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作物杂种优势与生物育种专辑 评 述

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水稻杂种优势遗传基础及机理解析研究进展

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摘要 杂种优势是指杂交F_1代在产量和抗逆性等方面显著超越亲本的现象, 作为现代作物育种的重要理论基础已被广泛应用. 随着基因组学与生物技术的快速发展, 该领域已取得系列突破性进展, 为揭示其分子机制和指导高效育种奠定了科学基础. 本文系统梳理了水稻杂种优势研究的遗传基础、分子机理及育种应用三方面进展: 在遗传解析层面, 显性互补、超显性和上位效应等经典假说被广泛证实, 能有效解释多数杂种优势现象, 文中重点归纳了已克隆的主效优势位点及其调控方式; 在分子机制层面, 系统阐释了基因组互补性、等位基因特异性表达及代谢通路协同增效等核心机理, 揭示杂种优势形成是多层次生物学过程动态调控的结果; 在育种应用层面, 总结了不同遗传背景下优势位点的系统组装与改良、分子预测模型构建等实践成果. 基于当前抗逆(特别是抗病虫)优势位点研究相对薄弱的现状, 本文建议从多环境优势位点挖掘、杂种优势群精细划分等方向深化研究, 为培育广适性优质杂交稻提供理论支撑.

关键词 杂交水稻, 杂种优势, 遗传基础, 分子机制, 杂种优势利用

杂种优势, 作为一种普遍存在于植物界的生物学现象, 表现为杂交后代在生长速度、生物量及环境适应等方面对亲本的显著超越, 其程度主要通过中亲或超亲优势率来评价[1]. 自1964年袁隆平先生发现雄性不育株以来[2], 我国水稻杂种优势利用研究历经60年发展, 不仅开创了三系法、两系法杂交水稻技术, 还培育出超级杂交水稻技术, 这些成果构建了科学、完整、成熟且独具特色的理论与技术体系, 使我国在杂交水稻领域始终保持国际领先地位. 当前, 杂交水稻全球推广面积超80亿亩, 稻谷增产超6000亿公斤, 杂交水稻技术被世界粮农组织视为解决粮食短缺的首选方案, 誉为农业生产的"第二次绿色革命"[3].

鉴于杂种优势在农业生产实践与科学探索中的核心价值, 科学家们长期聚焦于水稻杂种优势遗传基础与分子机理的深入剖析, 旨在为育种实践提供坚实的理论支撑、促进育种效率的显著提升. 本文综述了水稻杂种优势研究的主要进展, 内容涵盖杂种优势的遗传基础(优势位点定位与基因克隆)、分子机制(基因组变异、基因表达及生理生化途径)及实际应用(亲本遗传改良、杂种优势基因组装与分子预测)等, 并提出加强水稻杂种优势研究的见解与建议.

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1 水稻杂种优势的遗传基础

1.1 杂种优势位点的定位

作为典型的数量性状，杂种优势易受外界环境、遗传背景等影响，需借助遗传学手段对控制这些性状的数量性状基因座(quantitative trait locus, QTL)进行定位. 近五十年来, 研究人员利用不同种质资源及多个优势杂交组合衍生的F_2、回交和测交F_1群体, 广泛开展了杂种优势位点的发掘工作. 综合38篇水稻杂种优势遗传基础相关文献(表1)，对近3000个杂种优势相关QTL统计发现，主要涉及产量、抗性、品质等近50个具体优势性状. 其中每穗粒数、有效穗、单株产量为性状杂种优势前3名，品质相关优势位点较少，可能与其较难表现出杂种优势有关[41]，这些QTL遍布水稻12条染色体，其中1号染色体上位点相对较多(图1). 另外，杂种优势性状QTL与控制产量等性状的数量性状QTL重叠度因材料背景、目标性状等差异较大，低的仅14.6%[14]，高的可达65%[12]，暗示杂种优势和性状表现存在不同的遗传模式[9]. 研究同时发现大多数性状杂种优势与整体基因组杂合性之间不存在相关性，即在来自高度杂种优势杂交种的基因型中，杂合子也不一定对性状表现有利[42].

