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水稻对弱光胁迫的响应及适应机制研究进展*

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摘 要: 水稻是我国最重要的粮食作物之一, 光照对其产量和品质形成具有重要影响。随着全球气候恶化, 阴雨寡照天气频发, 随之带来的弱光胁迫已成为影响水稻高产稳产、优质生产的重要限制因素。水稻安全稳定、可持续生产对保障我国粮食安全、满足人们对粮食的需求具有重要意义。因此, 本文对近些年的研究成果进行总结, 综述了弱光胁迫对水稻根茎叶和花器官的形态特征、光合特性、花粉受精、同化物转运和淀粉合成酶的生理特征, 氮代谢、激素调节、光受体调节、抗氧化系统和渗透调节的生化特征, 以及对产量和品质的影响, 重点关注水稻对弱光胁迫的分子响应机制; 并展望未来水稻耐荫性研究的方向和热点, 指出未来要更加深入研究水稻在遗传水平上对弱光胁迫的适应机制以及相关耐荫基因的挖掘。本研究旨在全面了解水稻耐荫分子响应机制, 为选育耐荫品种提供新的思路和策略。

关键词: 水稻; 弱光胁迫; 产量和品质; 形态特征; 生理生化特征; 耐荫基因

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Research progress on the response and adaptation mechanism of rice to low-light stress*

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Abstract: Rice is one of the most important food crops in China, and light has an important effect on its yield and quality. With the deterioration of the global climate, the low light stress brought by the frequent rainy weather has become an important limiting factor affecting the high and stable yield and high quality production of rice. The safe, stable and sustainable production of rice is of great significance to ensure food security and meet people's demand for food. Therefore, this paper summarized the research results in recent years, and reviewed the effects of low light stress on rice morphological characteristics such as roots, stems, leaves and flower organs; physiological characteristics such as photosynthetic characteristics, pollen fertilization, assimilate transport and enzyme activities related to starch synthesis; biochemical characteristics such as nitrogen metabolism, hormone regulation, photoreceptor regulation, antioxidant system and osmotic regulation. The molecular response mechanism of rice to low light stress was emphasized, and the future research direction and hotspot of rice shade tolerance were prospected. In terms of morphological characteristics, shade-tolerant rice varieties can maintain higher root absorption area and α -naphthalamine oxidation capacity under low light stress, increase the content of non-structural carbohydrates and structural carbohydrates in stems, increase stomatal density and photosynthetic

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membrane area in leaf, and reduce stomata, so as to improve photosynthesis. In terms of physiological and biochemical characteristics, the shade avoidance response is regulated by photoreceptors, the content of osmoregulatory substances is increased, and the antioxidant system is activated to remove reactive oxygen species. In terms of molecular response, low light stress can be responded through the expression of shade tolerance genes, light signaling pathway genes and hormone pathway related genes, and the regulation of transcription factors. At present, most studies on shade tolerance of rice focused on the effects of low light stress on growth, yield and quality of rice, but its molecular response mechanism has not been clarified in detail. In this paper, it is pointed out that the adaptation mechanism of rice to low light stress at the genetic level and related shade tolerance genes should be further studied in the future. Studying its molecular regulation mechanism and combining genetic engineering with crop genetics and breeding technology will help us to dig out shade-tolerant genes in rice, select shade-tolerant rice varieties, and further improve cultivation techniques, so as to play a guiding role in actual production. The paper provides theoretical basis and practical basis for high yield, stable yield and high quality cultivation of rice.

Keywords: rice (*Oryza sativa* L.); low-light stress; yield and quality; morphological characteristics; physiological and biochemical characteristics; shade tolerance gene

水稻 (*Oryza sativa* L.) 是我国乃至世界的主要粮食作物之一, 是人类获取能量的重要物质来源, 水稻生产是影响世界粮食安全的重大问题^[1]。水稻生产主要由遗传因素决定, 也会受到环境条件的影响。在实际生产中水稻产量和品质与环境条件紧密联系, 恶劣的环境条件会降低水稻产量和品质, 而弱光胁迫是典型的逆境因素。因此, 弱光胁迫对水稻生产的影响不应忽视^[2]。水稻在生育过程中需要适宜的光照条件, 光照不足将影响水稻生长发育, 导致产量下降和品质变劣^[3-4]。近年来, 随着温室气体排放增加、快速城市化及工业化, 使得环境污染加剧, 阴雨寡照天气频发^[5], 加上大气层污染致使太阳照射到地面的光能逐年减少, 严重的雾霾和气溶胶污染可能会降低 28%~49% 的太阳辐照度^[6]。在我国西南地区, 弱光胁迫已成为制约四川盆地、云贵高原地区水稻生产的主要环境因素^[7]。有研究表明, 弱光胁迫对水稻产量的影响因生育期而不同, 分蘖期、拔节孕穗期和灌浆期遭受弱光胁迫分别减产 17.34%、41.35% 和 53.93%^[7]。在品质方面, Shang 等^[8]研究表明, 灌浆期遭受弱光胁迫使垩白度和垩白粒率分别比对照高 49.5% 和 41.0%, 显著降低了直链淀粉含量、峰值黏度和崩解值, 蛋白含量增加。弱光胁迫破坏淀粉结构, 导致大米的外观品质、蒸煮食味品质变差^[9]。弱光胁迫已成为威胁水稻高产稳产和优质生产的重要因素。因此, 了解弱光胁迫对水稻的影响, 探明水稻在弱光胁迫下的响应机制, 可为筛选耐荫水稻品种, 应对未来气候变化, 减少弱光胁迫对水稻生产的损失, 以及有效利用水稻淀粉结构和热力学特性来改善弱光地区的稻米品质提供有益参考。

植物在面对弱光胁迫时, 有其自身的应答机制, 如避荫 (shade avoidance) 和耐荫 (shade tolerance) 两

种方式。避荫反应是指植物光受体感受到弱光环境中红光和远红光比例的变化后, 引起株高增加、节间伸长和分枝减少等一系列反应。耐荫反应即通过生理的变化来适应弱光环境, 常表现为光合色素含量增加、光合电子传递速率增强、光合酶活性提高等, 以增强对低光量子密度的吸收, 充分利用光能, 并高效地转化为化学能^[10]。水稻在弱光胁迫下通常以避荫的方式来应答胁迫, 其中茎秆伸长和株高增加是典型的表现^[11], 而伸长的茎秆不仅易倒伏, 而且还会消耗过多的碳水化合物而影响产量的形成和品质的降低^[12]。因此, 选育耐荫水稻品种是弱光胁迫下保持高产稳产、优质生产的有效方法。目前虽有部分研究对弱光胁迫下水稻的形态、生理生化和品质的影响进行了总结, 但缺乏系统总结, 尤其是缺乏对水稻耐荫响应分子机制的系统性阐述。因此, 本文对近些年在水稻耐荫响应, 尤其是分子水平方面的研究成果进行了梳理, 为全面了解水稻耐荫响应机制和选育耐荫水稻品种提供参考。

