

# 水稻抗倒伏性状的分子机理研究进展

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## Advances in Molecular Understanding of Rice Lodging Resistance

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**Abstract:** Rice lodging is a serious problem impairing grain yield. Plant stature, culm structure and cell wall components play major roles in shaping rice lodging resistance. Genomic and genetic dissection of rice has generated insightful information into mechanistic elucidation of the rice lodging resistance. Here, we summarize the recent advances in molecular understanding of the lodging resistance in association with rice stature, culm character and chemical composition of cell walls. The knowledge helps to establish new molecular strategies for breeding rice varieties with enhanced lodging resistance properties.

**Key words:** rice; lodging; cell wall; culm

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**摘要:** 倒伏是水稻高产稳产的一个重要限制因素。水稻倒伏主要受植株形态、茎秆结构与细胞壁成分的影响。近年来,随着水稻基因组学和分子生物学的发展,水稻抗倒伏性状的研究已逐渐从植株表型分析发展到分子水平调控机理解析。本文综述了水稻株型、茎秆特性与细胞壁化学组成对水稻抗倒伏性状影响的分子机理。这些研究为水稻抗倒伏分子育种奠定了重要的理论基础。

**关键词:** 水稻; 倒伏; 细胞壁; 茎秆

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倒伏是影响水稻高产的主要限制因素之一。水稻倒伏多发生在谷粒灌浆后期,此时贮藏在水稻茎鞘中的光合产物与营养物质向籽粒中转移,造成茎秆机械强度下降,最终导致水稻茎秆从直立状态到倒伏状态。水稻倒伏可分为弯曲型倒伏(culm bending-type lodging)、挫折型倒伏(culm breaking)和扭转型倒伏(root lodging)<sup>[1]</sup>。弯曲型倒伏指作用于茎秆的负荷尚未达到使茎秆折断的强度,在穗重或风雨的作用下水稻上部节间呈弯曲状态。挫折型倒伏指当作用于茎秆的负荷超过抗折强度时,茎秆下部折断引起的倒伏,主要受茎秆结构及细胞壁化学组成的影响。扭转型倒伏是指水稻根系不发达不能支撑地上部的重量从而被直接从土壤中拔出的茎秆基部倒伏现象,多发生在直播稻中。水稻倒伏后,

植株生长状态变差,叶片光合效率锐减,光合产物运输受阻,最终导致产量降低<sup>[2]</sup>。

20世纪60年代,以作物矮化育种为目标的绿色革命使矮秆基因被广泛用于水稻抗倒伏品种的选育,曾为解决水稻倒伏问题发挥了关键作用。传统的矮秆品种由于自身生物量积累较少,进一步提高产量受到较大限制。随着超高产水稻品种的选育与推广,倒伏问题再次引起育种家重视。相关研究表明,水稻株型、茎秆结构、细胞壁化学成分是影响倒伏的主要因素<sup>[3,4]</sup>。随着分子生物学的发展,对水稻抗倒伏研究已从表型分析逐渐深入到抗倒伏性状QTL定位及相应分子机理的阐明。本文对该方面研究进展进行综述。