杂种优势遗传基础涵盖三大经典假说：显性互补假说[43]提出杂种优势源于显性有利等位基因对隐性有害突变的互补掩盖；超显性假说[44,45]强调杂合基因型(A1A2)通过功能增强或调控机制直接产生优势；上位性假说[46]则聚焦多基因互作网络对复杂性状的协同调控. 研究表明, 这三大假说(显性互补、超显性、上位效应)在籼籼交、籼粳交、粳粳交及野生稻参与的杂交组合中广泛存在，共同构成了水稻杂种优势的主要遗传基础[47]. 它们在不同杂交组合中的表现形式多样, 且并非相互独立或排斥, 而是存在交叉或重叠, 共同影响某一性状杂种优势[48]. Zhou等人[19]的研究表明，超显性对产量、每穗粒数和粒重的杂种优势贡献最大，显性×显性互作对分蘖数和粒重的杂种优势有重要影响, 同时也影响产量和粒数; Yu等人[5]的研究则揭示, 多位点间的频繁互作(即上位性)是杂种优势的主要成因. 尽管杂种优势的超亲表现主要受非加性效应(显性、超显性及上位效应)调控，但加性效应作为性状遗传的基础组分, 通过稳定传递优良等位基因型, 在杂种优势形成过程中发挥着不可或缺的作用[7,49,50]. Chen等人[12]基于籼型杂交稻(协青早B/9308)RILBCF$_1$群体的研究表明，20个杂种优势相关QTL中有13个与RIL群体QTL定位结果共定位，进一步证实了纯系产量性状加性效应对杂种优势形成的重要贡献.

以单核苷酸多态性(single nucleotide polymorphism, SNP)为代表的第三代分子标记[51]技术快速兴起，水稻杂种优势位点发掘进入大数据时代. 结合高效基因分型[52]、全基因组关联分析[53](genome wide association studies, GWAS)等技术，Huang等人[25,29]通过构建包含1495份优良杂交稻及其亲本的基因组图谱，鉴定出130个与产量相关性状(如穗粒数)相关的杂种优势位点，其中仅少数位点呈现超显性效应. 研究表明，高产品种较其亲本自交系携带更多优良等位基因，且正向显性效应位点的持续累积是杂种高产优势形成的重要遗传基础. 研究随后挑选17个代表性杂交稻构建了包含10074 株F_2用于位点定位, 发现三系、两系和亚种间杂交稻携带的主要杂种优势位点差异较大. 其中三系以*TAC1*[54]，*Hd3a*[55]为主，两系为*Ghd8*[56]和*LAX1*[57]，籼粳亚种间杂交稻以*Ghd7*[58]，*IPA1*[59]和*NAL1*[60]等为主效位点. 近期，Wang等人[39]对甬优4953等3个籼粳杂交稻的高产遗传机制进行了深入解析. 结果表明, 杂种基因组中约25%的区域为纯合籼型或粳型, 涵盖了杂种育性相关基因*Sd*[61], *Sc*[62], *f5*[63]和*qS12*[64]等. 其中, 关键育性位点*S5*[65]呈现无功能型与广亲和型的组合，确保了杂种的正常育性. 同时, 杂交种携带了株型与产量相关的优良纯合等位基因*sd1*[66]，*NAL1*，*Ghd7*和*Ghd8*等，以及杂合的*Tb1*[67]，*Gn1a*[68]，*DTH2*[69]和*IPA1*等功能位点. 这些基因共同作用产生正向的加性与显性效应, 构成籼粳杂交稻产量杂种优势的主要遗传基础. 值得注意的是，图1显示主要优势位点与相应染色体区域的杂种优势QTL分布密度高度一致. 在1，2和3号染色体的短臂、长臂末端以及10号染色体的长臂末端附近，杂种优势QTL和已克隆基因呈现密集分布，暗示这些区域可能蕴含影响杂种优势的新基因或等位变异，值得深入探究.

