塞抗性之间协调的重要性。总的来说,气孔安全边际随着栓塞抗性的增加而持续增加,并且气孔安全边际与水力安全边际相

关<sup>[53]</sup>。最重要的是,将气孔调节策略与木质部水力策略相结合有助于更全面地表达植物对干旱的适应<sup>[54]</sup>。

### 3.1.3 非结构性碳水化合物(NSC)

NSC 包括淀粉和可溶性糖<sup>[55-56]</sup>,在树木的抗旱性中发挥重要作用<sup>[57]</sup>。淀粉是一种长期的碳储存分子,它以一种紧凑的、不溶性的形式存在,允许植物在高光合速率的情况下储存碳水化合物。可溶性糖为植物提供能量和底物,同时也可充当中间代谢产物、信号分子或渗透物。植物通过光合作用将 CO<sub>2</sub> 固定为碳水化合物,然后用于呼吸、防御、生长、繁殖或在光合作用无法发生时(如夜间、休眠季节或环境压力时期)为植物提供能量储备<sup>[58]</sup>。在干旱胁迫下,NSC 扮演着两种角色<sup>[59]</sup>,缓冲了植物的碳供应不足<sup>[60-61]</sup>:1)作为“碳饥饿”的缓冲。在“碳饥饿”过程中,光合作用受到干旱胁迫,植物缓慢地消耗他们储存的碳水化合物直到死亡<sup>[8]</sup>。因此,生活在炎热和干燥气候中的植物比生活在潮湿气候中的植物分配更多的碳储存,作为应对干旱胁迫的保守缓冲<sup>[62]</sup>。2)作为渗透缓冲剂。当水分胁迫激活淀粉降解酶时,植物可以将不溶性淀粉转化回可溶性糖<sup>[63]</sup>。这种从淀粉到糖的转化可以降低植物的渗透势,从而在干旱期间维持细胞膨压<sup>[64-65]</sup>。因此,有人认为在干燥环境中进化或生长的植物将保持较高的 NSC 储存量,并保持更大比例的可溶性糖储存,以防止细胞失水,保持细胞稳定,在干旱条件下生存更长时间<sup>[41, 66-68]</sup>。

### 3.1.4 结构性状

结构性状可以很好地反映不同树种面对干旱胁迫时的适应能力。比如,叶片厚度(Leaf thickness, LT)与植物获取、利用资源的策略紧密相关。具有较高 LT 的植物可以增强蓄水能力,避免环境胁迫造成伤害。叶干物质含量(Leaf dry matter content, LDMC)常用干重和鲜重的比值来表示,干旱地区的植物 LDMC 也较高,对环境胁迫有较强的抗性<sup>[69]</sup>。比叶重(Leaf mass per unit area, LMA)和叶密度(Leaf density, LD)是表示干旱容忍能力的重要叶片功能性状,因为 LMA 较高和 LD 较高表明细胞壁较厚或者较密,从而能够较大程度地防止由于叶水势下降引起的变型诱导的损坏。LMA 常用叶片单位面积的干物质量来表示<sup>[70]</sup>。LMA 高的植物因其较强的碳同化能力能够更好地生长。干旱地区的植物通过提高比叶重来提高植物固持资源(碳、氮)的效率,从而提高竞争力。LD 反映叶片的紧实程度及植物对外界干旱环境的忍耐能力。具有较高 LD 的植物通常适应于干旱的生境。通常 LD 高,则叶片细胞小且细胞壁较厚,能够高效积累渗透物质同时减少水分损失,从而减弱水分可利用性低对叶片造成的破坏。胡伯尔值(AL:AS)与 WD 都是物种对不同水分可利用环境进行水力调节的重要性状。AL:AS 表征枝条对叶片的供水能力,反映蒸腾叶面积与茎输导供水之间的权衡<sup>[71-72]</sup>。低 AL:AS 可以避免蒸腾过程过度失水,促进叶片水平供水以适应干旱条件,降低水力紊乱的风险。WD 常用植物对单位体积木材投资的生物量来表示,反应植物机械支撑、水分运输和生长速率<sup>[73]</sup>。低 WD 意味着储水能力较高,有利于木质部再充水而修复栓塞;高 WD 意味着较厚的导管壁或较丰富的机械组织,结构紧密,相应的导管面积较小。在干旱胁迫的环境中,植物通常具有较高的 WD,保护木质部避免空穴化<sup>[72]</sup>。根系与土壤环境直接接触,负责吸收养分和水分,但由于其藏匿于地下,根系性状成为了植物对干旱响应的一个重要但被忽视的预测因子<sup>[74]</sup>。有关根系性状对干旱反应的数据仅限于少数几种植物<sup>[74]</sup>。因此,关于植物根性状响应策略的结论似乎很特殊,或者年代太久远<sup>[74]</sup>。例如,有研究报告称,一些植物种因干旱而产生更细的根,具有高比根长(Specific root length, SRL)和比根表面积(Specific root surface area, SRSA),这一策略被解释为以低投资改善水资源获取<sup>[75]</sup>。相比之下,其他研究报告称,植物种产生的根更粗,SRL 和 SRSA 较低,这已被证明可以降低水力失败的风险<sup>[76]</sup>。更粗的根与通过真菌营养获得高养分和高水分有关<sup>[77-78]</sup>,并与由于储存非结构性碳水化合物而产生的渗透调节有关<sup>[79]</sup>。

植物性状有助于预测树木对干旱的响应<sup>[73]</sup>。相比于常用功能性状,现在已经出现了一套经过充分研究的与耐旱性机制相关的水力性状(表 1),被寄予厚望用于预测植物对干旱胁迫的响应,这代表了未来研究的方向<sup>[9]</sup>。

表 1 与树木耐旱性相关的植物水力性状列表

Table 1 List of hydraulic traits (physiological, morphological, and anatomical) associated with drought tolerance in trees

性状 Trait	性状描述 Trait description	参考文献 References
叶片 Leaves		
气孔响应 Stomatal response	气孔闭合速率和敏感性对 VPD 和叶片水势变化	[80—87]
膨压消失点和渗透调节 Turgor loss point & osmotic regulation	叶片叶肉细胞失去膨压和叶片枯萎的水势,以及叶片叶肉细胞渗透含量的适应性调节	[41, 43, 88—98]
最小气孔导度 Minimum stomatal conductance	当气孔处于最小孔径时,叶片角质层的水分损失率	[99—101]
木质部外通路 Extraxylary pathways	液体和蒸汽通过叶肉和支持组织的阻力变化	[102—104]
叶脱落 Leaf shedding	在干旱期间通过叶片脱落减少叶面积可以减缓干燥速度,减轻水分对剩余叶片的压力	[87, 105—106]
气孔解剖结构 Stomatal anatomy	气孔的形状、大小和分布,影响失水相关的叶片生理性状	[42, 107]
根系 Roots		
皮层空腔形成 Cortical lacunae formation	根皮层细胞解体,使维管组织从表皮及周围干燥土壤分离	[33, 108—109]
细根损失 Fine root loss	细根脱落,减少根系与土壤接触的总面积,重新平衡根枝比	[33, 108—111]
根系深度 Rooting depth	深层根系生长,获得更稳定的水源	[112—118]
组织性状 Traits among tissues		
栓塞脆弱性 Vulnerability to cavitation	木质部汁液的负压导致木质部最大水力导度损失 50% 或 88%。如,裸子植物的生理临界点 ( $P_{50}$ ); 被子植物的生理临界点 ( $P_{88}$ )	[47—48, 100, 119—138]
水容 Capacitance	在木质部周围组织中储存的水分,可以缓冲导致空穴化事件的木质部汁液负压	[30, 113, 139—141]
细胞膜通透性 Cell membrane permeability	水通道蛋白的活性可以改变细胞膜的通透性,导致跨膜通路的水力导度降低	[32, 103, 142—143]
木质部解剖性状 Xylem anatomical traits		
木质部导管尺寸、数量和连通性 Xylem conduit	木质部导管(管胞和导管)的直径、长度和连通性影响最大水力导度和空穴化脆弱性。	[132, 144—145]
纹孔膜孔隙度/厚度 Pit membrane porosity/thickness	纹孔膜解剖结构决定了木质部导管之间的空气传播阈值,并影响水力导度和空穴化脆弱性。	[121—122, 131, 146—147]
木材密度 Wood density	木材密度由木质部解剖性状决定,并与许多生理性状相关。	[28, 127, 148]
连接性 Sectoriality	维管组织的空间分离,防止栓塞在分支间扩散	[149—154]