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## 1 水稻抗倒伏相关株型性状基因

### 1.1 株高

株高是影响水稻倒伏的重要因素之一,与倒伏指数呈显著正相关<sup>[5]</sup>。20世纪60年代作物育种的绿色革命即携带 *sd1* 半矮秆基因的品种取代传统的高秆品种,从而降低了节间长度和茎秆高度,提高了水稻的耐肥抗倒性,使粮食产量得到大规模提升<sup>[3]</sup>。*SD1* (*semi dwarf 1*) 编码赤霉素(gibberellic acid, GA)合成途径中的 GA<sub>20</sub>氧化酶,催化 GA<sub>53</sub> 转换为 GA<sub>20</sub>,是调控赤霉素合成的关键酶。该基因的变异导致赤霉素合成受阻,细胞伸长受到抑制<sup>[6-8]</sup>。*SD1* 基因具有明显的组织表达特异性,主要在茎秆中表达,含有 *sd1* 基因的矮秆品种只降低株高,产量不受影响<sup>[7,8]</sup>。利用 *SD1* 等位变异基因,生产上培育了大量的抗倒伏矮秆水稻品种<sup>[9,10]</sup>。虽然赤霉素合成受阻可以使水稻植株矮化从而提高抗倒伏性,但矮化植株无法在生物量积累上获得突破。Okuno等<sup>[11]</sup>研究水稻 GA 缺失突变体及 GA 过量合成突变体抗倒伏性及生物产量的结果显示,GA 缺失突变体株型偏矮,很少发生弯曲型倒伏,但容易发生挫折型倒伏且生物产量减少;GA 过量合成植株较易发生弯曲型倒伏,但木质素含量增加及茎秆增粗,抗挫折型倒伏的能力得到了增强,同时生物产量增加。因此,适当增加株高对增强茎秆抗倒伏能力及增加水稻生物学产量均有利。

### 1.2 分蘖夹角

分蘖夹角体现了水稻空间占有情况,若分蘖夹角过大,植株呈匍匐状生长,抗倒伏能力差,产量低;分蘖夹角适当减小,植株茎秆直立,抗倒伏能力增强,有利于水稻高产稳产<sup>[12]</sup>。在长期进化与栽培过程中,控制水稻分蘖夹角的基因受到了人工选择。*PROG1* (*PROSTRATE GROWTH 1*) 基因编码一个含有锌指结构的核转录因子,其蛋白序列 T152S 的氨基酸替换是栽培稻与野生稻相比分蘖夹角减小的主要原因<sup>[13,14]</sup>。*TAC1* (*tiller angle control 1*) 基因控制现有栽培稻分蘖角度,该基因表达量与分蘖角度正相关<sup>[15,16]</sup>。具有紧凑株型的粳稻该基因第4内含子3'端剪切位点处基因序列由“agga”突变为“ggga”,导致该内含子在 mRNA 加工过程中不能正常剪切,3'非翻译区改变,mRNA 稳定性降低,分蘖夹角减小<sup>[15,16]</sup>。Li等<sup>[17]</sup>利用水稻大分蘖夹角突变体克隆到基因 *LAI* (*LAZY1*),该基因通过调节生

长素的极性运输来调控水稻地上部的向重性,从而影响水稻分蘖角度的大小。*OsTB1* (*teosinte branched 1*) 是一个作用于独脚金内酯(strigolactones)下游的基因,编码 TCP 家族的一个转录因子,抑制水稻侧芽的生长,负调节水稻分蘖数<sup>[18-20]</sup>。包含 *OsTB1* 等位基因 *SCM3* (*strong culm 3*) 的水稻品种分蘖数虽然减少,但颖花数目增多、茎秆强度增大<sup>[21]</sup>。因此,适当减小分蘖夹角与分蘖数并不会造成减产,反而会使植株抗倒伏性增强而增加生物学产量。

### 1.3 穗型

同时改良穗型与抗倒伏性的基因对于水稻增产具有重要价值<sup>[22]</sup>。*DEP1* (*DENSE PANICLE 1*) 基因是控制我国北方粳稻直立穗型的主效基因<sup>[23,24]</sup>。该基因突变后促进细胞分裂,减小穗长并使稻穗变密、枝梗数增加、每穗籽粒数增多,从而促进水稻增产 15%~20%<sup>[23,25]</sup>。而具有直立穗型的粳稻品种茎秆抗折力增大,抗倒伏性显著增强<sup>[26]</sup>。*LP* (*large panicle*)/*EP3* (*erect panicle 3*) 基因编码一个 F-box 蛋白质,可能参与形成 SCF 复合体调节细胞分裂素氧化酶的蛋白水平<sup>[27,28]</sup>。该基因突变体一次枝梗数与每穗粒数增多,茎秆壁加厚,大小维管束数量增多,厚壁细胞层数增加,茎秆机械强度增大<sup>[28,29]</sup>。*OsAPO1* (*aberrant panicle organization 1*) 基因也编码一个 F-box 蛋白质,正调节水稻一次枝梗数目和维管束形成<sup>[30,31]</sup>。携带该基因功能获得型等位基因 *SCM2* (*Strong Culm 2*) 的近等基因系茎秆强度增大的同时每穗粒数增多,产量增加<sup>[32]</sup>。因此,将这些能同时改善穗型与茎秆强度的基因进行合理的聚合与应用,无疑会是调节高产与抗倒伏矛盾的有效途径。