1.2 已克隆的杂种优势基因

由于杂种优势性状的复杂性，精细定位并克隆的位点仍然有限，其中*RH8*[26](*rice heterosis* 8)为首个图位克隆的产量杂种优势主效位点. 在两优培九衍生的RIL及RILBCF$_1$群体研究中，鉴定到1个QTL簇*RH8*，同时调控开花期*qHD8*/*qhHD8*、株高*qPH8*/*qhPH8*及每穗颖花数*qSPP8.1*/*qhSPP8.1*等性状，最高解释了59.1%的

表 1　水稻杂种优势QTL定位群体及遗传基础a)

Table 1　The mapping population and genetic basis for quantitative trait loci (QTLs) of heterosis in rice

定位群体	主要遗传基础	参考文献	发表年份
388个RILBCF$_1$	显性互补	[4]	1995
250个$F_{2:3}$	上位性	[5]	1997
337个F_2	超显性	[6]	2000
349个RILBCF$_1$, 379个RILTCF$_1$	上位性互作导致的超显性	[7]	2001
171个F_2	超显性	[8]	2001
360个IMF$_2$	显性、超显性和上位性	[9]	2003
63个CSSLTCF$_1$	超显性、上位性	[10]	2005
281个RILBCF$_1$	上位性互作导致的加性和超显性	[11]	2009
281个RILBCF$_1$	加性	[12]	2010
265个ILBCF$_1$	显性	[13]	2011
175个IMF$_2$	超显性	[14]	2011
265个ILBCF$_1$	超显性	[15]	2012
156个ILBCF$_1$	上位性	[16]	2012
294个RILTCF$_1$	加性和非加性效应	[17]	2012
66个CSSLBCF$_1$	显性	[18]	2012
278个IMF$_2$	显性、超显性和上位性	[19]	2012
286个RILBCF$_1$	上位性	[20]	2012
66个CSSLBCF$_1$	显性	[21]	2013
286个RILBCF$_1$	超显性和上位性	[22]	2013
219个RILBCF$_1$	显性, 超显性	[23]	2014
832个RILBCF$_1$	显性、超显性和上位性	[24]	2015
1495个F_1	显性, 超显性	[25]	2015
219个RILBCF$_1$	显性, 超显性	[26]	2016
228个ILTCF$_1$	显性	[27]	2016
204个RILTCF$_1$	加性, 显性, 超显性	[28]	2016
17个F_1, 10074个F_2	加性, 部分显性、超显性	[29]	2016
105个IMF$_2$	显性, 超显性, 上位性	[30]	2016
79个ILTCF$_1$	部分显性, 显性, 超显性	[31]	2017
85个BILBCF$_1$	显性, 超显性	[32]	2020
551个F_1	显性互补	[33]	2020
382个RILTCF$_1$	上位性	[34]	2021
122个CSSLBCF$_1$, 244个CSSLTCF$_1$	显性, 超显性	[35]	2021
146个CSSLBCF$_1$, 146个CSSLTCF$_1$	超显性	[36]	2021
1061个RILBCF$_1$	超显性, 上位性	[37]	2022
382个RILTCF$_1$	完全显性	[38]	2022
300个$F_{2:3}$	加性, 显性	[39]	2022
33个CSSLBCF$_1$	显性	[40]	2023
2839个F_1, 9839个F_2	显性、超显性、上位性	[41]	2023

a) 永久F_2(immortalized F_2, IMF$_2$)群体, 重组自交系/导入系/代换系的回交F_1(a set of F_1 populations derived from a backcross between recombination inbred lines (RILs), introgression lines (ILs) or chromosome segment substitution lines (CSSLs) and their parents, RILBCF$_1$, ILBCF$_1$ or CSSLBCF$_1$), 重组自交系/导入系/代换系的测交F_1(a set of F_1 populations derived from a testcross between RILs, ILs or CSSLs and other tester lines, RILTCF$_1$, ILTCF$_1$ or CSSLTCF$_1$)

