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植物光合作用限制因素与植被生产力研究进展

邢红爽[1,2],乌佳美[1,2],陈　健[1,2],史作民[1,2,3,*]

1 中国林业科学研究院森林生态环境与自然保护研究所,国家林业和草原局森林生态环境重点实验室,北京　100091

2 米亚罗森林生态系统定位观测研究站,理县　623100

3 南京林业大学南方现代林业协同创新中心,南京　210037

摘要:随着全球气候变化的加剧,陆地生态系统中植物光合作用限制影响程度的增加已成为降低全球植被净初级生产力的主要因素。系统了解植物光合作用限制因素是科学评估植被生产力的重要前提,也是缓解植物光合作用限制,增加植物光合碳同化能力的先决条件。对植物光合作用限制因素进行了系统解析,分析了光合作用三种限制因素生化限制(Biochemical limitation,l_b)、气孔限制(Stomatal limitation,l_s)、叶肉限制(Mesophyll limitation,l_m)的环境响应,重点讨论了叶肉限制及其影响机理,述评了光合作用限制定量分析方法及改善措施,最后以提高植被生产力为驱使目标,对未来植物光合作用限制因素研究提出以下内容:(1)基因工程技术与系统生物学数据相结合提高植被生产力;(2)气孔响应速度对植物光合作用的影响机制;(3)水通道蛋白(Aquaporin,AQPs)和碳酸酐酶(Carbonic anhydrase,CAs)感知环境信号变化的驱动基因。以期为未来气候变化背景下,深入认识和降低植物光合作用限制,提高植物光合碳同化能力提供参考。

关键词:光合作用;生化限制;气孔限制;叶肉限制;植被生产力

Research progress on limiting factors of plant photosynthesis and vegetation productivity

XING Hongshuang[1,2], WU Jiamei[1,2], CHEN Jian[1,2], SHI Zuomin[1,2,3,*]

1 *Key Laboratory of Forest Ecology and Environment of National Forestry and Grassland Administration*, *Ecology and Nature Conservation Institute*, *Chinese Academy of Forestry*, *Beijing* 100091, *China*

2 *Miyaluo Research Station of Alpine Forest Ecosystem*, *Lixian* 623100, *China*

3 *Co-Innovation Center for Sustainable Forestry in Southern China*, *Nanjing Forestry University*, *Nanjing* 210037, *China*

Abstract: With the intensification of global climate change, the increase of plant photosynthetic limitations in terrestrial ecosystem has become the main internal factor to reduce the net primary productivity of global vegetation. It is an important prerequisite that we understand systematically the limiting factors of plant photosynthesis for the assessing vegetation productivity scientifically, alleviating photosynthetic limitations, and increasing the ability of plant photosynthetic carbon assimilation. The factors of plant photosynthetic limitations were explained systematically. The responses of three limiting factors of photosynthesis (biochemical limitation l_b, stomatal limitation l_s, mesophyll limitation l_m) to different environments were analyzed, and the mesophyll limitation and its influence mechanisms were discussed emphatically. The quantitative analysis methods and improvement measures of photosynthetic limitations were reviewed. Finally, the following suggestions for the future research of plant photosynthetic limitations driven by the goal of improving vegetation productivity were formulated: (1) Combing genetic engineering technology and system biology data to improve vegetation productivity; (2)

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* 通讯作者 Corresponding author.E-mail: shizm@ caf.ac.cn

The mechanism for the impact of stomatal response speed on plant photosynthesis; (3) Driving genes of aquaporin (AQPs) and carbonic anhydrase (CAs) to perceive changes of environmental signals. This review is expected to provide some references for further understanding and reducing plant photosynthetic limitations nd improving the ability of photosynthetic carbon assimilation under the background of future climate change.

Key Words: photosynthesis; biochemical limitation; stomatal limitation; mesophyll limitation; vegetation productivity

光合作用作为陆地生态系统植物生长和生产的主要驱动力,是植物维持生长所需能量的来源[1]。面对资源的限制以及气候变化的挑战,植物光合作用不但能够为日益增长的全球人口提供更多的燃料、纤维和食物,而且在大气净化和生态环境保护等诸多方面具有十分重要的意义[2—3]。然而,光合作用的过程较为复杂,且早前研究认为,其主要受生化因素(即生化限制,Biochemical limitation,l_b)和扩散因素(即气孔限制,Stomatal limitation, l_s)的影响[4],但随着科学技术的进步,研究者发现并确定了对 CO_2扩散起着关键作用的另一重要因素—叶肉限制(Mesophyll limitation,l_m)[5]。叶肉导度(Mesophyll conductance,g_m)是表征这一限制因素的重要指标[6],是控制 CO_2在叶肉细胞传导的关键限制因子[7]。1,5 二磷酸核酮糖羧化氧化酶(Rubisco)与 CO_2反应生成有机分子的速率(包括最大羧化速率,Maximum carboxylation rate of Rubisco,$V_{c\max}$、最大电子传递速率,Maximum rate of electron transport,$J_{\max}$)是影响植物叶片光饱和净光合速率(PPFD-saturated net photosynthesis rate under atmospheric CO_2 concentration,A_n)的主要生化限制因素,而气孔限制和叶肉限制是影响 CO_2在植物叶片细胞内部传导的两个主要扩散限制因素[8—10]。