1 弱光胁迫对水稻形态特性的影响

1.1 弱光胁迫对水稻根茎叶的影响

根茎叶是水稻重要的营养器官, 发达的根系, 粗壮的茎秆, 光合高效的叶片, 可为后期籽粒形成积累必要的营养元素和物质。弱光胁迫会对水稻根系的生长、茎叶的形态特征产生影响, 且在不同时期不同程度弱光胁迫的影响不同^[13]。如王丽等^[14]研究表明, 抽穗前进行弱光处理, 根系体积、总吸收面积和活跃吸收面积等指标随着弱光程度的增加而下降, 弱光抑制根系生长; 而始穗后轻度弱光 (53%) 处理则表现相反, 使根冠比增加, 促进根系生长, 表现出对弱光胁迫的积极响应, 始穗后重度弱光 (73%) 处理, 这些指标则降低, 且根系 α -萘胺氧化力下降, 不利于

其根系生长;表明轻度弱光胁迫可能刺激水稻根系防御机制的响应,重度胁迫则造成伤害。活跃的根系活力是水稻适应弱光胁迫的生理基础,有利于其对土壤养分和水分的吸收与利用。耐荫水稻品种在弱光胁迫下其根系能维持较高的根系体积、总吸收面积、根系 α -萘胺氧化力和较大的活跃吸收面积^[14]。因此,这些参数可以作为耐荫水稻品种选育的有效指标。

弱光胁迫会影响水稻茎秆的形态特征和抗倒伏性。据报道,弱光胁迫降低了重穗型水稻基部节间折断弯矩和茎秆的断面模数,增加了植株倒伏风险,且上部节间显著缩短,造成功能叶片密集叠加,导致叶片之间的遮挡,不利于后期群体的高光效^[15],且茎秆下部节间伸长变细,增加株高,导致抗倒伏性差,最终减少产量^[16]。因此,增加基部节间折断弯矩和茎秆断面模数是提高水稻在弱光胁迫下抗倒伏能力的有效方法。移栽到分蘖期遭受弱光胁迫会减少水稻分蘖数,且随着弱光胁迫程度的增加,分蘖进一步减少^[17-18]。拔节到抽穗期弱光胁迫会下调木质素和纤维素生物合成基因对节间伸长的表达水平,导致茎秆结构性碳水化合物(木质素和纤维素)的积累减少,降低茎秆机械强度^[19]。耐荫水稻品种在弱光胁迫下茎秆组织中非结构性碳水化合物(木质素、纤维素和半纤维素)含量增加,茎粗壁厚,以提高其抗倒伏性^[20]。叶片的形态结构对光合性能的调节起着至关重要的作用,适宜的叶片形态结构使植物能够在弱光胁迫下最大限度捕获光能、转化光能,提高光能利用效率。通常情况下水稻遭受弱光胁迫后其气孔密度、大叶脉和小叶脉密度均显著降低,上下表皮的气孔长度和保卫细胞长度都显著增加^[21];但也有研究指出,耐荫性不同的水稻品种叶片结构对弱光的响应不同。耐荫水稻品种在弱光环境下叶色变浅、叶片变薄,而气孔密度增加,剑叶气孔变小,面积变大,有利于气体交换,以提高光合性能^[22]。此外,王丽^[23]对不同水稻品种弱光处理后叶片解剖结构变化的研究表明,弱光处理后非耐荫品种的叶脉变短、叶脉维管束面积显著降低,而耐荫品种则表现相反。在自然条件下,由于叶片相互遮挡和太阳角度、云层的改变,叶片的形态结构会随之发生改变,以尽可能捕获光能^[24]。目前大多数研究表明弱光胁迫会使水稻的叶绿素含量升高,但也有研究得出相反的结论。如戈长水等^[25]研究表明,弱光胁迫下水稻叶绿素含量、比叶重显著降低,而弱光胁迫下水稻叶绿素含量的变化与基因型有关^[26]。抽穗前弱光胁迫会显著提高水稻叶基角、叶开角,披垂度变大^[27],而弱光胁迫