VPD: 饱和水汽压差 Vapor pressure deficit

### 3.2 植物水分利用策略

鉴于植物在异质环境中争夺空间、阳光、水和养分的策略多种多样,任何单一植物功能性状均不足以表征植物在干旱胁迫下的生存力,常需结合一系列形态功能性状、生理功能性状、生物化学功能性状来阐明植物的水分调节对策及机制,进一步揭示植物对气候变化的响应和适应<sup>[155]</sup>。

#### 3.2.1 等水和非等水调节策略

1936 年, Berger 提出等水/非等水概念,基于叶片水势或者蒸腾来描述植物昼夜水分调节关系。在昼夜转换间,等水植物会在正午来临时,及时关闭气孔,维持较高的正午叶片水势。而非等水植物气孔则持续张开,保持水碳交换,故而正午叶片水势较低。近期,研究者将等水/非等水概念用于长期干旱条件下的水分管理<sup>[86]</sup>。即随着土壤水势的持续降低,等水植物的叶片水势会保持较高水平,然后缓慢降低,而非等水植物的叶片水势会持续降低。等水植物的叶片蒸腾随着土壤变干而迅速降低,而非等水植物则先缓慢降低而后加快

降低。后来,多物种结果表明,大多数物种是按照等水/非等水连续体排序的,而非二分法分类且很少有物种严格遵循等水或非等水定义。基于气孔导度调节行为将林木沿“等水-非等水”谱进行划分是一种新兴的判断植物对干旱的适应策略的方法<sup>[156]</sup>。等水调节植物通过气孔控制水分散失到大气的速率来调节自身水分状况,使土壤-植物-大气水力系统的水分供应能力相匹配,是在水分条件变化下能维持最小叶水势相对稳定的物种。非等水物种在干旱早期关闭气孔,将更多地依赖储存的碳水化合物满足其呼吸、渗透调节或防御方面的碳需求,从而在干旱胁迫下更容易死于碳饥饿<sup>[8]</sup>。非等水调节植物则随着蒸发需求的增加,降低其叶水势,从而维持水由土壤到达叶片的驱动力。非等水物种在干旱时气孔关闭较晚,以牺牲水势为代价换取碳摄入,因而更容易死于水力失衡<sup>[8]</sup>。等水型植物常为在干旱初期减少蒸腾速率的保水植物(或避旱植物),而非等水型植物是在干旱胁迫下维持长时间气体交换的耗水植物(或耐旱植物)。与等水势调节植物相比,非等水势调节植物木质部对较负的水势有更强的抵抗力,在干旱环境下通常更具优势。在全球变化背景下,究竟是等水调节植物还是非等水调节植物的适应性更强尚无定论。

### 3.2.2 木质部效率-安全权衡策略

木质部的水力传导效率与安全性之间的权衡关系对于植物适应环境水分条件的变化具有重要意义。更高的效率意味着:1)在一定的压力梯度下,单位木质部横截面积的潜在蒸腾作用和光合作用更强;2)植物只需要形成较小的木质部横截面积就可以运输同样的水量;3)导致在给定的蒸腾拉力下不那么负的木质部水势,避免张力过大<sup>[157]</sup>。安全性是指抵抗栓塞形成和扩散的能力。更大的安全性意味着:1)植物可以在更大的木质部张力下运行;2)在给定的张力下,木质部导管内的气体阻塞更少。安全性好的植物仅需相对少的根系生长投入,具有耐盐碱性,且在一定程度缺水时仍可保持一定的气孔开放进行CO<sub>2</sub>固定<sup>[157]</sup>。基于全球数据集,Choat 等发现,在年平均降雨量较低的生境分布的物种表现出较强的气穴化栓塞抵抗力,而生长于年平均降雨量较高的生境的物种具有较高的木质部水分传输效率<sup>[48]</sup>。除此之外,森林恢复早期植被盖度低,物种之间对于土壤水分的竞争相对较小,而后期物种丰富度和森林郁闭程度增加,物种之间对水分的竞争激烈;因此早期较小的水分胁迫迫使木质部水分传导效率比较高的先锋物种能够迅速占领生境,而在恢复后期占据优势的物种则普遍具有较强的气穴化栓塞抵抗力,以应对由于竞争导致的水分胁迫程度的增加。这种跨物种的木质部水分传导效率-安全权衡关系是物种之间生态位分化的重要生理机制。Gleason 等对较少物种的研究进行划分,通过安全和效率值之间的线性相关性来衡量,约 25%的研究支持安全-效率权衡假说,75%的研究不支持<sup>[157]</sup>。根据 Sperry 等的观点,在单个膜孔水平上安全和效率之间的负相关是不可避免的,但随着分析水平扩大到整个膜、整个导管和整个木质部组织这种相关性可能会减弱。基于对全球 424 个树种(89 个裸子植物和 335 个被子植物)的木质部水力安全-效率权衡假说验证结果进一步显示:木质部安全、效率之间存在弱的权衡关系;几乎没有树种同时具有高的木质部效率和安全性,而许多树种是低效率、低安全物种<sup>[157]</sup>。Yao 等研究发现,干旱区域的锦鸡儿属植物同时具有高的水力效率和水力安全,这可能是由于该属植物在面对干旱胁迫时采取干旱避免策略,通过提高脱落酸浓度使气孔导度迅速下降以维持高的导水率<sup>[158]</sup>。对于相当数量的低效率和低安全的物种,似乎没有令人信服的解释,Gleason 等认为这可能与木材密度低、叶边材面积低和高度低有关<sup>[157]</sup>。目前,关于效率-安全权衡是否存在仍有争议。

### 3.2.3 保守型水分利用策略和索取型水分利用策略

Wright 等提出了全球叶经济型谱<sup>[159]</sup>:在谱的一端为“缓慢投资-收益型”物种,它们具有叶寿命长、叶片坚硬的特点,用于叶片结构构建的资源较多,所以减少了对光合和呼吸功能的资源投入,使光合速率和呼吸速率都偏低,这种类型的植物养分投资低且回收慢,因此生长速率和叶片周转速率均较慢,从而适宜生长在低资源环境的地区。相反,在谱的另一端为“快速投资-收益”型物种,它们具有光合及呼吸速率快、养分含量高,但叶寿命短、比叶重小、碳和养分归还快等特点,这种类型的植物养分投资高且回收快,可以支撑较高的生长速率和叶片周转速率,从而适宜生长在资源丰富的地区。然而,这个最初的叶经济型谱只包括了碳和养分经济性,并没有考虑到与水资源利用相关的性状,另外叶经济谱是否适用于根和茎尚不清楚。Reich 将原有的

叶经济谱扩展成包括叶-茎-根、碳-养分-水的普适性“快-慢”植物经济型谱,反映植物在生产-维持、生长-存活之间的权衡<sup>[160]</sup>;在快对策一端为索取型水分利用策略,物种表现为在资源丰富时能快速生长以掠夺更多资源,但需花费较大的投资建设成本,这对植物在资源受限时的适应不利,对干旱胁迫的容忍性较差;在慢对策一端为保守型水分利用策略,物种在资源受限时降低对资源的使用速率,通过对低资源环境较高的容忍能力以保证存活,但该对策的植物在资源丰富时的竞争力较弱,对干旱胁迫的容忍性较高。我们通过综述相关文献,从水力性状和碳经济性状两方面比较并归纳了保守型水分利用策略与索取型水分利用策略植物的差异(图3),其中多数性状的差异明显,但有些性状之间的相关性尚需更多的验证。