光合作用的改善是一个复杂的过程,科学缓解光合作用限制是提高植物光合碳同化能力的有效措施。与已实现光合作用最优化的 C4 植物相比[11—12],改善 C3 植物光合作用,减少光合作用限制相对困难。在 C3 植物中,气孔是 CO_2进出植物叶片内部的“大门”,改善植物气孔特征是降低植物气孔限制的有效措施[13],目前有关气孔结构及生化特征的研究已颇为详实[14],然而气孔分布对光合作用中 CO_2扩散的影响仍然不是很清晰。植物叶肉细胞是 CO_2在植物叶片内部扩散的“廊道”,其对 CO_2扩散的主要限制因素存在于细胞壁和叶绿体基质中,且叶肉导度极易受环境因素的影响[7]。水通道蛋白(Aquaporin, AQPs)和碳酸酐酶(Carbonic anhydrase,CAs)的表达及活性增强与其它生化因子的动态调节是改善植物叶肉限制的重要方式[15—16],然而,目前人们对叶肉导度感知环境信号变化及具体内在驱动机制的了解仍然存在盲区。Rubisco 作为有机碳的“制造商”,对固定 CO_2起到了重要作用。通过控制叶绿体基因转录后调节 Rubisco 与 CO_2反应的速率和特异性是有效降低生化限制,实现最佳碳固定的有效方式[17—18],然而,这项操作目前较为困难,且鲜少成功。因此,了解植物光合过程的内在限制因素及改善它们的潜在策略是提高植被生产力的重要前提。

本文通过分析国内外关于光合作用限制因素的最新研究成果,系统解析生化限制、气孔限制和叶肉限制对不同环境响应的生理生态机理,述评光合作用限制定量分析方法及改善措施,提出改善植物光合作用限制因素未来的研究重点,为提高和精准评估植被生产力提供科学参考。

1 影响光合作用的三种限制因素

植物生长与 CO_2的同化密切相关。自引用 Farquhar-von Caemmerer-Berry(FvCB)叶片光合作用模型以来,光合作用通常被认为仅受两个因素的限制,即气孔驱动的 CO_2扩散限制以及生物化学(Rubisco)和/或光化学(类囊体电子传递)调控的生化限制[19]。然而,20 世纪 80 年代末,随着光合作用中^{13}C 鉴别技术和叶绿素荧光气体交换技术等新方法的引入,研究者发现并确定了限制光合作用的第三种因素,即叶肉限制[20—21]。在绝大多数 C_3植物中,光合作用受到 CO_2扩散和 CO_2固定限制的影响,其中,CO_2在植物叶片内的扩散程度取决于气孔导度(Stomatal conductance,g_s)和叶肉导度,而 CO_2固定则由叶片光化学和/或光合酶的功能决定[22]。光合作用的调节涉及到 CO_2从气孔中扩散,通过气孔保卫细胞进入气孔下腔(气孔对 CO_2传导产生阻力的倒数

即为气孔导度)，从气孔下腔穿过一系列生物物理屏障，这一过程包括 CO_2从气孔下腔传导到叶肉细胞壁外表面的气相扩散途径(称之为气相导度，Gas-phase conductance，g_{ias})和 CO_2通过细胞壁(Cell wall conductance，g_{cw})、质膜(Plasma membrane conductance，g_{pl})、细胞质(Cytoplasm conductance，g_{cyt})、叶绿体膜(Chloroplast membrane conductance，g_{cm})和叶绿体基质(Chloroplast matrix conductance，g_{st})的液相扩散途径(称之为液相导度，Liquid-phase conductance，g_{liq})(CO_2 从气孔下腔到叶绿体羧化位点扩散阻力的倒数即为叶肉导度)，最后到达叶绿体羧化位点并由 Rubisco 协同所有的光化学和/或生物化学过程固定 CO_2等过程(图 1)[23]。植物光饱和净光合速率是衡量植物光合能力强弱的重要指标，植物的光合能力在物种间，以及在时间和空间上会因环境条件的改变而产生变化[24]。影响植物光合作用的三种限制因素(生化限制、气孔限制和叶肉限制)常常因环境条件的改变出现适应变化，进而影响光合作用。

