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植物叶肉导度影响因素研究进展

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摘要: 叶肉导度 (g_m) 是植物光合作用的重要限制因素之一, 用于表征 CO_2 从气孔下腔传输到叶绿体羧化位点的难易程度, 受到多种因素的影响, 包括内部生理状况和外部环境因素。本文重点介绍引起 g_m 变化的生物物理屏障, 主要包括细胞壁组分与厚度和面向细胞间隙的叶绿体面积, 以及生物化学因素如水孔蛋白和碳酸酐酶; 并阐述进化和驯化过程中 g_m 及其影响因素的变化; 分析 g_m 对外界环境如水分、温度、光照以及营养变化的响应及其内在的调控机制。

关键词: 光合作用; CO_2 传输; 细胞壁; 叶绿体; 进化; 驯化; 环境因素

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Research progress on the influencing factors of mesophyll conductance

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Abstract: Mesophyll conductance (g_m), one of the major limiting factors of photosynthesis, is used to characterize the accessibility of CO_2 transport from the sub-stomatal cavity to the carboxylation sites in the chloroplast stroma. It is influenced by multiple factors including internal physiological status and external environmental factors. This paper focuses on the biophysical barriers that contribute to the changes in g_m , mainly the components and thickness

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of the cell wall and the surface area of chloroplasts exposed to intercellular airspaces per unit leaf area, as well as the biochemical factors including aquaporins and carbonic anhydrase. On this basis, we expound the variations of g_m and its influencing factors during evolution and domestication. We also analyze the response of g_m and the internal regulatory mechanisms in response to external environmental changes of water, temperature, light and nutritional status.

Key words: photosynthesis; CO₂ diffusion; cell wall; chloroplast; evolution; domestication; environmental factor

植物的光合作用效率不仅受到叶绿体基质内核酮糖-1,5-二磷酸羧化酶/加氧酶(Rubisco)固定能力的影响,还受限于CO₂对光合机构的供应。CO₂供应效率取决于其吸收的CO₂从气孔进入后,传输到Rubisco羧化位点的能力。CO₂从气孔下腔传输到羧化位点的效率称为叶肉导度(g_m),这是一个复杂而漫长的传输过程,CO₂需要穿过叶片内不同介质,如细胞间隙(即气相导度, g_{ias})和一系列液相组分(即液相导度, g_{liq}),最终到达基质中的Rubisco羧化位点。由于气相限制非常小,整个气相阻力比液相路径的总阻力小两个数量级^[1],因此一般认为CO₂在叶片内部的扩散主要受到 g_{liq} 限制。 g_{liq} 由细胞壁(g_{cw})、质膜(g_{pm})、细胞质(g_{cvt})、叶绿体膜(g_{env})和叶绿体基质(g_{st})多种导度以串联的方式组成;同时还受到生物膜上水通道蛋白(AQPs)和叶绿体基质中碳酸酐酶(CA)的主动调节。由于 g_m 的改善可以提高光合速率5%~10%^[2],许多研究致力于探索 g_m ,尤其是 g_{liq} 的调控因素,并试图通过生物技术手段改善 g_{liq} 以增强光合作用^[3-4]。目前,随着同位素测定和荧光测定技术的发展,已建立多种估算 g_m 的方法,如叶绿素荧光和气体交换参数结合测定法、碳同位素测定法、氧同位素测定法、CO₂响应曲线拟合法以及叶片解剖结构法等。但鉴于每种方法自身的局限性,通常采用前两种方法进行测定,而其他方法则只用于辅助验证,具体测定方法和注意事项在其他综述中有详细介绍^[5-7]。本文主要概述引起 g_m 变化的生物物理因素和生物化学因素,前者是指细胞壁厚度和组分以及叶绿体面向细胞间隙的面积(S_c),后者是指调节CO₂跨膜运输的AQPs和CA的表达量及活性,并讨论这些因素在植物进化和驯化过程中的变化。此外,鉴于植物的结构和生化功能易受环境影响,因此本文也总结了当前环境变化(如水分、温度、光照和养分)引起的 g_m 变异,并进行了探讨。