抽穗期表现变异. 图位克隆揭示*RH8*与已克隆的*Ghd8*[56]等位, 编码一个CCAAT-box-binding转录因子的HAP3亚基, 该基因杂合态对株高、穗长、每穗粒数及产量等性状表现为超显性效应. 在调查的361个商业化杂交稻中, 约40%的两系杂交稻携带了杂合的*RH8*单倍型, 其杂种优势效应同时受基因型和背景影响. 携带

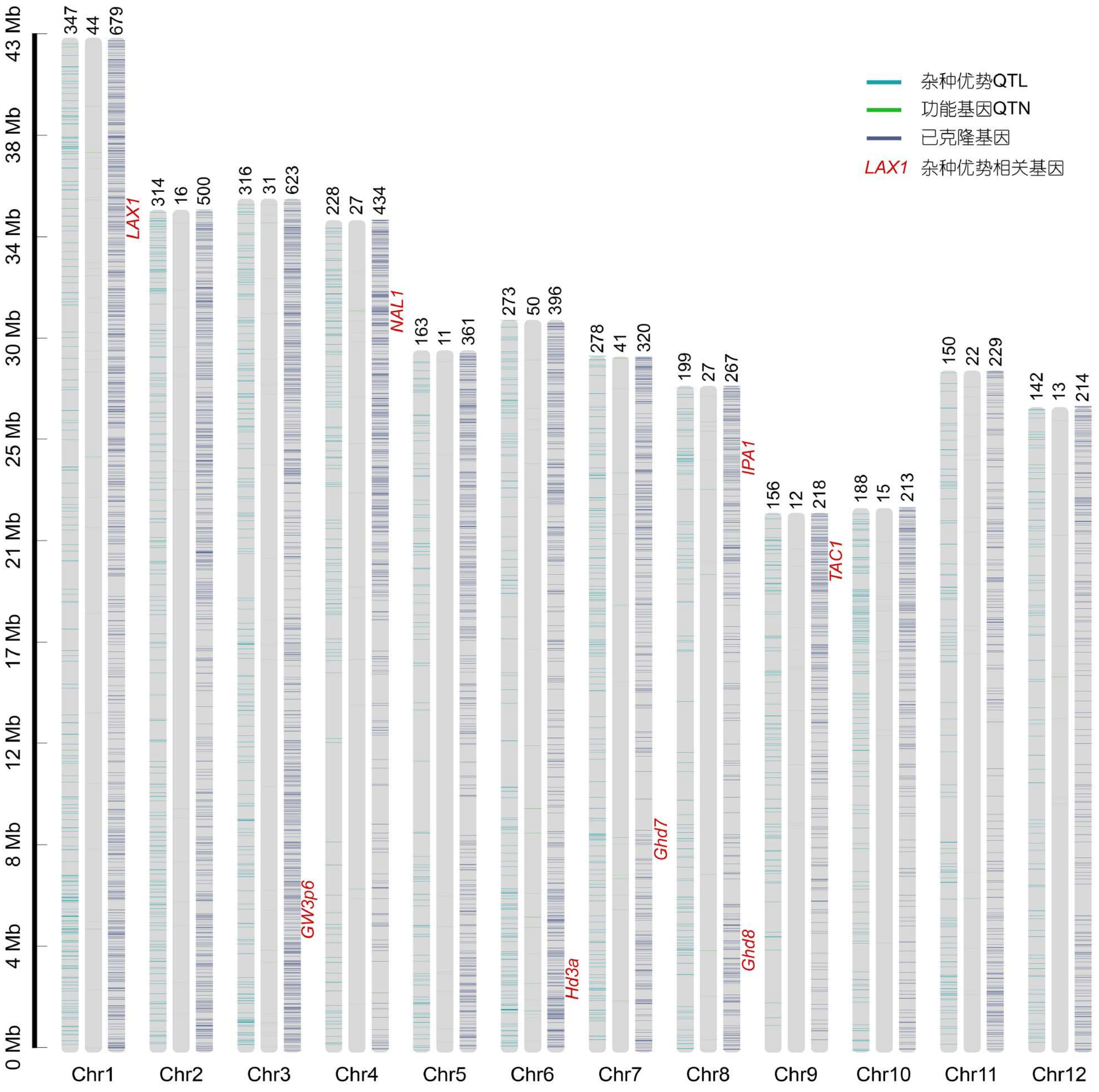

图 1　(网络版彩色)水稻杂种优势QTL、已克隆功能基因及其QTN的位置分布．已克隆基因及相关QTN信息分别源自：https://funricegenes.github.io/和http://www.xhhuanglab.cn/tool/RiceNavi.html

Figure 1　(Color online) The positional distribution of quantitative trait loci (QTLs) for hybrid vigor, cloned functional genes, and quantitative trait nucleotides (QTNs) in rice (The cloned genes and related QTN information were sourced from: https://funricegenes.github.io/ and http://www.xhhuanglab.cn/tool/RiceNavi.html, respectively)

