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·专题论坛·

水稻籽粒灌浆速率的分子机制与遗传调控研究进展

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摘要 水稻(*Oryza sativa*)的高产优质是我国粮食安全的重要保障, 也是育种家一直追求的目标。水稻籽粒灌浆速率(GFR)是一个重要而复杂的农艺性状, 直接影响籽粒充实度、粒重和米质。目前, 快速灌浆的优良水稻品种缺乏, 可供育种利用的相关优异基因资源有限, 已成为制约水稻产量和品质进一步提高的瓶颈。相对于水稻的其它农艺性状, GFR具有复杂的时空动态和环境可变性, 相关研究长期围绕灌浆过程的生理生化特性和栽培措施展开, 而分子机制和遗传调控研究启动较晚。该文以近年来国内外发现的水稻GFR相关基因为主线, 从糖类代谢和运输相关基因对GFR的影响、转录和翻译调控基因对GFR的调节、粒型和粒重等相关数量性状位点(QTL)对GFR的作用, 以及GFR相关QTL的分析和克隆4个方面, 对GFR分子机制与遗传调控进行综述; 并对GFR的研究策略特别是表型组学相关技术的应用前景进行展望, 以期推动该领域的基础研究和育种应用。

关键词 水稻, 籽粒灌浆速率, 分子机制, 遗传调控, 数量性状位点

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水稻(*Oryza sativa*)是我国最重要的粮食作物, 也是禾谷类植物分子生物学研究的模式物种。水稻经过开花、授粉和双受精之后, 子房发育为颖果, 随后进入籽粒灌浆(grain filling)时期。此时, 叶片等绿色组织光合作用产生和积累的同化物向颖果运输并转化, 最终颖果发育成为成熟籽粒。因此, 籽粒灌浆是稻米形成的关键阶段, 灌浆特性决定稻米的最终产量和品质。籽粒灌浆特性包括籽粒灌浆速率(grain-filling rate, GFR)、灌浆持续时间(grain-filling duration, GFD)以及与各种环境因子(温度、水分和氮肥等)的互作等(Jones et al., 1979; Jongkaewwattana and Geng, 2001; 施伟等, 2020)。其中, GFR一般定义为颖果日均积累的干重, 其直接影响籽粒的充实度、粒重和米质等, 是重要而复杂的农艺性状之一(Yang and Zhang, 2006, 2010; Liu et al., 2019)。GFR传统测量方法基于较长的时间窗口(天数), 而且耗时费力, 但最近X射线显微计算机断层扫描(computed tomography, CT)技术的运用有望实现水稻GFR的实时和精细测量(Hu et al., 2020b)。

目前, 我国多数水稻品种GFR较低, 快速灌浆的优良水稻种质比较缺乏, 可供育种利用的相关优异基因资源非常有限, 严重制约了水稻产量和品质的进一步提高(Yang et al., 2001; Yang and Zhang, 2010; Liu et al., 2019)。相对于水稻的其它农艺性状, GFR具有复杂的时空动态和环境可变性。研究人员长期围绕水稻籽粒灌浆过程的生理生化特性和栽培措施展开研究, 而分子机制和遗传调控相关研究启动较晚。尽管以GFR为直接研究性状及鉴定到的GFR调控基因相对较少, 但在水稻其它性状尤其是粒型性状研究中, 通过分析籽粒灌浆动态曲线发现一些基因可能与GFR有关。本文以近年来国内外发现的水稻GFR相关基因为主线(图1), 对已知的GFR分子机制和遗传调控研究进行综述, 并对研究策略进行展望, 希望能吸引更多研究者对GFR分子遗传学的兴趣和关注, 进

