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植物叶片机械强度与抗旱性耦合机制研究进展

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摘要:植物叶片机械强度(刚度和韧性)与其抗旱性之间存在一定的协同关系,是植物适应环境的重要策略。开展植物叶片机械强度与抗旱性耦合机制研究有助于理解和预测陆地植被对气候变化的响应和适应策略。由于缺少针对该协同关系驱动因素的系统性研究,当前对植物适应干旱的生理生态机制缺乏深入理解。从叶片机械结构、抗旱性状及驱动二者变化的相关解剖学/生理性状进行分析,在综述叶片机械结构与抗旱性状的基础上,阐明抗旱性与机械性状协同关系的解剖学和生理基础,以期为今后研究植物机械性状和抗旱协同适应策略提供参考。细胞壁厚度、膨压损失点(Ψ_{tlp})和主脉长度($\mathrm{VLA}_{\mathrm{maj}}$)在调节叶片机械强度和抗旱性的权衡关系中发挥重要作用:①较厚的细胞壁不仅能够降低细胞膨压损失后的皱缩和塌陷风险,也会保护叶片免受由细胞收缩引起的导管外水分运输能力下降,从而使得植物叶片有较强的耐旱能力;②叶脉维管束水分的运输在干旱下存在着由栓塞引发的被破坏风险,而单位面积较大的主脉长度($\mathrm{VLA}_{\mathrm{maj}}$)可以提供额外的水分替代途径向叶肉供应水分;③较厚的细胞壁厚度和较高的$\mathrm{VLA}_{\mathrm{maj}}$有助于增加叶片的机械强度。综上所述,在干旱生境中,尽管水分亏缺会降低叶片光合速率,但具有高机械强度和抗旱性的叶片却能延长其寿命,以保证叶片在恶劣生境中维持基本的气体交换和正碳收益。揭示了高机械性和抗旱性的耦合是植物适应干旱的内在机制,并对植物抗旱性的研究进行展望,强调未来研究在考虑植物机械性状的基础上,需要结合植物功能性状和生理因素如渗透调节能力、水分缓冲能力等协同探究植物的抗旱性,以期为未来植物抗旱协同策略提供指导。

关键词:比叶重;叶密度;细胞壁;粗脉密度;失膨点;叶水力导度

Research progress in the coordination between leaf mechanical structure and drought tolerance

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Abstract: There is a synergistic relationship between the mechanical strength (stiffness and toughness) of plant leaves and their drought resistance, which is an important strategy for plants to adapt to environment. Research on the interplay between the mechanical strength and drought resistance of plant leaves aids in understanding and predicting the responses and adaptive strategies of terrestrial plants to climate change. However, due to the lack of systematic research on the driving factors of this synergistic relationship, there is a lack of in-depth understanding of the physiological and ecological mechanisms of plant adaptation to drought. In this paper, leaf mechanical structure, drought resistance and related

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anatomical or physiological traits driving the relationship were analyzed, leaf mechanical structure and drought resistance were summarized, to clarify the anatomical basis of the synergistic relationship between drought resistance and anatomical or physiological traits, so as to provide reference for the future study of plant mechanical traits and drought resistance strategies. Among them, cell wall thickness, expansion pressure loss point (Ψ_{tlp}) and main vein length (VLA$_{\mathrm{maj}}$) play important roles in regulating the balance between leaf mechanical strength and drought tolerance, 1) a thicker cell wall not only reduces the risk of shrinkage and collapse after loss of cell bulging, but also protects the leaf from the reduction of extraductal water transport capacity caused by cell shrinkage, therefore, the plant leaves have strong drought resistance; 2) the transport of water in vascular bundle of leaf vein has the risk of being destroyed by embolism under drought, and the larger length of main vein per unit area (VLA$_{\mathrm{maj}}$) can provide an additional way to supply water to mesophyll; 3) thicker cell wall and higher VLA$_{\mathrm{maj}}$ help to increase the mechanical strength of leaves. In summary, although water deficit in arid habitats reduce the leaf photosynthetic rate, leaves with high mechanical strength and drought tolerance extend their lifespan to ensure that leaves maintain essential gas exchange and positive carbon gain in harsh habitats. It shows that coupling high mechanical resistance with drought tolerance is advantageous for plants in water-limited habitats. The research on plant stress resistance under global climate change is promising, and this study also emphasizes the need for future research to synergistically explore drought tolerance in plants by taking into account the mechanical characteristics of the plant in conjunction with its functional characteristics and physiological factors, such as osmoregulatory capacity and water buffering capacity. This could provide guidance on synergistic strategies of drought tolerance in plants in the future.