1.1 生化限制

C_3植物光合作用受限于类囊体中的电子传递速率(Electron transfer rate，ETR)、羧化速率和卡尔文循环中的 1,5 二磷酸核酮糖(RuBP)再生，导致光合碳同化速率降低的现象被称为生化限制[25]。Rubisco 是催化 CO_2固定的关键酶，同时也是叶绿体中最丰富的可溶性蛋白，Rubisco 的活性及含量对光合碳同化速率存在显著影响，是影响植物光合碳同化能力的主要因素之一[26]。Rubisco 动力学特征对 CO_2 固定速率的影响取决于酶催化位点上 CO_2和 O_2的浓度及温度，环境 CO_2和 O_2的浓度及温度是导致 Rubisco 催化性质改变的主要环境因素[27—29]。

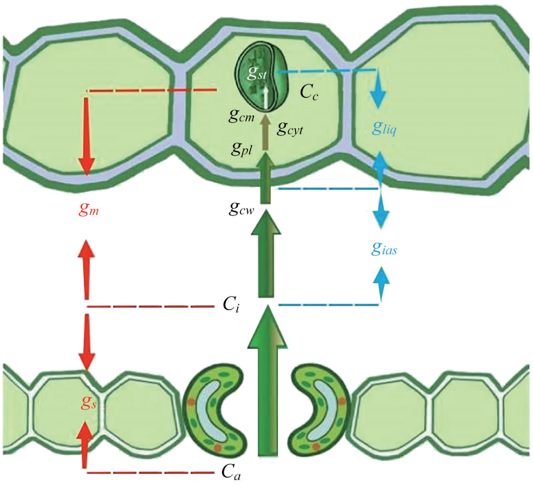

图 1 光合作用中 CO_2的传递途径

Fig.1 Transmission pathway of CO_2 in photosynthesis

C_a：大气中的 CO_2浓度；C_i：细胞间隙 CO_2浓度；g_s：气孔导度；g_m：叶肉导度；g_{ias}：气相导度；g_{liq}：液相导度，其包括 CO_2穿过细胞壁(g_{cw})、质膜(g_{pl})、细胞质(g_{cyt})、叶绿体膜(g_{cm})和叶绿体基质(g_{st})的导度；C_c：羧化位点 CO_2浓度。改自 Gago 等[23]

CO_2的同化速率受叶绿体羧化位点上 CO_2浓度的影响，当 CO_2浓度较低时，Rubisco 的活性与含量是影响 CO_2同化速率的主要因素，随着 CO_2浓度的升高，RuBP 再生速率成为影响光合作用的重要因素，当底物 CO_2浓度进一步升高时，ETR 成为限制光合速率大小的主要原因[30]。因此，在一定范围内，随着大气中 CO_2浓度的增加，CO_2/O_2的比率增加，有利于 RuBP 再生，提高羧化效率[31]。但也有研究表明，较高浓度的 CO_2不仅会降低植物羧化速率，而且也会导致 Rubisco 的活性及含量下降，这可能是因为植物光合作用受到除 CO_2浓度以外的其他因素干扰，也有可能是植物光合碳同化能力超过转移与储藏碳水化合物的能力造成了负反馈调节[26]。温度也是影响植物羧化能力的重要环境因子，在较温暖的环境下，叶绿体中溶解的 CO_2/O_2的比率随温度的增加而降低，从而导致植物羧化能力下降[28]。温度本身也直接影响 Rubisco 的催化性能，随着温度的升高，Rubisco 特异性因子降低，CO_2的米氏常数(Michaelis constant of CO_2，K_C)增加，直接导致 CO_2同化速率降低[32]。在干旱胁迫环境条件下，植物气孔关闭会干扰 CO_2的摄入，进而改变酶活性，破坏细胞膜，减少三磷酸腺苷(ATP)合成和 RuBP 的再生，从而抑制 Rubisco 活性，降低羧化效率[33—35]。同样，弱光胁迫也会导致 Rubisco 活性降低，电子传递能力下降[36]，强光会破坏捕光复合物，导致光系统 II (PSII)反应中心的功能失效引起光抑制[35]。此外，臭氧[37—38]等非生物环境因子对植物叶片的羧化能力均会产生一定影响。

1.2 气孔限制

二氧化碳从外界空气中到达植物叶片表层，通过气孔进入植物叶片内部，导致细胞间隙 CO_2浓度(Intercellular CO_2 concentration，C_i)降低，这种由气孔导致光合作用受限的现象被称为气孔限制[14]。气孔导