### 1.4 其他株型性状

水稻理想株型育种策略之一是适当增加株高以提高生物学产量,但同时必须增强植株的抗倒伏能力<sup>[33,34]</sup>。研究表明,通过改变 *OsmiR156* 对 *OsS-PL14* 基因的调控可以塑造出既高产又抗倒伏的水稻理想株型<sup>[35,36]</sup>。*OsSPL14* (*SOUAMOSA PROMOTER BINDING PROTEIN-LIKE 14*)/*IPA1* (*ideal plant architecture 1*)/*WFP* (*WEALTHY FARMER'S PANICLE*) 基因编码一个植物特有的转录因子,是 *OsmiR156* 的直接作用靶标,并参与调控水稻株型与穗型的发育<sup>[37]</sup>。该基因 *OsmiR156* 靶点处的一个点突变干扰了 *OsmiR156* 对 *OsS-*

*PL14* 的调控,使水稻分蘖数减少、每穗粒数和千粒重增加,同时茎秆变粗壮,抗倒伏能力增强<sup>[35,36]</sup>。编码 *OsmiR156* 前体的基因 *OsmiR156h* 的功能获得型突变体 *sdt* 中 *OsmiR156* 成熟体表达水平增加,使水稻分蘖数增多、植株变矮、抗倒伏性增强<sup>[38]</sup>。通过聚合 *sdt* 基因与 *sd1* 基因,使水稻产量在目前超级稻的基础上提高了 20%<sup>[38]</sup>。由此可见,将调控株型基因进行合理聚合对于培育水稻高产抗倒伏新品种具有重要意义。

## 2 水稻抗倒伏相关茎秆性状基因

### 2.1 茎秆物理特性

水稻茎秆支撑着水稻植株的重量,因此茎秆形态及强度决定了植株的抗倒伏性<sup>[3,4]</sup>。Kashiwagi 和 Ishimaru<sup>[39]</sup>通过对 Nipponbare 与 Kasalath 杂交组合后代茎秆相关表型分析,找到 5 个与抗压力相关的 QTL 和 6 个与茎秆直径相关的 QTL,并发现多个茎秆直径相关 QTL 的组合可能会提高水稻茎秆强度及抗倒伏能力<sup>[40]</sup>。Hirano 等<sup>[41]</sup>对水稻茎秆抗折突变体 *smos1* (*small organ size 1*) 进行研究,发现秆壁厚度对水稻抗倒伏也起到重要作用。*SMOS1* 基因编码一个 AP2-type 转录因子,通过生长素依赖形式调节细胞伸展。*smos1* 基因突变导致细胞延展能力下降,但细胞数目却增多,秆壁厚度与茎秆直径明显增加,导致茎秆抗折力增大<sup>[42]</sup>。目前,*smos1* 基因已被用于厚壁粗秆抗倒伏水稻品种的培育<sup>[42]</sup>。刘慧娟等<sup>[43]</sup>研究发现叶鞘包裹茎秆增强了茎秆的物理强度,且位于第 4 染色体上 RM548—RM6997 区间的 QTL 是同时调控水稻叶鞘长、干质量及叶鞘厚的主效基因座。

### 2.2 茎秆化学成分

水稻属于喜硅作物,其植株中  $\text{SiO}_2$  含量高达 20%<sup>[44]</sup>。编码水稻硅转运蛋白基因的突变体植株地上部分硅含量降低,对病虫害很敏感,产量受到严重影响<sup>[45-47]</sup>。水稻茎秆基部秆壁厚度和抗折力与茎秆  $\text{SiO}_2$  的含量显著相关<sup>[48]</sup>;施加硅肥后,水稻茎秆粗壮、机械强度增大<sup>[49]</sup>;且抗倒伏能力强的水稻品种茎鞘中硅含量明显高于抗倒伏能力弱的品种<sup>[50]</sup>。

