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# 稻米品质的遗传研究及分子育种进展

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**摘要** 水稻是我国最主要的粮食作物之一,高产优质不仅是水稻基础研究的重点,更是水稻育种应用的主要方向。稻米品质主要包含加工碾磨品质、外观品质、蒸煮食味品质和营养品质,是受遗传与环境因素共同影响的复杂性状。本文对稻米品质性状的分类、影响因素、遗传研究进展和稻米品质育种改良现状进行了综述,并对稻米品质研究进行总结和展望,以期对稻米品质遗传改良以及优质稻品种培育提供指导。

**关键词** 稻米;外观品质;加工碾磨品质;营养品质;感官食味品质;遗传改良;分子育种;优质稻

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水稻作为我国超过 60%人口的主要能量来源,在保障我国粮食安全和促进农业发展上占据着重要地位。自新中国成立以来,我国水稻在经历了半矮秆化、杂种优势的利用以及绿色超级稻的培育后,产量达到了质的飞跃。随着社会的发展,我国已经基本实现从“吃不饱”到“吃得饱”再到以“吃得好”为目标的重大转变。2019年,指导“三农”工作的中央一号文件明确指出要深入推进优质粮食工程,要推进农业由增产转向为提质。因此,研究和改良稻米的品质具有十分重要的意义。

稻米品质是由遗传与环境因素共同影响的复杂性状,它不仅是决定稻米是否好吃的关键,也是决定消费者喜爱度以及稻米市场价格的重要因素<sup>[1]</sup>。此外,随着人们健康意识的提高,具有保健作用的糙米以及有色米越来越受欢迎<sup>[2-3]</sup>。从消费者的角度看,优质稻米是指好看、好吃且营养健康的稻米;而从育种家的角度来看,优质稻则需符合我国优质稻米国家标准(下文简称国标)。国标经过多次修改,所包含的指标要求也逐渐提高(表 1)。国标要求的提高,一方面促进了科学家进行稻米品质相关的研究,另一方面也加快了优质稻培育的速度。截至目前,已有大批品质相关基因被克隆,稻米品质的影响因素也得到了一定解析,优质稻的培育也取得了显著的成果<sup>[4-5]</sup>。

本文对稻米品质性状的分类和影响因素进行了简要的介绍,重点介绍了稻米品质性状的遗传研究进展,分析了我国优质稻米研究的现状,并探讨了分子育种和基因编辑育种在稻米品质改良上的应用现状以及前景,以期对稻米品质的深入研究和稻米品质的遗传改良提供一定的思路和借鉴价值。

## 1 稻米品质性状分类与影响因素

### 1.1 稻米品质性状的分类

稻米从种植到最终食用涉及多个过程,其生产、加工、烹饪以及最终食用都与稻米的品质密切相关。为了便于研究,通常将稻米品质划分为加工碾磨品质、外观品质、感官食味品质和营养健康品质<sup>[6]</sup>。

加工碾磨品质不仅是稻米生产上最重视的品质,还是优质稻谷评价的重要性状(表 1),一般包含 3 个指标:糙米率、精米率和整精米率。糙米率也称为出糙率,是指净稻谷脱壳后糙米占试样质量的百分比。精米率是指糙米加工碾磨成一定精度的大米占供试稻谷质量的百分比,整精米率则是指精米长度达到完整米粒平均长度 2/3 的精米质量占供试稻谷质量的百分比。

外观品质是最直观的品质性状,消费者肉眼就能进行分辨,主要包括稻米粒形、垩白和透明度,其

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中粒形和垩白是最重要的外观品质性状(图 1A、B)。粒形是指稻米的粒长、粒宽、粒厚和长宽比;垩白是指稻米中白色不透光部分,可以根据垩白的部位将垩白分为腹白、心白和背白(图 1B),生产上会根据垩白占的比率和垩白在米粒中的面积大小,即垩白率和垩白度表征垩白情况(表 1)。

稻米的感官食味品质是稻米作为食品最重要的品质性状,主要是指稻米蒸煮品质以及米饭的外观、香味、口感等,通常用直链淀粉含量、糊化温度(ge-

latinization temperature,GT)(碱消值,alkali digestion value)、胶稠度、黏度特性和食味值来表征。稻米的直链淀粉含量(amylose content,AC)一般在 0~30%。糊化温度是指稻米中淀粉遇水完成糊化变成半透明胶状所需的温度,或者是淀粉晶体丧失双折射性时的温度。胶稠度(gel consistency,GC)是指稻米糊化冷却后于水平放置的试管中延伸的凝胶长度。黏度特性是指米饭蒸煮过程的黏度变化,利用快速黏度分析仪(rapid viscosity analyzer,RVA)