度控制着叶片和外界大气之间的气体交换，是判断气孔限制大小的重要指标，由气孔的类型、孔径大小及密度共同决定[38—40]。气孔由两个保卫细胞组成，保卫细胞在结构上有很大的差异，通常将其划分为哑铃型和肾型两大类[42]。哑铃型保卫细胞通常存在于禾本科植物和其它单子叶植物中[43]。肾形保卫细胞大约在 4 亿年前首次出现[44]，并在大多数双子叶植物和一些单子叶植物中发现[45]。已有研究表明，哑铃型气孔的环境响应敏感度通常要高于肾型气孔，气孔应对外界环境变化的敏感程度是植物适应环境的重要体现[42—43, 46]。最大气孔导度（Maximum stomatal conductance，$g_{s\max}$）指在所有气孔完全打开状态下的最大潜在气体交换，它是由气孔的密度、最大气孔面积（根据气孔长度计算）和气孔深度（由保卫细胞宽度估算）共同决定，计算公式如（1）[14]，同时三者的改变已经成为植物响应环境变化的重要适应性策略[42]。植物叶片气孔组织结构会因温度、光照、水分和 CO_2 浓度等环境因子的改变产生适应性变化，从而调节气孔导度，改变气孔限制。

$$g_{s\max}=\frac{\frac{D_w}{v}SD\times Pa_{\max}}{P_D+\frac{\pi}{2}\sqrt{Pa_{\max}/\pi}} \tag{1}$$

D_w 为 25 ℃时水蒸气在空气中的扩散率（0.0000249 m^2/s），v 为空气的摩尔体积（0.0245 m^3/mol），SD 为气孔密度（每 m^2 叶片的气孔），$Pa_{\max}$ 为最大气孔面积（m^2），P_D 为气孔深度（m）。

温度是影响植物气孔导度变化的关键环境因子之一，在全球气候变化背景下，高温会对植物光合碳同化能力产生显著影响，它可以在气孔乃至非气孔水平上影响碳同化途径[47]。Rodrigues 等在咖啡（*Coffea* spp.）的光合作用研究中发现，高温会降低咖啡叶片的气孔导度和气孔密度，气孔关闭是影响光合速率降低的主要限制因素[48]。Greer 在葡萄（*Vitis vinifera*）光合作用的气孔限制研究中也得到了类似的结果，发现从低温到高温，葡萄叶片的气孔限制从 20%增加到 45%[49]。Hendrickson 等在葡萄的光合作用研究中发现叶片气孔导度对温度的响应速率在 15 ℃以下时有所下降，低温条件下光合作用的抑制并非由气孔限制主导，非气孔成分抑制作用较为强烈[50]。气孔对光照强度的变化极其敏感，这完全取决于保卫细胞的类型，高敏感度的哑铃型气孔能够快速感知光照变化并作出应答，这对提高植物光能利用效率具有十分重要的意义[46]。多数研究发现对于相同结构类型的气孔来说，较小的气孔孔径和较大的气孔密度拥有较快的光照变化响应速度[46,51]，但 Elliott-Kingston 等发现并不是所有物种都存在这种现象，部分植物叶片气孔导度的降低与气孔组织结构并不存在显著联系[52]。在全球气候变暖的背景下，地下水可利用性的降低导致干旱现象时有发生，植物生长受到严重抑制，导致植被生产力显著降低[2]。研究表明，在干旱胁迫条件下，保卫细胞膨胀压力降低，导致气孔孔径和气孔导度减小，植物叶片气孔限制增强，细胞间隙 CO_2 浓度降低，光合作用会受到明显抑制[53]。水分限制条件下，植物叶片的气孔面积和气孔深度明显减小，这直接降低了气孔扩散 CO_2 的能力[54—55]。Campos 等在灯笼椒（*Capsicum annuum*）水分胁迫的研究中发现，在重度水分胁迫条件下，由于植物叶片气孔的关闭导致气孔限制增加，光合作用显著下降[54]。李周等对草本植物进行了不同水分处理，同样证实了水分胁迫会对植物叶片气孔导度产生极显著的影响，且随着水分的减少，光合作用的气孔限制逐渐增强[55]。环境大气 CO_2 浓度的降低会导致植物叶片气孔密度显著增加，气孔孔径显著降低，这说明较大的气孔密度和较小的气孔孔径更有利于提高叶片气孔导度，保证植物在低 CO_2 浓度环境条件下有足够的 CO_2 供应能力，降低叶片气孔限制，增强植物光合作用能力[56]。此外，有研究从另一面同样证实了这一结论，即随着 CO_2 浓度的升高，绝大多数植物叶片的气孔密度有所降低[43]。气孔一直是光合作用研究的重点，关于不同环境下气孔组织结构及分布对光合作用的影响研究已较为深入[48, 53, 56]，但对气孔环境响应速度的内部影响机制的认识仍然存在不足，需要继续开展深入研究。