Ghd8$^{\mathrm{NIP}}$互补转基因系与NIL-*Ghd8*$^{\mathrm{ZS97}}$杂交，F_1的产量和有效穗数的平均中亲优势分别提高了17.1%和8.4%，同时对产量表现出正向的超显性效应，表明等位基因*Ghd8*$^{\mathrm{NIP}}$和*Ghd8*$^{\mathrm{ZS97}}$在ZS97背景下对中亲优势表现出强烈的相互作用[36]．*RH8*杂种优势的具体机制尚不明了，推测*RH8*/*Ghd8*杂合态可能通过改变组蛋白折叠结构域，影响*Ghd7*-*Ghd8*-*OsHAP5C*三元复合物的组装[70]，进而干扰下游光周期基因如*Hd3a*的表达，致使杂交种表现出抽穗期超中亲及产量性状超高亲的现象．验证此推测或需借助冷冻电子显微镜解析、双分子荧光互补等技术手段．

水稻籼粳亚种间存在显著的杂种优势，但生殖隔离导致的杂种不育限制了其直接利用．广亲和品种作为一类特殊种质资源，能够与籼稻和粳稻杂交产生高

育性后代. Chen等人[65]通过图位克隆鉴定了广亲和性主效基因*S5*，该基因编码一个定位于细胞壁的天冬氨酰蛋白酶，调控胚囊育性. 研究发现，籼稻*S5-i*和粳稻*S5-j*在第273位氨基酸存在苯丙氨酸/亮氨酸差异，导致胚囊败育；而广亲和基因*S5*-n由于N端大片段缺失，引起蛋白亚细胞定位异常和功能丧失. 进一步研究发现[71]，*S5*位点是一个由三个紧密相连的开放阅读框(ORF3，ORF4和ORF5)编码的“杀手-保护者”系统，籼稻中3号和5号基因有功能(3+/5+)，4号基因没有功能(4–)，粳稻则相反. 在杂种雌配子形成过程中，4号和5号基因共同作用杀死配子，籼型配子由于3+的保护，正常存活，粳型配子无3+的保护而死亡，籼粳杂种表现为半不育.

