



# “绿色革命”新进展：赤霉素与氮营养双重调控的表观修饰助力水稻高产高效育种

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**摘要** 以半矮秆育种为代表的“绿色革命”极大地提高了作物产量, 但也带来氮营养利用效率降低的严重问题。“绿色革命”主要基于调控赤霉素的代谢和信号转导而实现。前期的研究发现, 赤霉素信号转导关键因子DELLA蛋白通过调控GRF4而负调控氮素的吸收利用, 为半矮秆品系氮利用效率低的问题提供了解决方案。最近的一项研究进一步揭示了GA信号途径与氮响应交叉互作的新机制。该研究发现水稻(*Oryza sativa*) *NGR5*是氮素调控分蘖数目的一个关键基因, 其表达受氮诱导。通过招募PRC2, *NGR5*对*D14*和*OsSPL14*等分蘖抑制基因所在位点进行H3K27me3甲基化修饰, 从而抑制其表达。而在半矮秆背景下超表达*NGR5*可以提高低氮水平下的水稻产量。*NGR5*同时也被发现为赤霉素受体GID1的一个新靶标, 受到其负调控。该研究发现了调控赤霉素信号通路的新机制, 并对高产高效的新一代“绿色革命”育种实践具有重要启示。

**关键词** 水稻, 分蘖数, 氮利用效率, 组蛋白修饰

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氮素是植物蛋白质、叶绿素以及激素等重要物质组分, 因此氮素营养是植物生长发育及作物产量最重要的限制因素之一(Crawford and Forde, 2002)。20世纪初, Haber-Bosch合成氨技术的成功使得农作物生产中大规模施用氮肥成为可能, 因此世界粮食产量得以迅速提高。然而, 氮肥增多也带来作物营养过剩、植株徒长和容易倒伏的问题, 有时甚至导致产量下降。为了解决这一问题, 20世纪中叶出现了以半矮化育种为主要特征的农业“绿色革命”(Green Revolution), 不仅解决了高肥情况下的倒伏问题, 也促进光合产物向籽粒分配, 进一步促进了谷类作物的产量提升(Khush, 1999; Pingali, 2012)。

“绿色革命”中的半矮秆育种主要通过调控植物激素赤霉素(gibberellin, GA)的代谢和信号转导来实现。活性GA与其受体蛋白GID1 (GIBBERELLIN INSENSITIVE DWARF1)结合后促进后者与生长抑制转录因子DELLA蛋白互作, 使DELLA蛋白能被

SCF (Skp, Cullin, F-box)泛素连接酶复合体泛素化, 并进入26S蛋白酶体中降解(Sasaki et al., 2003; Murase et al., 2008; Shimada et al., 2008; Harberd et al., 2009)。水稻(*Oryza sativa*)矮秆育种主要利用赤霉素合成酶基因*SD1*的突变, 该基因突变导致赤霉素不能正常合成, 从而抑制水稻生长, 产生半矮秆表型(Sasaki et al., 2002; Spielmeyer et al., 2002)。而小麦(*Triticum aestivum*)中利用的半矮秆基因*Rht1*则是DELLA蛋白编码基因的一个显性突变座位, 该显性突变使其编码的DELLA蛋白难以被降解, 从而使DELLA蛋白在细胞中积累, 进而产生半矮秆性状(Peng et al., 1999; Zhang et al., 2014)。

半矮秆水稻品种株高较低、抗倒伏性强, 但同时也存在一个显著缺陷, 即氮的吸收和利用效率显著降低(Gooding et al., 2012)。该缺陷导致其最大产量潜力必须依靠施用大量氮肥来实现, 使农民不得不大量增加化肥施用量, 增加农业生产成本的同时还

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加剧了氮肥流失, 导致土壤酸化和水系富营养化等一系列环境问题(Kong et al., 2008; Guo et al., 2010)。理解株高与氮素利用效率正相关的分子机制, 进而使两者解偶联, 无疑是进一步解决产量与氮素利用效率矛盾的关键。2018年, 中国科学院遗传与发育生物学研究所傅向东课题组在攻克这一问题上取得突破性进展, 他们探明水稻株高与氮素正相关的原因在于DELLA蛋白在控制株高的同时也控制氮素的吸收和同化(Li et al., 2018)。该研究进一步表明, 水稻生长调节因子GRF4 (GROWTH-REGULATING FACTOR 4)可与GIF1 (GRF-INTERACTING FACTOR 1)结合, 并激活下游氮素吸收和同化相关基因, 而DELLA蛋白则抑制GRF4与GIF1的结合。因此当DELLA蛋白积累时, GRF4与GIF1的互作被抑制, 氮素的吸收和同化也因此降低。此外, GRF4还促进碳