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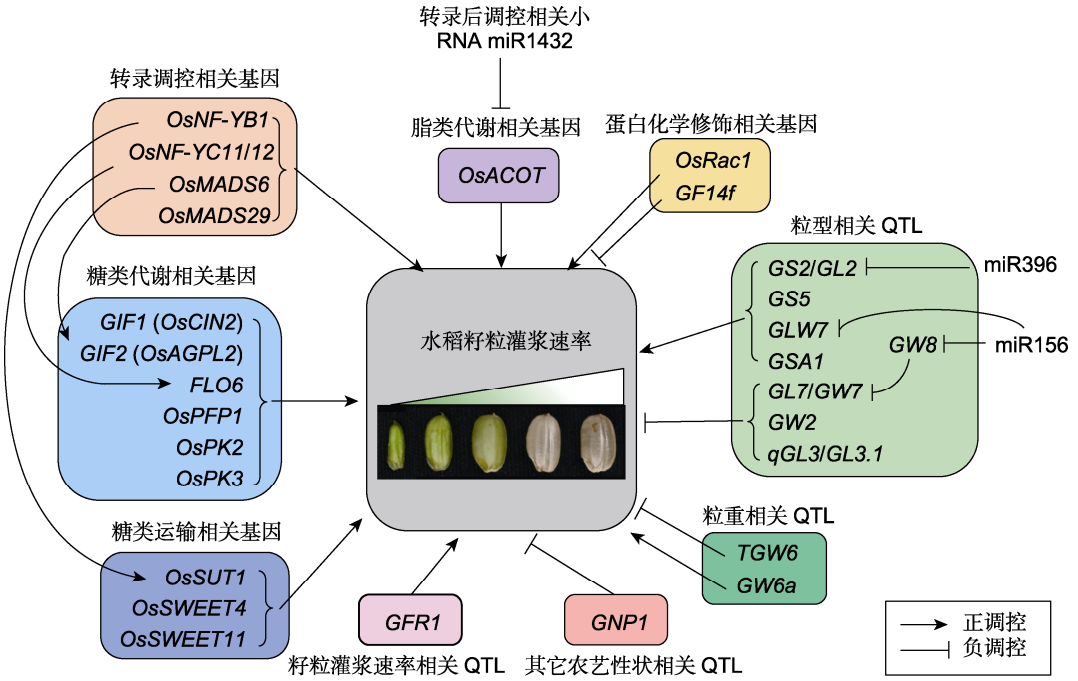

图1 已报道的水稻籽粒灌浆速率相关基因

Figure 1 The known genes related to grain-filling rate in rice

一步推动该领域的基础研究和育种应用。

1 糖类代谢和运输相关基因对GFR的影响

1.1 糖代谢酶相关基因

水稻籽粒的主要内含物是淀粉，因此糖类代谢和运输在籽粒灌浆过程中至关重要。目前，在已报道的水稻GFR相关基因中，相当一部分是糖类代谢酶相关基因。光合作用产生的蔗糖需要转化为己糖磷酸酯才能进入籽粒细胞，细胞壁转化酶(cell-wall invertase, CIN)在此过程中发挥至关重要的作用。CIN作为一类定位于细胞壁的蔗糖酶，可将质外体中的蔗糖催化水解为葡萄糖和果糖(Sturm and Tang, 1999)。Hirose等(2002)从水稻灌浆籽粒中克隆到1个CIN基因*OsCIN1*。该基因在灌浆早期高丰度表达，可能在籽粒灌浆中发挥重要作用，但其对GFR的影响未知。Wang等(2008)筛选到1个灌浆不完全突变体*gif1* (*grain incomplete filling 1*)，其GFR降低。图位克隆结果表明，*GIF1*编码水稻CIN (OsCIN2)，在籽粒灌浆早期控制蔗糖在胚乳中的卸载。在长期驯化过程中，*OsCIN2*基因启动子明显受到人工选择，使得栽培稻*OsCIN2*等位基因主要在胚珠脉管部位表达，而普通野生稻(*O. rufipogon*) *OsCIN2*等位基因具有广泛的时空表达；将后者导入栽培稻中，会显著降低栽培稻的GFR (Wang et al., 2008)。进一步研究发现，OsCIN2主要在灌浆过程中发挥作用，而OsCIN1酶活较低，可能主要参与调控其它生物学过程(Wang et al., 2010)。通过研究另一个灌浆缺陷突变体*gif2*，鉴定到腺苷二磷酸葡萄糖焦磷酸化酶(ADP-glucose pyrophosphorylase, AGPase)的大亚基基因*OsAGPL2* (Wei et al., 2017)。AGPase是淀粉合成的限速酶，催化1-磷酸葡萄糖与ATP反应生成腺苷二磷酸葡萄糖(淀粉合成的前体)，其突变会影响籽粒中淀粉的合成，导致GFR降低(Wei et al., 2017)。*FLO6* (*FLOURY ENDOSPERM 6*)编码参与淀粉合成的含有C末端糖结合域48的蛋白CBM48，该蛋白定位于质体上，其C端与淀粉结合，而N端与异淀粉酶1 (isoamylase1, ISA1)结合，介导ISA1对淀粉的结合(ISA1无法直接与淀粉结合)；其可能是ISA1的底物识别亚基，*FLO6*突变导致GFR降低(Peng et al., 2014a)。