水稻灌浆后期茎秆中贮藏物质的多少对维持茎秆强度有重要作用<sup>[50]</sup>。Kashiwagi 等<sup>[39]</sup>鉴定到一个与水稻茎秆下部节间抗压力相关的主效 QTL *prl5*。该位点能够在籽粒干物质形成后减缓叶绿体退化、延迟叶片衰老,使茎鞘中碳水化合物重新积

累;从而提高亲本茎秆下部节间的干质量、碳水化合物的含量及密度,增强茎秆抗压力<sup>[51]</sup>。Ishimaru 等<sup>[52]</sup>鉴定到一个与水稻茎秆上部节间抗压力相关 QTL *lrt5*;该位点能够增加水稻倒 2 叶的叶绿体数量,进而提高茎秆上部节间的淀粉含量;茎秆密度与茎秆直径也相应增大,抗压力增强,使茎秆上部节间在遭受台风袭击后仍然保持相对直立。

## 3 水稻抗倒伏相关次生细胞壁性状基因

次生细胞壁是决定水稻茎秆机械强度的物质基础,其成分结构与水稻抗倒伏性直接相关<sup>[53]</sup>。作为次生细胞壁主要成分之一的纤维素的含量与茎秆抗折力密切相关<sup>[54]</sup>。水稻次生细胞壁纤维素合酶单体 *OsCESA9* 与 *OsCESA4* 的错义突变会直接导致次生细胞壁纤维素合成受阻、含量下降,茎秆易折断<sup>[55-57]</sup>。而其他一些基因突变也会间接影响次生细胞壁纤维素合成从而降低水稻抗倒伏能力。水稻动力蛋白基因 *OsDRP2B* 突变会导致水稻植株纤维素含量下降 28%~36%,从而使厚壁组织次生细胞壁变薄,茎秆机械强度减弱<sup>[58]</sup>;水稻类几丁质酶基因 *BC15/OsCTL1* 的突变会引起茎秆厚壁细胞纤维素含量降低,次生细胞壁变薄,茎秆机械强度严重下降<sup>[59]</sup>;编码水稻 UDP-葡萄糖核糖转运因子的基因 *BC14* 错义突变会引起细胞壁多糖糖基合成缺陷,次生细胞壁纤维素合成受阻,从而导致植株机械强度降低<sup>[60]</sup>;水稻糖基转移酶 *BC10* 可通过调节细胞壁纤维素合成和阿拉伯半乳糖蛋白含量来控制水稻植株机械强度<sup>[61]</sup>。水稻 MYB 转录因子 *Os-MYB103L* 可以调控纤维素合成酶基因(*CesAs*)的表达水平,进而使植株纤维素含量及茎秆强度发生改变<sup>[62]</sup>。Huang 等<sup>[63]</sup>对不同类型水稻 GA 突变体的研究表明,水稻 DELLA 蛋白 SLR1 可以与正调控水稻 CESA 表达的转录因子 NAC29/31<sup>[64]</sup> 互作,促进 NAC29/31 的降解从而抑制 *CesA* 基因的表达。当 GA 存在时,抑制作用被解除,*OsCesA* 基因表达量升高,纤维素含量增加,茎秆强度增大。纤维素的结晶化程度及微纤丝排列方向的改变也会间接造成次生壁的变化进而影响植株抗倒伏性<sup>[65]</sup>。*BC1* 基因编码一个胞外磷脂酰肌醇(GPI)锚定 COBRA 蛋白<sup>[66]</sup>,其 N 端碳水化合物结合结构域(CBM)可以特异结合结晶态纤维素,通过调节纤维素微纤丝结晶度来影响次生细胞壁的薄厚及茎秆机械强度<sup>[67]</sup>。水稻驱动蛋白基因 *kinesin-4* 缺失突变