1 引起 g_m 变化的主要生物物理和生物化学因素

1.1 生物物理因素

细胞壁是CO₂从细胞间隙进入叶肉细胞的第

一道障碍,其对 g_m 的影响已在众多研究中得到证实^[8-11]。细胞壁对 g_m 的影响主要取决于其孔隙度和曲折度^[3,12]。由于这些参数难以直接测量,研究者通常通过分析细胞壁厚度和组分来推断其与 g_m 之间的关系^[12-15]。细胞壁厚度(T_{cw})这一二维指标已在数百个物种中得到量化,研究发现不同植物类群的 T_{cw} 与 g_m 呈现出显著负相关性^[16]。系统发育分析显示,细胞壁变薄与 g_m 提高往往同步发生^[17]。虽然多项研究证实 T_{cw} 在 g_m 变化中的重要作用,但在针叶树种的比较中发现,种间水平上 g_m 的变化与 T_{cw} 关联并不显著^[12]。从二维视角看, T_{cw} 增加意味着CO₂扩散路径变长,但气体传输的实际扩散路径取决于细胞壁成分的三维排列方式^[14,18-19]。细胞壁主要由纤维素、半纤维素和果胶构成。然而,这些组分与 g_m 之间的关系并未明确,可能是因为组分变化影响了细胞壁内部气体传输路径,而这种影响并非通过简单的线性关系就能反映出来^[20]。在半纤维素缺失突变体研究中发现, T_{cw} 与 g_m 并无直接联系。但半纤维素的缺失改变了内部结构,导致有效气体传输路径减少,进而影响了 g_m ^[21]。在 $xxt1\ xxt2$ 半纤维素突变体中也观察到,其纤维素排列较野生型更加一致且紧密,这种致密排列不利于气体传输^[22-23]。尽管一些研究结果表明纤维素或木质素含量与 g_m 存在一定关系^[24-25],但多项研究表明,细胞壁组分中的果胶因其既能形成孔隙又能形成凝胶,在调控 g_m 方面发挥重要作用^[21,26-27]。果胶的增加会降低孔隙度,从而减缓CO₂通过细胞壁的传输速率,对于干旱条件下麦类作物的研究表明果胶含量与 g_m 呈负相关^[15]。与此同时,也有研究表明果胶并不能单独调控 g_m ,果胶与其他细胞壁组分之间的相对比例才是关键^[12]。在葡萄树、向日葵、烟草或某些针叶树种的环境胁迫研究中,发现果胶和 g_m 之间可能不存在显著关系^[12,21,24-25]。这表明果胶对 g_m 的调控方式并不统一。针对这一现象,有研究认为可能是由于果胶的块状和非块状甲酯化导致的,前者更容易形成凝胶阻碍CO₂传输,后者则易于在细胞壁上形成孔隙;换言之,果胶理化特性的不同

导致其调控 g_m 的机制也不同^[14, 28-29]。细胞壁对 g_m 的调控是一个复杂的过程, 不仅受细胞壁结构影响, 还涉及多种生化因素。值得注意的是, pH 值、温度以及与其他离子的相互作用也可能影响果胶等细胞壁组分的性质, 进而影响气体穿过细胞壁的速度^[8]。

单位面积内叶绿体面向细胞间隙的面积 (S_c) 是另一个主要的结构限制因素。通常, S_c 与 g_m 呈正相关, 较大的 S_c 有助于增加 CO_2 的平行扩散路径^[10, 30-32]。高 S_c 意味着更多的叶绿体暴露于 CO_2 , 这可大大提高羧化位点的 CO_2 浓度。但 S_c 在物种间存在较大差异, 同时也易随环境发生变化^[32-37]。与结构特征中的 T_{cw} 相比, S_c 对环境的响应更为迅速, 因为叶绿体可以在细胞质内移动, 而细胞壁厚度则很难快速响应环境变化^[38-39]。Tholen 等^[39] 发现叶绿体的短期避光运动能够降低 S_c , 进而通过减小 g_m 限制光合作用, 并通过缺乏叶绿体运动的光敏色素突变体进一步证实了叶绿体运动对 g_m 的影响。