Key Words: leaf mass per area; leaf density; cell wall; thick vein density; turgor loss point; leaf hydraulic conductance

叶片形态和结构作为植物自然选择进化的结果,与其生理过程紧密相关,是影响植物环境适应性的重要因素[1]。因此,从叶片形态和结构入手揭示植物的生理过程和生态适应策略是一种行之有效的研究手段。比叶重(leaf mass per area, LMA)作为表征叶片解剖结构特征的综合指数, 直接决定了植物叶片的机械强度(如刚度、韧性、穿透力及撕裂力等)[1—2],是反映植物功能的重要结构参数。研究表明,陆地植物的LMA存在极大的种间变异,一般情况下,生长缓慢的常绿树种具有较高的LMA和机械抗性,而生长快速的落叶树种则与之相反[3],即在机械强度方面也存在巨大差异。但在全球或区域尺度上的研究发现,LMA呈现出一致的生物地理格局,存在明显的纬度和海拔变化趋势[4]。通常,在环境胁迫条件下(如强光、高温、水分胁迫等), 植物会呈现出较高的LMA[5—8],而与此协同的高叶片机械强度在抵御草食动物或其他物理因素(如强风,强光)可能导致的机械损伤方面具有明显优势[9—11]。尽管这些具备高机械强度的叶片会导致植物呈现出较低的光合能力和缓慢的生长速率[5, 12],但却延长了叶片寿命,从碳捕获时间上补偿植物叶片构建过程中的碳消耗[13—15],保证了植物的长期碳收益。综上所述,高机械强度的叶片在环境胁迫条件下通常具备生存和生长优势,而探明LMA表征的机械强度与植物环境适应性之间的关系至关重要,有助于理解和预测陆地植被对气候变化的响应和适应策略。

与植物抗逆性(Stress-resistance) 相关的功能性状是反映植物适应胁迫生境策略的重要指标。叶片机械抗性与功能性状之间的关系一直是生态学家关注的热点,二者关系的探究对于明确植物在气候变化背景的生存策略至关重要。值得注意的是,在受胁迫生境中,植物叶片除了具备高机械强度外,还会表现出强抗逆性。然而,高机械强度(韧性、硬度、刚度)的叶片在应对非生物胁迫是否会表现出强抗逆性还不清楚,即机械强度与抗逆性之间的协同关系还未有定论。特别是在当前全球气候变化导致的干旱事件发生强度和频率都逐步加强的背景下[16],探究植物叶片机械强度与抗旱性相关功能性状的关系及其驱动因素,对于揭示植物适应干旱生境的生态适应策略具有重要意义。然而,目前针对此问题的结论并不统一,早期研究发现叶片机械强度与抗旱性之间没有相关性[17—19],但是近期的研究却支持了高机械强度叶片更能抵抗水分亏缺的假设,原因在于叶片的解剖/生理性状[20—21],这些结果表明高机械强度的叶片具有更强的抗旱性,如较厚的细胞壁厚度或

较高的主脉长度能够保护叶片免受由细胞收缩引起的水分运输能力下降,或者能够为叶肉提供额外的水分,从而提高植物的抗旱能力[3, 22—23]。这两种观点的差异一方面反映了不同物种的系统发育轨迹,但也从另外一个角度证明了影响叶片厚度/密度的不同解剖性状的改变会引起叶片 LMA 的变化,且这些性状与表征植物抗旱性的生理性状之间也可能存在一定的关联。