最近的研究表明，多个水稻糖酵解途径相关酶基因与GFR相关，而糖酵解可以促进淀粉合成和代谢。*OsPFP1*编码糖酵解途径中的焦磷酸:果糖-6-磷酸1-

磷酸转移酶(pyrophosphate:fructose-6-phosphate 1-phosphotransferase, PFP)的β亚基，与3个α亚基共同形成异源四聚体，催化果糖-6-磷酸与果糖-1,6-二磷酸间的可逆反应，其突变导致籽粒造粉体和淀粉颗粒发育异常，淀粉含量和GFR降低(Duan et al., 2016a; Chen et al., 2020)。丙酮酸激酶(pyruvate kinase, PK)催化糖酵解途径的最后一步反应，即磷酸烯醇式丙酮酸和ADP转化生成丙酮酸和ATP，是糖酵解途径的重要限速酶之一。*OsPK2*编码1个位于质体的PK (PKpα1)，与其它3个质体同工酶PKpα2、PKpβ1和PKpβ2形成异源复合体，其突变导致籽粒淀粉合成异常，复合淀粉颗粒显著减少，GFR降低(Cai et al., 2018)。*OsPK3*编码1个位于线粒体的PK，其突变导致灌浆中后期GFR下降; OsPK3可以招募另外2个同功酶OsPK1和OsPK4，分别形成2种不同的异二聚体，在籽粒不同灌浆阶段发挥作用(Hu et al., 2020a)。*OsPK3*还在叶片中高表达，特别是叶肉细胞和韧皮部伴胞中，而*ospk3*突变体的叶片中会发生蔗糖和淀粉积累，说明OsPK3还影响蔗糖从源到库的转运和卸载(Hu et al., 2020a)。上述糖类代谢酶相关基因均参与GFR的正调控，其突变可导致GFR降低，籽粒灌浆异常。

1.2 糖转运蛋白基因

蔗糖转运蛋白(sucrose transporter, SUT)基因是最早被发现与水稻籽粒灌浆相关的糖转运蛋白基因，在水稻中有5个同源基因(Ishimaru et al., 2001; Aoki et al., 2003)。其中，*OsSUT1*主要在灌浆颖果的糊粉层表达，抑制该基因的表达导致严重的灌浆缺陷，表明GFR可能降低，但是叶片的光合作用不受影响，其可能负责将蔗糖从叶片质外体转运到灌浆籽粒基部的韧皮部(Ishimaru et al., 2001; Scofield et al., 2002, 2007)。*OsSUT2*编码的SUT位于液泡膜上，负责将蔗糖从液泡转运至胞质，其在叶肉细胞和维管束鞘中高表达，在籽粒灌浆初始阶段的小穗枝梗及灌浆后7–8天的种皮中也有显著表达。*ossut2*突变体籽粒的千粒重下降，但其对GFR的影响尚属未知(Eom et al., 2011)。通过同源比对调控玉米(*Zea mays*)籽粒灌浆的己糖和蔗糖转运蛋白SWEET (sugars will eventually be exported transporters)基因*ZmSWEET4c*，鉴定了水稻中的同源基因*OsSWEET4*，其负责将葡萄糖和果糖等己糖通过基底胚乳转移层从韧皮部运输到胚乳，功能缺失突变体表现出严重的灌浆缺陷(Sosso et al., 2015)。对水稻灌浆籽粒中表达的其它*SWEET*基因进行研究，发现*OsSWEET11*和*OsSWEET15*分别参与珠心组织突起处蔗糖的外排，以及珠心表皮层和糊粉层交界处的糖类转运，其中*OsSWEET15*的突变导致GFR显著降低(Ma et al., 2017; Yang et al., 2018)。