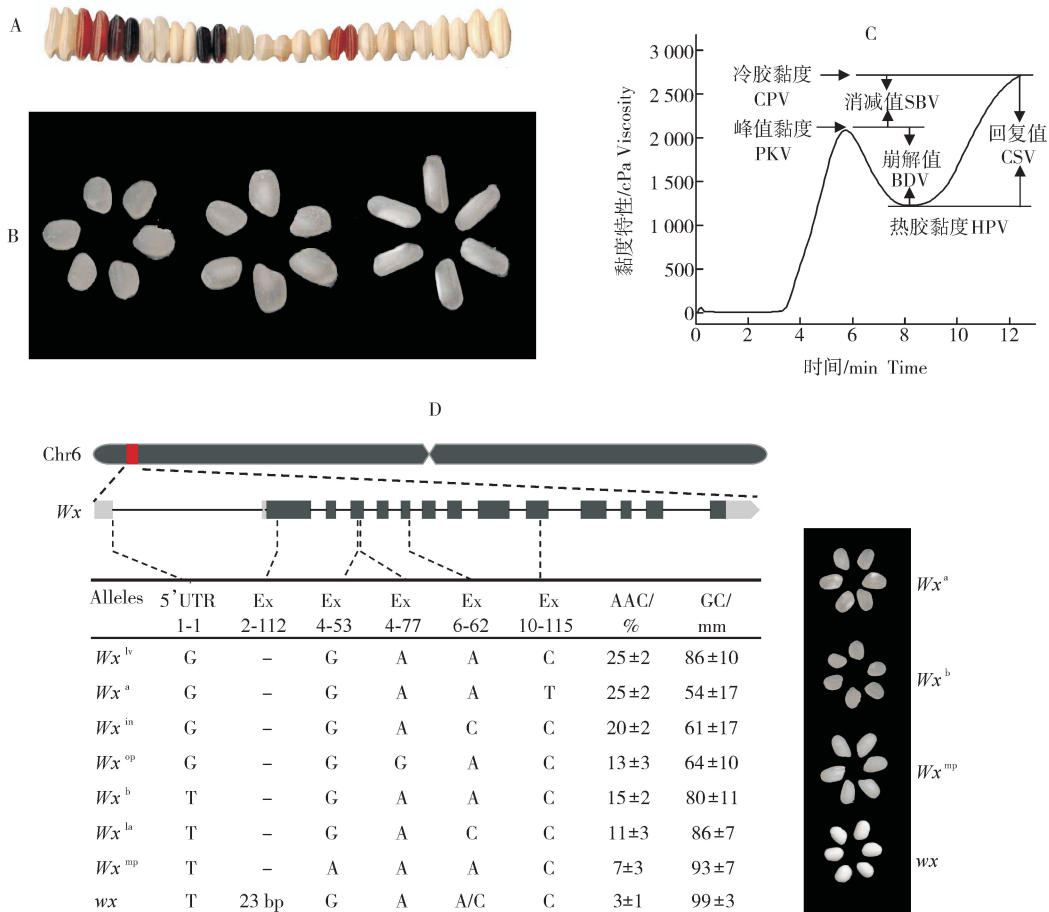


图 1 糙米外观品质、RVA 曲线及 *Wx* 的自然变异  
 A: 糙米的外观品质; B: 精米垩白表型, 左为无垩白, 中间为心白, 右为腹白; C: 精米粉的 RVA 曲线; D: 栽培稻 *Wx* 的不同等位型与对应表型。A: The appearance of brown rice; B: The chalky phenotype of milled rice, grains in the left circle represent the grains without chalk, grains in the middle circle represent white core, the grains in the right circle represent white belly; C: The RVA plot of milled rice powder; D: The different *Wx* alleles in cultivated rice and the corresponding phenotype. PKV: Peak viscosity; HPV: Hot viscosity; CPV: Cold viscosity; BDV: Breakdown viscosity; SBV: Setback viscosity; CSV: Consistence viscosity; AAC: Apparent amylose content; GC: Gel consistency.

图 1 糙米外观品质、RVA 曲线及 *Wx* 的自然变异  
 Fig.1 The appearance quality, RVA plot of rice and the natural variation of *Wx*

分析并绘制黏度曲线(图 1C)。食味值是品尝人员对米饭的气味、外观结构、适口性、滋味和冷饭质地的综合评分。

稻米的营养健康品质是稻米营养品质的扩展,

既包含稻米中的有益营养元素,也包含对稻米中有害健康物质的限制。稻米中有益健康的成分主要有蛋白质、氨基酸、维生素、矿物质和花青素等<sup>[2,7]</sup>,有害物质则主要是重金属和农药残留等。

## 1.2 影响稻米品质的因素

稻米品质主要是由环境、基因以及基因与环境互动共同决定的,且不同的品质性状受这 3 个因素的影响并不相同。

1) 环境因素。水稻的种植条件、化肥施用、灌溉情况、光照、温度和病虫害等因素,均能影响稻米品质<sup>[8]</sup>。研究表明肥料的种类(有机肥和氮肥)、肥料用量以及施加时期均能影响稻米的品质,施用氮肥可以在一定程度上改善稻米的加工品质和外观品质,但具体情况也会随水稻品种和环境条件而有所差异<sup>[9-10]</sup>。高温会降低外观品质,增加稻米的垩白率和垩白度<sup>[11-12]</sup>。灌溉方法不仅会影响稻米氮素的吸收利用,还会对稻米的外观品质、加工碾磨品质以及食味品质造成不同程度的影响<sup>[13]</sup>。此外,CO<sub>2</sub> 浓度、病虫害、杂草、盐胁迫、重金属等也对稻米品质产生较大影响<sup>[11,14]</sup>。

2) 遗传因素。在品种和环境一定的情况下,遗传因素就会成为影响稻米品质的主要原因,且不同品质性状受到的遗传因素影响并不相同<sup>[15]</sup>。蛋白质、精米率和整精米率的遗传力不高,容易受到环境的影响<sup>[16]</sup>。Zhang 等<sup>[17]</sup>认为胶稠度常表现为数量性状,是受多基因共同控制的,而糊化温度和直链淀粉含量则是由一个主效基因和多个微效基因控制。目前已经定位并克隆了包含影响稻米感官食味品质的主效基因 *Wx*、控制稻米外观品质性状的 *GS3*、*GW5* 以及控制蛋白质含量的 *OsAAP6* 和 *OsGluA2* 等大量品质相关基因。这些基因的克隆及其功能研究有利于稻米品质的分子遗传改良。

## 2 稻米感官食味品质的遗传基础

稻米的感官食味品质是与米饭“是否好吃”密切相关的重要品质性状,已有研究表明,*Wx* 是影响该性状的最主效基因。

### 2.1 *Wx* 是影响稻米直链淀粉含量的主效基因

早在 20 世纪初,科学家就发现一个决定稻米糯与非糯的 *Wx* 连锁群,之后科学家们克隆了 *Wx* 基因,并发现该基因功能缺失会形成糯米。*Wx* 编码一个颗粒结合型淀粉合成酶(granule-bound starch synthase I, GBSSI),直接影响稻米中直链淀粉的合成,且 *Wx* 的表达量和成熟 mRNA 的含量与稻米直链淀粉含量显著正相关<sup>[18-19]</sup>。后续研究发现 *Wx* 具有多种自然变异,这些变异形成不同功能等位型,并导致不同的直链淀粉含量。位于 *Wx* 基因 5' UTR