因此,想要回答叶片机械抗性和抗旱性是否关联以及它们之间的关系,需要弄清以下问题 1) 哪些性状能够赋予叶片应对水分亏缺的能力？2)这些性状的机械强度如何？3)它们是如何相互关联的？从目前已发表的文章来看,从机制上阐述二者内在关联的综合性报道仍较为缺乏。叶片的解剖学和生理性状作为同时影响植物抗旱性和叶片机械强度的关键因素,在决定二者间功能权衡方面发挥着重要作用。因此,本文从形态和生理角度,厘清二者之间的内在关系,为阐明植物生态适应策略开辟新思路。本文以表征植物机械强度的关键指标 LMA 为着眼点,梳理过往的研究,重点讨论叶片 LMA 的解剖学决定因素、叶片抗旱性的生理决定因素及其与 LMA 的关系,以期为今后更深入的研究提供借鉴和参考。

1　叶片机械强度的解剖学决定因素

Villar 等[24]将引起 LMA 变化的原因分解为叶片整体、组织和细胞三个水平。从叶片整体水平出发,引发 LMA 增加的原因可能是由于叶片厚度(LVA)变厚、密度(LD)的增大或者是二者同时增加[24—26]。其中,为了涵盖所有的叶形,Poorter 等[3]将叶片厚度定义为单位叶面积的体积,其大小取决于单位叶面积内细胞的数量而并非单个细胞或细胞组织解剖结构的变化[7]。叶片密度则表示的是单位体积的干物质的数值,其大小强烈依赖于细胞和组织的解剖结构[27]。20 世纪 90 年代以来,诸多学者针对不同植物的 LMA 做了大量的研究,并讨论了 LVA 和 LD 与 LMA 之间的关系,结果发现 LD 贡献了 80% LMA 的变异,而 LVA 贡献了剩余的 20%,这表明与驱动 LD 变化的相关解剖学特征会显著影响叶片机械强度的变化[3, 28—29]。研究表明,LD 与细胞壁的厚度(T_{cw})和组成密切相关,可以贡献高达 70%的 LMA 变异[3, 14]。综上所述,T_{cw}作为直接驱动 LD 变化的关键解剖性状,与 LMA 紧密相关并对其大小起决定性作用。

另外一个驱动 LD 变化的重要因素是叶脉密度(VLA)(单位叶表面积的叶脉长度),尤其是主脉密度(1—2 级脉,VLA_{maj})[25, 30—32]。Niinemets 等[33]通过研究大量草本植物发现叶片主脉部分的 LMA 比其余部分的 LMA 高,且他们之间的差异能够达到 6 倍,他们认为这种差异一方面是由于物种特异性,另外一方面则可能是因为主脉中含有的较多的厚壁组织、厚角组织或纤维细胞。无论原因如何,这些结果证明 VLA 与 LMA 紧密相关并决定 LMA 的大小。事实上,主脉也发挥着重要的结构作用,因为他们包含许多具有较厚次生壁的细胞,并且占据了很大的空间[3, 34—35],总体上增加了叶片单位体积干物质的量。综上可知,叶片的解剖学特征显著影响了其机械强度的变化:即单位叶面积内细胞的数量越多,细胞壁越厚,而较厚的细胞壁和较高的 VLA 有助于增加叶片的机械强度。