图3 保守型水分利用对策与索取型水分利用对策植物的性状对比

Fig.3 Contrasting plant traits between conservative and risk-taking regulation strategies

#### 4 与干旱相关的死亡机制假说

干旱最显著的影响表现在区域尺度的森林死亡事件中,可以在短时间内杀死数百万棵树木<sup>[9]</sup>。近年来,很多研究者对干旱导致树木死亡机理进行了大量研究,但至今尚未获得干旱导致树木死亡确切的生理学机制,这限制了我们准确预测全球气候变化条件下植被分布的变化,也影响到应对气候变化相应策略的制定。目前为止,干旱导致树木死亡的假说主要包括:水力失败假说,碳饥饿假说和生物攻击假说。

##### 4.1 水力失败假说

水力失败假说是指干旱胁迫引起植物水势下降,当水势下降超过水势阈值时,木质部张力的增加可能会导致木质部导管中的水柱中断或产生不可恢复的气穴化,使得导水率严重受损,造成将水分从根际供应至叶片的传输系统通道受阻,植物因“水力失衡”而死亡<sup>[128, 161-163]</sup>。水力失败假说的依据是完全干燥会导致细胞死亡。如果干旱足够严重,植物在耗尽碳之前耗尽水,则水力失败就可能发生<sup>[8]</sup>。现有研究表明,小型植物

中会发生水力失败,盆栽的干旱试验通常会导致快速死亡。因为与具有较大根系的植物相比,幼苗有限的生根量使他们面临更负的土壤水势,从而降低了土壤到根系的水力传导,缩小  $E$  和  $E_{crit}$  之间的安全边际。而对于成熟树木,在没有昆虫或病原体侵袭的情况下,有许多轶事性的死亡,水力失败或其他机制是否是导致死亡的原因尚不清楚。墨西哥果松(piñon)与杜松(juniper)的对比研究表明:与等水调节策略的墨西哥松相比,非等水调节策略的杜松更容易死于水力失败。干旱期间,持续的蒸腾作用使杜松土壤水势降低至  $-6.9\text{MPa}$ ,在根系和茎中分别引起 40%—60% 的栓塞,接近水力失败。如果干旱持续时间较长,最终可能会导致冠层枯梢,考虑到更大的干旱强度和更长的干旱持续时间,水力失败可能导致非等水调节策略植物的全株死亡。干旱期间,墨西哥松气孔关闭使其木质部水势保持在  $-2.5\text{MPa}$  以上,仅在根系中引起 5%—40% 的栓塞。即使在极端干旱条件下,等水调节策略的墨西哥松也能防止过度空穴化,不太可能发生水力失败。有明确的证据表明,等水和非等水植物的部分和完全死亡与水力失败有关<sup>[164]</sup>。然而,没有任何水力失败试验排除了碳饥饿或其他过程作为死亡率有关的机制。

#### 4.2 碳饥饿假说

碳饥饿假说是指当土壤水分降低时,植物会关闭气孔来减少蒸腾作用散失的水分,气孔关闭导致  $\text{CO}_2$  同化减少,植物光合作用、可调动非结构性碳水化合物和液泡蛋白质水解的碳供应低于呼吸、生长和防御的碳消耗,非结构性碳水化合物被持续消耗,长期碳失衡最终导致植物死亡(在植物死亡时可测量的非结构性碳水化合物不一定为零,但其剩余量必须不能用于新陈代谢)。环境胁迫下,非结构性碳水化合物的变化大致可分为 3 个阶段:1)碳剩余:在干旱早期,非结构性碳水化合物含量增加;2)碳限制:在长期干旱中,光合作用显著减少,非结构性碳水化合物被消耗以维持呼吸代谢和渗透调节等细胞生存,其含量最终将下降<sup>[164—166]</sup>;3)碳亏损:在长期干旱后,由于长时间碳消耗大于碳供应,可能会导致植物因碳饥饿而死亡。现代分子手段证实碳饥饿现象的存在:各种降低光合作用的实验(如,盐胁迫、光胁迫、温度胁迫和水分胁迫)均观察到,在胁迫早期光合产物分配到储存的增加与植物下调呼吸和生长,上调能量储存的分子信号有关<sup>[167]</sup>。这些分子信号的改变并非对短期环境变化的反应而与 NSC 的可利用性有关<sup>[168]</sup>。碳饥饿(全株植物光合作用下降)的最初驱动因素实际上是淀粉产量随环境胁迫相对增加<sup>[169]</sup>。植物淀粉含量最终下降则是由于胁迫条件下,植物叶面积下降,光合作用下降至最低水平,可利用 NSC 不能满足代谢需求<sup>[167]</sup>。以上研究从分子和生理角度总结出一致现象:胁迫早期,植物碳水化合物含量增加;胁迫后期(长时间低光合作用下),植物出现碳饥饿现象。然而,一方面由于碳饥饿与:1)利用能量储存进行新陈代谢和防御;2)碳水化合物的运输以及 3)维持膨压和光合能力所需的能量以及碳骨架这 3 个过程密切相关;另一方面在胁迫过程中均发现 NSC 含量上升,这就引发了研究者们对于碳饥饿机制的争议<sup>[164]</sup>:有学者认为水分胁迫会通过水力失败,限制 NSC 的利用或是使植物更易受到病虫害攻击而致死,碳饥饿过程并不重要,但 McDowell 则认为,由于干旱引起水力传输、NSC 传输障碍,从而使用于新陈代谢和抵御病虫害的 NSC 减少,进一步影响 NSC 含量,这一负反馈最终引起植物死亡。

#### 4.3 生物攻击假说

生物攻击假说表明,干旱会引起生物致死因子(如昆虫和病原体)的统计学变化,从而独立地或与干旱引起的寄主植物生理状况变化一起导致树木死亡<sup>[8]</sup>。这一假说源于经常观察到的干旱与昆虫爆发之间的时间相关性:1)温度升高会增加生物致死因子数量(如生长率和繁殖的增加)<sup>[170]</sup>;2)与异常温暖的天气相关的干旱将对昆虫种群动态的许多特征产生影响(如种群内在增长率,每年产生的世代数,关键发育阶段的同步性,冬季死亡率和地理范围)<sup>[170]</sup>;3)干旱通过影响主要捕食者和共生动物的丰度来影响昆虫和病原体种群,这种影响的方向和强度在很大程度上是未知的<sup>[171]</sup>。总之,温暖干旱可能会增加生物致死因子爆发的强度而不依赖于与干旱相关的树木生理状况的变化,生物致死因子的数量变化必须覆盖宿主植物生理状况的变化,以引起广泛的死亡事件<sup>[8]</sup>。然而,干旱不可能对所有杀死树木或所有地方的昆虫都有利,与干旱相关的死亡率并不总是包括明显的生物致死因子<sup>[172]</sup>,因此生物攻击假说最多只能解释一部分树木死亡现象<sup>[8]</sup>。

部分学者认为水力失败是导致干旱胁迫下木本植物死亡的主要原因,而另一部分学者认为碳饥饿是导致

木本植物死亡的主要原因。McDowell 等认为水力失败、碳饥饿的发生与水分胁迫的强度和持续时间有关:植物暴露在低强度但持续时间长的干旱中,可能会使水分状态保持在临界水势阈值以上,但会耗尽储存的碳水化合物至致命限度;相反,在高强度干旱条件下,植物不能将水分状态调节到临界阈值以上,在耗尽碳之前耗尽水,将导致木质部空穴化和脱水死亡<sup>[8]</sup>。越来越多的研究指出,树木死亡并非由单一机制造成,而是水力失败和碳饥饿共同作用的结果<sup>[173-174]</sup>。除此之外,树木还经常遭受生物攻击引起的组织损伤(比如虫害爆发)。水力失败和碳饥饿加剧生物攻击(由于树脂等碳基防御性化合物的减少,吸引昆虫的乙醇等挥发性物质的增加,以及昆虫食物质量的改变会导致生物攻击加剧)<sup>[8]</sup>;生物攻击也可以加剧水力失败(当甲虫用木质部封闭真菌接种边材时,会阻碍木质部水分运输)<sup>[175]</sup>和碳饥饿(通过生产树脂来增加碳损失)<sup>[176]</sup>。目前,木本植物面对死亡的机制没有一个统一的定论。