上 G>T 的变异,会使成熟胚乳中 *Wx* 的成熟 mRNA 含量降低,并使稻米中直链淀粉含量从 24% 降低到 18% 左右<sup>[20]</sup>。*Wx* 基因所在区段的重组率大约是基因组平均重组率的 10 倍,表明 *Wx* 基因更容易发生基因重组<sup>[21]</sup>。Mikami 等<sup>[22]</sup>发现籼稻中存在 *Wx<sup>a</sup>*、*Wx<sup>in</sup>*、*Wx<sup>b</sup>* 和 *Wx<sup>op</sup>* 等多种等位型,不同等位型对应不同的直链淀粉含量,其中 *Wx<sup>op</sup>* 是一种有垩白但直链淀粉含量偏低的等位型,该等位型的 GBSS 酶活大约降低了一半,然而其在 5' UTR 上是高直链淀粉的 G 等位型。Zhang 等<sup>[23]</sup>发现 *Wx<sup>lv</sup>* 是 *Wx* 的祖先等位型,该等位型对应最高的直链淀粉含量。*Wx<sup>la</sup>*/*Wx<sup>mv</sup>* 是新发现的一种低直链淀粉含量且外观是透明的优质等位型,可以用来改良稻米的品质<sup>[24-25]</sup>。迄今为止,已经发现了至少 8 种 *Wx* 等位型,不同等位型材料对应不同的直链淀粉含量(图 1D)。

### 2.2 *Wx* 同时影响稻米的胶稠度、RVA 和食味

胶稠度、RVA 和食味值都是影响稻米感官食味品质的重要性状,研究发现 *Wx* 对这些性状也有影响<sup>[26]</sup>。Tian 等<sup>[27]</sup>和 Ge 等<sup>[28]</sup>同时发现,*Wx* 除了影响稻米的 AC,还是影响 GC 的主效基因,同时还会影响米饭的吸水性、延伸性和膨胀度,这一结果被 Qiu 等<sup>[29]</sup>通过 3 000 核心种质关联分析和转基因验证予以证实。Wang 等<sup>[30]</sup>通过对由珍汕 97 和德隆 208 构建的重组自交系的 27 个品质性状进行 QTL 定位,在 *Wx* 位置定位到了影响 AC、GC 和 RVA 的主效 QTL 簇,同时微效影响 GT 等相关性状。进一步研究发现,位于第 10 外显子上 C>T 的变异被发现是影响稻米 GC 和 RVA 的主要功能变异位点<sup>[31]</sup>。Zhou 等<sup>[25]</sup>通过对多样性栽培稻的感官食味品质进行 QTL 定位,发现 *Wx* 不仅影响 AC、GC 和 RVA,同时还影响稻米的食味。因此,*Wx* 具有一因多效性,是影响稻米感官食味品质的主效基因(图 1D)。

### 2.3 稻米糊化温度和香味的主效基因

稻米的糊化温度是评价稻米蒸煮食味品质的重要指标,一般由碱消值表示,研究发现 *ALK* 是影响稻米糊化温度的主效基因。*ALK* 基因编码 1 个可溶性淀粉合酶(starch synthase IIa, SSIIa),包含 8 个外显子,其中位于第 8 外显子上 G>A 和 GC>TT 这 2 种变异是该基因的功能变异。这 2 种变异会引起氨基酸的改变,并改变产物的酶活,进一步影响中等长度支链淀粉的合成,改变晶体层结构,最终引起糊化温度发生改变<sup>[32-33]</sup>。此外,研究发现,同时

抑制 *ALK* (*OsSSIIa*) 和 *OsSS III a* 会使稻米出现粉质胚乳、直链淀粉含量增加、糊化温度升高和黏度减小的现象,同时降低了聚合度 5~6 的短支链淀粉并增加了聚合度 7~11 的中长型支链淀粉含量<sup>[34]</sup>。

米饭的香味主要来源于芳香族化合物 2-乙酰-1-吡咯啉,简称 2-AP,研究发现该物质主要由 1 个隐性 QTL 位点 *fragrance* 调控,简称 *fgr*,后续基因克隆发现 *OsBADH2* 为 *fgr* 的功能基因,编码甜菜醛脱氢酶,它可以消耗 2-AP 的前体物质 4-氨基丁醛 (AB-ald) 从而抑制 2-AP 的合成,位于该基因第 2 和第 7 外显子的缺失会形成有香味的 2 种等位型 *badh2-E2* 和 *badh2-E7*<sup>[35-36]</sup>。此外, Lin 等<sup>[37]</sup> 发现 1 个新的香味突变体 SA0420,并预测了其候选基因 *OsGAPDHB*。

### 3 稻米其他品质性状的遗传基础

目前学者已经对水稻不同品质性状进行了大量的研究,定位到了很多 QTL 并克隆了一批影响稻米品质的主效基因,如 *GS3*、*GW5*、*Chalk5*、*Wx*、*ALK* 和 *OsAAP6* 等,并对稻米品质形成的分子调控机制进行了一定的解析(表 2)。