2 转录和翻译调控基因对GFR的调节

2.1 转录因子相关基因

在水稻籽粒灌浆过程中，糖类等物质代谢与运输以及胚乳发育受到转录水平、转录后水平、翻译水平和翻译后水平等多级复杂调控。目前研究较多的是基因转录水平上的籽粒灌浆调控机制，已发现数个相关转录因子。MADS-box (MCM1、Agamous、Deficiens和SRF-box)转录因子因其包含高度保守的MADS结构域而得名，多数参与花器官形态建成等发育过程。水稻MADS-box转录因子基因*OsMADS6*可调控多个AGPase基因(*OsAGPS1*、*OsAGPL2*和*OsAGPL3*)的表达，其突变体籽粒灌浆发生严重缺陷，淀粉积累减少(Zhang et al., 2010)。另一个MADS-box转录因子基因*OsMADS29*通过调控半胱氨酸蛋白酶和核苷酸结合位点-富含亮氨酸重复蛋白等基因的转录来调节授粉后母体组织的降解，保证胚乳正常起始发育；抑制*OsMADS29*的表达导致GFR下降，籽粒发育异常(Yin and Xue, 2012)。NF-Y (nuclear factor-Y)转录因子一般由3种不同的亚基组成(NF-YA、NF-YB和NF-YC)，是一类异源多聚体转录因子。水稻NF-YB亚基基因*OsNF-YB1*在灌浆籽粒糊粉层中特异表达，抑制*OsNF-YB1*的表达会降低GFR (Xu et al., 2016)。OsNF-YB1可以与NF-YC亚基OsNF-YC11/12以及AP2/ERF (APETALA2/ethylene-responsive factor)家族转录因子OsERF115互作形成蛋白复合体，通过结合GCC盒和AP2/ERF转录因子结合基序，在转录水平上直接调控参与糖和氨基酸等同化物转运的基因，包括*OsSUT1* (Xu et al., 2016; Xiong et al., 2019)。NF-YC12在胚乳中还与*FLO6*和胞质谷氨酰胺合成酶基因*OsGS1;3*的启动子结合，直接调控后者的转录(Xiong et al., 2019)。

此外, 水稻bZIP (basic leucine zipper)转录因子家族基因*RISBZ1* (又名*OsbZIP58*)、DOF (DNA binding with one finger)转录因子家族基因*RPBF*和*OsDOF11*、AP2/ERF转录因子家族基因*SERF1*和*RSR1*都参与调控灌浆相关基因的转录表达, 但其对GFR的具体作用还有待深入研究。RISBZ1与RPBF共同形成转录激活子正调控籽粒贮藏蛋白基因的表达(Onodera et al., 2001; Kawakatsu et al., 2009; Wang et al., 2013), *OsDOF11*直接正调控糖类转运蛋白基因*OsSUT1*、*OsSWEET11*和*OsSWEET14*的表达(Wu et al., 2018)。SERF1直接负调控*RPBF*以及淀粉粒结合淀粉合成酶基因*GBSSI*的转录(Schmidt et al., 2014)。RSR1负调控一系列I型淀粉合成酶基因的表达(Fu and Xue, 2010)。多梳蛋白(polycomb group)基因*OsFIE2*编码1个组蛋白H3甲基转移酶, 在染色质水平抑制HLH (helix-loop-helix)转录因子家族基因的转录, 进而影响一系列淀粉合成酶和贮藏蛋白相关基因的表达(Na et al., 2012; Nallamilli et al., 2013; Li et al., 2014; Liu et al., 2016; Cheng et al., 2020)。

2.2 microRNA

microRNA通过介导靶基因信使RNA的切割和降解, 在转录后水平调节靶基因的表达。microRNA在水稻籽粒灌浆过程中发挥重要的调节作用, 推测多个microRNA通过调节同化物代谢、基因转录调控和植物激素稳态等相关基因的表达而影响籽粒灌浆(Peng et al., 2013, 2014b; Yi et al., 2013)。Zhao等(2019)报道了1个在籽粒灌浆过程中表达量逐渐升高的microRNA——miR1432, 其通过靶向酰基辅酶A硫酯酶基因*OsACOT*的信使RNA, 影响脂肪酸代谢以及生长素和脱落酸的合成, 进而负调控GFR; 抑制miR-1432的表达可以提高GFR, 过表达miR1432结合位点发生突变的*OsACOT*同样可提高GFR (Zhao et al., 2019)。该研究表明, miR1432的靶基因*OsACOT*可以正调控GFR; *OsACOT*参与脂肪酸去饱和及其碳链延长, 因此脂肪酸代谢可能也与GFR密切相关。