除 S_c 外, 其他特征也可能影响 g_m , 如细胞质。细胞质对 CO_2 传输的阻力相对较小, 通常认为低于液相传输阻力的 10%^[10, 40-41]。因为 CO_2 穿过细胞膜后需要跨越细胞质才能到达叶绿体膜, 为缩短 CO_2 的扩散距离, 叶绿体往往紧贴细胞膜。但也有研究表明缺钾植物叶绿体与质膜分离, 扩大细胞质阻力, 从而导致 g_m 降低^[34]。在棉花驯化过程中, 叶绿体与质膜分离抵消了细胞壁变薄带来的 CO_2 扩散优势, 因此 g_m 未发生显著变化^[42]。

1.2 生物化学特性

CO_2 扩散至羧化位点需要跨越细胞膜和叶绿体膜, 它们均为磷脂双分子层, 含有多种蛋白质, 可以在一边或两边进行整合或延伸——这有助于增加膜渗透性通道, 但也严重阻碍 CO_2 扩散, 因此需要转运蛋白的参与^[13, 43]。一些研究表明细胞膜上的 AQPs 可以促进 CO_2 跨膜运输^[43-46], 在 g_m 中发挥重要作用。Uehlein 等^[45] 通过改变烟草 *NtAQPI* 基因表达, 为体内 CO_2 运输的蛋白质介导途径提供了证据; 进一步研究发现 *NtAQPI* 位于叶绿体内膜, 降低 *NtAQPI* 的表达可使叶绿体膜 CO_2 通透性减少 89%, g_m 降低 20%, 但不影响质膜的 CO_2 渗透性。该研究通过对比分析发现, 质膜对 CO_2 的渗透性是叶绿体膜的 5 倍^[47], 表明质膜和叶绿体膜的内外膜对 CO_2 的通透性可能存在差异。现在越来越多直接或间接证据支持 AQPs 在促进 CO_2 扩散中的作用^[48-50]。然而, 最近一项研究通过 4 种不同方法敲除拟南芥的 *AtPIP1;2*、*AtPIP1;3*、*AtPIP2;6* 后, 发现其 g_m 和

光合速率均无显著变化, 这可能与 AQPs 家族内的功能冗余、生长条件及其他生理功能的变化有关^[51]。Clarke 等^[52] 通过在烟草中异位表达 *AtPIP1;2* 或 *AtPIP1;4* 也发现, 简单改变 AQPs 的表达不会导致 g_m 或光合速率的变化, 他们指出植物生长和环境条件可能在 AQPs 改变 g_m 中发挥重要作用, 但需要通过进一步研究来更好地了解 AQPs 的功能。此外, AQPs 还可以作为信号分子响应不同的环境刺激, 调节气孔动力学^[53], 以响应生长条件变化和非生物胁迫。

CA 作为一种高效的催化剂, 能够促进 CO_2 与碳酸氢根离子 (HCO_3^-) 之间的相互转化, 有利于 CO_2 在叶绿体基质中的扩散。在光合组织中, CA 通过维持细胞质和叶绿体内 CO_2 与 HCO_3^- 的平衡来加强 g_m , 从而促进 Rubisco 对 CO_2 的固定^[54-55]。CA 在叶绿体基质和细胞质中含量丰富, 并与各种膜的组分有关。虽然 CA 被认为是光合过程中 CO_2 传输和固定的重要组成部分, 但其对 g_m 的影响仍存在争议: 有研究认为叶绿体基质中 CA 的缺失会影响烟草的发育, 但不影响光合作用^[56]; 也有研究表明即使叶绿体 CA 活性降低 98% 也不会显著降低其 CO_2 同化速率^[57]。这可能与叶片中 CA 的类型复杂性、细胞器中的丰度水平、多种代谢途径中的潜在作用以及活性有关。相反, 移除细胞质中的 CA 使 g_m 下降 44%^[58]。有研究表明 CA 的活性具有物种依赖性, 在细胞壁对 CO_2 扩散阻力较大的物种如硬叶植物中, CA 对 g_m 具有明显的调节作用^[59]。在 C_4 植物中, 叶绿体中的 CA 协助碳浓缩机制为 Rubisco 提供较高浓度的 CO_2 , 因此 CA 的活性对其光合作用至关重要。然而, 在 C_3 植物中 CA 的作用尚不确定, 因为通过使用抑制剂、突变体或水分胁迫改变 CA 的表达或活性未得到肯定结果。因此, CA 如何影响 g_m 仍然是一个值得探讨的问题。