#### 3.1 *GS3* 和 *GW5* 是影响稻米粒形的主效基因

稻米的外观品质是最直观的品质性状,也是研究最为深入的品质性状<sup>[38]</sup>。目前已经报道和克隆的粒形和垩白基因已有上百个,遍布水稻 12 条染色体,其中 *GS3*、*GW5* 以及 *Chalk5* 分别是影响稻米粒长、粒宽以及垩白率变异的最主效基因<sup>[39]</sup>。*GS3* 基因编码 1 个 G 蛋白  $\gamma$  亚基,负调控水稻的粒长,起源于温带粳稻的位于第 2 外显子 C>T 的无义突变是 *GS3* 最主要的功能变异,该变异会增加粒长,并且在热带粳稻和籼稻中受到了选择<sup>[40-41]</sup>。*GS3* 参与 G 蛋白途径调控水稻粒长,*GS3* 蛋白通过与另外 2 个  $\gamma$  亚基 *DEP1* 和 *GGC2* 竞争性结合 G 蛋白  $\beta$  亚基,抑制了 *DEP1* 和 *GGC2* 的功能,从而负调控水稻的粒长<sup>[41]</sup>。*GW5* 编码 1 个钙调素结合蛋白的基因,负调控水稻的粒宽<sup>[42-43]</sup>。*GW5* 启动子的变异是引起 *GW5* 功能以及水稻粒宽变异的主要原因,大多数粳稻因启动子 1 212 bp 的缺失而表现为宽粒表型,部分籼稻因启动子区域 957 bp 的缺失而表现为宽粒。进一步研究发现,*GW5* 是通过油菜素内酯信号途径调控水稻粒宽,它通过抑制该途径中关键负调控因子 *GSK2* 的激酶活性,使细胞核中未磷酸化的 *OsBZR1* 和 *DLT* 蛋白得到积累,调控油菜素

内酯响应基因表达水平和生长响应。此外,从自然变异及突变体中还克隆了大批粒形相关基因,如 *GL2*、*GW2*、*GL3.1*、*GL3.3*、*GS5*、*GS6*、*TGW6*、*GL7*、*GW8*、*BG1*、*SRS3*、*D2* 等,这些基因大多通过激素途径、G 蛋白途径、蛋白酶体降解等途径来调控水稻粒形<sup>[44-63]</sup>(表 2)。

#### 3.2 垩白的遗传研究进展

稻米的垩白是由淀粉颗粒的疏松和不规则排布引起,表现为胚乳不透明的表型。关于稻米垩白的遗传基础,学者做了大量研究,并定位了一大批垩白相关的 QTL,这些 QTL 基本遍布水稻 12 条染色体<sup>[64-69]</sup>。Yun 等<sup>[66]</sup> 对 1 个籼粳交群体的垩白性状进行了连续 2 a 的考察,共检测到 10 个与垩白率相关的 QTL,包含 5 个影响腹白率的 QTL 和 5 个影响心白率的 QTL,其中影响腹白率的 *qWBR2*、*qWBR5*、*qWBR6* 和 *qWBR8* 以及影响心白率的 *qWCR1* 和 *qWCR4* 被重复检测到。Gao 等<sup>[67]</sup> 利用培矮 64S 和 9311 构建的重组自交系进行垩白相关性状的 QTL 定位,一共检测到位于第 1、4、6、7、9 和 12 号染色体上的 19 个相关 QTL,对影响垩白度的 *qACE9* 进行精细定位,并最终预测 1 个候选基因 *OsAPS1*,该基因与淀粉合成相关,双亲在该基因的 2 个 SNP 变异会导致氨基酸的变异,并引起直链淀粉含量的差异。Wu 等<sup>[69]</sup> 对前期珍汕 97 和德隆 208 的重组自交系鉴定的心白位点 *qWCR7* 进行精细定位,将之定位在 65 kb 的区段内,并预测了候选基因,此外 *qWCR7* 还能影响稻米中淀粉和储藏蛋白的含量。

*Chalk5* 是影响栽培稻垩白率变异的主效基因,该基因编码 1 个液泡  $H^+$ -焦磷酸转移酶 (*V-PPase*),在胚乳中特异性表达,正调控稻米的腹白率;位于该基因启动子的 2 个 SNP 变异导致该基因表达量下降,垩白率降低,而且这 2 个 SNP 变异是籼稻腹白率遗传多样性的一个重要原因;*Chalk5* 通过调节种子内膜系统的 pH 值来影响蛋白体的形成,并影响胚乳中储藏物质的空间结构最终导致垩白的形成<sup>[70]</sup>。粉质胚乳突变体从胚乳透明度以及淀粉颗粒性状和排列来看,与垩白十分相似,可以算是垩白的极端情况。目前克隆了十几个与粉质胚乳相关的基因,如 *flo2*、*flo5*、*flo8*、*flo10* 和 *flo11* 等,这些基因大多与淀粉合成和能量代谢等相关<sup>[71-78]</sup>。Lou 等<sup>[77]</sup> 鉴定到一个粉质胚乳突变体 *flo19*,该突变体是由于编码二类草酰乙酸转氨酶的

表 1 国标优质稻谷各项品质要求  
Table 1 GB high quality rice requirements

国标类型 GB types	类别 Category	等级 Level	出糙率/% BRR $\geq$	整精米率/% MRR $\geq$			粒长/mm			长宽比 LWR	食味品质分 TS $\geq$	胶稠度/ mm GC $\geq$	直链淀粉 粉含量 (干基)/% AC	黄粒 米率/% YGR $\leq$
				长粒 LG	中粒 MG	短粒 SG	长粒 LG	中粒 MG	短粒 SG					
GB/ T17891— 2017	籼稻谷 Xian rice	1	—	56	58	60	$\geq 6.5$	5.6~6.5	$< 5.6$	—	90	—	14.0~24.0	—
		2	—	50	52	54	—	—	—	—	80	—	—	—
		3	—	44	46	48	—	—	—	—	70	—	—	1.0
GB/ T17891— 1999	粳稻谷 Geng rice	1	—	—	67	—	—	—	—	90	—	—	14.0~20.0	—
		2	—	—	61	—	—	—	—	80	—	—	—	—
		3	—	—	55	—	—	—	—	70	—	—	—	—
GB/ T17891— 1999	籼稻谷 Xian rice	1	79	—	56	—	—	—	—	$\geq 2.8$	9	70	17.0~22.0	—
		2	77	—	54	—	—	—	—	$\geq 2.8$	8	60	16.0~23.0	—
		3	75	—	52	—	—	—	—	$\geq 2.8$	7	50	15.0~24.0	—
GB/ T17891— 1999	粳稻谷 Geng rice	1	81	—	66	—	—	—	—	9	80	—	15.0~18.0	0.5
		2	79	—	64	—	—	—	—	8	70	—	15.0~19.0	—
		3	77	—	52	—	—	—	—	7	60	—	15.0~20.0	—

注 Note: BRR: Brown rice rate; MRR: Milled rice rate; LG: Long grain; MG: Middle grain; SG: Short grain; CR: Chalky grain rate; CD: Chalky degree; GL: Grain length; LWR: Grain length-width ratio; TS: Taste score; GC: Gel consistency; AC: Amylose content; YGR: Yellow grain rate.