近期，控制籼粳亚种间杂种花粉不育的主效位点*RHS12*[72]/*Se*[73]/*pf12*[74]被克隆，该位点位于水稻第12染色体的一个存在缺失变异(presence absence variation，PAV)中，由两个基因(*iORF3*/*DUYAO*和*iORF4*/*JIEYAO*)组成，编码一个毒素-抗毒素系统. 在该系统中，*DUYAO*编码一个靶向线粒体的蛋白，并与*OsCOX11*互作，触发细胞毒性和细胞死亡；而*JIEYAO*则通过编码一个竞争性结合DUYAO的互作蛋白，防止*DUYAO*与*OsCOX11*产生低聚体，将其重新定位到自噬体中进行降解，解除DUYAO毒性. 在籼粳杂交种中，粳型单倍型花粉因缺乏*ORF4*的保护而受到籼型单倍型花粉*ORF3*的毒性作用，导致选择性败育；而*RHS12-i*型花粉则因*JIEYAO*的保护而优先传递给后代，形成天然的基因驱动机制. 目前，已有14个籼粳杂种育性相关的主效位点被克隆，其作用机制主要涉及单基因座孢子-配子体互作和双隐性致死配子等模型. 这些位点的功能解析不仅揭示了生殖隔离的遗传基础，也为籼粳杂交稻的分子设计育种提供了重要理论依据[75,76].

综上，解析、利用水稻杂种优势的关键在于分离主效功能基因，并深入剖析其生物学功能. 为此，Wang等人[77]开发了一种新的数量性状作图方法，即Graded-Pool-Seq(GPS)，用于快速绘制QTL图谱，其通过对F_2后代的梯度池样本进行全基因组测序，然后进行集群分离分析(bulked segregant analysis，BSA). 通过该方法结合图位克隆技术，从广占63-4s中成功分离出杂种优势QTL *GW3p6*. 该位点为*OsMADS1*[78]的等位基因，编码一种MIKCc型MADS-box转录因子，属于调控水稻花器官发育的E类基因. 近等基因系表型分析表明，*GW3p6*对粒长表现为不完全显性，其杂合态的籽粒长度接近纯合母本基因型，同时显著提高千粒重和单株产量，可解释27.8%的杂种优势效应. 将*GW3p6*与母本来源的分蘖杂种优势基因*PN3q23*聚合后，产量得到进一步提升，最高可解释55.7%的优势变异率，证实母本来源的少数杂种优势位点对产量杂种优势的形成具有重要贡献.

目前，在已克隆的产量相关基因中，除番茄成花素同源基因*SFT*[79]外，尚未发现其他基因在水稻杂种优势中表现出典型的超显性特征[80]. 尽管*Ghd8*，*Hd3a*，*IPA1*等位点的杂合态在每穗粒数、单株产量等性状上呈现超显性效应，但其效应值在不同杂交组合中存在较大变异，难以重现*SFT*在不同遗传背景下的稳定超显性表现. 关于单位点超显性的分子机制仍不明确，可能源于以下两种假设：(1) 该位点通过调控多个产量相关性状的综合效应呈现超显性[81]；(2) 两个紧密连锁基因的相斥作用导致拟超显性现象的产生[82].

2 水稻杂种优势的分子机制

2.1 基因组变异(genomic variation, GV)与杂种优势

基因组变异包含SNP和结构性变异(structural variation，SV)，是优势亲本之间遗传多样性产生的重要基础，其中SV，PAV等的数量与杂种优势强烈相关，而SNP、插入和缺失(insertions and deletions，InDels)的数量与杂种优势相关性较弱[83]. 水稻中的GV多源于不同血缘材料间的遗传互渗，Lin等人[84]研究揭示两系杂交稻父本含少量外源基因组导入(5.74%)，母本比例较高(22.57%)，尽管粳稻血缘仅贡献少量基因组，但其影响了约50%的杂种优势位点，广泛的遗传互补显著促进了产量性状的杂种优势表现，其中显性位点对杂种优势的贡献大于超显性位点. 研究进一步表明，亲本间的部分遗传变异可追溯至野生稻，这些杂种优势位点在现代水稻杂交育种过程中经历了定向选择，有害效应的位点被逐步淘汰，而具有正向效应的位点则被稳定保留并固定. Zhang等人[85]完成了4个杂交稻亲本的无缺口基因组组装，鉴定出56,817个非冗余SVs，其中PAV达52,943个. 在三系杂交稻中，738个互补基因被利用，而两系杂交稻则利用593698个互补基因，其中仅有46个为两者共有，表明其PAV基因存在显著差异. 基于Y58S/9311和LK638S/WSSM杂交种的RNA-seq分析显示，超显性表达的互补基因占比分别为27.7%和26.1%，提示结构变异在杂种优势形成中具有重要作用.