2.3 蛋白化学修饰相关基因

研究发现, 编码Rho家族GTPase的水稻基因*OsRac1*在翻译后蛋白化学修饰水平上正调控GFR; 其负责丝裂原活化蛋白激酶OsMAPK6的磷酸化, 过表达该基因可以促进细胞分裂, 使籽粒增大、GFR升高, 而敲除该基因导致GFR降低(Zhang et al., 2019a)。另一项研究发现, 水稻14-3-3蛋白家族基因*GF14f*在蛋白化学修饰水平上负调控稻穗下部弱势粒的GFR, 其编码蛋白涉及蛋白丝氨酸残基磷酸化; GF14f与蔗糖水解、淀粉合成、三羧酸循环和糖酵解相关酶类存在互作, 而抑制*GF14f*的表达会使籽粒中AGPase、蔗糖合成酶和淀粉合成酶的活性增强(Zhang et al., 2019b)。

3 粒型和粒重等性状相关QTL对GFR的作用

3.1 粒型相关QTL

根据作物产量生理的源-库-流理论(source-sink-translocation theory), 更大的颖壳意味着更大的库容量, 其与GFR存在一定的相关性。目前发现已克隆的一些水稻粒型相关数量性状位点(quantitative trait locus, QTLs)也影响GFR。其中, 至少有5个粒型相关QTLs可能正调控GFR, 分别是*GS5*、*GS2*/*GL2*/*GLW2*、*GW8*、*GLW7*和*GSA1*。编码丝氨酸羧肽酶的*GS5*启动子区域2个SNP影响该基因在幼穗中的表达, *GS5*表达增强可使颖壳增宽、GFR升高(Li et al., 2011; Xu et al., 2015)。GS5通过竞争性结合油菜素内酯(brassinosteroid, BR)相关受体激酶OsBAK1-7的富含亮氨酸重复结构域, 抑制后者与膜类固醇结合蛋白OsMSBP1的互作, 进而阻止OsBAK1-7的胞吞作用而影响BR信号(Xu et al., 2015)。*GW8*编码1个受miR156调控的SPL (SQUAMOSA promoter-binding protein-like)家族转录因子OsSPL16, 其直接与另一个粒型相关QTL基因*GL7*/*GW7*的启动子结合, 抑制后者的表达(Wang et al., 2012)。*GW8*启动子区域的变异导致该基因的表达量改变, 其高表达促进横向细胞分裂, 抑制纵向细胞伸长, 因此使粒宽和GFR增高。*GLW7*编码另一个SPL转录因子OsSPL13, 在大粒热带粳稻中, 该基因5′UTR上一段串联重复导致其表达增强, 使细胞体积增大、粒长变长, 同时使GFR增高(Si et al., 2016)。*GS2*/*GL2*/*GLW2*编码受miR396调控的生长调控因子OsGRF4, miR396结合

位点突变的等位基因在使水稻籽粒增大的同时，也使GFR大幅升高(Hu et al., 2015; Che et al., 2016; Duan et al., 2016b; Li et al., 2016; Sun et al., 2016; Chen et al., 2019)。GS2/GL2/GLW2与转录共激活因子OsGIF1/2/3互作，正调控多个粒型相关QTL基因(如*GS5*和*GW8*)、糖类代谢和运输相关基因(如*OsCIN2*和*OsSWEET11*)、光合作用相关基因以及BR信号途径相关基因的表达(Hu et al., 2015; Che et al., 2016; Li et al., 2018)。*GSA1*编码1个糖基转移酶UGT83A1，影响黄酮介导的生长素极性运输及生长素相关基因的表达，进而调控细胞分裂和增殖。非洲栽培稻(*O. glaberrima*) *GSA1*等位基因编码蛋白的保守氨基酸变异导致GSA1酶活降低，使粒型变小、GFR降低(Dong et al., 2020)。