## 5 研究展望

植物水分生理学对理解树木如何响应干旱胁迫以及干旱致死机理至关重要。对植物水力性状的研究有助于加强我们对植物运输水分策略的认识,扩展我们对植物与环境因子间相互作用的了解,逐步揭示植物对环境的适应机制,为气候变化背景下植被分布的预测提供理论依据。目前仍有部分问题在未来研究中有待加强。

### 5.1 加强纳入水力性状阐明植物对干旱胁迫的响应和调节机制。

木本植物的干旱致死和地区性植被枯死在世界各地广泛存在,然而面对未来的全球干旱趋势,预测某一区域哪种植物最具耐受性仍然是一项挑战。相比于常用植物功能性状,水力性状可能更好地描述植物对干旱胁迫的响应。因此纳入水力性状阐明植物对干旱的响应和调节机制,对于理解和预测全球变化背景下植物生存、生长、分布以及死亡有着重要意义。目前仅有的关于水力性状的研究大多停留在物种水平的比较上,干旱条件下群落水平的水力性状研究仍十分有限。将水力性状纳入植物群落的响应对策中,可以极大地改善极端干旱环境下植物性状对群落稳定性变化的解释能力。

### 5.2 加强从全株植物的角度考虑植物不同组织性状间的关系。

目前已有研究大多集中在叶和根的资源获取性状上,而没有考虑其他重要的组织系统(例如树皮),而且对不同组织(例如根、茎、叶)功能性状之间的关系没有达成共识。全植物经济型谱是植物多个器官,多个功能性状之间的权衡策略,这些性状通常被看作是植物适应环境的指示器,能够揭示植物在生态系统中的分布特征、预测群落组成。因此从全株植物的角度考虑植物不同组织性状之间的关系是十分有必要的。

### 5.3 深入探究树木干旱致死机理。

干旱导致的树木死亡现象越来越普遍。部分学者认为水力失败是导致干旱胁迫下木本植物死亡的主要原因;部分学者认为碳饥饿是导致木本植物死亡的主要原因;越来越多的研究表明水力失败、碳饥饿和生物攻击在植物干旱致死过程中相互影响,不能将这三个过程作为相互独立的机制对待。目前干旱导致植物死亡背后的精确生理机制尚不清楚,有待深入研究。

## 参考文献(References):

- [1] Christidis N, Jones G S, Stott P A. Dramatically increasing chance of extremely hot summers since the 2003 European heatwave. *Nature Climate Change*, 2015, 5(1): 46-50.
- [2] Easterling D R, Meehl G A, Parmesan C, Changnon S A, Karl T R, Mearns L O. Climate extremes: observations, modeling, and impacts. *Science*, 2000, 289(5487): 2068-2074.
- [3] Trenberth K E, Dai A G, van der Schrier G, Jones P D, Barichivich J, Briffa K R, Sheffield J. Global warming and changes in drought. *Nature Climate Change*, 2014, 4(1): 17-22.
- [4] Duan H L, Duursma R, Huang G M, Smith R A, Choat B, O'Grady A, Tissue D. Elevated [CO<sub>2</sub>] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant Cell & Environment*, 2014, 37(7): 1598-1613.
- [5] Allen C, Breshears D, McDowell N. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the

- Anthropocene. *Ecosphere*, 2015, 6: 1-55.
- [ 6 ] Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas, J. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the national academy of sciences of the united states of america*, 2011, 108(4): 1474-1478.
- [ 7 ] Narisma G T, Pitman A J, Eastman J, Watterson I G, Pielke R Sr, Beltrán-Przekurat A. The role of biospheric feedbacks in the simulation of the impact of historical land cover change on the Australian January climate. *Geophysical Research Letters*, 2003, 30(22): 1345-1360.
- [ 8 ] McDowell N, Pockman W T, Allen C D, Breshears D D, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams D G, Yezpe E A. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *The New Phytologist*, 2008, 178(4): 719-739.
- [ 9 ] Choat B, Brodribb T J, Brodersen C R, Duursma R A, López R, Medlyn B E. Triggers of tree mortality under drought. *Nature*, 2018, 558(7711): 531-539.
- [ 10 ] Roscher C, Gubsch M, Lipowsky A, Schumacher J, Weigelt A, Buchmann N, Schulze E D, Schmid B. Trait means, trait plasticity and trait differences to other species jointly explain species performances in grasslands of varying diversity. *Oikos*, 2018, 127(6): 865.
- [ 11 ] F. D. Transpiration and the Ascent of Sap in Plants. *Nature*, 1915, 94:558-559.
- [ 12 ] Chen L T, Zhang Y, Nunes M H, Stoddart J, Khoury S, Chan A H Y, Coomes D A. Predicting leaf traits of temperate broadleaf deciduous trees from hyperspectral reflectance: can a general model be applied across a growing season? *Remote Sensing of Environment*, 2022, 269: 112767.
- [ 13 ] Kattge J, Ogle K, Bönisch G, Díaz S, Lavorel S, Madin J, Nadrowski K, Nöllert S, Sartor K, Wirth C. A generic structure for plant trait databases. *Methods in Ecology and Evolution*, 2011, 2(2): 202-213.
- [ 14 ] Greenwood S, Ruiz - Benito P, Martínez - Vilalta J, Lloret F, Kitzberger T, Allen C, Fensham R, Laughlin D, Kattge J, Bönisch G, Kraft N J B, Jump A. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 2017, 20(4): 539-553.
- [ 15 ] Harrison S, LaForgia M. Seedling traits predict drought-induced mortality linked to diversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, 2019, 116(12): 5576-5581.
- [ 16 ] Anderegg W R L, Trugman A T, Bowling D R, Salvucci G, Tuttle S E. Plant functional traits and climate influence drought intensification and land-atmosphere feedbacks. *Proceedings of the National Academy of Sciences of the United States of America*, 2019, 116(28): 14071-14076.
- [ 17 ] Wiczyński D J, Boyle B, Buzzard V, Duran S M, Henderson A N, Hulshof C M, Kerkhoff A J, McCarthy M C, Michaletz S T, Swenson N G, Asner G P, Bentley L P, Enquist B J, Savage V M. Climate shapes and shifts functional biodiversity in forests worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, 2019, 116(2): 587-592.
- [ 18 ] Brodersen C R, Roddy A B, Wason J W, McElrone A J. Functional status of xylem through time. *Annual Review of Plant Biology*, 2019, 70: 407-433.
- [ 19 ] Katul G, Leuning R, Oren R. Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model. *Plant, Cell & Environment*, 2003, 26(3): 339-350.
- [ 20 ] Cowan I R, Farquhar G D. Stomatal function in relation to leaf metabolism and environment. *Symposia of the Society for Experimental Biology*, 1977, 31(4): 471-505.
- [ 21 ] Dixon H H, Joly J. Ascent of Sap. *Nature*, 1900, 62: 572.
- [ 22 ] Scholander P F, Plumb R C, Bridgman W B, Hammel H T, Plumb R C, Bridgman W B, Richter H H, Plumb R C, Bridgman W B, Levitt J, Storvick T S, Plumb R C, Bridgman W B. On the ascent of sap. *Science*, 1973, 179(4079): 1248-1250.
- [ 23 ] Tyree M T, Sperry J S. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? : answers from a model. *Plant Physiology*, 1988, 88(3): 574-580.
- [ 24 ] Mott K A, Parkhurst D F. Stomatal responses to humidity in air and helox. *Plant, Cell and Environment*, 1991, 14(5): 509-515.
- [ 25 ] Sperry J S, Hacke U G. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology*, 2002, 16(3): 367-378.
- [ 26 ] Martin-StPaul N, Delzon S, Cochard H. Plant resistance to drought depends on timely stomatal closure. *Ecology Letters*, 2017, 20(11): 1437-1447.
- [ 27 ] Hochberg U, Windt C W, Ponomarenko A, Zhang Y J, Gersony J, Rockwell F E, Holbrook N M. Stomatal closure, basal leaf embolism, and shedding protect the hydraulic integrity of grape stems. *Plant Physiology*, 2017, 174(2): 764-775.
- [ 28 ] Li X M, Blackman C J, Choat B, Duursma R A, Rymer P D, Medlyn B E, Tissue D T. Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. *Plant, Cell & Environment*, 2018, 41(3): 646-660.
- [ 29 ] Kerstiens G. Cuticular water permeability and its physiological significance. *Journal of Experimental Botany*, 1996, 47(12): 1813-1832.
- [ 30 ] Borchert R, Pockman W T. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiology*, 2005, 25(4): 457-466.
- [ 31 ] Zhang Y J, Rockwell F E, Graham A C, Alexander T, Holbrook N M. Reversible leaf xylem collapse: a potential circuit breaker against cavitation.