表 2 稻米品质相关基因  
Table 2 Rice quality related genes

品质性状 Quality trait	基因 Gene	基因号 Locus	功能 Function	参考文献 Reference
粒形 Grain shape	GS3	Os03g0407400	G protein $\gamma$ subunit, negatively regulates grain length through G protein pathway	[40-41]
	GW5	LOC_Os05g09520	Calmodulin binding protein, negatively regulates grain width through BR signaling pathway	[42-43]
	GS5	LOC_Os05g06660	Serine Carboxypeptidase, positively regulates grain shape	[44]
	GW2	LOC_Os02g14720	E3 ligase, negatively regulates grain width through proteasome pathway	[45]
	GW8	LOC_Os08g41940	OsSPL16, positively regulates grain width	[46]
	GS2	LOC_Os02g47280	OsGRF4, positively regulates grain shape through BR signaling pathway	[47]
	GL3.2	LOC_Os07g41240	Cytochrome P450, positively regulates grain shape through phytohormone	[48]
	GW7/GL7	LOC_Os07g41200	LONGIFOLIA protein, negatively regulates grain length through interacting with GW8	[49-51]
	GLW7	LOC_Os07g32170	OsSPL13, positively regulates grain length	[52]
	GS6	LOC_Os06g03710	GRAS family protein, negatively regulates grain width through BR signaling pathway	[53]
	GL3.1	LOC_Os03g44500	PPKL family protein, positively regulates grain length through activating cell division	[54]
	GL3.3	LOC_Os03g62500	OsGSK5, negatively regulates grain length through IAA pathway	[55]
	srs1	LOC_Os07g42410	Expressed protein, loss-of-function produces small and round grains	[56]
	smg1	LOC_Os02g54600	OsMKK4, positively regulates grain length and grain width	[57]
	smg11/d2	LOC_Os01g10040	BADH acyltransferase, positively regulates grain shape through BR signaling pathway	[58]
	srs3	LOC_Os08g44840	Microtubule Depolymerase, positively regulates grain length and negatively regulates grain width	[59]
	rgg2	LOC_Os05g06280	G protein $\gamma$ subunit, positively regulates grain length and negatively regulates grain width	[60]
srg1	LOC_Os02g04520	Kinesin protein, positively regulates grain length and negatively regulates grain width	[61]	
srs5	LOC_Os09g02650	$\alpha$ -tubulin, positively regulates grain length	[62]	
	LOC_Os11g14220		[63]	

续表 2 Continued Table 2

品质性状 Quality trait	基因 Gene	基因号 Locus	功能 Function	参考文献 Reference
	<i>Chalk5</i>	<i>LOC_Os05g06480</i>	Vacuolar H <sup>+</sup> -translocating pyrophosphatase, positively regulates grain white belly rate	[70]
蛋白	<i>flo8</i>	<i>LOC_Os09g38030</i>	UDP-glucose pyrophosphorylase, loss-of-function causes floury endosperm	[71]
Chalkiness	<i>flo5</i>	<i>LOC_Os08g09230</i>	Soluble starch synthase IIIa, loss-of-function causes floury endosperm	[74]
	<i>flo2</i>	<i>LOC_Os04g55230</i>	Tetratricopeptide repeat domain containing protein,	[75-76]
	<i>flo10</i>	<i>LOC_Os03g07220</i>	PPR protein, loss-of-function reduces ATP and causes floury endosperm	[73]
	<i>flo11</i>	<i>LOC_Os12g14070</i>	Heat shock protein, loss-of-function causes floury endosperm	[72]
直链淀粉含量 AC	<i>Wx</i>	<i>LOC_Os06g04200</i>	GBSS, positively regulates amylose content and gel consistency	[23-25]
糊化温度 GT	<i>ALK</i>	<i>LOC_Os06g12450</i>	Starch synthase II, negatively regulates amylopectin and gelatinization temperature	[33]
香味 Fragrance	<i>fgr</i>	<i>LOC_Os08g32870</i>	Betaine aldehyde dehydrogenase, negatively controls rice fragrance	[35]
	<i>OsAAP6</i>	<i>LOC_Os01g65670</i>	Amino acid transporter, positively regulates rice storage protein content	[82]
储藏蛋白	<i>OsGluA2</i>	<i>LOC_Os10g26060</i>	Glutelin precursor, positively regulates rice protein content	[83]
Storage protein	<i>GPA1</i>	<i>LOC_Os12g43550</i>	Small GTP binding protein, loss-of-function causes accumulation of glutelin precursor	[86]
	<i>GPA3</i>	<i>LOC_Os03g61950</i>	Regulator of post-Golgi vesicular traffic, loss-of-function causes accumulation of glutelin precursor	[85]
	<i>GOT1B</i>	<i>LOC_Os03g11100</i>	Golgi Transport 1, loss-of-function causes accumulation of glutelin precursor	[84]
脂质 Lipids	<i>PAL6</i>	<i>LOC_Os06g05130</i>	Myristoyl-acyl carrier protein thioesterase, positively regulates C16:0 content	[91]
	<i>LIN6</i>	<i>LOC_Os06g40500</i>	Expressed protein, positively controls the conversion of C18:1 and C18:2	[91]
花青素	<i>Rc</i>	<i>LOC_Os07g11020</i>	bHLH transcription factor, positively regulates proanthocyanin biosynthesis in rice pericarp	[95]
Anthocyanin	<i>Rd/DFR</i>	<i>LOC_Os01g44260</i>	DFR, positively controls anthocyanin and proanthocyanin biosynthesis	[95]
	<i>OsB2</i>	<i>LOC_Os04g47059</i>	bHLH transcription factor, positively regulates anthocyanin biosynthesis in rice pericarp	[97]