下散射光占主导,因此水稻剑叶的表现利于截获更多的光能,以适应弱光环境。

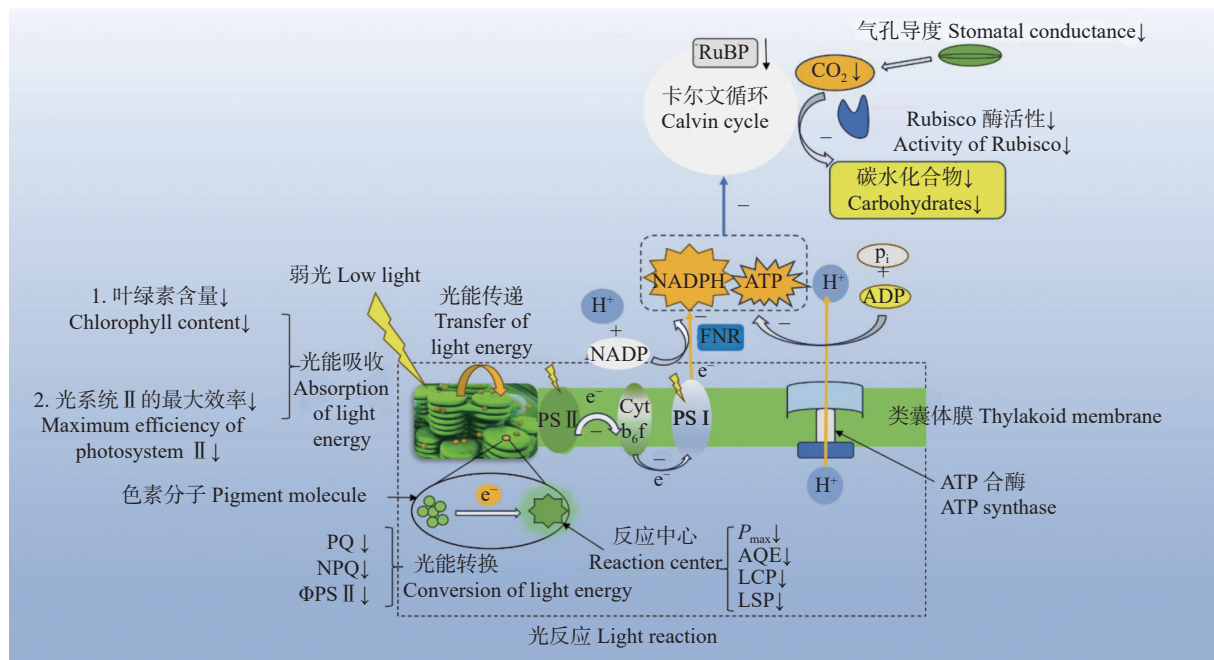
1.2 弱光胁迫对水稻花器官的影响

水稻花器官发育是其生殖生长的重要部分,弱光胁迫严重影响水稻穗部发育和各种生命活动,进而影响产量和品质。水稻在不同生育阶段遭受弱光胁迫都会对其产量构成因子产生不利影响。研究发现,孕穗期遭受弱光胁迫主要影响水稻穗的分化程度,包括枝梗形成和每穗颖花数^[28],以及推迟扬花时期且延长扬花时间^[10]。始穗期遭受弱光胁迫主要造成水稻抽穗推迟和结实率下降^[29]。水稻的花药开裂和花粉管生长易受环境因素的影响,且整个生命活动中在减数分裂期、抽穗扬花期对光照最为敏感^[30]。抽穗扬花期弱光胁迫显著降低了花药开裂率、花粉萌发率,使柱头的花粉粒数量减少,导致产量显著下降^[22]。但目前有关弱光调控水稻花粉管生长鲜有报道,其中的生理机制有待进一步研究。灌浆结实期弱光胁迫会导致每穗颖花数、结实率、千粒重急剧下降,籽粒充实度降低,造成减产^[31]。

2 弱光胁迫对水稻生理特性的影响

2.1 弱光胁迫对水稻光合作用的影响

为了适应弱光环境,植物可以通过提高其光合效率来适应弱光环境^[32]。植物提高光合效率的途径主要基于光反应和暗反应:光反应主要依赖于原初反应的光能捕获、传递、转化,以及光合电子传递和光合磷酸化的高效进行;暗反应主要依赖1,5-二磷酸核酮糖羧化酶/加氧酶(ribulose-1,5- bisphosphate carboxylase/oxygenase, Rubisco)活性、气孔导度和1,5-二磷酸核酮糖(ribulose-1,5- bisphosphate, RuBP)再生能力^[33]。弱光胁迫下这两个反应过程都会受到影响(图1)。原初反应包含光能的吸收、传递和转换,叶绿素荧光特性能够精确反映作物在遭受弱光胁迫时光能吸收和转化效率、电子传递速率等光化学反应过程生理指标的变化^[34]。如原初光能转化效率表示光系统Ⅱ(PSⅡ)反应中心光能捕获率。弱光胁迫下,原初光能转化效率下降,从而降低水稻叶片光化学效率^[25]。有研究表明,耐荫性强的水稻品种在弱光胁迫下原初光能转化效率增加,表明其启动了相应的防御机制,以提高对光能的捕获率^[23]。此外,光能的吸收还与光合色素有关。光合色素在光合作用中起着至关重要的作用,其中叶绿素在光合作用中有着举足轻重的地位。研究光合认为弱光胁迫使水稻叶绿素a(chlorophyll a, Chl a)、叶绿素b(chlorophyll b,



RuBP: 1,5-二磷酸核酮糖; Rubisco: 1,5-二磷酸核酮糖羧化酶/加氧酶; NADPH: 还原型烟酰胺腺嘌呤二核苷酸; ATP: 腺嘌呤核苷三磷酸; NADP: 烟酰胺腺嘌呤二核苷酸; FNR: 光合电子传递链的末端氧化酶; ADP: 二磷酸腺苷; PQ: 光化学猝灭系数; NPQ: 非光化学猝灭系数; $\Phi PS II$: PS II 光化学反应中心实际光化学效率; P_{max} : 最大净光合速率; AQE: 表观量子效率; LCP: 光补偿点; LSP: 光饱和点; -: 抑制; Cyt b_6f : 细胞色素 b_6f ; ↓: 减少。RuBP: ribulose-1,5-bisphosphate; Rubisco: ribulose-1,5-bisphosphate carboxylase/oxygenase; NADPH: nicotinamide adenine dinucleotide phosphate; ATP: adenosine triphosphate; NADP: amidate adenine dinucleotide phosphate; FNR: oxidase at the end of the photosynthetic electron transport chain; ADP: adenosine diphosphate; PQ: photochemical quenching; NPQ: non-photochemical quenching; $\Phi PS II$: actual photochemical efficiency of PS II; P_{max} : the maximum net photosynthetic rate; AQE: apparent quantum efficiency; LCP: light compensation point; LSP: light saturation point; -: restrain; Cyt b_6f : cytochrome b_6f ; ↓: reduce.

图1 弱光胁迫对水稻光合作用的影响

Fig. 1 Effects of low light stress on photosynthesis in rice

Chl b) 和总叶绿素含量增加, 叶绿素 a/b (Chl a/b) 和净光合速率下降, 叶片变薄, 叶色变浅^[35-36]。叶绿素含量增加有利于吸收弱光环境下漫射光中的蓝紫光, 提高对光的捕获和利用能力^[37]; Chl a/b 值降低可提高对光量子的捕获效率^[35]。而朱筱芸^[38]研究表明, 弱光胁迫下剑叶的 Chl a、Chl b 和总叶绿素含量表现为随弱光胁迫强度先升后降; 有研究分析指出造成弱光环境下叶绿素含量变化差异的主要原因是品种差异和弱光处理时间^[39]。因此, 能否将叶绿素含量作为耐荫水稻筛选指标还有待研究。光化学猝灭系数 (photochemical quenching, PQ) 反映 PS II 所捕获的光量子转化为化学能的效率, PQ 越高, 光能转化效率越高; PS II 中光化学反应中心的实际光化学效率 (actual photochemical efficiency of PS II, $\Phi PS II$) 指植物 PS II 在特定环境条件下的光能利用能力^[40]。研究表明, 弱光胁迫下耐荫水稻品种较非耐荫品种能够维持较高的 PQ 和 $\Phi PS II$ ^[23]; 非光化学猝灭系数 (non-photochemical quenching, NPQ) 指植物 PS II 反应中心的天线色素吸收的光能不能用于光合电子传递,

而是以热能的形式被耗散掉, 防止光抑制破坏光合机构^[41]。耐荫水稻品种的 NPQ 低于非耐荫品种^[23]。综上, PS II 反应中心具有较高的光化学猝灭系数、较低的非光化学猝灭系数, 则有利于光反应过程中电荷分离, 使叶片有更高的光能利用率和电子传递速率^[26], 有效缓解弱光引起的光合速率下降^[23]。因此, 较高的叶片实际光化学效率、电子传递速率、光化学猝灭系数和较低的非光化学猝灭系数可以作为筛选耐荫品种的潜在指标。弱光胁迫还会降低最大净光合速率 (maximum net photosynthetic rate, P_{max})、表观量子效率 (apparent quantum efficiency, AQE)、光补偿点 (light compensation point, LCP) 和光饱和点 (light saturation point, LSP), 从而使水稻在弱光下的光合能力下降^[22]。不同水稻品种的净光合速率不同。弱光胁迫下, 低光合速率品种在 50% 的弱光处理剑叶净光合速率比对照品种明显下降^[42], 高光合速率品种在一定时期内能保持较高的表观量子效率^[43]。光合电子传递链由 PS II、细胞色素 b_6f 复合体 (cytochrome b_6f complex, Cyt b_6f) 和光系统 I (PS I) 3 个