除此之外,叶片力学性状也可以表征叶片抵抗外界环境变化的能力。其中,叶片穿透力和撕裂力是人们通常测定的叶片力学性状,可以表征叶片的机械抗性[36]。理论上,叶片机械抗性较高的植物往往有较高的叶片穿透力和撕裂力。前人的研究表明,叶片穿透力与比叶面积呈显著负相关,说明植物在低比叶面积(高 LMA)下有较高机械抗性,这可能是比叶面积值越低,叶肉细胞壁和叶片角质层所占的叶片体积比例越大,植物对于构建叶片保卫结构或叶肉组织投入越多,从而能够更好地外界不良环境(如干旱等)[36—37]。此外,叶脉含有厚壁组织和纤维细胞,具有较高的机械阻力和弹性,对叶片的机械支撑和防御等具有重要作用。Hua 等[38]发现 VLA 与叶片撕裂力和叶片穿透力呈正相关关系,认为叶脉的机械特性是影响叶片机械阻力和结构的潜在因素。因此,综上可知,叶片解剖学与力学性状是密切相关的,较大的 VLA 和较厚的细胞壁往往伴随着较大的叶片穿透力和撕裂力,共同作用影响着植物抗旱性。因此,要厘清叶片机械强度与抗旱性之间的内在联系,关键在于确定影响叶片解剖学驱动因素是否与表征植物抗旱性的生理指标之间存在相关性。

2 叶片抗旱性的生理决定因素及其与 LMA 的关系

2.1 膨压损失点

现有研究发现叶片抗旱性与两个重要的生理指标密切相关：叶失膨点水势（Ψ_{tlp}）和叶水力脆弱性[39]。一般用引起叶片导水率（K_{leaf}）损失 50%时的叶水势来表示叶水力脆弱性（P_{50}）[40]。尽管目前对于 Ψ_{tlp}的准确性提出了质疑[41]，但其仍然是使用最为广泛的抗旱性指标。Ψ_{tlp}的大小与细胞生理功能密切相关，是细胞丧失其生理功能的极限。当叶片水势低于 Ψ_{tlp}时，会导致气孔关闭，细胞质与细胞壁分离、细胞塌陷且无法维持正常的生理功能，从而增加植物死亡的风险[42—44]。因此，具有低 Ψ_{tlp}的物种能更好抵抗干旱[21, 45—46]，并且这些物种更多的分布在水分限制的生境中[20, 39, 47]。研究表明，物种间 Ψ_{tlp}的差异主要由细胞饱和渗透（π_0）[39, 48]，和细胞壁弹性模量的改变（ε）来决定的[39]，即取决于细胞壁的厚度和组成[49—50]。虽然 Ψ_{tlp}和 π_0在机制上的正相关关系已经被很好的证明[48]，但是 Ψ_{tlp}和 ε 的负相关关系表明，低 π_0的细胞在其充分水合时产生的高膨压，可能需要通过强化细胞壁韧性来支持。此外，细胞壁厚度和机械阻力的增加，以及细胞尺寸的减小，也可能有利于细胞在低于 Ψ_{tlp}的水势下存活。事实上，已知一些物种的叶细胞可以通过维持负膨压来避免质壁分离后细胞的破裂[51]，且较厚的细胞壁和小的细胞被证明在细胞塌陷之前会维持更多的负膨压[52]。由于单位体积细胞数的增加（会改变叶片厚度）和单个细胞壁的厚度变化都会对 LMA 产生影响，因此在一些研究中机械强度（LMA）、Ψ_{tlp}和细胞抗塌陷和死亡能力之间会出现显著的相关关系，支持了叶片机械强度与抗旱性相协调的观点[12]。

2.2 叶水力导度和水力安全

维持蒸腾叶片充足的液态水供应是维持水合作用和保证植物光合碳获取的基础，因为从大气中吸收不可避免地伴随着大量的水汽损失。即使在缺水条件下，气孔关闭后，也需要通过水分运输来维持叶片的水分状况，从而避免叶片失水、脱落，最终导致植株因水力失败（hydraulic failure）而死亡[53]。因此，即使在水分限制条件下，理论上其水力运输效率（K_{leaf}）也应保持较高且恒定的值。