基因发生突变而产生的,该突变会影响水稻正常的碳氮代谢并影响水稻的生长。*gwc1* 是 1 个垩白率和垩白度增加、糙米率和整精米率都降低的突变体,该突变体是由位于第 8 号染色体上的 *WTG1* 发生突变形成,该基因是通过影响蔗糖代谢以及淀粉合成相关途径来影响稻米的外观品质<sup>[78]</sup>。

### 3.3 营养健康品质的调控基因

蛋白质、氨基酸、脂质和花青素等是影响稻米营养健康品质的主要营养物质。蛋白质是稻米中仅次于淀粉的第二大储藏物质,可以分为清蛋白、球蛋白、醇溶蛋白和谷蛋白 4 种储藏蛋白。Chen 等<sup>[81]</sup>通过对 527 份多样性栽培稻 4 种储藏蛋白的全基因组关联分析,鉴定到了许多已知和未知的 QTL,并分析了蛋白相关基因 *OsAAT2*、*RA17*、*RM1*、*RP6* 和已克隆淀粉代谢相关基因 *AGPS2a*、*ISA2*、*PUL* 的自然变异对各种储藏蛋白含量的影响。Peng 等<sup>[82]</sup>克隆了首个调控稻米储藏蛋白的基因 *OsAAP6*,该基因编码 1 个氨基酸转移酶,正调控稻米中 4 种储藏蛋白含量,负调控食味相关性状。Yang 等<sup>[83]</sup>克隆了 *OsGluA2*,该基因编码二型谷蛋白前体,也是 4 种储藏蛋白的正调控因子。位于该基因启动子上的变异会影响其表达量,从而影响蛋白质的含量,并且该变异存在籼粳差异。此外,从突变体克隆的 *GPA1*、*GPA3* 和 *GOT1B* 等基因,主要通过蛋白合成、加工和运输等方面,来影响稻米中蛋白质的含量<sup>[84-86]</sup>。

稻米中的脂质主要为棕榈酸、油酸和亚油酸,主要存在于稻谷的胚和糊粉层中。学者利用不同群体和不同方法,对稻米中油脂组分和含量进行 QTL 定位和分析,分别在第 1、2 和第 5 号染色体上定位到与稻米脂肪含量相关的 QTL<sup>[87-88]</sup>,此外还发现 *OsFAD2* 和 *OsFAD3* 可以分别调控稻米中亚油酸和亚麻酸的含量<sup>[89-90]</sup>。Zhou 等<sup>[91]</sup>通过对 533 份多样性栽培稻的全基因组关联分析和 3 个重组自交群体的连锁分析,鉴定到 99 个脂肪酸组分和浓度相关的 QTL,并发现 *PAL6*、*LIN6*、*MYR2* 和 *FAE6* 分别是调控稻米中软脂酸、油酸、豆蔻酸(C14:0)和长链脂肪酸组分的主效基因。

抗性淀粉具有降低血糖的作用,在稻米中与直链淀粉的含量正相关。Zhou 等<sup>[92]</sup>发现 *SS III a* 的突变体中直链淀粉含量和抗性淀粉含量显著提高,尤其是在强功能的 *Wx* 基因背景下,抗性淀粉含量能达到 6%。Bao 等<sup>[93]</sup>通过对稻米抗性淀粉含量的全

基因组关联分析,发现 *Wx*、*SS II a*、*ISA1* 和 *AGPS14* 个淀粉合成途径相关基因共同影响抗性淀粉的自然变异。

花青素和原花青素作为水溶性色素,具有很强的抗氧化活性<sup>[94]</sup>。水稻中,原花青素和花青素分别存在于红米和黑米的果皮中。红米的果皮颜色由水稻第 7 染色体的 *Rc* 基因和第 1 染色体的 *Rd* 基因共同调控,*Rc* 和 *Rd* 分别编码 1 个 bHLH 型转录因子和 1 个黄烷酮醇还原酶。位于 *Rc* 第 6 外显子上 1 个 14 bp 的缺失或者 G-A 的变异均会使造成 *Rc* 的功能缺失,只有 *Rc* 和 *Rd* 同时有功能,才能表现为红米表型,*Rd* 有功能而 *Rc* 缺失功能的时候会形成白米,而 *Rc* 有功能、*Rd* 功能缺失就会形成浅棕米<sup>[95]</sup>。黑米的形成受 3 个基因的调控,分别为 *Kala1*、*Kala3* 和 *Kala4*,其中 *Kala1* 即 *Rd* 基因,*Kala3* 为 1 个 R2R3-Myb 转录因子,*Kala4* 为 1 个 bHLH 转录因子,只有这 3 个基因都有功能才能形成黑米。值得注意的是 *Kala4* 为 1 个功能获得型的突变,位于其启动子区域大片段的插入会引起该基因表达量的上升,从而形成黑米<sup>[96-97]</sup>。