复合体串联组成^[44]。在弱光环境下,光系统反应中心的活动减弱,高能电子的产生及电子传递速率降低,导致质子动力驱动腺嘌呤核苷三磷酸(adenosine triphosphate, ATP)和还原型烟酰胺腺嘌呤二核苷酸磷酸(reduced form of nicotinamide-adenine dinucleotide phosphate, NADPH)的合成减弱,进而影响暗反应过程^[45]。光合磷酸化活性是叶绿体在光照条件下形成ATP的能力,光合效率与光合磷酸化活性呈正相关^[46]。光合磷酸化反应过程都需要光的参与,光的强弱影响着光合磷酸化的效率,弱光下可通过假环式光合磷酸化来供应需要额外的ATP^[47]。暗反应阶段水稻的光合生理限制因素包括: Rubisco 酶的活性、气孔导度、RuBP 再生能力。Rubisco 是叶绿体中最为丰富的可溶性蛋白,该酶活性受光的诱导,在转录水平上由核基因编码的小亚基启动子上存在光调节元件。在弱光胁迫下, Rubisco 大小亚基的含量明显减少,阻碍了 Rubisco 的合成,且弱光抑制其活性,从而降低光合速率^[38]。因此,在弱光条件下,为了保持叶片生理特性的稳态,气孔导度会降低^[45],造成CO₂在叶绿体中的浓度降低并导致净光合速率降低,促进光呼吸的形成,增加能量消耗^[48]。此外,当CO₂浓度下降到一定程度时,光合速率主要限制因素转为 RuBP 的再生能力,而弱光胁迫会降低 RuBP 的再生能力^[35]。研究发现, RuBP 的再生能力与 Cyt b₆f 复合体的含量以及 1,6-二磷酸果糖酶的活性(FBPase)密切相关^[49],这为研究如何增加 RuBP 再生能力提供了新的思路。

植物碳同位素分辨率是光照影响植株光合速率、气孔导度等光合活动,从而影响碳同位素组分在植株中分布的参数^[50]。王丽^[23]对杂交水稻对穗后弱光胁迫响应机制的研究表明,弱光胁迫下,各器官特别是茎鞘的净光合速率与成熟期茎鞘碳同位素分辨率呈显著正相关关系,因此,碳同位素分辨率可以作为筛选耐荫水稻品种的潜在指标。

2.2 弱光胁迫对水稻花粉受精的影响

水稻抽穗扬花期是决定产量的关键时期,花粉活力、花药开裂、花粉萌发和花粉管生长是成功授粉的关键,其对产量形成至关重要。因此,抽穗扬花期若遭受弱光胁迫将导致小穗败育和空粒的产生,降低产量^[51]。弱光胁迫通过抑制授粉过程,特别是减少花药开裂和花粉的释放来降低受精率。花期成功授粉归因于雄蕊发育的3个过程,包括:1)花粉成熟,花粉活力高是植物成功受精的生理基础;2)花丝伸长,使花药接近柱头;3)花药开裂,花粉粒从花药中释放出来^[52],并落在柱头细胞上,发生花粉萌发,花粉

管出现并穿过花柱向子房延伸^[53]。弱光影响水稻扬花和花粉受精。Wang 等^[54]利用转录组测序研究了水稻成花基因与弱光胁迫的关系,结果表明,弱光胁迫抑制水稻成花基因 *OsFKF1*、*OsDof12* 和开花位点 1 (RFT1) 的表达水平,抑制了柱头的外露和花粉萌发,降低花药开裂率和花粉活性,使水稻颖花的受精率降低,最终导致结实率显著下降。这与王方^[55]和 Kobata 等^[56]的研究一致。Deng 等^[57]研究也表明,弱光胁迫显著降低了花药的开裂率,导致花粉粒数减少。综上所述,未来应关注弱光胁迫下花药开裂率较高的水稻品种的选育和进一步探究影响水稻花药裂开的生理生化机制。

2.3 弱光胁迫对水稻同化物转运的影响

同化物转运是指植物叶片通过光合作用将二氧化碳固定合成的有机化合物,经各种蔗糖转运蛋白装载和卸载从韧皮部长距离运输到“库”器官(如穗部)的过程^[58]。同化物的高效转运是高产的基础,弱光胁迫不仅影响同化物的转运效率,还会影响其分配。蔗糖转运蛋白(sucrose transporters, SUTs)和己糖和蔗糖转运蛋白(sugars will eventually be exported transporters, SWEETs)是最常见的蔗糖转运蛋白^[59]。同化物的运输主要以蔗糖的形式通过韧皮部进行长距离运输,其整个过程中装载与卸载需要依靠各种转运蛋白的协助来完成^[60]。因此, SUTs 转运蔗糖是逆浓度梯度需要消耗 ATP 的主动转运,而弱光胁迫会阻碍细胞中 ATP 的合成,无法满足主动转运所需的能量供给,从而降低同化物转运效率。此外, *OsDOF11* 转录因子通过促进 *OsSWEET* (*OsSWEET11*、*OsSWEET14*) 和 *OsSUTs* (*OsSUT1*、*OsSUT3*、*OsSUT4*、*OsSUT5*) 的表达编码蔗糖转运蛋白,促进蔗糖在水稻中转运^[61]。弱光胁迫下同化物的转运还与激素调控有关,但在水稻中的研究鲜有报道,进一步研究激素调控籽粒同化物转运的相关作用对于减少弱光胁迫下水稻产量下降具有重要意义。