1.3　叶肉限制

二氧化碳通过植物叶片内部结构最终扩散到叶绿体基质内的 Rubisco 羧化位点，这种主要由叶肉细胞导致 CO_2 传递受阻进而影响植物光合作用的现象被称作叶肉限制[57]。叶肉限制大小的重要表征参数为叶肉导

度，它的大小直接决定了 CO_2在叶片内部的扩散量，进而影响植物光合作用效率的高低。然而，叶肉导度并不能直接测量，需根据相应的计算方法进行估算获得，常见的估测方法有气体交换与叶绿素荧光相结合法、曲线拟合法、瞬时碳同位素（$^{13}CO_2$）辨别法[58]及一维气体扩散模型法[59]，叶肉导度的估算对于植物光合碳同化能力的评估意义重大。此外，植物细胞组织结构及内部生化因素被认为是影响叶肉导度的关键因子[60—62]，叶肉导度对调控不同环境条件下植物光合作用的叶肉限制发挥着重要作用[63—65]。

植物叶片解剖特征和生化因素会影响 CO_2在细胞内的扩散，进而调控叶肉导度，改变叶肉限制[60, 66—68]。影响植物叶片叶肉导度的主要叶片解剖特征参数有细胞壁厚度（Cell wall thickness，T_{cw}）、单位叶面积面向细胞间隙的叶绿体表面积（The chloroplast surface area exposed to intercellular airspace per leaf area，S_c/S）和面向细胞间隙的叶肉细胞表面积（The surface area of mesophyll cell exposed to intercellular airspace per leaf area，S_m/S）等。研究表明细胞壁厚度与叶肉导度呈负相关关系，与叶肉限制呈正相关关系[60, 68—69]；S_c/S 和叶肉导度呈正相关关系，与叶肉限制呈负相关关系[60, 68,70]；S_m/S 的增加会扩大 CO_2与叶肉细胞的接触面积，提高 CO_2扩散效率，进而增加叶肉导度，降低叶肉限制[62,71]。影响叶片叶肉导度的生化因素主要指叶片中可以改变 CO_2扩散介质性质的水通道蛋白和改变 CO_2扩散分子性质的碳酸酐酶[67]。水通道蛋白家族作为小分子的扩散促进剂，可以增加生物膜的通透性，可能是 CO_2在生物膜（质膜和叶绿体被膜）上有效扩散的必要条件[72]。多项研究表明，某些特定水通道蛋白与叶肉导度存在正相关关系，例如水通道蛋白 PIP1（PIP1）和水通道蛋白 PIP2（PIP2）的过表达能够显著降低叶肉限制[73—75,61]，水通道蛋白活性的增加也可以较好地促进 CO_2的扩散，降低叶肉限制[62,76]。二氧化碳除了通过细胞壁和生物膜扩散外，还通过细胞质和叶绿体基质进行扩散[77]。碳酸酐酶家族可以调控细胞质基质和叶绿体基质中的 CO_2和 HCO_3^-的相互转化，增强 Rubisco 对 CO_2的吸收同化，进而提高叶片叶肉导度，降低叶肉限制[78]。有研究通过调控不同碳酸酐酶同工型基因的表达验证了碳酸酐酶在叶片叶肉导度调控中具有重要作用[78—79]；也有研究通过控制环境条件或添加抑制剂来探讨碳酸酐酶活性对叶片叶肉导度影响，发现碳酸酐酶活性与叶片叶肉导度有较好的正相关关系[80—82]。除了水通道蛋白和碳酸酐酶之外，其它代谢过程与叶肉导度之间也存在着某种联系[83]，例如细胞氧化还原调节相关的代谢组分（线粒体电子传递复合物、硫氧还原蛋白等）[84—85]。虽然多项研究表明植物具有多种调控叶片叶肉导度的生化因素[86—87]，但对其确切的调控机制以及操作方式的认识仍然不是很全面。