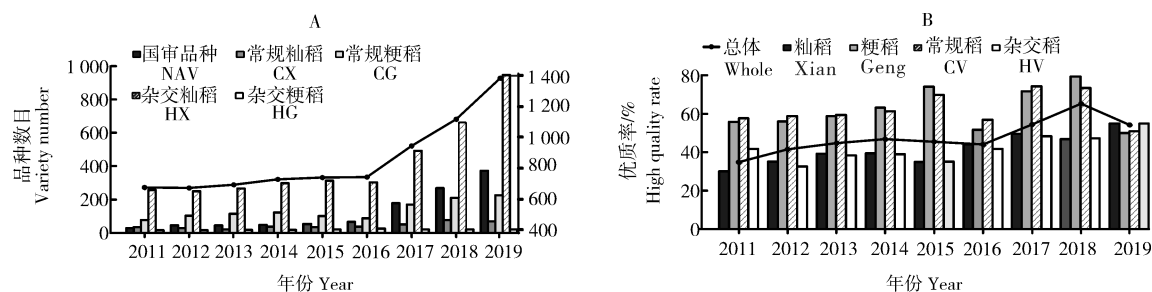
### 3.4 加工碾磨品质的遗传基础

不同水稻品种的加工品质差异显著,通过对稻米加工品质的遗传研究,学者们定位到了一些糙米率、精米率和整精米率的 QTL,但尚未克隆到直接影响加工品质的基因<sup>[98-99]</sup>。Ren 等<sup>[99]</sup>利用籼稻台中 1 号和粳稻春江 6 号构建的 DH 群体在第 10 染色体定位到 1 个控制糙米率(brown rice rate, BRR)的主效 QTL,命名为 *qBRR-10*,该 QTL 能够解释 23.1% 的表型变异,来源于春江 6 的等位基因能够增加约 7% 的糙米率。通过细胞学分析发现,*qBRR-10* 通过降低颖壳细胞的大小从而降低颖壳的厚度,最终导致稻谷中颖壳的比重减小,从而提高糙米的相对产量。许多影响稻米精米率和整精米率的 QTL 都是与已克隆的粒型垩白基因共定位,*Chalk5* 基因表达量的提高增加了稻米的腹白率,也导致了整精米率的下降<sup>[90]</sup>。稻米上的裂缝会直接导致精米率和整精米率下降。Pinson 等<sup>[100]</sup>利用高裂缝抗性的栽培稻 *Cypress* 和低抗性材料 *Lagruet* 构建的重组自交系群体定位了 3 个裂缝抗性 QTL,命名为 *qFIS1-1*、*qFIS1-2* 和 *qFIS8*,其中来源于 *Cypress* 的 *qFIS1-2* 位点能够降低 12% 的裂缝率,Sater 等<sup>[101]</sup>进一步将其定位到标记 RM1361 和 RM3482 之间,约 640 kb 区间。

## 4 稻米品质的遗传改良

在 20 世纪和 21 世纪初,增产一直是水稻生产的主要目标,经过绿色革命和杂交稻育种,我国水稻产量稳步提升,但是稻米品质却普遍偏差<sup>[102]</sup>。随着人们生活水平以及对物质生活需求的提高,人们对

稻米品质的要求也日益增加,优质稻米培育也变得愈发重要。经过科学家的不断努力,稻米品质相关的遗传基础得到了一定的解析,分子标记辅助选择技术以及转基因技术在育种上的应用,加速了水稻品质的遗传改良,我国的优质稻谷达标率也逐年上升(图 2)。



NAV:国审品种 National audit variety; CX:常规籼稻 Conventional *xian*; CG:常规粳稻 Conventional *geng*; HX:杂交籼稻 Hybrid *xian*; HG:杂交粳稻 Hybrid *geng*; PAV:省审品种 Provincial audit variety; CV:常规稻 Conventional variety; HV:杂交稻 Hybrid variety.

图 2 我国 2011—2019 年水稻审定的品种数及优质率情况

Fig.2 Certified rice variety number and high-quality-variety rate in 2011–2019 during China

### 4.1 优质稻培育现状

我国稻米品质的总体特征是粳稻品质优于籼稻,常规稻的品质优于杂交稻<sup>[103]</sup>。近 10 年来,我国培育的优质稻品种逐渐增多,一级优质稻品种也有所增加(2019 年 13 个达到一级优质稻谷标准,2013 年为 7 个),籼稻和杂交稻的品质改良也有了很大进步(图 2)<sup>[104-107]</sup>。不同地区材料的品质达标率也有较大差异,东北地区的稻米品种优质率相对最高,其次是两广地区和江淮地区<sup>[106]</sup>。黑龙江地区主要推广的是粳稻品种,由黑龙江从日本引进并改良的空育 131 是品质佳且种植面积最广的品种之一。江淮地区也以粳稻更受欢迎,南粳系列的粳稻是江苏地区大面积推广的优质稻,如南粳 46 和南粳 5055 等。广东、广西主要种植籼稻,黄华占是由广东省农业科学院水稻研究所培育的米质达到国标一级的绿色超级稻常规籼稻品种,是我国审定次数最多且适种范围最广的优质稻品种,同时还是陕西、重庆和湖北的省区试对照品种。

### 4.2 分子标记辅助育种

分子标记辅助选择育种(molecular marker assisted selection, MAS)是利用与基因紧密连锁的分子标记来选择对应性状的方法,相比于传统回交育种,该方法从基因层面实现性状的选择,具有效率高、时间短、选择更精准的特点,目前该方法已经被广泛地运用在水稻产量、抗病以及品质改良上<sup>[4-5,108-114]</sup>。Jin 等<sup>[108]</sup>利用分子标记辅助选择的方

法,在 II-32B 中对 *Wx*、*SS II a* 和 *fgr* 基因进行选择,最终选育出了有香味且低直链淀粉和低糊化温度的 II-32B 品质改良材料。Ni 等<sup>[113]</sup>通过分子标记辅助选择的办法,将高产品种协优 57 的 *Wx<sup>a</sup>* 基因替换成 *Wx<sup>b</sup>*,使其蒸煮食味品质得到了改善。Liu 等<sup>[114]</sup>通过聚合选择 *Pi1*、*Xa23* 和 *Wx*,最终培育出抗稻瘟病和白叶枯并且为软米的三级优质稻的新恢复系粤恢 88。Wang 等<sup>[49]</sup>通过该方法将 *GL7* 和 *gs3* 导入到籼稻不育系粤丰中,极大地改善了该品种的外观品质并提高了产量。Wang 等<sup>[50]</sup>通过聚合 *gs3* 和 *GW7*,培育出了高产且品质改良的籼稻杂交材料,如泰丰优 55 和泰丰优 208。