体 *bc12* 中细胞骨架微管排列方向紊乱,纤维素微纤维沉积方向改变,次生细胞壁变薄,茎秆机械强度下降<sup>[68]</sup>。

次生细胞壁半纤维素含量的变化也会引起茎秆机械强度的改变<sup>[54]</sup>。 $\beta$ -(1,3)-(1,4)葡聚糖是禾本科植物特有的半纤维素多糖,负责合成该类多糖的类纤维素合酶 F(OsCSLF) 亚家族的主效基因 *CS-LF6* 突变体中  $\beta$ -(1,3)-(1,4)葡聚糖含量显著降低,幼苗及成熟期茎秆细胞壁变得脆弱,茎秆机械强度明显降低<sup>[69-70]</sup>。Li 等<sup>[71]</sup>通过对 36 株不同水稻细胞壁突变体次生壁成分与抗倒伏关系的研究,发现纤维素结晶度与水稻植株抗倒伏性呈负相关,而半纤维素阿拉伯糖可能通过与纤维素  $\beta$ -(1,4)葡聚糖发生交联后负调纤维素结晶度从而提高水稻的抗倒伏性。

次生细胞壁木质素含量的变化同样会造成水稻茎秆机械强度改变,水稻对香豆酸辅酶 A 连接酶是木质素单体合成过程中关键酶<sup>[72]</sup>;编码水稻对香豆

酸辅酶 A 连接酶(4-coumarate:CoA ligase,4CL)基因 *Os4CL3* 的表达量下调的植株大部分发生矮化且茎秆强度显著低于野生型<sup>[73]</sup>。肉桂醇脱氢酶(cinnamyl alcohol dehydrogenase,CAD)在木质素单体合成过程中最后一步将醛类中间产物进一步还原为相应的木质醇<sup>[74]</sup>。编码水稻肉桂醇脱氢酶的基因 *OsCAD7* 突变后,肉桂醇脱氢酶活性显著降低,木质素含量下降、细胞壁变薄,最终导致该突变体茎秆机械强度减弱<sup>[75]</sup>。Ookawa 等<sup>[76]</sup>从另一个水稻肉桂醇脱氢酶突变体 *gh2/OsCAD2*<sup>[77]</sup>与粗秆品种水稻杂交后代中选育出木质素单体含量偏低但茎秆粗壮的抗倒伏品种。这些研究为水稻抗倒伏分子育种提供了重要的基因资源<sup>[65]</sup>。

#### 4 结语

培育抗倒伏能力强的水稻品种是实现水稻高产稳产所面对的重要课题。矮化品种的推广曾为解决水稻倒伏问题发挥了重要作用<sup>[78]</sup>,但世界人口总数

表 1 已知水稻抗倒伏基因

Table 1. Reported Lodging resistance genes in rice.