2 进化和驯化过程中 g_m 的变异

2.1 进化过程中 g_m 的变异

植物在系统发育过程中经历了从苔藓植物、拟蕨类植物、蕨类植物、裸子植物到被子植物的进化。在这一过程中, 光合速率和 g_m 呈显著同步增加趋势, 苔藓和拟蕨类植物具有陆生植物中最高 g_m 限制, 随着气孔发育的完善, 在蕨类植物和裸子植物中光合开始受到 g_m 和 g_s 共同限制, 最终在被子植物中, 光合作用受到 g_m 、 g_s 以及生化因素的综合限制^[16-17]。进一步分析发现在系统发育中光合作用的改善主要

与 CO_2 扩散能力的提高有关,而与生化能力的关系较弱^[16]。Flexas 和 Carriqui^[60] 通过叶绿素荧光和气体交换参数结合测定与解剖结构模型两种独立的方法估测了 g_m , 认为其在很大程度上取决于解剖结构特征 T_{cw} 和 S_c 。苔藓类植物具有最小 g_m 的结构特征,即最小的 S_c 和最大的 T_{cw} ; 而被子植物则表现出非常大的 S_c 和较低的 T_{cw} , 同时也表现出较高的 g_m ^[16-17]。 S_c 随着进化表现出增加趋势,而 T_{cw} 则表现出下降趋势,这共同导致了 g_m 增加^[17]。 S_c 和 T_{cw} 在进化中也存在显著负相关性,这表明其在叶片发育过程中可能存在协调性,被认为是未来优化研究以实现最大的 g_m 的重要方向^[17,60]。Huang 等^[16] 进一步对 S_c 和 T_{cw} 的增幅变异情况进行分析,发现系统发育过程中 g_m 的提高主要受到 T_{cw} 而不是 S_c 制约,这表明通过调节 T_{cw} 进一步改善植物的光合作用更易实现。

2.2 驯化过程中 g_m 的变异

在作物驯化过程中,叶片生理和结构特征通常会因人类选择、环境条件和农田管理方式而发生变化^[42,61-64],厘清驯化对 g_m 的影响有助于剖析叶片光合变异的复杂机制以及明确产量提升的有效途径^[65]。然而,驯化过程中 g_m 变异比较复杂。例如,Nadal 和 Flexas^[66] 观察到木本作物(包括落叶植物和常绿植物)与其野生祖先具有相似 g_m ; Eriksen 等^[67] 发现栽培莴苣叶片的 g_m 低于野生莴苣;而小麦现代品种的 g_m 高于地方品种^[68];同样,在栽培种水稻中也发现了更高的 g_m ^[69-70]。棉花栽培种比野生型的光合速率更高,但不论使用气体交换和叶绿素荧光法估算的 g_m 还是以解剖学特征建模计算的 g_m , 野生型和栽培种之间均无差异^[42]。

