

提高现代超级稻产量潜力的栽培生理研究途径探讨

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摘要:水稻籽粒灌浆期同化物供应不足会导致籽粒灌浆不充分, 从而影响产量, 这种现象在大穗型、高库容的现代超级稻品种中尤为明显, 直接限制了超级稻品种产量潜力的发挥。灌浆期水稻同化物的供给主要来源于花前同化物的积累与花后同化物的合成, 它们均依赖于冠层群体光合能力。因此, 加强相关过程的生理生态研究对揭示制约现代超级稻产量潜力的关键性因素具有重要意义。作者综述了相关领域的研究进展, 并从叶片光合生理、冠层光氮匹配和根-冠水分平衡等方面, 对提高现代超级稻产量潜力的栽培生理途径进行了探讨。同时, 作者总结了模型分析在综合栽培生理认识、发现超级稻产量潜力限制性因子及其生理机制等方面的作用。

关键词:光合作用; 产量潜力; 冠层光氮匹配; 根-冠水分平衡

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现代超级稻品种穗型大, 穗粒数多, 有极高的库容, 产量潜力能够达到 1 000 kg/667 m² 以上^[1]。但是在实际生产中, 以江苏为例, 超级稻单产只在 600~700 kg/667 m² 之间, 且表现出灌浆不充分、结实率低, 影响了产量潜力的发挥。超级稻品种的结实率往往比常规稻品种低 10% 以上^[2]。现代超级稻品种灌浆不充分、结实率低, 主要原因是灌浆期同化物的供给不充分所造成。要是能突破灌浆期同化物供应的瓶颈, 将有望进一步提高我国超级稻的产量。

灌浆期水稻同化物的供给主要来源于两个方面(图 1): 一是花前累积的同化物, 它们来源于花前冠层群体的光合, 主要以非结构性碳水化合物的形式贮存在茎鞘中, 对产量的贡献为 30% 左右^[3-4]; 二是花后冠层群体的光合, 其中剑叶光合对产量贡献较大。以下将分别从叶片光合与冠层光合角度来分析提高水稻净同化力的限制性因子。

1 叶片光合作用

光合作用是指绿色植物通过叶绿素吸收光能, 同化 CO₂ 和 H₂O, 制造有机物并释放 O₂ 的过程, 根据是否需要光的参与, 分为光反应和暗反应两个过程。在光反应过程中, 类囊体上的电子传递链捕获和利用光能, 合成暗反应需要的能量 ATP 和还原剂 NADPH。光反应形成的 ATP 和 NADPH 供给暗反应同化 CO₂ 形成碳水化合物。在暗反应中, CO₂ 受体为 1, 5-二磷酸核酮糖(RuBP), 在核酮糖二磷酸羧化酶(Rubisco)等一系列酶的作用下, CO₂ 被还原成磷酸丙糖 3-磷酸甘油醛(3-

GAP)。磷酸丙糖不能直接透过叶绿体内膜, 其必需由磷酸运转器与 Pi 对等交换才能出入叶绿体。当 Pi 不足或长期光照时, 磷酸丙糖会在叶绿体内积累, 形成淀粉粒。

因此在低光强下, 囊体上的电子传递受限, 影响 ATP 的合成, 从而影响 RuBP 再生(RuBP 再生限制); 在饱和光强下, 暗反应关键酶 Rubisco 的数量与活性, 及反应底物 CO₂ 的浓度是限制光合作用的最关键因素(Rubisco 羧化限制); 在长期光照下, 大量形成的光合产物需要借助叶绿体被膜上的磷酸运转器及时运转出叶绿体, 此时光合速率受细胞质中无机磷运转速率限制(磷酸丙糖运转限制)^[5-6]。根据叶片光合的限制性因子, 国内外学者开展了很多研究, 希望突破叶片光合限制, 提高同化物的供给, 例如, 通过提高 Rubisco 活化酶(RCA)的活性来改善 Rubisco 活性^[7], 通过提高 Rubisco 酶对 CO₂(相对于 O₂)的专一性(Sc/o)来改善 Rubisco 活性^[8], 降低光呼吸损耗^[9], 过表达 *SBPase* 基因改善 RuBP 的再生能力^[10-11], 通过增加细胞色素 b6f 复合体含量提高叶绿体电子传递^[12], 引入蓝细胞的 CO₂ 浓缩机制来提高反应底物 CO₂ 浓度^[13], 过表达水通道蛋白 NtAQP1

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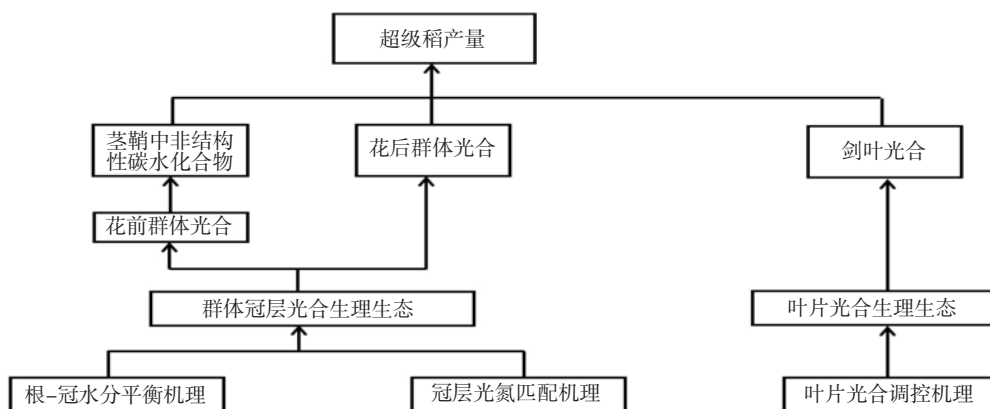