2.4 弱光胁迫对水稻淀粉合成相关酶的影响

光合产物主要以蔗糖的形式运输到籽粒中,水稻籽粒灌浆充实是淀粉等物质的合成与积累的过程,淀粉积累过程受到淀粉合成相关酶的调控^[62]。灌浆结实期是水稻进行籽粒充实,提高产量的关键时期,在这过程中,光照是不可缺少的条件,弱光胁迫会影响淀粉合成相关酶的活性,导致淀粉含量下降^[63]。淀粉的合成始于葡萄糖-1-磷酸,在腺苷二磷酸葡萄糖焦磷酸化酶(ADP-glucose pyrophosphorylase, AGPase)的催化作用下产生腺苷二磷酸葡萄糖(adenosine

diphosphate glucose, ADPG), 因此, AGPase 是淀粉合成限速酶。随后蔗糖合成酶 (sucrose synthase, SS) 以 ADPG 为底物, 在淀粉体中合成葡聚糖链, 一方面由淀粉分支酶 (starch branching enzyme, SBE) 和颗粒结合型淀粉合成酶 I (granule bound starch synthase I, GBSS I) 合成支链淀粉, 另一方面在可溶性淀粉合成酶 (soluble starch synthase, SSS) 和颗粒结合型淀粉合成酶 II (granule bound starch synthase II, GBSS II) 的作用下进行直链淀粉的合成^[64], 之后 SBE 负责将直链淀粉转化为支链淀粉^[65]。SBE 包括: 可溶性淀粉分支酶 (可溶性 Q 酶) 和颗粒结合型淀粉分支酶 (颗粒结合型 Q 酶)。水稻在灌浆结实期遭受弱光胁迫, 腺苷二磷酸葡萄糖焦磷酸化酶、蔗糖合成酶、可溶性淀粉合成酶和颗粒结合型淀粉合成酶活性降低, 导致淀粉合成受阻^[66], 但淀粉分支酶活性反而升高^[67], 是因为直链淀粉在总淀粉量中的占比减少所导致^[63]。鉴于此, 淀粉合成相关酶的活性受弱光胁迫影响, 使籽粒淀粉形成受到阻碍。

3 弱光胁迫对水稻生化特性的影响

3.1 弱光胁迫对水稻氮代谢的影响

氮代谢是涉及植物体内含氮化合物的分解、合成与再利用的重要代谢过程, 与产量和品质密切相关。水稻在生育后期氮代谢显著增强^[68]。硝酸还原酶 (nitrate reductase, NR) 不仅是氮代谢过程的限制性关键酶和限速酶, 还是一种光诱导酶, 因此光照强度对 NR 活性影响很大^[69]。高等植物氮同化途径主要由谷氨酰胺合成酶 (glutamine synthetase, GS) 和谷氨酸合成酶 (glutamate synthase, GOGAT) 构成循环反应, 在氮素利用及氮同化过程中起重要作用^[70]。有研究指出, 弱光胁迫下 NR 和 GS 活性随着弱光程度的增加而逐渐降低^[71]。转氨基作用是植物体内重要的氮代谢过程, 这一过程最主要的转氨酶有谷氨酸-草酰乙酸转氨酶 (glutamic-oxaloacetic transaminase, GOT) 和谷氨酸-丙酮酸转氨酶 (glutamic-pyruvic transaminase, GPT)。有研究指出, GOT 和 GPT 的活性随着弱光程度的增加而增加, 从而促进转氨基作用, 适应弱光环境^[71]。弱光胁迫下, 氮的分配也会受到影响。弱光胁迫使分配到叶片、茎鞘中的氮素增加, 而分配到穗中的氮素减少, 此时作物合成含氮化合物主要用于叶片、茎鞘的生长^[72], 以维持水稻植株生长。

3.2 弱光胁迫对水稻激素的影响

植物激素是植物自身代谢产生的小分子有机化

合物, 细胞的分裂、伸长、分化乃至生根、发芽、开花、结实、胁迫应答都受到植物激素的调控^[73]。不同程度的弱光胁迫对水稻秧苗内源激素含量的影响不同。据报道, 弱光胁迫下, 主要通过脱落酸 (abscisic acid, ABA)、生长素 (indole acetic acid, IAA)、赤霉素 (gibberellin, GA) 以及油菜素内酯 (brassinolide, BR) 来调控避荫反应^[74]。其中, 弱光胁迫程度增大, ABA 含量呈上升趋势, 说明弱光胁迫下可以诱导水稻产生抗逆激素 ABA^[75]。拔节期弱光处理导致 GA 含量升高, 株高增加^[76]。水稻可通过激素信号通路基因表达来应答胁迫, 缓解弱光胁迫带来的伤害^[77]。弱光胁迫下, 生长素响应基因 *IAA19* 被诱导表达^[78]; IAA 合成关键基因 *YUCCAs*, 包括 *YUC2/3/5/8/9* 迅速诱导合成生长素, 促进叶片的生长, 因此耐荫水稻品种通过促进 IAA 信号转导途径中相关基因的表达来提高耐荫性^[79]。DELLA 蛋白家族是 GA 信号通路中重要的负调控因子, DELLAs 通过和光敏色素互作因子 PIFs 互作, 使转录因子的 APA 或 APB 结构无法与 DNA 结合, 从而调控下游基因的表达, 诱导弱光下 GA 的合成, 促进 DELLAs 的降解, 解除对 PIFs 的抑制作用, 进一步调控避荫反应^[80]。细胞分裂素通路基因在植物避荫反应中起到积极作用。细胞分裂素介导信号传导涉及双组分信号磷酸介质和组氨酸磷酸转移蛋白以及不同的反应调节因子。弱光胁迫下, 组氨酸磷酸转移蛋白基因 *PHP3*、A 型反应调节因子 *RR9* 介导细胞分裂素通路基因的表达, 如介导 *OsCKX11*、*LOGL3* 基因对穗发育的正调控^[81]。此外, *OsbHLH153* 是一种油菜素类固醇信号通路基因, 可调控水稻旗叶角, 以提高弱光胁迫下光合效率^[82]。

3.3 弱光胁迫对水稻光受体的影响

光不仅为植物光合作用提供光量子, 还作为一种信号物质, 调控植物的生命活动。植物中能感受到光信号, 引发相应细胞反应的一类生物大分子物质称为光受体。完善的光受体系统可以感受来自环境中的光信号, 调整合适的生理状态以更好地适应环境和生长发育, 主要包括光敏色素受体 (phytochrome, phy)、隐花色素 (cryptochrome, cry)、向光素 (phototropin, phot) 和 ZTL 家族蛋白以及 UV-B 受体。光敏色素基因家族有 *PHYA*、*PHYB*、*PHYC*、*PHYD* 和 *PHYE*, 分别编码对应的光敏色素蛋白。在水稻基因组中只存在 *PHYA*、*PHYB* 和 *PHYC*。*PHYA* 的表达可以通过增强生长素信号早期响应因子 *AUX/IAA* 的稳定性来负向调控弱光胁迫^[83], *phyA* 与 *phyB* 共同调控水稻花药发育和花粉活力, 水稻 *phyA* 还可

通过极低辐照度反应(very low fluence response, VLFR)介导光形态建成,以适应弱光环境^[84]。蓝光受体包括隐花色素、向光素和 ZTL 受体。*CRY2* 基因编码隐花色素蛋白 cry2, 主要调控光周期诱导的开花反应, 其可抑制 *OsCRY1a* 基因的表达, 推迟水稻开花期^[85]。ZTLs 家族属于蓝光受体蛋白, 包括 ZTL/FKF1/LKP2, 水稻可通过基因表达来提早扬花以躲避逆境, 如 *Os-FKF1* 主要通过上调 *Ehd2* 和下调 *Ghd7* 表达, 激活 Ehd1-Hd3a/RFT1 通路, 提早扬花避开弱光胁迫^[86]。在光信号通路中鉴定出的基因在耐荫水稻品种的成穗中上调表达, 如 *BBX* 基因和促进开花的 *FLT6*、*FACTOR1* 和控制开花时间的 *COL4*、*COL5* 和 *COL3*^[87], 使水稻在弱光下成穗。