驯化过程中 g_m 的改变主要归因于叶肉细胞解剖结构的变化,包括 T_{cw} 、 S_c 、单位面积叶肉细胞面向细胞间隙的表面积 (S_m) 和细胞间隙占横截面的比例^[6,8,10,40,71-72],这些结构特征的变化与叶肉细胞的分布和形态变化密切相关^[26,73]。野生稻和栽培稻 g_m 的差异与 S_m 和 T_{cw} 的变异有关,但与 S_c 无关^[74]。Scafaro 等^[75] 发现,与野生稻相比,栽培稻的 g_m 较大与其较薄的 T_{cw} 有关,这与进化过程中的变化相一致^[76]。棉花驯化过程中 T_{cw} 减小导致 g_{cw} 增加,但细胞质距离增加导致 g_{cyt} 减小,两者相互抵消使 g_m 保持不变^[42]。因此,在未来育种中打破 g_{cw} 和 g_{cyt} 的相互抵消关系是增加 g_m 和光合能力从而提高产量的关键所在。

3 不同环境条件下 g_m 的变化

植物能够通过调节 g_m 来响应水分、温度、光

照以及养分等环境因素的变化。通常来说,短期响应主要通过 AQPs 和 CA 引起 CO_2 渗透性变化实现,而结构性变化则需要更长的时间来发生^[13,77-79]。

3.1 干旱胁迫条件下 g_m 的变化

干旱是影响植物光合作用的重要环境因素之一,多项研究表明干旱胁迫会降低植物 g_m ^[37,80-83],这取决于胁迫时间和程度。Flexas 等^[84] 观察到在干旱胁迫初期,光合作用主要受到 g_s 限制,在胁迫适应过程中转变为受 g_s 和 g_m 的共同限制。Zou 等^[37] 发现随着干旱胁迫的持续和加剧,光合速率下降最初由 g_s 限制主导,随后转变为受 g_s 和 g_m 共同限制,最后演变为包含生化因素的共同降低。干旱胁迫下 g_m 的降低主要归因于 S_c 的减小、细胞壁厚度和组分的变化、AQPs 和 CA 活性及含量的改变。干旱胁迫会引起叶绿体的萎缩、数量的减少和排列方式的改变,从而导致 S_c 减小^[39,81,85-86]。在干旱条件下,植物可能通过叶绿体运动减少沿膜排列,以避免因光能过剩引起光合机构损伤^[39]。研究发现,干旱胁迫对细胞壁的影响存在明显物种依赖性,如欧洲山杨 g_m 降低源于 S_c 减小和 T_{cw} 增厚^[87],而在棉花中 T_{cw} 无明显增加^[81]。水分对细胞壁的影响,不仅表现在厚度上,还可能通过改变细胞壁孔隙度及细胞壁组分中果胶、纤维素、半纤维素含量及其比例等物理化学特性,进而影响 CO_2 扩散^[14,21,24,88]。然而,叶肉结构特征并不能完全解释 g_m 的变化^[89],生化因素如 CA 和 AQPs 活性也发挥着重要作用^[85]。干旱胁迫通常会引起 CA 表达量下调,以应对由较低 g_s 和 g_m 引起的胞间 CO_2 浓度降低。如 Han 等^[81] 发现,在长期干旱条件下,棉花的 g_m 降低可能受到 CA 基因调控。但在橄榄树短期水分胁迫和恢复研究中发现,CA 的表达对 g_m 影响较弱^[90],也有研究表明 CA 活性极度降低不会严重限制光合作用^[56]。因此,关于 CA 对 g_m 的调节作用目前存在较大争议,还需进一步验证。Perez-Martin 等^[90] 在橄榄树短期干旱实验中强调了 AQPs 在 g_m 中的主要调节作用,植物通过下调 AQPs 表达降低膜的水渗透性并限制细胞水损失,但也影响了 CO_2 跨膜运输,从而降低了 g_m 。在桑树干旱胁迫研究中发现,AQPs 转录丰度更高的桑树品种具有更强的光合能力, g_m 受到干旱的影响更小^[91]。干旱胁迫也可降低烟草的 AQPs 活性,从而降低其 g_m ^[92]。与此相反,一项研究发现拟南芥 AQPs 敲除株系与对照的 g_m 无显著差异^[51]。此外,Han 等^[81] 的研究也发现,尽管干旱胁迫导致海岛棉中 *GhPIPI.1* 基因表达发