- Plant Physiology, 2016, 172(4): 2261-2274.
- [32] McElrone A J, Bichler J, Pockman W T, Addington R N, Linder C R, Jackson R B. Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant, Cell & Environment*, 2007, 30(11): 1411-1421.
- [33] Cuneo I F, Knipfer T, Brodersen C R, McElrone A J. Mechanical failure of fine root cortical cells initiates plant hydraulic decline during drought. *Plant Physiology*, 2016, 172(3): 1669-1678.
- [34] Tyree M T, Zimmermann M H. The cohesion-tension theory of sap ascent. *Xylem Structure and the Ascent of Sap*. Berlin, Heidelberg: Springer Berlin Heidelberg, 2002: 49-88.
- [35] Choat B, Brodersen C R, McElrone A J. Synchrotron X-ray microtomography of xylem embolism in *Sequoia sempervirens* saplings during cycles of drought and recovery. *The New Phytologist*, 2015, 205(3): 1095-1105.
- [36] Brodribb T J, Skelton R P, McAdam S A M, Bienaimé D, Lucani C J, Marmottant P. Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. *The New Phytologist*, 2016, 209(4): 1403-1409.
- [37] Tyree M T, Cochard H, Cruiziat P, Sinclair B, Ameglio T. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell & Environment*, 1993, 16(7): 879-882.
- [38] Rood S B, Patiño S, Coombs K, Tyree M T. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees*, 2000, 14(5): 248-257.
- [39] Li J L, Chen X P, Niklas K, Sun J, Wang Z Y, Zhong Q L, Hu D D, Cheng D L. A whole - plant economics spectrum including bark functional traits for 59 subtropical woody plant species. *Journal of Ecology*, 2021, 110: 248-261.
- [40] Bartlett M K, Zhang Y, Kreidler N, Sun S W, Ardy R, Cao K F, Sack L. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters*, 2014, 17(12): 1580-1590.
- [41] Bartlett M K, Scoffoni C, Sack L. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters*, 2012, 15(5): 393-405.
- [42] 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 & Environment*, 2003, 26(8): 1343-1356.
- [43] Lenz T I, Wright I J, Westoby M. Interrelations among pressure-volume curve traits across species and water availability gradients. *Physiologia Plantarum*, 2006, 127(3): 423-433.
- [44] Lawlor D W, Cornic G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant, Cell & Environment*, 2002, 25(2): 275-294.
- [45] Lamy J B, Delzon S, Bouche P S, Alia R, Vendramin G G, Cochard H, Plomion C. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *The New Phytologist*, 2014, 201(3): 874-886.
- [46] Lobo A, Torres-Ruiz J M, Burlett R, Lemaire C, Parise C, Francioni C, Truffaut L, Tomášková I, Hansen J K, Kjær E D, Kremer A, Delzon S. Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. *Forest Ecology and Management*, 2018, 424: 53-61.
- [47] Maherali H, Pockman W T, Jackson R B. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, 2004, 85(8): 2184-2199.
- [48] Choat B, Jansen S, Brodribb T J, Cochard H, Delzon S, Bhaskar R, Bucci S J, Feild T S, Gleason S M, Hacke U G, Jacobsen A L, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell P J, Nardini A, Pittermann J, Pratt R B, Sperry J S, Westoby M, Wright I J, Zanne A E. Global convergence in the vulnerability of forests to drought. *Nature*, 2012, 491(7426): 752-755.
- [49] Blackman C J, Brodribb T J, Jordan G J. Leaf hydraulic vulnerability influences species' bioclimatic limits in a diverse group of woody angiosperms. *Oecologia*, 2012, 168(1): 1-10.
- [50] Wason J W, Anstreicher K S, Stephansky N, Huggert B A, Brodersen C R. Hydraulic safety margins and air-seeding thresholds in roots, trunks, branches and petioles of four northern hardwood trees. *The New Phytologist*, 2018, 219(1): 77-88.
- [51] Powers J S, Vargas G G, Brodribb T J, Schwartz N B, Pérez-Aviles D, Smith-Martin C M, Becknell J M, Aureli F, Blanco R, Calderón-Morales E, Calvo-Alvarado J C, Calvo-Obando A J, Chavarría M M, Carvajal-Vanegas D, Jiménez-Rodríguez C D, Murillo Chacon E, Schaffner C M, Werden L K, Xu X T, Medvigy D. A catastrophic tropical drought kills hydraulically vulnerable tree species. *Global Change Biology*, 2020, 26(5): 3122-3133.
- [52] Skelton R P, West A G, Dawson T E. Predicting plant vulnerability to drought in biodiverse regions using functional traits. *Proceedings of the National Academy of Sciences of the United States of America*, 2015, 112(18): 5744-5749.
- [53] Chen Z C, Li S, Luan J W, Zhang Y T, Zhu S D, Wan X C, Liu S R. Prediction of temperate broadleaf tree species mortality in arid limestone habitats with stomatal safety margins. *Tree Physiology*, 2019, 39(8): 1428-1437.
- [54] Chen Z C, Li S, Wan X C, Liu S R. Strategies of tree species to adapt to drought from leaf stomatal regulation and stem embolism resistance to root properties. *Frontiers in Plant Science*, 2022, 13: 926535.
- [55] Tomasella M, Casolo V, Aichner N, Petruzzellis F, Savi T, Trifilò P, Nardini A. Non-structural carbohydrate and hydraulic dynamics during drought and recovery in *Fraxinus ornus* and *Ostrya carpinifolia* saplings. *Plant Physiology and Biochemistry*, 2019, 145: 1-9.