通常，K_{leaf}大小取决于叶片中导管系统（例如叶脉，K_{x}）与导管外系统，也就是叶肉部分的水力学特性（K_{ox}）[54—56]。植物遭遇干旱水势下降时，K_{leaf}的下降主要就是因为这两部分中不同的生理过程而导致的。首先，细胞脱水可能会抑制水通道蛋白的表达，降低细胞膜通透性，进而降低 K_{ox}[57—59]。此外，膨压丧失会导致细胞和叶片皱缩，限制叶肉中的质外体的水分流动，降低 K_{ox}[60—61]。因此，较低的 Ψ_{tlp}和相关细胞特征（主要是细胞壁厚度）降低了细胞塌陷和叶片萎蔫的风险，有助于叶片在干旱条件下也能保持相对恒定的 K_{ox}，降低了叶片的水力脆弱性，从而提升叶片的水力安全（P_{50}），增强了抗旱性。因此，Ψ_{tlp} 和 P_{50}之间显著的相关关系[19—20, 62]，进一步说明 LMA 和 P_{50}之间存在密切联系。

水分胁迫下 K_{leaf}下降的另一个重要决定因素是木质部栓塞在叶脉系统中的积累，导致维管束水分运输受阻[63—65]。研究表明，干旱胁迫诱导木质部压力的逐渐下降，最终超过栓塞形成和扩散的临界阈值，导致植物发生水力失败[66—68]。这在最近的研究中观察到[64]，与水力脆弱性高的物种（如 *Lantana camara* 和 *Hedera canariensis*）相比，水力脆弱性较低的物种（如 *Comarostaphylis diversifolia*）通常显示出狭窄但却非常丰富的叶脉系统。此外，木质部导管细胞较厚的细胞壁，降低了木质部因强负压而发生坍塌的风险[19]。这种改变维管系统以提高植物栓塞抗性的方式，同时也驱动了叶片组织密度的变化，从而直接影响叶片的机械强度。

物种间栓塞脆弱性的差异还与主脉（1—2 级）密度（$\mathrm{VLA}_{\mathrm{maj}}$）有关。一般来说具有较高 $\mathrm{VLA}_{\mathrm{maj}}$的物种通常表现出更负的 P_{50}，因为更多的主脉为叶片上的水流提供了更多的替代途径，以防止部分叶脉被木质部栓塞堵塞，从而缓解干旱对 K_{x}的负面影响[45, 66, 69]。此外，高 $\mathrm{VLA}_{\mathrm{maj}}$代表着密度较高的叶片结构[25]，而这些叶片也倾向于具有较高的 LMA 值[20, 70]，使得叶片 $\mathrm{VLA}_{\mathrm{maj}}$与 LMA 之间存在正相关关系[69—72]。上述结果均表明，LMA，P_{50}，$\mathrm{VLA}_{\mathrm{maj}}$之间紧密相关，尽管这些性状之间的相关性并不总是显著的[38]。不同物种的叶片通常表现出不同

的 P_{50}值,这与不同的植物适应策略有着内在的联系,因此相对于中生植物[62, 73],旱生植物 P_{50}更趋于负值。目前,关于 LMA 和 P_{50}是否存在直接的相关性还存在分歧,一些研究认为这些性状之间缺乏相关性或协调性[19, 62, 74—75],但由于大量的研究证明了细胞和叶脉特征与维持 K_{ox}和 K_x之间存在机制上的相关性,因此一些研究也同样显示出 P_{50}与 LMA 之间的显著相关性[20, 69,72, 76]。

2.3　其他相关生理因素

除了上述提到的水分相关决定因素外,其他生理因素如渗透调节能力、水分缓冲能力(叶水容)等也直接决定了植物的抗旱性。渗透调节是植物在干旱逆境下的一种重要防御方式,近年来受到了广泛的研究,渗透调节物质可分为有机和无机两大类,有机物质主要以脯氨酸、可溶性糖、甜菜碱等为主,其主要功能为在调节细胞质的渗透势的同时保护酶蛋白质和生物膜系统[77];无机离子主要包括 K^+、Ca^{2+}等,等其主要功能是维持细胞膨压调节液泡的渗透势。其中无机离子与细胞饱和渗透(π_0)直接相关,间接调控了植物的失膨点水势[78]。但目前并未见到相关报道试图探究渗透调节物质浓度与 LMA 的关系。此外,有机物质及叶水容与叶片结构性状之间的关系也未被证明。未来对于上述与植物抗旱性密切相关的生理因素研究应重点探究其与结构性状之间的关系,为今后进一步的研究植物耐旱策略提供理论依据。