生变化, 但并未对 g_m 造成影响。Zou 等^[37] 发现棉花 g_m 降低的主要因素因干旱持续时间和干旱程度不同而异。干旱首先影响叶绿体基质中 CA 活性以及质膜或叶绿体膜上水孔蛋白相关基因表达, 而叶片结构变化则是长期效应^[93]。综上, 干旱胁迫下 g_m 变化受植物种类、胁迫时间和胁迫程度等诸多因素影响, 其响应机制较为复杂, 目前尚无明确定论。

3.2 g_m 对温度变化的响应

研究表明, g_m 能够迅速响应温度变化。Flexas 等^[94] 观察到诱导温度改变会使甘蓝 g_m 在 20~30 min 内发生显著变化。然而, g_m 对温度的响应往往因物种而异, 可能随着温度升高呈现出增加、不敏感或先增加后减少的变化趋势^[13, 70, 95-97]。Bernacchi 等^[98] 发现, 在 10~40 °C 的温度范围内, g_m 随温度指数增长, 在 35~37 °C 时达到峰值, 随后逐渐下降。通过分析 g_m 变化系数, 推测其对温度的响应可能涉及酶促反应, 因为 CA 和 AQPs 均为蛋白质, 其活性易受温度影响, 从而影响 CO₂ 传输。Warren^[99] 发现橡树叶片的 g_m 在 20~35 °C 之间相对恒定, 表明 g_m 不可能仅由简单的蛋白质促进过程决定, 而可能是由不同温度敏感性的多个过程共同决定的复杂温度响应。Evans^[13] 总结发现, C₃ 植物 g_m 对温度的响应存在显著差异, 而 C₄ 植物 (狗尾草除外) g_m 对温度的响应非常强烈, 推测可能是质膜渗透性在温度响应中发挥了重要作用。von Caemmerer 和 Evans^[97] 比较了多种植物 g_m 的温度依赖性, 发现烟草、棉花、大豆和桉树的 g_m 在 15~40 °C 之间增加了两至三倍, 而木麻黄和小麦的变化较小。为了解释不同物种间的温度响应差异, 他们提出一种双组分模型, 将 g_m 分为液相和膜相两部分, 并考虑了膜通透性的温度依赖性和液相的有效路径长度。通过模拟发现, 不同物种 g_m 的温度响应差异主要由膜活化性渗透能和液相扩散路径调控。Li 等^[100] 的研究发现, 叶片水势在 g_m 对温度的响应中起着重要作用, 这可能与膜透性、叶绿体表面积和细胞壁特性等因素有关。该研究团队进一步强调了叶片解剖结构是 g_m 对温度响应种间变异的主要决定因素^[95]。目前, 关于 g_m 液相和膜相组分对温度响应的生理机制尚不明确, 缺乏直接证据。

3.3 不同光照强度对 g_m 的影响

植物会改变自身形态和生化特征以适应生长的光环境, 长期生长在高光照强度下的植物, 其叶片通常具有较高的 g_m 、光合能力和与之匹配的结构特

征^[101-105]。植物往往具有较厚的叶片和栅栏组织厚度^[103, 106-108], 高光照强度有助于光线在叶片内穿透, 提高光合组织光能利用效率, 从而促进单位面积光合速率和 g_m ^[109]。在高光照条件下生长的叶片, 常通过增加栅栏细胞层数和扩大叶肉细胞体积来增加叶片厚度, 进而提高 S_c 和 S_m ^[3, 87, 103, 105, 107, 110-111]。也有研究指出, 叶绿体对光环境的适应性较强, 当长期生长在荫蔽环境的植物被转移到高光环境时, S_c 会增加, 但 S_m 的增加并不明显^[108]。关于 T_{cw} 对光照变化响应的研究结果存在很大差异, 可能随着光照强度的增加而增加^[112], 或保持不变^[3, 107, 112-113], 或降低^[103, 113], 但目前的机理尚不清楚。