同化相关基因的表达, 通过调节碳氮平衡提高水稻氮素利用效率和产量(Li et al., 2018)。

最近, 傅向东课题组又在水稻赤霉素与氮素响应方面取得重要进展(Wu et al., 2020)。他们通过筛选以半矮秆品种9311为背景的EMS突变体库, 得到1个分蘖数目减少的氮不敏感突变体*ngr5* (*nitrogen-mediated tiller growth response 5*)。图位克隆和遗传互补实验显示, *NGR5*编码1个AP2 (APETALA2)结构域转录因子。不同于对照株系随着氮供应的增加分蘖数目和产量都相应增加的表型, *ngr5*突变体的分蘖数目和产量在不同氮水平下都无显著变化, 表明氮促进水稻分蘖的调控依赖于*NGR5*。进一步研究发现, 氮响应的*NGR5*通过招募PRC2 (POLYCOMB REPRESSIVE COMPLEX 2)对*D14* (*Dwarf14*, 编码植物激素独脚金内酯的受体蛋白)和*OsSPL14* (编码SQU-

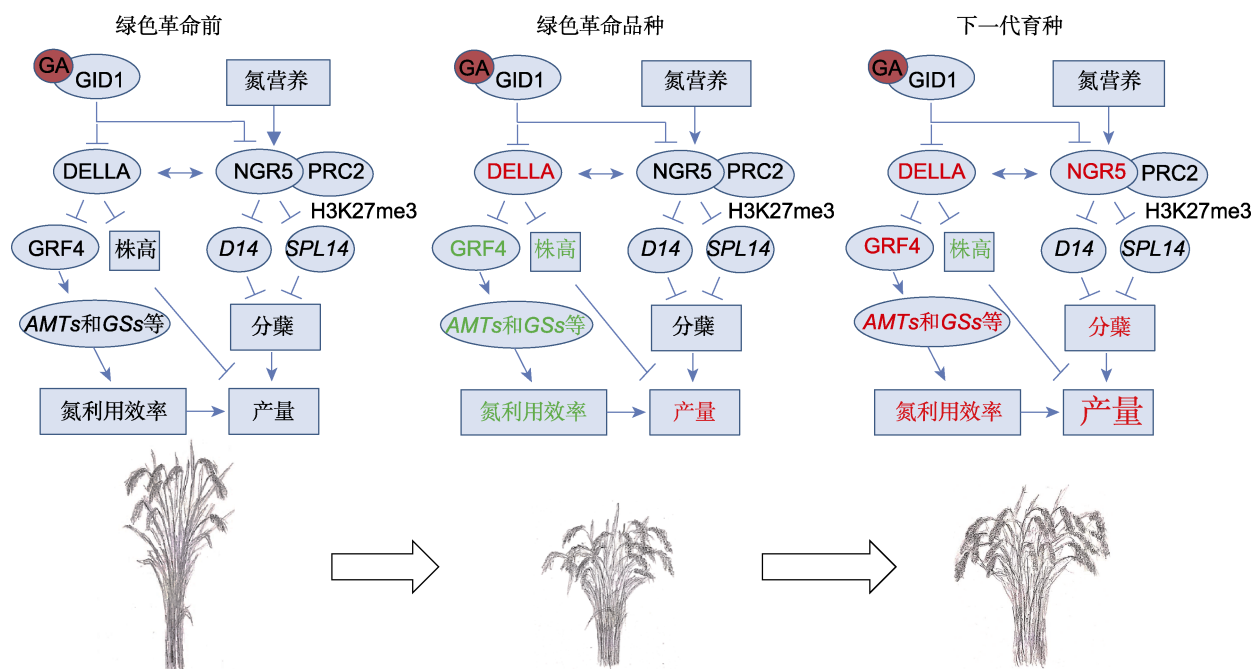


图1 “绿色革命”和下一代育种靶标及分子机制

在“绿色革命”中, 抑制GA信号通路导致DELLA蛋白积累, 产生半矮秆表型, 但同时也抑制GRF4的活性进而降低植物氮利用效率。GRF4以及NGR5为下一代高产高效的育种目标提供了优秀的靶点。增强它们的活性可以兼顾高产和营养高效, 突破以肥增产的瓶颈。红色及大号代表增加, 而绿色和小字号代表降低。