环境因子会改变叶片叶肉导度，进而影响叶肉限制[88—90]。植物叶片叶肉导度是温度依赖性的，不同温度条件下植物叶片叶肉导度对光合作用限制的影响力不同[64,91—92]。例如，Sáez 等对两种南极植物进行了 5 ℃、10 ℃和 16 ℃的温度处理，发现叶肉限制随温度的升高而显著降低[93]。光照能够调控植物叶肉导度，影响叶肉限制[65—66,89, 94]。Liu 等对拟南芥（*Arabidopsis thaliana*）进行了光诱导过程中光合作用限制研究，发现在整个光诱导期间，叶肉限制可高达 35%[90]。Kazuma 等在不同光照强度条件下对烟草（*Nicotiana tabacum*）的光合作用进行了研究，发现叶肉导度为适应光环境变化同样会产生一定适应变化，叶肉限制虽不是限制烟草光合作用的主要因素，但也占据了相当大的比重[95]。在水分胁迫条件下，植物叶片叶肉导度显著降低，叶肉导度与气孔导度是限制光合作用的主要因素[63, 96—97]。水分亏缺会导致植物叶绿体表面积（Chloroplast surface area，S_c）降低，细胞壁厚度增加，水通道蛋白和碳酸酐酶活性改变，抑制叶片组织内部 CO_2的传递，导致叶肉限制占比加大[59]。同样，Guo 等对不同水分条件下的火炬松（*Pinus contorta*）和云杉（*Picea engelmannii*）进行了光合作用限制定量分析，发现两种树种叶片叶肉导度会随着水分条件变化产生适应性变化，其中叶肉限制达到了 5%—17%[98]。二氧化碳浓度对植物叶片叶肉导度具有一定的影响，短期 CO_2浓度的增加降低了叶肉导度，叶肉限制所占比重加大[99—101]，这可能是由于高 CO_2浓度下导致 HCO_3^-在通过叶绿体被膜时产生泄露而引起[102]，也可归因于影响叶片扩散特征的生化成分的变化[89]；长期 CO_2浓度改变对叶片叶肉导度往往没有或仅有轻微的影响，叶肉限制所占比重因气孔和生化因素有所波动[88, 103—104]。目前关于叶片叶肉导度对环境适应变化的研究多集中在叶肉细胞组织结构及生化层面，不同环境条件下叶肉限制占比很少被提及。

2　光合作用限制定量分析

在大多数环境条件下,C3 植物光合作用会受到三种限制因素的影响,光合作用限制定量分析不但解答了三种限制因素如何限制光合作用的疑问[4],而且还可以提示植物应该在哪里投资以获得光合作用的最大效益。量化生化限制和 CO_2扩散限制(气孔限制和叶肉限制)对光合碳同化的贡献率,对深入理解植物光合碳同化过程具有十分重要的意义。

目前对植物光合作用限制定量分析通常根据 Grassi 和 Magnani 的方法进行[105]。量化三个限制因素的前提需已知植物叶片叶肉导度及叶绿体羧化位点的 CO_2浓度(the CO_2 concentration inside the chloroplast,C_c),然而,两者均不能通过仪器直接进行测量,需根据相应的计算方法估算获得[58—59]。*J* 变量法是气体交换与叶绿素荧光相结合方法中的一种,一般在正常大气条件下测定,该方法相较于其他方法来说具有较高的操作性[58]。以 *J* 变量法估算获得叶肉导度[21],量化分析光合作用三种限制因素为例:

利用 *J* 变量法估算得到叶肉导度

$$g_m = \frac{A_n}{C_i - \left\{ \frac{\Gamma^* \times [J_f + 8 \times (A_n + R_d)]}{J_f - 4 \times (A_n + R_d)} \right\}} \tag{2}$$

A_n为光饱和净光合速率(μmol m^{-2} s^{-1})、C_i为细胞间隙 CO_2浓度(μmol/mol),A_n和 C_i由饱和光量子通量密度(PPFD)大气 CO_2浓度下的气体交换测定得到,R_d为光下暗呼吸速率(μmol m^{-2} s^{-1}),是暗呼吸速率(R_n)的一半[63],R_n是 PPFD 为 0 时大气 CO_2浓度下的净光合速率;Γ^* 为 CO_2补偿点,根据 Bernacchi 等[108]的研究,25℃时为 37.4 μmol/mol;J_f为光合电子传递速率(μmol m^{-2} s^{-1}),根据 Loreto *et al*.进行估算[107]:

$$J_f = \frac{\Delta F}{F_m{'}} \times \mathrm{PPFD} \times \alpha \times \beta \tag{3}$$

PPFD 可直接测量得出;$\Delta F/F_m$为光系统Ⅱ的实际光化学效率,由饱和 PPFD 大气 CO_2浓度下的叶绿素荧光参数测定得到;α 为叶片吸收系数,取值为 0.82—0.85[108];β 为所吸收光能在光系统 I 和光系统 II 之间的分配比例,取值 0.5[107]。