在自然环境中生长的植物常面临剧烈的光强波动 (从毫秒到数小时), 研究发现 g_m 对短期光照强度有不同响应。例如, 烟草、3 种桉树和 7 种班克木属植物的 g_m 在短期光照强度增加时有所提高^[94, 114-117]。而在小麦、烟草和 9 种杜鹃花属植物中, 却发现 g_m 对光照强度无响应^[118-120]。Yamori 等^[119] 认为 g_m 会随生长光照强度的增加而增加, 但不随测量光照强度变化。有学者表示, 由于在研究中未考虑到光呼吸等因素, 部分 g_m 的快速响应结果可能是测定和计算错误造成的假象^[121]。但 Douthe 等^[114] 认为, g_m 对光照变化的响应不太可能是计算误差, 虽然使用不同的模型参数值会改变 g_m 的绝对值, 但不会影响对其辐照度的相对响应。目前的研究认为, g_m 对短期光照强度的快速响应主要源于 CO₂ 扩散特性的生化成分变化, 如 CA 和 AQPs^[122]。

3.4 不同营养条件下 g_m 的变化

养分亏缺会通过影响叶片形态结构和细胞水平等一系列特征, 对植物生长造成阻碍, 但不同营养元素的缺失对植物的影响并不相同^[123]。高氮环境一方面通过增加 S_c 来增加平行扩散路径, 另一方面降低 T_{cw} 缩短扩散路径^[36, 124-125]。李勇等^[78] 认为高氮环境下 S_c 增加主要由叶绿体增大造成。除了观察到解剖性状协同变化外, 其他过程如 AQPs 基因表达也受到营养条件的影响, 例如氮营养水平可以调节 AQPs 基因的表达和含量^[126-128]。钾供应情况对高等植物的光合能力有显著影响, Jin 等^[129] 发现 g_m 与山核桃幼苗的钾供应密切相关, 推测 g_m 的增加可能是供应钾引起的生化修饰和 (或) 叶片结构适应的结果。Hu 等^[130] 证明钾亏缺会引起 S_m 和 S_c 减小, 阻碍 CO₂ 扩散, 从而降低光合速率。进一步研究发现, 钾营养水平有效调节叶肉细胞形态和排列, 有利于形成疏松的叶肉细胞和较小的海绵组织

细胞, 增加叶肉孔隙率以提高 S_m 和 S_c , 从而增加 g_m ^[131]。这表明在钾亏缺条件下, S_c 对 g_m 有重要调控作用。此外, 有研究表明钾可以通过调节碳代谢来调控甘蓝型油菜叶片 CO_2 的运输和同化^[132]。目前关于磷对 g_m 影响的研究较少, 一些研究表明缺磷会降低叶片 g_m ^[133-134], 也有研究指出低磷胁迫会严重破坏大豆叶肉细胞和叶绿体, 减少叶绿体数量^[135]。但对于低磷胁迫下 g_m 变化是否与叶片结构有关尚不清楚。关于营养元素如何通过结构调控和生化调控机制影响 g_m 还需深入研究。

4 总结及展望

g_m 作为光合作用的重要限制因素之一, 因其内在复杂性, 其生理调控机制尚未被完全阐明。本文主要在细胞结构水平上总结了决定其变化的主要内部因素: T_{cw} 和化学组成、叶绿体运动引起的 S_c 变化、AQPs 介导的 CO_2 跨膜运输和 CA 介导的 CO_2 转运调控。这一系列内部影响因素在植物驯化过程中, 以及在不同水分、温度、光照和营养环境条件下的响应性明显不同, 同时也因物种和环境胁迫而产生不同响应机制。未来需要深入探究植物 g_m 与细胞结构和生化特性以及环境适应性的关系, 为提高植物内部 CO_2 扩散调控提供理论指导。

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