3.4 弱光胁迫对水稻抗氧化系统的影响

长期弱光胁迫下, 水稻会积累活性氧(reactive oxygen species, ROS), 包括单线态氧、 H_2O_2 和 $O_2^{\cdot-}$, 其含量过高且无法被及时清除则会损伤结构, 发生毒害作用^[88]。植物体内活性氧的清除主要依赖于酶促和非酶促机制。酶促机制在细胞水平上的抗氧化物酶的活性强弱, 直接关系到 ROS 的清除效率。抗氧化酶有超氧化物歧化酶、过氧化物酶、过氧化氢酶、抗坏血酸过氧化物酶、谷胱甘肽过氧化物酶和单脱氢抗坏血酸还原酶, 这些酶相互协作清除植物体内多余的活性氧与自由基, 使植物内膜系统稳定平衡^[89]。弱光胁迫下不同水稻品种的超氧化物歧化酶、过氧化物酶和过氧化氢酶的活性水平存在差异, 可相互协调以清除 ROS^[90]。弱光胁迫使耐荫性强的品种抗坏血酸过氧化物酶、谷胱甘肽过氧化物酶和单脱氢抗坏血酸还原酶的活性仍维持在一定水平, 以清除体内积累的 ROS 和自由基^[91-92]。非酶促机制主要包括: 抗坏血酸、谷胱甘肽、 α -生育酚、类胡萝卜素、黄酮类化合物和生物碱等^[93], 对水稻活性氧的清除十分重要。

3.5 弱光胁迫对水稻渗透调节的影响

细胞的生命活动依赖于稳定的渗透环境, 以维持细胞内环境的稳态。渗透调节物质在维持细胞动态平衡当中发挥重要作用。水稻长期遭受弱光等胁迫, 当其体内 ROS 的积累到一定程度时, 产生膜脂过氧化作用, 最终产生丙二醛, 丙二醛的大量积累, 会导致植株的相对电导率增加, 膜透性增加, 细胞膜系统破坏, 电解质外渗加剧^[94], 对细胞造成不可逆伤害。研究表明, 耐荫水稻能够保持较低的丙二醛含量和相对稳定的细胞膜的结构和功能^[95]。脯氨酸作为一种亲和性渗透调节物质, 在应激过程中可作为抗氧

化防御分子和信号分子^[96], 水稻脯氨酸转运蛋白家族基因(*OsProT*)中 *OsProT1* 主要在营养生长阶段的叶鞘中表达, *OsProT2* 主要在剑叶中表达, *OsProT3* 主要在穗中表达, 协同转运脯氨酸分配到水稻不同部位^[97], 以维持细胞与环境的渗透平衡。因此, 脯氨酸含量可作为选择耐荫水稻品种的潜在指标。此外, 弱光胁迫下, 水稻还通过增加叶片可溶性蛋白质和可溶性糖含量来适应弱光环境^[98]。

4 弱光胁迫对水稻产量和品质的影响

水稻在生育期不同阶段遭受弱光胁迫都会影响产量的形成。前人研究^[99-100]表明, 弱光胁迫不利于产量形成, 其中拔节孕穗期、抽穗扬花期和灌浆结实期是易受逆境危害的敏感时期。水稻产量构成因子由单位面积有效穗数、每穗颖花数、结实率和千粒重构成^[101]。弱光胁迫显著降低水稻产量, 主要原因是单位面积有效穗数、每穗粒数和千粒重降低^[15]。抽穗后遭受弱光胁迫严重阻碍了水稻籽粒的充实过程(特别是穗下部), 造成空粒增加^[23,102]。耐荫水稻品种减产幅度显著小于敏感型水稻品种^[103]。因此, 水稻产量构成因子可作为耐荫水稻材料选育的产量指标。不同时期遭受弱光胁迫对水稻产量影响不同^[36,104]。水稻分蘖期弱光胁迫显著减少植株的有效分蘖^[99], 孕穗期则主要影响穗的分化, 抽穗扬花期主要影响授粉受精^[105], 齐穗期和灌浆结实期主要影响籽粒灌浆结实, 导致结实率和千粒重下降^[105]。从生理角度来说, 弱光胁迫虽然使水稻叶片变薄, Chl a 和 Chl b 含量增加, Chl a/b 值降低, 但降低了 Rubisco 和 Rubisco 活化酶的活性, 导致净光合速率降低, 最终导致减产^[106-107]。水稻产量的形成主要由花前储藏的非结构性碳水化合物转运再利用和花后光合产物的直接供给所决定^[105], 其中杂交水稻产量 90% 来自花后光合产物供给^[108]。弱光胁迫降低了齐穗后水稻节间的非结构性碳水化合物积累量, 使各节间非结构性碳水化合物转运量降低^[105]。

水稻遭受弱光胁迫不仅会影响产量, 还会影响稻米品质。稻米品质又可分为碾米品质、蒸煮和食味品质、外观品质和营养品质。普遍研究^[109-112]认为: 弱光胁迫会使水稻的糙米率、精米率和整精米率降低; 但也有研究认为弱光胁迫可以显著提高整精米率^[27,113], 其原因是弱光胁迫使水稻颖壳体积变小, 接受同化物能力减弱, 籽粒获得了良好的充实, 使得籽粒容重增加, 从而提高了整精米率^[114]。弱光胁迫会使水稻垩白粒率和垩白度增加^[66], 同时籽粒蛋

白质含量增加,这是由于水稻在灌浆结实期遭受弱光胁迫会促进叶片中的可溶性蛋白向籽粒中运输,促进籽粒的蛋白质合成,但直链淀粉含量、糊化温度、胶稠度降低^[115]。此外,淀粉 RVA 谱特征和热力学特征与稻米食味品质密切相关,水稻淀粉 RVA 谱是指一定量的米粉在快速加热和冷却过程中其米浆的黏滞性所表现的一系列变化特征。因此,淀粉 RVA 谱特征值是评价稻米食味品质优劣的重要指标。有研究指出,食味品质好稻米的峰值黏度、胶稠度和崩解值较大,消碱值绝对值较小,糊化温度较低^[116]。随着光照强度的减弱,峰值黏度、最终黏度、崩解值逐渐降低,消碱值绝对值变大、糊化温度升高^[117-119]。淀粉热力学特性是反映作物籽粒淀粉品质的重要指标之一^[120],其中淀粉回生度与米饭适口性呈负相关,回生度越高,米饭会越硬,适口性也越差^[121]。在弱光胁迫下淀粉回生度显著增加,从而降低了稻米品质^[67]。综上,稻米直链淀粉含量和胶稠度以及峰值黏度和崩解值等可作为耐荫水稻材料选育的品质指标^[103]。