Figure 1 The targets and molecular mechanisms of Green Revolution and next generation breeding

In Green Revolution, suppression of GA signaling leads to accumulation of DELLA protein that results in semi-dwarf phenotype, but it also inhibits activity of GRF4 and subsequently decreases nitrogen use efficiency of crops. GRF4 and NGR5 provide excellent targets for next generation breeding which aims to crops with high nitrogen use efficiency and high yield. Improvement of these two genes helps to achieve yield with low nitrogen input and break through the bottle neck of fertilizer dependent yield increasing. The font size and color of the characters represent increase (red and larger font) or decrease (green and smaller font).

AMOS PROMOTER BINDING PROTEIN LIKE-14 转录因子)等分蘖抑制基因所在位点进行H3K27me3 甲基化修饰,从而抑制其表达,并促进水稻分蘖。

NGR5不仅受到氮的诱导,同时也被GA信号负向调控。研究发现,类似于DELLA蛋白,结合活性GA的GID1亦可与NGR5直接结合,并促进NGR5蛋白的泛素化降解。但无论在DELLA蛋白缺失突变体还是在高积累突变体中,NGR5蛋白的降解依然发生,表明NGR5的降解可能不依赖于DELLA蛋白的降解。然而,水稻中DELLA蛋白SLR1也可直接与NGR5互作,且该互作对于GID1与NGR5的互作具有竞争作用,从而减弱NGR5的降解。上述结果表明,除了传统的GA-GID1-DELLA信号通路外,还存在一条依赖于NGR5的重要GA信号调控通路,完善了我们对于GA信号转导的认知。研究者进一步找到了1种NGR5的单倍型,将其在含半矮秆基因的9311品系中过表达,可实现在不改变半矮秆表型的情况下提高水稻产量和氮利用效率。此外,在9311中同时过表达2个GA信号及氮利用偶联因子基因(*GRF4*和*NGR5*)可进一步提高水稻产量,尤其在低氮供应条件下,显示出全面挖掘GA信号和氮利用偶联因子的重要应用意义。

Wu等(2020)的研究工作不仅首次发现了H3K27me3组蛋白修饰参与氮营养促进的分蘖过程,揭示了一条全新的GA信号转导通路,同时也进一步阐明了GA信号通路与氮素分配利用交叉的关键分子机制,为进一步推进“绿色革命”高产高效的目标提供了新的靶点(图1)。因此,该研究不仅是植物激素信号转导、植物发育生物学和植物营养学交叉的典范,也为降低氮肥施用的同时提高水稻产量提供了一种策略,更为进一步找到更多关键因子、促进新一代“绿色革命”早日到来夯实理论基础。

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## A New Progress of Green Revolution: Epigenetic Modification Dual-regulated by Gibberellin and Nitrogen Supply Contributes to Breeding of High Yield and Nitrogen Use Efficiency Rice

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**Abstract** The Green Revolution represented by the breeding of semi-dwarf crops greatly promoted agriculture yield, but it also unfortunately led to the problem of low nitrogen use efficiency (NUE). The achievement of Green Revolution was mainly based on modification of gibberellin (GA) metabolic or signaling pathways in crops. A previous study has found that the central regulator of GA signaling pathway DELLA protein negatively regulates NUE through suppressing GRF4, an essential NUE regulator, which provided a resolution for improving NUE of semi-dwarf rice. A recent study further revealed a novel mechanism underlying the crosstalk between GA signaling and nitrogen response. The study revealed that *NGR5* is a key gene controlling tiller number changes under different nitrogen conditions, which is inducible by nitrogen. Further investigation established that the *NGR5* suppresses branching inhibitory genes, such as *D14* and *OsSPL14*, through nitrogen-dependent recruitment of polycomb repressive complex 2 that promotes histone H3 lysine 27 tri-methylation in the regions harbouring the branching suppressors. In addition to be responsive to nitrogen, *NGR5* is also negatively regulated by GA and its receptor GID, and overexpression of *NGR5* in the semi-dwarf background is thus able to significantly improve rice yields under low nitrogen conditions. This study not only uncovered a new mechanism of GA signaling, but also enlightens the new generation of Green Revolution by breeding high yield crops with enhanced NUE.

**Key words** rice, tiller number, nitrogen use efficiency, histone modification

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