图1 提高现代超级稻产量潜力的栽培生理途径分解

提高叶肉导度从而提高反应底物 CO_2 浓度^[14-15],将高效的 C_4 途径引入水稻来消除光合作用的氧抑制^[16]。但是将这些分子生物学成果运用于水稻的大田生产中,预计需要 15 年甚至更长的时间^[16-17]。针对大田生产中广泛使用的粳型超级稻品种沈农 265 和农家早稻品种毫格劳,我们对它们及它们杂交组合后代进行了遗传与生理分析,发现气孔与叶肉导度是高光强下影响光合最主要的限制性因子^[18-19]。Adachi 等^[20-22]研究发现,水稻品种 Takanari 干物质积累比水稻品种 Koshihikari 高 20%~30%,主要是因为 Takanari 根系具有较高的导水率,能够维持高的叶片水势,保持气孔开发,有较高的气孔导度。Yang 等^[23]也发现,目前大田高氮肥施用条件下氮素利用效率降低是由于水稻根系导水率低,吸水能力不足,气孔开放程度低,气孔导度小所致。因此,如何通过栽培措施调节根系、根系-叶片水分平衡,提高气孔导度,可能是提高水稻光合能力的一个潜在的靶标。

2 冠层光合作用

相对于叶片光合,冠层群体的光合与水稻干物质的积累、同化物的供应联系更紧密^[24]。冠层结构大大提高了作物光能利用效率。对于水稻等 C_3 作物叶片来说,当光合有效辐射(Photosynthetically active radiation, PAR)达到 $700\sim 1\,000\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$ 时,叶片的光合值达到上限,光合能力不再随着光强的提高而增加,称为光饱和点。而当光合有效辐射增加到 $2\,000\ \mu\text{mol}/(\text{m}^2\cdot\text{s})$,冠层光合仍然没有达到饱和,此时,冠层光合是叶片光合的 3 倍^[25-26]。这是因为除了冠层顶部的光饱和叶(如剑叶等),冠层内阴影部分 70% 的叶片能够吸收占总光能 30% 的散射光与漫射光,贡献冠层约 50% 的光合能力^[27]。因此,研究整个冠层的光合生理生态对水稻

的干物质积累非常重要。合理的冠层结构历来受到国内外育种和栽培生理专家的重视与关注^[24,28-29]。相关研究普遍认为,茎叶夹角小、直立叶片构成的冠层有利于群体受光,对群体光合作用和物质生产有利。但在水稻高产实践中发现,基于株型选择的,具有矮秆、直立叶片等特性的新株型(New type plant-NTP)水稻品种的产量往往比基于产量选择的超级稻品种的产量低^[29],说明人们对群体冠层结构和功能的认识仍然是片面的,不系统的,需要深入理解作物高产群体冠层结构的生理生态基础及其与光温等生态因子的匹配机理。

3 提高冠层光合作用的途径

光是绿色植物进行光合作用的能量来源。优良的冠层结构有利于光在群体中的分布,有利于群体受光。除了光的分布,氮素作为 Rubisco 酶与叶绿体的重要组成部分,它在冠层中的分布也是限制植物体内物质合成的关键因素^[30-32]。和光一样,氮素在冠层内的分布也呈现顶部高、基部低的梯度分布。这种氮素的梯度分布相对于均匀分布,冠层光合提高了 20%^[33],这种现象被认为是植物对外界光环境的适应,是为了提高冠层光合同化力和氮素利用效率^[33-35]。但是通常冠层中氮素的分布并不是最优的^[36-38],Hikosaka 等^[39]通过研究发现,如果能够调控冠层中的氮素分布,使之与光的分布一致,达到最优,冠层光合能额外再提高 20%。Dingkuhn 等^[40]在 1991 年就提出,优化冠层氮的分布(即加大氮素的分布梯度差,增加上部叶片含氮量,减少下部叶片含氮量)应该作为育种中的重要选择靶标。但是,氮素在冠层中的分布调控机理非常复杂,除了光强外,也受其他因素调控,如环境中红光/远红光比例^[41]、植株体内激素^[42]、叶龄^[32]、库源关系^[31]等。在栽培调控措施方面,Hikosaka 等^[34,43-44]的研究表明,高施氮水平能够改善氮

素与光的梯度分布,但是受发育时期影响^[45]。而 Sinclair 等^[46-47]却持不同观点,认为氮肥水平对光、氮的分布没有影响。因此,在生产中栽培措施能否优化光、氮分布,充分利用植株体内氮素与光合效率空间梯度特点,实现作物群体光合效率的最大化,值得深入探讨。鉴于冠层光合的复杂性,冠层中的光、氮分布及其对冠层光合的贡献研究常常借助于模型模拟分析^[27,39,48-50]。同时,植物冠层群体是动态变化的,苗期叶片的快速生长与冠层结构的建成,有利于光的有效截获和花前干物质的积累^[40,51]。开花后作物氮素吸收、分配与植株体内氮素代谢影响着冠层光合持续期长短及其与光温资源的合理匹配,最终决定品种产量潜力是否能充分发挥。以往的作物模型研究结果^[50,52]为定量评价这些因子对提高超级稻产量潜力的影响打下了很好的基础。

综上所述,作者建议从叶片光合生理(光合电子传递、Rubisco 酶含量与活性、气孔与叶肉导度、叶绿体发育状况、磷酸丙糖运转等)、冠层光氮匹配(冠层光氮分布、氮素代谢、激素调控等)和根-冠水分平衡(根茎叶木质部发育、根系导水率、水通道蛋白表达等)这几个方面开展下一步研究,并在此基础上利用模型分析方法为辅助,揭示现代超级稻品种实现产量潜力的关键制约因素及其生理调控基础,并提出相应的栽培调控手段。

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