目前至少发现3个粒型相关QTLs负调控GFRs，分别为*GW2*、*qGL3*/*GL3.1*和*GL7*/*GW7*。控制粒宽和粒厚的*GW2*编码1个RING型E3泛素连接酶，参与泛素化蛋白降解，其功能缺失性等位基因可使颖壳细胞数目增加、GFR升高(Song et al., 2007)。*GW2*在染色体上紧邻泛素特异性蛋白酶基因*OsUBP15*，两者在遗传上可能存在相互作用；*OsUBP15*编码1个去泛素酶，在水稻显性大粒突变体*lg1-D*中，OsUBP15稳定性增强，导致粒宽增加和GFR升高(Shi et al., 2019)。控制水稻粒长的*qGL3*/*GL3.1*编码1个丝氨酸/苏氨酸磷酸酶OsPPKL1，功能缺失性等位基因使粒长增加、GFR升高(Qi et al., 2012; Zhang et al., 2012)。qGL3/GL3.1通过调控细胞周期蛋白Cyclin-T1; 3去磷酸化影响细胞分裂(Qi et al., 2012)。Gao等(2019)研究发现，qGL3/GL3.1可以通过调控蛋白激酶OsGSK3去磷酸化来影响BR信号通路，进而发挥其调控作用。调控粒型的*GL7*/*GW7*编码1个与拟南芥LONGIFOLIA (又称TON1 RECRUITING MOTIF 2)蛋白同源的微管相关蛋白，该位点17.1 kb的串联重复或者启动子区域变异均能上调*GL7*/*GW7*的表达量，使颖壳纵向细胞分裂，并减少横向细胞分裂，导致颖壳变细长，同时提高稻米品质，但降低籽粒灌浆中期的GFR (Wang et al., 2015a, 2015b)。

3.2 粒重相关QTL

已克隆的2个粒重相关QTLs (*TGW6*和*GW6a*)也影响GFR。*TGW6*编码吲哚乙酸-葡萄糖水解酶，通过控制吲哚乙酸供应影响胚乳合胞体阶段到细胞化阶段的转变，从而控制胚乳细胞的数目和籽粒长度，而功能缺失性等位基因导致粒重和粒长增加、GFR升高；*TGW6*不仅直接调控胚乳长度，还间接参与从源到库的碳水化合物运输(Ishimaru et al., 2013)。*GW6a*编码1个拥有组蛋白乙酰转移酶活性的类GNAT蛋白OsglHAT1，调控组蛋白H4的乙酰化水平，其启动子区域的变异导致*GW6a*的表达增强，促进细胞分裂，从而使粒重和粒长增加、GFR升高(Song et al., 2015)。

3.3 穗粒数相关QTL

GNP1 (*Grain Number per Panicle 1*)是调控水稻穗粒数的QTL，其编码1个赤霉素(GA)氧化酶OsGA-20ox1，催化GA生物合成的倒数第2步反应(Wu et al., 2016)。*GNP1*启动子区域的变异导致该基因表达量上升，通过转录因子KNOX的反馈调节增强穗分生组织中的细胞分裂素活性，进而增强另一个GA分解代谢酶基因*GA2oxs*的表达，降低2种GA (GA1和GA3)的积累，最终提高籽粒数目和产量，但同时降低结实率、穗数、粒重以及GFR (Wu et al., 2016; Zhai et al., 2020)。

4 GFR相关QTL的分析和克隆

跟粒型和粒重一样，GFR也是复杂的数量性状，对其进行QTL分析是鉴定育种可用的优异等位基因的有效策略。由于对GFR的测定费时费力，水稻GFR相关QTL的研究相对缺乏，对其遗传调控位点及分子机制所知甚少。由于水稻茎秆和叶鞘是源组织，其中储存的非结构碳水化合物对于灌浆初期胚乳的发育非常重要(Tsukaguchi et al., 1996)。Nagata等(2002)利用回交自交系，以灌浆期水稻茎秆和叶鞘中非结构碳水化合物的积累量(绝对总含量、每株含量和每穗含量)为指标，在不同年份分别检测到9个和14个可能影响籽粒灌浆的QTLs，其中有5个在不同年份被重复检测到。Takai等(2005)利用重组自交系，进一步对水稻茎秆和叶鞘中非结构碳水化合物含量以及每穗籽粒充实率相关QTLs开展了3个不同灌浆时期的动态分析，鉴定到2个分别位于第8和12号染色体上影响籽粒灌