3　植物的抗逆策略:变硬、变韧

综上所述,叶片的机械强度和抗旱性存在协同关系。这种协同关系通过改变诸如细胞壁厚度[79]、主脉密度[30]以及木质部导管的大小和密度[64]来确保叶片在逐步脱水的过程中更好的维持膨压和水力运输能力(图1)。因此,高机械强度和抗旱性的协同是植物适应水分限制生境的重要策略。虽然无论是高机械强度还是高抗旱性都意味着叶片水平的光合速率的降低,但是这种负效应会通过延长叶片寿命而抵消。此外,在外部环境变严峻时,较强的抗旱性也有利于其维持基本的气体交换和正的碳增益。在未来,气候变化引起的降水格局的改变,以及干旱事件发生频率和强度的变化有可能会驱动植被变化[80—81],使其向着有利于高机械强度且耐旱的物种或者基因型方向扩张[82]。值得注意的是,这种机械抗性和抗旱性之间协同关系会因物种的差异(如针叶和阔叶、种间和种内)[3]、环境变化剧烈程度(如石砾含量变化,红树林与喀斯特地区等)[83—84]而变化,例如,阔叶的抗旱性和机械强度弱于针叶,落叶弱于常绿[3]。此外,在水分亏缺的高石砾土壤中生长的耐旱物种表现出更高的叶脉密度及 LMA[84],而这一现象也同样被发现在受严重水分胁迫的红树林中。

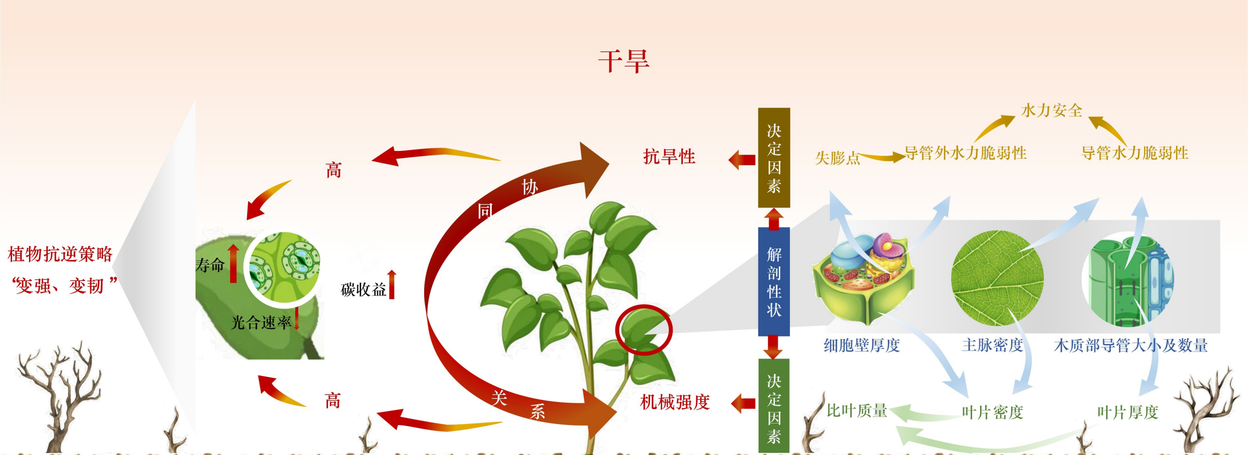

图 1　叶片机械性状调控植物抗旱性的路径示意图

Fig.1　Schematic diagram of the pathways of leaf mechanical traits regulating plant drought resistance