2.2 等位基因特异性表达(allele-specific expression, ASE)与杂种优势

ASE是一种特殊的基因表达模式，表现为杂交种中亲本等位基因表达的不均衡性，可分为一致性等位基因特异性表达基因(allele-specific expression genes, ASEGs)和不一致性ASEGs. 其中，不一致性ASEGs包含方向转变ASEGs，其特征是表达偏向性随组织或环境条件的变化而发生改变. 在不同组织和实验环境中，ASEG均无明显的亲本偏向性[86]，但逆境相关基因常表现为方向一致性的ASEG[87]，表明杂交种能选择性表达有利亲本等位基因以适应生存环境. 在四种实验环境的水稻幼芽中，汕优63均偏向于表达*TAC1*，而在低温短日照的剑叶、高温长日照及低温短日照的稻穗，表达偏向于*tac1*(株型更紧凑)[86]. 叶瘟抗性基因*RGA4*在Y900幼穗发育早期特异性表达Y58S^{C}(不抗稻瘟病)，在始穗期的茎秆和剑叶组织中偏向于表达抗稻瘟病单倍型R900^{G}[87]. 基于ASEG研究，科学家提出“方向变换的等位基因特异表达”假说，认为一致ASEGs可能产生显性效应，方向转变ASEGs可能导致超显性[86].

水稻中ASE调控机制复杂，DNA甲基化作为关键表观遗传修饰，对调控基因表达和维持杂种优势稳定有重要作用[88]. 多数ASEG存在加性甲基化修饰，即亲本偏好型表达由另一亲本等位基因的高CHG甲基化抑制其自身表达所致[89]. 而杂种中亲本特异DNA甲基化与组蛋白修饰相关，低甲基化区域富集激活性修饰(H3K4me3，H3K27ac)，高甲基化区域则富集抑制性H3K9me2修饰[90]. 研究还发现，DNA甲基化与染色质可及性动态变化正相关，杂种中染色质活跃状态由父本高表达基因和母本低表达基因共同塑造，进而影响杂种优势形成[91]. 此外，水稻不同组织中ASEG的调控模式存在显著差异：茎秆和叶片主要受反式作用调控，而幼穗则倾向于顺式调控，其中反式调控在超显性基因表达中起关键作用. 这些调控模式与基因组变异及籼粳分化区域显著相关，共同参与杂种优势形成的动态精细调控过程[87].

2.3 生理生化途径与杂种优势

在杂种优势转录组研究中，研究人员通过对杂交稻及其亲本的根、幼穗、剑叶和茎秆等组织进行大量RNA-seq分析，发现不完全显性、显性和超显性等表达模式是杂种优势差异基因的主要表现形式. 这些基因表达模式具有显著的组织特异性，例如茎秆中超显性表达基因的数量显著高于幼穗和剑叶[87]. 这些基因涉及光合作用[92]、激素代谢与活性氧调控[93]、昼夜节律与缺水响应[94]，以及DNA整合、细胞壁修饰和类囊体功能[95]等多种生物学途径和代谢通路.