5 水稻耐荫胁迫的分子响应机制

水稻耐荫基因的筛选可通过耐荫基因家族、耐荫相关转录因子来鉴定。现代分子生物学已广泛应用于作物育种,分子标记辅助选择技术(MAS)与QTL结合可有效提高优良品种的选育效率。耐荫性是一个受多基因表达共同调控的数量性状,在选育耐荫水稻品种时可通过分子标记多个QTL定位,从中发掘耐荫基因,再通过生物技术和分子标记辅助选择进行杂交,以获得耐荫水稻品种。例如将药用野生稻(*Oryza officinalis*)总DNA导入‘恢复系R225’中,通过测定耐光氧化指数,最终筛选到耐荫、耐光氧化的3个导入系,并发现标记RM219和RM5490很可能与耐荫QTL位点紧密连锁^[122]。

OsSUTs 基因家族中的 *OsSUT1/2/4* 的表达对弱光胁迫响应明显,弱光胁迫下这3个基因表达上调,使其上游序列中的顺式元件G-box和ACE参与弱光胁迫的应答^[123]。*MicroRNAs* 对水稻在避荫反应中发挥重要作用,调节其对各种环境胁迫的反应^[124-125]。*MicroRNAs* (*miRs*) 是长度为21~24个核苷酸的非编码RNA。*miRs* 对耐荫性的调节主要包括 *miRs* 本身的失活,导致其靶标上调,弱光胁迫会诱导 *MicroRNAs* 中的 *miR5144-5p* 的差异表达以及对 *OsWD40-24* 的靶向切割,能对水稻在弱光胁迫下产量的维持起调节作用;*miRs* 的靶标 *OsSLAC*、*OsLOG1* 的表达正调控穗长,*OsBRITTLE1-1* 表达促进籽粒形成,*OsC-*

sIF9 降低茎的机械强度,*OsGns9*、*OsCPI1* 和 *Osahlh-153* 促进弱光下花粉发育^[39]。水稻重组自交系(BILs)通过控制 *miR2877*、*miR530-5p* 和 *miR396h* 靶基因的表达,促进其籽粒的灌浆过程^[126]。*OsCesA* 基因家族属于纤维素合成基因,在水稻茎秆中表达,*OsCesA4*、*OsCesA7*、*OsCesA9* 编码次级细胞壁中纤维素合成,在弱光胁迫下,其表达上调,合成纤维素,增强茎秆机械强度,防止植株倒伏导致减产^[19]。

NAC、HD-Zip、PIF4 转录因子可调控水稻对弱光胁迫的应答。NAC 转录因子是植物中与逆境相关的转录因子家族,在其C端含有1个转录结构域,具有转录激活和抑制的功能,可调控下游次生壁中纤维素、半纤维素和木质素的合成,提高水稻抗倒伏能力^[82]。此外,亮氨酸拉链蛋白(homeodomain-leucine zipper protein, HD-Zip) 转录因子通过响应外界信号,在避荫反应中参与维管束的分化过程,提高水稻植株抗倒伏能力^[76]。水稻中 *WSL214* 通过激活过氧化氢酶基因 *OsCATC* 的表达,使细胞内清除 ROS 的酶系活性提高^[127]。水稻染色质重塑因子 *OsINO80* 表达促进 ABA、乙烯、BR 等植物激素的合成来正向调控避荫反应^[128]。水稻 *OsGAPB* 基因过表达可提高 CO₂ 的利用率,增加叶绿素含量和提高光合速率以促进水稻在弱光胁迫下的光合作用^[129];光敏色素互作因子(phytochrome interacting factors, PIFs) 属于 bHLH 家族的第15亚族,作为光敏色素介导的光信号传导途径的枢纽,在调控植物的生长发育和信号转导中发挥重要作用。PIFs 家族成员可通过 APA 结构域与光敏色素 A (phyA) 相结合来调控植物的形态建成^[130]。在弱光胁迫下,生长素响应因子 ARF18 的表达水平被 PIFs 抑制,阻碍了生长素合成途径以调控弱光胁迫下叶片生长和植物代谢^[131],以促进植物的耐荫性。*OsPIL15* 基因过表达正调控叶鞘长度、叶角大小和气孔密度,防止叶片之间相互遮挡^[132]。PIFs 还可以与 MIR156 启动子的 G-box 基序结合,抑制多种 *mir156* 基因家族的表达,从而显现出更强的避荫反应^[133]。Jiang 等^[134] 通过 QTL 分析发现,PIF3、PIF4、PIF7 可以与耐荫反应负调节因子 PRR5 和 PRR7 相互作用,实现对其的转录抑制,防止植物因茎秆过细弯曲致死。

综上所述,培育耐荫品种是应对弱光胁迫最有效的方法,未来要更加深入研究水稻在遗传水平上对弱光胁迫的适应机制以及挖掘相应的耐荫基因。这不仅对水稻育种工作具有重要意义,更有利于水稻实际生产应用。明确弱光胁迫下水稻的分子响应