对羧化位 CO_2浓度(C_c,μmol/mol)由以下公式进行计算:

$$C_c = C_i - \frac{A_n}{g_m} \tag{4}$$

光合作用限制因素生化限制(l_b)、气孔限制(l_s)和叶肉限制(l_m)($l_b + l_s + l_m = 1$)的计算公式如下:

$$l_b = \frac{g_{\mathrm{tot}}}{g_{\mathrm{tot}} + \frac{\partial A_n}{\partial C_c}} \tag{5}$$

$$l_s = \frac{\frac{g_{\mathrm{tot}}}{g_s} \times \frac{\partial A_n}{\partial C_c}}{g_{\mathrm{tot}} + \frac{\partial A_n}{\partial C_c}} \tag{6}$$

$$l_m = \frac{\frac{g_{\mathrm{tot}}}{g_m} \times \frac{\partial A_n}{\partial C_c}}{g_{\mathrm{tot}} + \frac{\partial A_n}{\partial C_c}} \tag{7}$$

$$g_{\mathrm{tot}} = \frac{g_s \times g_m}{g_s + g_m} \tag{8}$$

g_{tot}为CO_2的总导度(mol CO_2 m^{-2} s^{-1}); g_s为气孔导度(mol CO_2 m^{-2} s^{-1});$\partial A_n / \partial C_c$为$C_c$范围在50—100 μmol/mol的$A_n / Cc$响应曲线的斜率[68]。波动光下叶片光合作用的动态影响植物的碳增益。

Grassi和Magnani的方法在绝大多数环境条件下均能够很好的量化植物光合作用三种限制因素的影响力[105]。动态光环境下叶片光合作用的波动会影响植物的净碳增益,充分了解光诱导过程中植物光合作用限制因素是提高植被生产力的可能途径,尽管如此,很少有研究量化光诱导过程中生物化学限制和扩散限制[109],这可能是因为光诱导下气孔导度、叶肉导度和Rubisco等因素的动态变化为光合作用限制定量分析增加了难度。Deans等基于Grassi和Magnani的方法,推导了两种方法来计算光诱导期间包括生物化学和扩散效应在内的限制[25]。第一种是消除法,通过依次消除每个限制的影响来计算限制[4,110—111]。第二种方法是差分法,通过线性化每个限制对同化率的影响来分配限制[4, 105, 111]。然而,Deans等在推导过程中只考虑了气孔限制和生化限制,叶肉限制作为研究的重点被弱化。Liu等基于Grassi和Magnani和Deans等的计算方法对光诱导期间植物光合作用限制因素进行了分析,修改了衍生过程,加入了叶肉限制成分,重点解析了叶肉限制,发现叶片叶肉导度在光诱导过程中对光合作用存在明显限制[90]。进一步改进和发展适用于变化环境下植物光合作用限制因素的科学计算方法,量化光合作用各种限制因素的影响力,有助于了解并改善各种限制因素,可为提高植被生产力提供更多可能。

3 光合作用限制的改善措施

面对全球人口的不断增加和气候变化的不确定性,增强植物光合作用效率成为缓解社会和自然压力的有效方式[18,112—113]。然而,此项研究工作一直收效甚微,研究者普遍认为光合作用已经优化,很难改善[114—115],因为降低这三个限制因素中的任何一个都会立即使其他两个成为最大的限制因素,提高植物光合碳同化能力的可能性被大大削弱[116]。近年来,针对如何提高植物光合作用效率做了大量研究工作[117—119],且随着时间的推移,传统技术方法已达到顶峰,新方法和新技术的发展为增强植物光合作用,改善光合作用限制提供了可能。

基因工程技术因其具有精准、高效、可持续等特点一直是植物生理生态研究领域关注的焦点,许多提高植被生产力的研究多以调控相关基因变化来增强植物光合能力[120]。然而,提高植物光合碳同化能力的措施并非只有基因工程这一种,针对植物光合作用限制因素,改善植物光合作用的技术及方法层出不穷,了解CO_2的传递途径及其内在限制因素,分析改善它们的潜在策略是提高植被生产力的理想途径。国内外众多研究者针对植物叶片生化限制、气孔限制和叶肉限制提出了一系列改善植物光合作用限制的措施[121—123]。Rubisco在光合作用碳同化方面扮演了十分重要的角色,因此,针对生化限制,研究者提出优化Rubisco动力学性质[124]、增加Rubisco活性[109]、优化Rubisco性能、电子传递效率和CO_2同化率的遗传变异[125]等一系列措施,为减少因生化限制导致光合碳同化能力下降的现象提供了可能。针对气孔限制,Hu等提出改变气孔CO_2响应的方法来改善光合作用限制[126],类似的方法也出现在后续研究中[127],Lawson和Vialet - Chabrand在研究提高气孔对环境变化的反应速度,增强植物光合碳同化能力方面也取得了显著效果[128]。针对叶肉限制,改善叶肉解剖结构和细胞形态来减少CO_2扩散路径的长度[129—130]、增加叶绿体中碳酸酐酶丰富度和活性[16]、调节CO_2转运蛋白相关基因来增强细胞膜水平上的CO_2扩散能力[131],增强水通道蛋白活性[62]等都是减少叶肉阻力,促进CO_2在叶肉细胞内扩散的理想方法(表1)。