- [56] Zhang H X, Li X R, Guan D X, Wang A Z, Yuan F H, Wu J B. Nitrogen nutrition addition mitigated drought stress by improving carbon exchange and reserves among two temperate trees. *Agricultural and Forest Meteorology*, 2021, 311: 108693.
- [57] Signori-Mueller C, Oliveira R S, Barros F D V, Tavares J V, Cilpin M, Diniz F C, Zevallos M J M, Yupayccana C A S, Acosta M, Bacca J, Chino R S C, Cuellar G M A, Cumapa E R M, Martinez F, Mullisaca F M P, Nina A, Sanchez Jm B, Silva L F D, Tello L, Tintaya J S, Ugarteche M T M, Baker T R, Bittencourt P R L, Borma L S. Non-structural carbohydrates mediate seasonal water stress across Amazon forests. *Nature Communications*, 2021, 12(1): e206.
- [58] Landhäusser S M, Chow P S, Dickman L T, Furze M E, Kuhlman I, Schmid S, Wiesenbauer J, Wild B, Gleixner G, Hartmann H, Hoch G, McDowell N G, Richardson A D, Richter A, Adams H D. Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiology*, 2018, 38(12): 1764-1778.
- [59] Blumstein M, Gersony J, Martínez-Vilalta J, Sala A N. Global variation in nonstructural carbohydrate stores in response to climate. *Global Change Biology*, 2023, 29(7): 1854-1869.
- [60] Furze M E, Huggett B A, Aubrecht D M, Stolz C D, Carbone M S, Richardson A D. Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *The New Phytologist*, 2019, 221(3): 1466-1477.
- [61] Martín-Gómez P, Aguilera M, Pemán J, Gil-Pelegrín E, Ferrio J P. Contrasting ecophysiological strategies related to drought: the case of a mixed stand of Scots pine (*Pinus sylvestris*) and a submediterranean oak (*Quercus subpyrenaica*). *Tree Physiology*, 2017, 37(11): 1478-1492.
- [62] Wiley E, Helliker B. A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytologist*, 2012, 195(2): 285-289.
- [63] Takahashi K, Furuhashi K. Shoot growth and seasonal changes of nonstructural carbohydrate concentrations at the upper and lower distribution limits of three conifers. *Landscape and Ecological Engineering*, 2016, 12(2): 239-245.
- [64] Blum A. Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant, Cell & Environment*, 2017, 40(1): 4-10.
- [65] Guo J S, Gear L, Hultine K, Koch G, Ogle K. Non-structural carbohydrate dynamics associated with antecedent stem water potential and air temperature in a dominant desert shrub. *Plant Cell & Environment*, 2020, 43(6): 1467-1483.
- [66] Dickman L T, McDowell N G, Grossiord C, Collins A D, Wolfe B T, Detto M, Wright S J, Medina-Vega J A, Goodsman D, Rogers A, Serbin S P, Wu J, Ely K S, Michaletz S T, Xu C G, Kueppers L, Chambers J Q. Homeostatic maintenance of nonstructural carbohydrates during the 2015-2016 El Niño drought across a tropical forest precipitation gradient. *Plant, Cell & Environment*, 2019, 42(5): 1705-1714.
- [67] O'Brien M J, Leuzinger S, Philipson C D, Tay J, Hector A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change*, 2014, 4(8): 710-714.
- [68] O'Brien M J, Reynolds G, Ong R, Hector A. Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. *Nature Ecology & Evolution*, 2017, 1(11): 1643-1648.
- [69] Mudrák O, de Bello F, Doležal J, Lepš J. Changes in the functional trait composition and diversity of meadow communities induced by *Rhinanthus minor* L. *Folia Geobotanica*, 2016, 51(1): 1-11.
- [70] Feng Z Z, Büker P, Pleijel H, Emberson L, Karlsson P E, Uddling J. A unifying explanation for variation in ozone sensitivity among woody plants. *Global Change Biology*, 2018, 24(1): 78-84.
- [71] Rosana L, Javier C F, MartinStPaul Nicolas K, Hervé C, Brendan C. Coordination of stem and leaf traits define different strategies to regulate water loss and tolerance ranges to aridity. *New Phytologist*, 2021, 230(2): 497-509.
- [72] Xu H Y, Wang H, Prentice I C, Harrison S, Wright I. Coordination of plant hydraulic and photosynthetic traits: confronting optimality theory with field measurements. *New Phytologist*, 2021, 232(3): 1286-1296.
- [73] Serra-Maluquer X, Gazol A, Anderegg W R L, Martínez-Vilalta J, Mencuccini M, Camarero J J. Wood density and hydraulic traits influence species' growth response to drought across biomes. *Global Change Biology*, 2022, 28(12): 3871-3882.
- [74] Lozano Y M, Carlos A A T, Flaig Isabel C, Matthias C R. Root trait responses to drought are more heterogeneous than leaf trait responses. *Functional Ecology*, 2020, 34(11): 2224-2235.
- [75] Comas L H, Becker S R, Cruz V M V, Byrne P F, Dierig D A. Root traits contributing to plant productivity under drought. *Frontiers in Plant Science*, 2013, 4: 442.
- [76] Zufferey V, Cochard H, Ameglio T, Spring J L, Viret O. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *Journal of Experimental Botany*, 2011, 62(11): 3885-3894.
- [77] Brundrett M C. Coevolution of roots and mycorrhizas of land plants. *The New Phytologist*, 2002, 154(2): 275-304.
- [78] Comas L H, Mueller K E, Taylor L L, Midford P E, Callahan H S, Beerling D J. Evolutionary patterns and biogeochemical significance of angiosperm root traits. *International Journal of Plant Sciences*, 2012, 173(6): 584-595.
- [79] Yang Q P, Zhang W D, Li R S, Xu M, Wang S L. Different responses of non-structural carbohydrates in above-ground tissues/organs and root to extreme drought and re-watering in Chinese fir (*Cunninghamia lanceolata*) saplings. *Trees*, 2016, 30(5): 1863-1871.
- [80] Brodrribb T J, McAdam S A, Carins Murphy M R. Xylem and stomata, coordinated through time and space. *Plant, Cell & Environment*, 2017, 40

- (6) : 872-880.
- [81] Deans R M, Brodribb T J, McAdam S A M. An integrated hydraulic-hormonal model of conifer stomata predicts water stress dynamics. *Plant Physiology*, 2017, 174(2) : 478-486.
- [82] Drake P L, Froend R H, Franks P J. Smaller, faster stomata: scaling of stomatal size, rate of response, and stomatal conductance. *Journal Experimental Botany*, 2013, 64(2) : 495-505.
- [83] Irvine J, Perks M P, Magnani F, Grace J. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiology*, 1998, 18(6) : 393-402.
- [84] Lawson T, Blatt, M R. Stomatal Size, speed, and responsiveness Impact on photosynthesis and water use efficiency. *Plant Physiology*, 2014, 164(4) : 1556-1570.
- [85] Saliendra N Z, Sperry J S, Comstock J P. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. *Planta*, 1995, 196(2) : 357-366.
- [86] Tardieu F, Davies W J. Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. *Plant, Cell & Environment*, 1993, 16(4) : 341-349.
- [87] Vilagrosa A, Bellot J, Vallejo V R, Gil-Pelegrín E. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *Journal of Experimental Botany*, 2003, 54(390) : 2015-2024.
- [88] Baltzer J L, Davies S J, Bunyavejchewin S, Noor N S M. The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. *Functional Ecology*, 2008, 22(2) : 221-231.
- [89] Bartlett M K, Zhang Y, Kreidler N, Sun S W, Ardy R, Cao K F, Sack L. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters*, 2014, 17(12) : 1580-1590.
- [90] Chaves M M, Flexas J, Pinheiro C. Photosynthesis under drought and salt stress; regulation mechanisms from whole plant to cell. *Annals of Botany*, 2009, 103(4) : 551-560.
- [91] Dichio B, Xiloyannis C, Sofo A, Montanaro G. Osmotic regulation in leaves and roots of olive trees during a water deficit and rewatering. *Tree Physiology*, 2006, 26(2) : 179-185.
- [92] Logullo M A, Salleo S. Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *The New phytologist*, 1988, 108(3) : 267-276.
- [93] Hinckley T M, Duhme F, Hinckley A R, Richter H. Water relations of drought hardy shrubs - osmotic potential and stomatal reactivity. *Plant, Cell & Environment*, 1980, 3(2) : 131-140.
- [94] Martínez-Vilalta J, Prat E, Oliveras I, Piñol J. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia*, 2002, 133(1) : 19-29.
- [95] Morgan J M. Osmoregulation and water-stress in higher-plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 1984, 35:299-319.
- [96] Patakas A, Nikolauou N, Zioziou E, Radoglou K, Noitsakis B. The role of organic solute and ion accumulation in osmotic adjustment in drought-stressed grapevines. *Plant Science*, 2002, 163(2) : 361-367.
- [97] Pita P, Pardos J A. Growth, leaf morphology, water use and tissue water relations of *Eucalyptus globulus* clones in response to water deficit. *Tree Physiology*, 2001, 21(9) : 599-607.
- [98] Tyree M T, Hammel H T. Measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany*, 1972, 23(74) : 267-282.
- [99] Barnard D M, Bauerle W L. The implications of minimum stomatal conductance on modeling water flux in forest canopies. *Journal of Geophysical Research: Biogeosciences*, 2013, 118(3) : 1322-1333.
- [100] Delzon S, Douthe C, Sala A N, Cochard H. Mechanism of water-stress induced cavitation in conifers; bordered pit structure and function support the hypothesis of seal capillary-seeding. *Plant, Cell & Environment*, 2010, 33(12) : 2101-2111.
- [101] Jordan G J, Brodribb T J. Incontinence in aging leaves: deteriorating water relations with leaf age in *Agastachys odorata* (Proteaceae), a shrub with very long-lived leaves. *Functional Plant Biology*, 2007, 34(10) : 918-924.
- [102] Barbour M M, Farquhar G D, Buckley T N. Leaf water stable isotopes and water transport outside the xylem. *Plant, Cell & Environment*, 2017, 40(6) : 914-920.
- [103] Scoffoni C, Albuquerque C, Brodersen C, Townes S V, John G P, Cochard H, Buckley T, McElrone A, Sack L. Leaf vein xylem conduit diameter influences susceptibility to embolism and hydraulic decline. *New Phytologist*, 2017, 213(3) : 1076-1092.
- [104] Trifiló P, Raimondo F, Savi T, LoGullo M A, Nardini A. The contribution of vascular and extra-vascular water pathways to drought-induced decline of leaf hydraulic conductance. *Journal of Experimental Botany*, 2016, 67(17) : 5029-5039.
- [105] Williams L J, Bunyavejchewin S, Baker P J. Deciduousness in a seasonal tropical forest in western Thailand: interannual and intraspecific variation in timing, duration and environmental cues. *Oecologia*, 2008, 155(3) : 571-582.
- [106] Williams R J, Myers B A, Muller W J, Duff G A, Eamus D. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology*, 1997, 78(8) : 2542-2558.