机制和构建水稻耐荫性评价体系^[135], 对于选育耐荫水稻品种意义重大。虽有耐荫相关基因被鉴定出来, 但仍有大量潜在基因等待挖掘(表 1)。

6 总结与展望

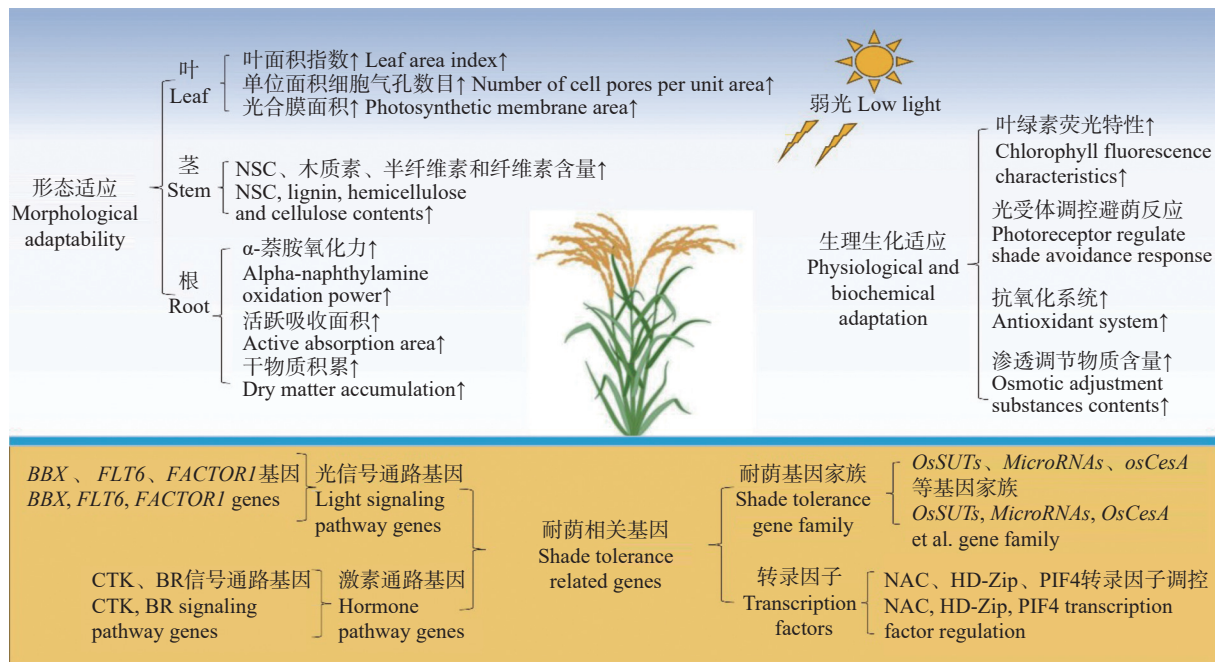
随着持续阴雨寡照天气的频发, 弱光胁迫对水稻产量及稻米品质的影响不容忽视, 选育耐荫水稻品种是保证粮食安全的重要任务。因此, 研究弱光胁迫对水稻形态、生理生化特征的影响及其分子适应机制对水稻高产稳产、优质生产至关重要。根系总吸收面积、根系活力和根系 α -萘胺氧化力、茎基部节间折断弯矩和断面模数、叶角开度、气孔密度和剑叶面积可作为水稻耐荫性选育的形态特征指标; 叶片实际光化学效率和电子传递速率、光化学猝灭系数、非光化学猝灭系数, 以及成熟期植株碳同位

素分辨率可作为水稻耐荫性选育的生理特征指标; 脯氨酸含量、抗氧化酶的含量及活性可作为水稻耐荫性选育的生化特征指标。相关耐荫转录因子的超表达可提高水稻植株的耐荫性, 对 QTL 的精细定位有助于挖掘新的耐荫基因。因此, 完善水稻的耐荫响应机制和发现新的耐荫基因是保障全球粮食安全的主要根基(图 2)。

目前, 有关水稻的耐荫性研究多侧重于弱光胁迫对水稻生长发育、产量和品质的影响, 而对其分子调控应答路径鲜有报道, 其分子响应机制还未得到详细阐明, 且目前对水稻是如何在蛋白质组学、代谢组学和多基因组学上的应答机制未形成体系^[130], 这也是今后水稻耐荫性研究的热点方向。研究其分子调控机制, 将基因工程和作物遗传育种技术有机结合, 有助于我们挖掘水稻耐荫相关基因, 选

表 1 水稻耐荫基因表达及其调控方式
Table 1 Shade tolerance related genes and their modes of regulation

基因 Gene	编码蛋白 Coding protein	调控影响 Regulatory influence	调控方式 Control method	文献 Reference
耐荫反应相关基因 Shade tolerance genes				
<i>RGA1</i>	G蛋白 α 亚基 G protein alpha subunits	正向调控 Positively regulate	提高ATP产生效率 Improve ATP production efficiency	[92]
<i>OsWRKY42</i>	WRKY转录因子 WRKY transcription factor	正向调控 Positively regulate	提高防御相关基因表达 Increased expression of defense-related genes	[136]
<i>MicroRNA</i>	RNA结合蛋白HYL1 RNA binding protein HYL1	负向调控 Negatively regulate	降解HYL1, 激活沉默基因启动弱光反应 HYL1 was degraded and the silencing gene was activated to initiate shading response	[137]
籽粒形成相关基因 Genes related to seed formation				
<i>OsSUT1</i>	蔗糖转运蛋白 Ucrose transporter protein	正向调控 Positively regulate	促进蔗糖分子转运 Promote sucrose molecular transport	[123]
<i>OsBT1</i>	ADP-葡萄糖转运蛋白 ADP-glucose transporter protein	正向调控 Positively regulate	正调控籽粒形成 Positive regulation of seed formation	[138]
<i>OsCIN3</i>	细胞壁转化酶 Cell wall invertase	正向调控 Positively regulate	正调控蔗糖卸载 Positive regulation of sucrose unloading	[139]
植物激素相关基因 Plant hormone related genes				
<i>OsGA20ox1</i>	GA20氧化酶 GA20 oxidase	正向调控 Positively regulate	提高赤霉素含量 Increase gibberellin content	[140]
<i>YUCCAs</i>	YUCCA转录因子 YUCCA transcription factor	正向调控 Positively regulate	提高生长素(IAA)含量 Increase indole acetic acid content	[141]
光信号相关基因 Light signal related genes				
<i>PHYA</i>	phyA蛋白激酶 phyA protein kinase	负向调控 Negatively regulate	抑制油菜素内酯合成及信号转导 Inhibition of brassinolide synthesis and signal transduction	[126]
<i>OsPIL1</i>	PIL转录因子 PIL transcription factor	正向调控 Positively regulate	增加节间细胞大小, 促进节间伸长 Increase internode cell size and promote internode elongation	[142]
叶绿体合成相关基因 Chloroplast synthesis related genes				
<i>OsClpP6</i>	Chla相关蛋白 Chla-related proteins	正向调控 Positively regulate	促进叶绿素a合成 Promote chlorophyll a synthesis	[143]
<i>OsCAOI</i>	Chlb相关蛋白 Chlb-related proteins	正向调控 Positively regulate	促进叶绿素b合成 Promote chlorophyll b synthesis	[144]
<i>OsPORA</i>	还原型烟酰胺腺嘌呤二核苷酸磷酸 NADPH	正向调控 Positively regulate	催化原叶绿素酸酯还原成叶绿素酸酯 Catalyze the reduction of protochlorophyllin ester to chlorophyllin ester	[145]



PIFs: 光敏色素互作因子; HD-Zip: 亮氨酸拉链蛋白转录因子; CTK: 细胞分裂素; BR: 油菜素甾醇; ↑: 增加; NSC: 非结构性碳水化合物。PIFs: phytochrome interacting factors; HD-Zip: homeodomain-leucine zipper protein; CTK: cytokini; BR: brassinosteroids; ↑: increase; NSC: non-structure carbohydrate.

图2 水稻对弱光胁迫的响应机制
Fig. 2 Response mechanism of rice to low light stress

育耐荫水稻品种,同时进一步完善栽培技术措施,以期在实际生产中起指导作用,为水稻高产、稳产、优质栽培、保障国家粮食安全提供理论依据和实践基础。

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