与抗倒伏相关表型性状 Phenotype related to lodging resistance	基因名称 Gene name	TIGR 基因编号 TIGR gene code	基因功能注释 Gene function annotation	参考文献 Reference	
株型 Plant architecture	<i>SD1</i>	LOC_Os01g66100	Gibberellin 20 oxidase 2	[6-8]	
	<i>PROG1</i>	LOC_Os07g05900	C2H2 zinc finger protein	[13-14]	
	<i>TAC1</i>	LOC_Os09g35980	Expressed protein	[15-16]	
	<i>LA1</i>	LOC_Os11g29840	Expressed protein	[17]	
	<i>OsTB1/FC1/SCM3</i>	LOC_Os03g49880	TCP family transcription factor	[18-21]	
	<i>DEP1</i>	LOC_Os09g26999	Keratin-associated protein 5-4	[23-25]	
	<i>LP/EP3</i>	LOC_Os02g15950	OsFBK5-F-box domain and kelch repeat containing protein	[27-29]	
	<i>OsAPO1/SCM2</i>	LOC_Os06g45460	OsFBX202-F-box domain containing protein	[30-32]	
	<i>IPAI/WFP/OsSPL14</i>	LOC_Os08g39890	SBP-box gene family member	[35-37]	
	<i>SDT</i>	LOC_Os06g44034	OsmiR156h microRNA precursor	[38]	
	茎秆 Culm	<i>SMOS1</i>	LOC_Os05g32270	AP2 domain containing protein	[41-42]
		<i>LSH</i>	LOC_Os02g51110	Silicon influx transporter	[45]
		<i>LS12</i>	LOC_Os03g01700	Silicon efflux transporter	[46]
		<i>LS16</i>	LOC_Os06g12310	Silicon influx transporter	[47]
<i>PRL5</i>		Uncloned	Unknown	[51]	
<i>LRT5</i>		Uncloned	Unknown	[52]	
次生细胞壁 Secondary cell wall	<i>BC6</i>	LOC_Os09g25490	OsCESA9-cellulose synthase	[55]	
	<i>BC7/BC11</i>	LOC_Os01g54620	OsCESA4-cellulose synthase	[56-57]	
	<i>BC3</i>	LOC_Os02g50550	Dynamain	[58]	
	<i>BC15/OsCTL1</i>	LOC_Os09g32080	CHIT13-chitinase family protein precursor	[59]	
	<i>BC14/OsNST1</i>	LOC_Os02g40030	Golgi-localized nucleotide sugar transporters	[60]	
	<i>BC10</i>	LOC_Os05g07790	Glycosyltransferase family protein	[61]	
	<i>OsMYB103L</i>	LOC_Os08g05520	MYB-like DNA-binding domain containing protein	[62]	
	<i>OsNAC29/OsSWN2</i>	LOC_Os08g02300	NAC transcription factor	[64]	
	<i>BC1</i>	LOC_Os03g30250	COBRA-like protein precursor	[66-67]	
	<i>BC12</i>	LOC_Os09g02650	Kinesin motor domain containing protein domain of unknown function 266	[68]	
	<i>CSLF6</i>	LOC_Os08g06380	CSLF6-cellulose synthase-like family F; beta1,3;1,4 glucan synthase	[69-70]	
	<i>Os4CL3</i>	LOC_Os02g08100	4-coumarate-CoA ligase	[72-73]	
	<i>OsCAD7/FC1</i>	LOC_Os04g52280	Cinnamyl alcohol dehydrogenase	[74-75]	
	<i>OsCAD2/gh2</i>	LOC_Os02g09490	Cinnamyl alcohol dehydrogenase	[76-77]	

不断增长对粮食产量提出了新要求。传统的矮秆品种由于自身生物量积累较少,进一步提高产量受到较大限制。增加株高可以提高生物学产量,但株高增加又会引入新的倒伏问题,为了保证现有生物学产量不变就必须增强植株的抗倒伏能力<sup>[33]</sup>,对抗倒伏性状分子调控机理的解析就显得非常重要。如表1所示,影响水稻抗倒伏性的基因相继被克隆并进行了功能解析,这些基因除控制株高外,还包括控制分蘖夹角、茎鞘内化学元素和可溶性糖含量、茎秆厚壁组织层数及次生细胞壁组成与结构等。其中一些关键基因在高产抗倒伏品种选育中也已得到成功应用,如 *DEP1* 基因已成功用于我国北方粳稻直立穗型高产抗倒伏品种的选育<sup>[23-24]</sup>。对 *OsmiR156* 与 *OsSPL14* 基因关系的解析对于水稻理想株型育种也具有重要应用价值<sup>[35-38]</sup>。另外,水稻根系结构对抗倒伏的影响也受到了关注,一些相关基因也得到了鉴定和克隆<sup>[79]</sup>。因此,未来对水稻抗倒伏的研究应进一步结合分子遗传方法,挖掘有利于提高水稻抗倒伏能力的基因,全面系统解析水稻抗倒伏性状的分子机制,构建抗倒伏性状的分子调控网络,在此基础上通过分子标记辅助育种方法将有利于水稻抗倒伏的不同基因进行聚合,从而选育出更多高产抗倒伏的优良水稻品种。

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