- [107] Brodribb Tim J, Jordan Greg J, Carpenter Raymond J. Unified changes in cell size permit coordinated leaf evolution. *The New Phytologist*, 2013, 199(2): 559-70.
- [108] North G B, Nobel P S. Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of agave-deserti (Agavaceae). *American Journal of Botany*, 1991, 78(7): 906-915.
- [109] Zhu J M, Brown K M, Lynch J P. Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays*L.). *Plant, Cell & Environment*, 2010, 33(5): 740-749.
- [110] Jackson R B, Mooney H A, Schulze E D. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences of the United States of America*, 1997, 94(14): 7362-7366.
- [111] Lopez B, Sabate S, Gracia C. Fine roots dynamics in a Mediterranean forest: effects of drought and stem density. *Tree Physiology*, 1998, 18(8-9): 601-606.
- [112] Bleby T M, Mcelrone A J, Jackson R B. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell & Environment*, 2010, 33(12): 2132-2148.
- [113] Bréda N, Huc R, Granier A, Dreyer E. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 2006, 63(6): 625-644.
- [114] Canadell J, Jackson R B, Ehleringer J R, Mooney H A, Sala O E, Schulze E D. Maximum rooting depth of vegetation types at the global scale. *Oecologia*, 1996, 108(4): 583-595.
- [115] Mcelrone A J, Pockman W T, Martínez-Vilalta J, Jackson R B. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *The New Phytologist*, 2004, 163(3): 507-517.
- [116] Padilla F M, Pugnaire F I. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, 2007, 21(3): 489-495.
- [117] Pinheiro H A, Damatta F M, Chaves A R M, Loureiro M E, Ducatti C. Drought tolerance is associated with rooting depth and stomatal control of water use in clones of *Coffea canephora*. *Annals of Botany*, 2005, 96(1): 101-108.
- [118] Schulze E D, Mooney H A, Sala O E, Jobbagy N, Buchmann N, Bauer G, Canadell J, Jackson R B, Loreti J, Oesterheld M, Ehleringer J R. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia*, 1996, 108(3): 503-511.
- [119] 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. *The New Phytologist*, 2010, 188(4): 1113-1123.
- [120] Brodribb T J, Bowman D M J S, Nichols S, Delzon S, Burrett R. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *The New Phytologist*, 2010, 188(2): 533-542.
- [121] Choat B, Ball M, Lully J, Holtum J. Pit membrane porosity and water stress-induced cavitation in four co-existing dry rainforest tree species. *Plant Physiology*, 2003, 131(1): 41-48.
- [122] Choat B, Jansen S, Zwieniecki M A, Smets E, Holbrook N M. Changes in pit membrane porosity due to deflection and stretching: the role of vestured pits. *Journal of Experimental Botany*, 2004, 55(402): 1569-1575.
- [123] Dalla-Salda G, Martínez-Meier A, Cochard H, Rozenberg P. Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (*Pseudotsuga menziesii* (Mirb.)). *Annals of Forest Science*, 2011, 68(4): 747-757.
- [124] Fonti P, Vonarx G, García-González I, Eilmann B, Sass-Klassen U, Gärtner H, Eckstein D. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *The New Phytologist*, 2010, 185(1): 42-53.
- [125] Baas P. Functional and Ecological Xylem Anatomy. *Iawa Journal*, 2015, 36(3): 359-360.
- [126] Hacke U G, Sperry J S, Pittermann J. Analysis of circular bordered pit function - II. Gymnosperm tracheids with torus-margo pit membranes. *American Journal of Botany*, 2004, 91(3): 386-400.
- [127] Hacke U G, Sperry J S, Pockman W T, Davis S D, Mcculloh K A. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 2001, 126(4): 457-461.
- [128] Hoffmann W A, Marchin R M, Abit P, Lau O L. Hydraulic failure and tree dieback are associated with high wood density in a temperate forest under extreme drought. *Global Change Biology*, 2011, 17(8): 2731-2742.
- [129] Jansen S, Baas P, Gasson P, Lens F, Smets E. Variation in xylem structure from tropics to tundra: Evidence from vestured pits. *Proceedings of the National Academy of Sciences of the United States of America*, 2004, 101(23): 8833-8837.
- [130] Jansen S, Baas P, Gasson P, Smets E. Vestured pits: Do they promote safer water transport? *International Journal of Plant Science*, 2003, 164(3): 405-413.
- [131] Pittermann J, Sperry J S, Hacke U G, Wheeler J K, Sikkema E H. Torus-margo pits help conifers compete with angiosperms. *Science*, 2005, 310(5756): 1924.
- [132] Sperry J S, Hacke U G, Pittermann J. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, 2006, 93(10): 1490-1500.
- [133] Wheeler J K, Sperry J S, Hacke U G, Hoang N. Inter-vessel pitting and cavitation in woody Rosaceae and other vesselled plants: a basis for a