浆的主效QTLs。

近年来，先后有3项研究涉及水稻GFR相关QTL的分析。贾小丽等(2012)利用重组自交系在2个不同环境下对单个时期的GFR进行了QTL分析，共鉴定到6个和4个加性QTLs以及4个环境互作QTLs。Liu等(2015)利用95个水稻品种对5个灌浆期GFR进行QTL分析，共检测到31个位点。Liu等(2019)进一步利用回交自交系，对GFR进行条件QTL分析和时序QTL分析，分别检测到7个(其中1个在2个时期)和3个(其中1个在2个时期) QTLs，共有3个QTLs同时被2种方法检测到，并克隆了其中1个位于10号染色体长臂末端的GFR主效QTL——*GFR1* (*GRAIN-FILLING RATE 1*)。*GFR1*编码1个膜蛋白，与二磷酸合酮糖羧化酶小亚基OsRbcS互作，可能通过参与卡尔文循环促进GFR。来自穆稻的*GFR1*等位基因存在非同义突变，该等位可以加快光合速率，促进胚乳细胞分裂，增强*OsCIN1*的表达，使胚乳和剑叶中的蔗糖、葡萄糖及果糖含量增加(Liu et al., 2019)。

5 总结与展望

GFR是重要的农艺性状和复杂的数量性状，对GFR调控基因和优异等位变异进行挖掘和研究，有助于实现水稻快速灌浆特性的精准育种，从而提升水稻的产量和品质。目前，关于GFR遗传分析的研究才刚刚起步，对于GFR的分子调控机制和网络的认识还非常有限，对GFR等灌浆相关特性和性状的分子遗传机制进行解析将是水稻等农作物研究领域的热点和突破点。随着显微CT等表型组学相关技术运用于籽粒灌浆研究(Hu et al., 2020b)，将有望实现水稻不同穗(主穗和分蘖穗)、不同穗位籽粒(强势粒与弱势粒)和不同环境条件下GFR的高通量实时测量，推动GFR时空复杂性和环境可变性背后的分子遗传机制解析。

具体地说，今后应重点在以下几方面开展研究。(1) 以GFR为直接研究对象的遗传和分子生物学研究相对有限，未来需要运用显微CT等表型组学技术，以特定部位和环境下的GFR为测量性状和直接指标，开展诸如突变体库筛查、全基因组关联分析和多组学联合分析，对GFR调控基因和等位变异进行系统鉴定和研究；(2) 粒型及其相关基因可以作用于GFR，而GFR也会影响粒型，但GFR是否对于粒型调控基因存在反馈调节机制目前并不清楚，未来需要开展水稻粒型和GFR互作机制的相关研究；(3) 已知GFR相关基因主要影响库和流，而较少影响源，未来需要更多地聚焦于源组织调控相关基因对GFR的作用，特别是对叶片和光合作用相关突变体进行GFR考察，检测其是否影响或调控GFR；(4) GFR在籽粒灌浆过程中是动态变化的，不同时期、不同穗和不同穗部的GFR可能受不同基因的影响，涉及的分子调控机制也不同，未来关于GFR的分子遗传研究仍需在时空调控上进一步细化；(5) GFR受多种环境因子的影响，其背后的分子响应和调节机制有待详细解析，尤其是涉及的关键调控位点和优异等位基因亟需鉴定，其将有助于培育GFR对不良环境钝感的优良水稻品种。

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Advances in the Molecular Mechanism and Genetic Regulation of Grain-filling Rate in Rice

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Abstract High yield and good quality of rice are important guarantees for food security in China, as well as the objective which breeders are pursuing. Grain-filling rate (GFR) is an important and complex agronomic trait in rice, directly affecting grain plumpness, weight, and quality. To date, elite rice germplasm with rapid GFR is rare, and valuable gene resources for breeding remain limited, which has become a bottleneck for further improvement of yield and quality in rice breeding. Comparing with other rice agronomic traits, GFR is highly complex for its spatio-temporal dynamics and environment-dependent variability, the research of which has long been concentrated on the physiological and biochemical characteristics and cultivation measure control of grain-filling period. The study on the molecular mechanism and genetic regulation of GFR has arisen relatively recently. Here, focusing on the GFR-related genes in rice identified recently, we reviewed the preliminarily known molecular mechanism and genetic regulation of GFR, including the influence of sugar metabolism and transport-related genes on GFR, the transcriptional and translational regulatory genes in GFR, the function of grain size and weight-related quantitative trait loci (QTLs) of GFR, and the analysis of GFR-related QTLs; we also discussed the future perspective of the research strategies for GFR, especially the application potential of phenomics-related technologies for GFR research, in order to promote the foundational research and application in rice breeding.

Key words rice, grain-filling rate, molecular mechanism, genetic regulation, quantitative trait locus

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