4 研究展望

准确评估与系统预测植被产力始终是全球变化研究的重要议题。系统了解植物光合作用限制因素是科学评估植被生产力的重要前提,也是缓解光合作用限制,增加植物光合碳同化能力的先决条件。尽管对于光合作用限制已开展较多研究,并且针对光合作用限制因素提出了一定的改善措施,但关于光合作用限制内在影响机理的认识仍然不深入,未来应该重点加强以下几个方面的研究。

表 1　针对光合作用限制因素改善植物光合作用的策略

Table 1　Strategies to improve plant photosynthesis by targeting intrinsic photosynthetic limitations

CO_2的扩散与吸收 Diffusion and absorption of CO_2	限制来源 Source of limitation	提高光合作用的策略 Strategies for improving photosynthesi
CO_2的同化 CO_2 assimilation	生化限制	优化 Rubisco 动力学性质[124,132]
		增加 Rubisco 活性[109,133—135]
		优化 Rubisco 性能、电子传递效率和 CO_2同化率的遗传变异[125]
CO_2扩散途径 CO_2 diffusion pathways	气孔限制	改变气孔的 CO_2响应[95,126—127, 136—137]
		提高气孔对环境变化的反应速度[128]
	叶肉限制	改善叶肉解剖结构(减少扩散路径长度)和叶肉细胞形态或孔隙率[129—130]
		增加叶绿体中碳酸酐酶丰富度[16,138]
		上调 CO_2转运蛋白基因改善细胞膜水平上的 CO_2扩散[131]

(1)基因工程技术与系统生物学数据相结合提高植被生产力

随着基因工程技术的快速发展,通过编码光合作用相关基因提高植被生产力已成为可能。系统生物学数据的应用也为成功实现基因工程技术提供了有力支持。基于系统生物学数据,通过编码参与 CO_2羧化过程中 Rubisco 等相关物质的基因来调控生化限制程度,增强植物对未来气候限制的耐受性,是提高植被生产力的有效方式。基因工程技术与系统生物学数据的广泛结合为降低生化限制,提高植物光合作用能力开辟了新的途径。

(2)气孔响应速度对植物光合作用的影响机制

植物叶片表面的气孔覆盖程度较大,达到了 0.3%—5%,其中 95%的叶片和周围大气之间的气体交换都通过气孔完成[14]。气孔会根据外部环境变化进行调整,较快的气孔反应速度能够降低光合作用对 CO_2需求的限制,改善植物性能和资源的利用。然而,有关于气孔对外部环境信号的感知机制仍然不是很清晰。虽然有研究表明气孔类型会影响气孔对环境的感知速度[42, 46],但保卫细胞应对环境变化的内部生理反应机制仍然是一个未知难题。深入研究气孔响应环境变化的速度和机理,进而调控气孔响应速度,可为增强植物适应气候变化能力,提高植被生产力提供科学支撑。

(3)水通道蛋白和碳酸酐酶感知环境信号变化的驱动基因

植物细胞组织结构及生化因素是调控植物叶肉导度的重要内部影响因素,关于细胞组织结构对叶肉导度的影响研究已日渐丰富,如植物细胞壁的厚度及组成成份、细胞膜的结构及功能等。水通道蛋白和碳酸酐酶是影响叶肉导度的主要生化因素,对于两者的研究也已深入到分子水平,然而,调控水通道蛋白和碳酸酐酶的基因研究绝大多数都是基于已知基因组的物种,对于未知基因组的物种来说,判断不同环境尤其是复杂环境条件下影响叶肉导度的水通道蛋白和碳酸酐酶调控基因相对来说较为困难,尤其是不同物种之间基因的特异性也为相关研究工作增加了难度。系统研究环境变化条件下不同物种间水通道蛋白和碳酸酐酶的调控基因,有助于丰富和完善植物光合作用叶肉限制的改进措施,增强植物适应环境的能力,提高植被生产力。

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