- safety versus efficiency trade-off in xylem transport. *Plant, Cell & Environment*, 2005, 28(6) : 800-812.
- [134] Willson C J, Jackson R B. Xylem cavitation caused by drought and freezing stress in four co-occurring *Juniperus* species. *Physiologia Plantarum*, 2006, 127(3) : 374-382.
- [135] Choat B. Predicting thresholds of drought-induced mortality in woody plant species. *Tree Physiology*, 2013, 33(7) : 669-671.
- [136] Pockman W T, Sperry J S. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany*, 2000, 87(9) : 1287-1299.
- [137] Tyree M T, Sperry J S. Vulnerability of Xylem to Cavitation and Embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, 1989, 40: 19-36.
- [138] Urli M, Porté A J, Cochard H, Guengant Y, Burelett R, Delzon S. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*, 2013, 33(7) : 672-683.
- [139] Goldstein G, Andrade J L, Meinzer F C, Holbrook N M, Cavelier J, Jackson P, Celis A. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ*, 1998, 21(4) : 397-406.
- [140] Meinzer F C, Johnson D M, Lachenbruch B, McCulloh K A, Woodruff D R. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology*, 2009, 23(5) : 922-930.
- [141] Meinzer F C, McCulloh K A. Xylem recovery from drought-induced embolism: where is the hydraulic point of no return? *Tree Physiology*, 2013, 33(4) : 331-334.
- [142] Maurel C, Verdoucq L, Luu D T, Santoni V. Plant aquaporins: Membrane channels with multiple integrated functions. *Annual Review of Plant Biology*, 2008, 59: 595-624.
- [143] Vandeleur R K, Mayo G, Shelden M C, Gilliham M, Kaiser B N, Tyerman S D. The Role of Plasma Membrane Intrinsic Protein Aquaporins in Water Transport through Roots: Diurnal and Drought Stress Responses Reveal Different Strategies between Isohydric and Anisohydric Cultivars of Grapevine. *Plant Physiology*, 2009, 149(1) : 445-60.
- [144] Loeffe L, Martinez-Vilalta J, Piñol J, Mencuccini M. The relevance of xylem network structure for plant hydraulic efficiency and safety. *Journal of Theoretical Biology*, 2007, 247(4) : 788-803.
- [145] Martinez-Vilalta J, Mencuccini M, Alvarez X, Camacho J, Loeffe L, Pinol J. Spatial distribution and packing of xylem conduits. *American Journal of Botany*, 2012, 99(7) : 1189-1196.
- [146] Li S, Lens F, Espino S, Karimi Z, Klepsch M, Schenk H J, Schmitt M, Schuldt B, Jansen S. Intervessel pit membrane thickness as a key determinant of embolism resistance in angiosperm xylem. *Iawa Journal*, 2016, 37(2) : 152-171.
- [147] Pittermann J, Choat B, Jansen S, Stuart S A, Lynn L, Dawson T E. The relationships between xylem safety and hydraulic efficiency in the Cupressaceae: the evolution of pit membrane form and function. *Plant Physiology*, 2010, 153(4) : 1919-1931.
- [148] Chave J, Coomes D, Jansen S, Lewis S L, Swenson N G, Zanne A E. Towards a worldwide wood economics spectrum. *Ecology Letters*, 2009, 12(4) : 351-366.
- [149] Ellmore G S, Zanne A E, Orians C M. Comparative sectoriality in temperate hardwoods: hydraulics and xylem anatomy. *Botanical Journal of the Linnean Society*, 2006, 150(1) : 61-71.
- [150] Orians C M, Babst B, Zanne A E. Vascular Constraints and Long Distance Transport in Dicots. 2005.
- [151] Orians C M, Smith S D P, Sack L. How are leaves plumbed inside a branch? Differences in leaf-to-leaf hydraulic sectoriality among six temperate tree species. *Journal of Experimental Botany*, 2005, 56(418) : 2267-2273.
- [152] Schenk H J. Clonal splitting in desert shrubs. *Plant Ecology*, 1999, 141(1-2) : 41-52.
- [153] Schenk H J, Espino S, Goedhart C M, Nordenstahl M, Cabrera H I M, Jones C S. Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proceedings of the National Academy of Sciences of the United States of America*, 2008, 105(32) : 11248-11253.
- [154] Zanne A E, Sweeney K, Sharma M, Orians C M. Patterns and consequences of differential vascular sectoriality in 18 temperate tree and shrub species. *Functional Ecology*, 2006, 20(2) : 200-206.
- [155] Werden L K, Averill C, Crowther T W, Calderón-Morales E, Toro L, Alvarado J P, Gutiérrez L M, Mallory D E, Powers J S. Below-ground traits mediate tree survival in a tropical dry forest restoration. *Philosophical Transactions of The Royal Society B Biological Sciences*, 2023, 378(1867).
- [156] Yi K, Dragoni D, Phillips R P, Roman D T, Novick K A. Dynamics of stem water uptake among isohydric and anisohydric species experiencing a severe drought. *Tree Physiology*, 2017, 37(10) : 1393.
- [157] Gleason S, Westoby M, Jansen S, Choat B, Hacke U, Pratt R, Bhaskar R, Brodribb T, Bucci S, Cao K, Cochard H, Delzon S, Domec J, Fan Z, Feild T, Jacobsen A, Johnson D M, Lens F, Maherali H, Martínez - Vilalta J, Mayr S, McCulloh K, Mencuccini M, Mitchell P, Morris H, Nardini A, Pittermann J, Plavcová L, Schreiber S G, Sperry J, Wright I, Zanne A. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, 2016, 209(1) : 123-136.
- [158] Yao G Q, Nie Z F, Turner N, Li F M, Gao T P, Fang X W, Scoffoni C. Combined high leaf hydraulic safety and efficiency provides drought tolerance in *Caragana* species adapted to low mean annual precipitation. *The New Phytologist*, 2020, 229: 230-244.

- [159] Wright I J, Reich P B, Westoby M, Ackerly D D, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen J H C, Diemer M, Flexas J, Garnier E, Groom P K, Gulias J, Hikosaka K, Lamont B B, Lee T L, Lee W, Lusk C, Midgley J J, Navas M L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov V I, Roumet C, Thomas S C, Tjoelker M G, Veneklaas E J, Villar R. The worldwide leaf economics spectrum. *Nature*, 2004, 428(6985): 821-827.
- [160] Reich P B. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, 2014, 102(2): 275-301.
- [161] Anderegg W R L, Berry J A, Smith D D, Sperry J S, Anderegg L D L, Field C B. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences of the United States of America*, 2012, 109(1): 233-237.
- [162] Mantova M, Herbette S, Cochard H, Torres-Ruiz J M. Hydraulic failure and tree mortality: from correlation to causation. *Trends in Plant Science*, 2022, 27(4): 335-345.
- [163] Anderegg W R L, Klein T, Bartlett M, Sack L, Pellegrini A F A, Choat B, Jansen S. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences of the United States of America*, 2016, 113(18): 5024-5029.
- [164] McDowell N G. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*, 2011, 155(3): 1051-1059.
- [165] Klein T, Hoch G, Yakir D, Körner C. Drought stress, growth and nonstructural carbohydrate dynamics of pine trees in a semi-arid forest. *Tree Physiology*, 2014, 34(9): 981-992.
- [166] Sevanto S, McDowell N G, Dickman L T, Pangle R, Pockman W T. How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment*, 2014, 37(1): 153-161.
- [167] Hummel I, Pantin F, Sulpice R, Piques M, Rolland G, Dauzat M, Christophe A, Pervent M, Bouteillé M, Stitt M, Gibon Y, Muller B. Arabidopsis plants acclimate to water deficit at low cost through changes of carbon usage: an integrated perspective using growth, metabolite, enzyme, and gene expression analysis. *Plant Physiology*, 2010, 154(1): 357-372.
- [168] Stitt M, Lunn J, Usadel B. Arabidopsis and primary photosynthetic metabolism-more than the icing on the cake. *The Plant Journal*, 2010, 61(6): 1067-1091.
- [169] Gibon Y, Pyl E T, Sulpice R, Lunn J E, Höhne M, Günther M, Stitt M. Adjustment of growth, starch turnover, protein content and central metabolism to a decrease of the carbon supply when Arabidopsis grown in very short photoperiods. *Plant, Cell & Environment*, 2009, 32(7): 859-874.
- [170] Khaitran J K, Ylioja T, Billings R F, Régnière J, Ayres M, Ayres M. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications*, 2007, 17(3): 882-899.
- [171] Ayres M P, Lombardero M J. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*, 2000, 262(3): 263-286.
- [172] Lloret F, Siscart D, Dalmases C. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, 2004, 10(12): 2092-2099.
- [173] Andrea N, Marta B, Tadeja S. Shoot desiccation and hydraulic failure in temperate woody angiosperms during an extreme summer drought. *The New Phytologist*, 2013, 200(2): 322-329.
- [174] Anderegg W, Berry J, Smith D D, Sperry J, Anderegg L, Field C. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *National Acad Sciences*, 2012, 109(1): 233-237.
- [175] Wullschlegel S D, McLaughlin S B, Ayres M P. High-resolution analysis of stem increment and sap flow for loblolly pine trees attacked by southern pine beetle. *Canadian Journal of Forest Research*, 2004, 34(11): 2387-2393.
- [176] Wallin K F, Kolb T E, Skov K R, Wagner M R. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology*, 2003, 32(3): 652-661.