### 4.3 转基因育种

转基因育种是通过导入外源片段来改变水稻本身基因的表达或者基因的功能,从而改变水稻的表型。各国科学家通过转基因育种的方法对稻米品质进行了改良,如富含维生素 A 的黄金大米<sup>[115]</sup>和富含花青素并且胚乳也是黑色的紫晶米<sup>[116]</sup>。近几年,基因编辑技术得到了飞速的发展,目前已经广泛运用在植物遗传和育种研究中<sup>[117]</sup>。Tang 等<sup>[118]</sup>敲除华占和隆科 685S 中的 *OsNramp5* 基因,并进一步对敲除成功的材料进行杂交,最终获取了没有差异产量的低镉含量且不含转基因片段的杂交材料。Zhou 等<sup>[119]</sup>通过 CRISPR/Cas9 的方法,对 *GS3*、*GW2* 和 *Gn1a* 进行基因编辑,三基因敲除材料的粒长、粒宽和穗粒数都有增加。Abe 等<sup>[120]</sup>通过敲除



*OsFAD2* 基因, 获得了高油酸低亚油酸的材料。Zeng 等<sup>[121]</sup>通过对泰丰 B 中 *Wx* 基因的 5'UTR 区上的顺式作用元件进行编辑, 成功获得了产量没有变化但直链淀粉含量显著降低且不是糯米的材料, 并且这些材料的品质性状与优质稻黄华占很相似。Huang 等<sup>[122]</sup>利用相同的方法对日本晴的 *Wx* 基因启动子上的 TATA 框附近进行基因编辑, 也获得了直链淀粉降低、蒸煮特性与 *Wx<sup>mp</sup>* 等位型材料相似的优质突变材料。Huang 等<sup>[123]</sup>利用 CRISPR/Cas9 的方法对淀粉合成基因 *Wx* 和 *SS II α* 进行编辑, 获得了蒸煮食味品质改良的材料。Guo 等<sup>[124]</sup>对低谷蛋白材料 LGC-1 中的淀粉分支酶基因 *SBE II b* 进行编辑, 获得了利于肾脏疾病患者食用的高抗性淀粉水稻材料。Hui 等<sup>[125]</sup>利用 CRISPR/Cas9 的方法对籼稻材料黄华占的香味基因 *OsBADH2* 进行编辑, 并将有香味的黄华占转基因材料与不育系桃农 1A 杂交, 最后得到了一个有香味的三系杂交稻 B-桃优香占, 该三系杂交稻相对于野生型桃优香占其香味和胶稠度都有提升。

## 5 展 望

水稻是我国主要的粮食作物, 保证稻米的产量和改良稻米的品质, 是保证我国粮食安全和满足人民日益增长的物质需求的主要办法。目前, 我们对稻米的需求就是好看好吃且营养健康, 因此培育晶莹有光泽、口感鲜香软糯并且富含营养的稻米品种具有重要意义。此外, 除了做成米饭, 大米还能以不同的方式来食用, 如炒饭、年糕、煮等。通常, 中等偏低直链淀粉含量的大米品种煮成米饭和粥, 会更加软糯, 适口性更好; 高直链淀粉含量的大米口感偏硬且不粘连, 适宜做成炒饭和米粉; 直链淀粉低于 2% 的糯米可以用来做年糕或者米酒; 有颜色的大米如黑米或者红米, 则可以糙米的形式食用, 具有更加丰富的营养价值。

在我国, 国家优质稻谷标准是评价稻米品质的唯一指标, 但除了部分指标可以准确地测定外, 食味值这个十分重要的指标在测定时却会有很大偏差。目前是根据人为品尝来打分, 但不同品尝人会有不同的喜好, 难免会出现打分不准确的情况。因此, 急需建立更准确的品质分析方法, 如日本大多数采用机器对大米的粒形、整精米率、垩白度和食味值等指标进行测定, 不仅可以更好地屏蔽人为操作带来的误差, 还可以加快稻米品质的评定进程。

整精米率和垩白度是影响稻米优质的关键指标, 其遗传和调控机制尚不清楚, 因此, 进一步解析稻米垩白度和整精米率的遗传和调控网络, 是当下稻米品质研究的重要方向。此外, 由于杂交稻利用  $F_1$  的杂种优势,  $F_1$  植株的种子形成  $F_2$  分离群体, 而双亲在品质相关性状的差异会发生分离, 这也是杂交水稻品质相对较差的原因之一。所以, 对杂交水稻品质的遗传改良需要同时对双亲进行改良, 达到二者品质基因型等位以提高品质的改良效果。此外, 高产和优质常常会表现出矛盾, 如大粒品种垩白度高等。因此, 改良品质需平衡其与产量的关系, 同时大力挖掘优质高产协同相关基因与资源, 将分子育种与常规育种相结合, 也是将来水稻品质遗传改良的重点研究方向。

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## Progress on genetic study and molecular breeding of rice quality

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**Abstract** Rice is one of the staple food crops in China. High yield with good quality is not only the focus of rice basic studies, but also the main goal of rice breeding. Rice qualities mainly include milling quality, appearance quality, sensory quality, and nutritional quality, which are complex traits affected by both genetic and environmental factors. This article systematically reviews the classification of rice quality traits, influencing factors, the progress of the genetic basis and molecular improvement of rice quality. The prospects of studying rice quality are discussed. Sensory trait controlled by the major gene *Wx* is a key quality that determines whether rice is delicious or not. *Wx*, encoding a granular-bound starch synthase, is the major gene that affects the amylose content, gel consistency, RVA and taste of rice. Variation on *Wx* leads to the difference of amylose content ranging from 0-30%, the different gel consistency and taste score. *ALK* responsible for gelatinization temperature and *fgr* for fragrance of rice affect rice sensory quality as well. *GS3*, *GW5* and *Chalk5* are the major genes responsible for the diversity of the major components of rice appearance quality including grain length, grain width and grain chalkiness of rice. Molecular marker-assisted selection and genome editing of these important rice quality genes have achieved great progresses. Yet, the genetic basis of rice overall quality is still rarely understood. The quality of most commercial rice varieties in China is still not good. More studies are still needed to fully uncover the genetic basis of rice quality and to improve the quality of elite rice varieties. It will provide guidance for the genetic improvement of rice quality and the breeding of rice varieties with high-quality.

**Keywords** rice; appearance quality; milling quality; nutritional quality; sensory quality; genetic improvement; molecular breeding; high-quality rice

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