4 未来的研究方向

伴随全球变暖,降水格局改变以及极端干旱等事件的频繁发生成为当前气候变化的重要特征之一。干旱能够显著影响树木生长发育相关的一系列生理代谢功能,从而严重威胁森林生物多样性维持以及生态系统功能发挥[16]。深入解析植物抗旱性与叶片机械强度之间的关系及其内在驱动因素应成为未来的研究方向,对于揭示植物的抗旱生态适应策略具有重要意义,是理解和预测森林生态系统功能对气候变化响应的关键。尽管本文从解剖和生理学角度表明高叶片机械强度有利于提高植物的抗旱性,但其他方面的调控因子及作用途径还需要深入分析,如功能性状和其他生理过程等。

1)植物机械性状与功能性状关系方面的研究,一方面客观反映了植物个体对外部环境的适应能力,以及植物个体内部不同功能间的协同与平衡;另一方面有助于准确预测气候变化背景下植物群落和生态系统的功能发挥与过程变化[85—86]。植物叶片作为受环境影响最为强烈的器官,在植物功能表现中发挥着关键作用,并最终影响生态系统过程[87—89]。近年来,叶经济谱(Leaf economics spectrum)的提出[90], 使得现有研究在全球尺度上定量分析了植物功能性状及其关系,有助于量化和概括协调、权衡策略的变化规律和内在机制。然而,目前大多数研究仅分析了功能性状的变化,对于更深层次驱动因素的研究相对不足,严重限制了对于叶经济谱的机制性认识,无法为未来有效利用叶经济谱理论解决实际生态问题提供充分依据。因此,从解剖学、分子生物学、多组学等角度探索功能性状关系之间的驱动因素应成为今后功能生态学的前沿领域。因此,本文建议在未来对植物机械性状与功能性状的关系研究中可以重点关注以下几个方面:

①LMA 作为受植物内在遗传特性和环境胁迫双重影响的综合结构性状,受到物种和环境因素的共同影响[3]。目前,有关叶机械性状与抗旱性生理性状之间机制性关系的结论更多是基于同一环境下的多物种研究,而对于单一物种分布在不同环境条件的情况极少涉及,尤其种内是否存在叶片机械性状和抗胁迫性之间的协同关系还不清楚,且其背后的解剖学驱动因素是否与上述因素相同也未可知。这限制了对于单一物种分布范围的预测及其生态适应策略的准确认识。

②由于根系分支系统的复杂性、根际过程的不确定性以及根系取样的困难,目前针对植物根系抗旱性相关生理性状和机械性状的研究还相对较少[91—92],特别是细根作为吸收水分的直接器官,其结构性状与抗旱性之间的机制性关系也仍然没有被证明。是否存在与叶片类似的协同关系? 如果存在,背后的驱动因素是什么? 这些问题的回答能够为建立和完善从“个体植物结构-个体植物功能”到“生态系统结构-生态系统功能”体系提供重要的理论依据。

2)除了解剖性状和水力等生理因素外,叶片渗透调节和抗氧化物质与机械强度之间的关系对于提高植物抗旱性也有着重要作用。一般来说,受到干旱胁迫时,植物会产生一些具有保水作用的渗透调节物质,如脯氨酸、可溶性糖和可溶性蛋白等物质,以及一些能够清除自由基的抗氧化酶(超氧化物歧化酶 SOD 和过氧化物酶(POD))等提高植物的抗旱性[77]。其中,可溶性蛋白的亲水胶体性质强,能够增强植物细胞的持水力,以束缚更多的水分,而 POD 在植物细胞壁中的主要功能是催化细胞壁中各种大分子,如蛋白质及半纤维素等,从而能够促进木质素合成,使得机械强度增强,提高植物抗旱性[78]。因此,在考虑机械强度和抗旱性之间关系时,其他生理指标在未来的研究中也需要纳入。

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