随着蛋白质组学、代谢组学和表观遗传学等组学技术的快速发展及成本优化，水稻杂种优势研究已从单一组学分析转向多组学技术的综合应用，使研究人员能够从多维度深入解析水稻杂种优势形成的分子机制. Ma等人[96]通过整合蛋白组、细胞能量代谢、基因表达调控及翻译后修饰等多层面数据，揭示了杂种幼穗中雷帕霉素靶蛋白复合物介导的能量代谢—赖氨酸乙酰化—生长/生殖发育蛋白调控网络，这一发现对杂交稻优势穗型形成及产量杂种优势至关重要. 近期，Xie等人[97]基于大规模杂种群体表型、杂种优势QTL、转录组数据、动力学模拟及酵母实验结果，提出了HoIIB模型，用以阐释杂种优势的核心分子机制. 该模型指出，在背景不足条件下，纯合子亲本中无法激活的功能，在杂种中可激活等位基因的全部功能，从而赋予杂合子相对于纯合子的相对优势.

3 水稻杂种优势遗传及分子应用

3.1 优势位点利用

水稻杂种优势位点的发掘与鉴定已积累丰富数据，如何有效聚合这些位点以创制强优势杂交种，成为验证其应用价值的关键. 为此，Shen等人[98]利用汕优63双亲的染色体代换系，鉴定出9个具显性遗传效应的产量杂种优势QTL，涉及*Ghd7*，*Ghd7.1*，*Hd1*，*GS3*等功能基因. 随后，于珍汕97背景下选取其中8个对产量贡献显著的位点进行组装，发现4位点组装F_1产量可以达到汕优63的68.3%~80.9%，8位点组装F_1产量则接近汕优63水平，表明通过聚合关键产量优势基因，可有效组装获得水稻的主要杂种优势. 为探索籼粳杂种间强大杂种优势的直接利用，Zhou等人[74]在优良恢复系9311背景下构建并组装了*S5*，*Sc*，*pf12*和*f5*等位基因的不同组合，结果表明籼粳杂种的花粉育性随着组装的亲和模块的增加可提高至90%以上，表现出明显的剂量效应. 而杂种花粉育性位点*f5*，*pf12*和*Sc*在对应广亲和等位基因聚合系中，对胚囊育性的提高表现出协同效应，籼粳杂种的平均结实率达84.75%，该方案将有助于未来重新设计更高产量潜力的亚种间杂交水稻.

借助生物育种技术，Wang等人[99]成功诱导杂种优势基因*GW3p6*的3′可变剪接，相较于杂交种对照，产量平均提升40.8%. 进一步，将编辑后的恢复系与不育系杂交，所得F_1的产量显著超越广两优676的同时，也较荃优丝苗增产3.4%以上，证实通过CRISPR-Cas9技术叠加单个杂种优势基因在提高杂交水稻产量方面的巨大潜力. 近期, Paril等人[1]提出一种作物改良新策略: 运用现代遗传工程技术，通过整合多个杂种优势基因为单一遗传单元以形成超级基因，其在维持显性、超显性及上位性共致的杂种优势基础上，导入目标受体以培育优良品系. 该计划在实施前仍需解决两大挑战: 一是需有效识别并验证足量杂种优势位点及等位基因，以显著提升作物优势，二是需确保多个等位基因融合不影响杂种优势效应.

3.2 杂种优势预测

早期水稻性状杂种优势的预测方法主要包括配合力法、生理生化法、分子标记法等，但因标记数量、定位精度及模型算法等限制, 预测效果有待提升. 随着多组学、生物信息学等技术的进步，表观遗传、标志代谢物、全基因组选择等技术在水稻杂种优势预测中展现出巨大潜力. 对五个F_1杂交种的转录、甲基化组分析发现，亲本外显子中CG背景下差异甲基化区域与转录起始位点的比例，与杂交种杂种优势水平显著负相关. 此比例在25个水稻品系的对比中得到验证, 且亲本在早期生长阶段该比例小于5，可能是F_1表现超亲优势的关键预测指标[100]. Dan等人[101]采用非靶向代谢组学技术, 结合差异代谢网络分析发现, 氨基酸和碳水化合物代谢途径的代谢物水平对产量杂种优势具有显著预测力, 其曲线下面积(area under the curve, AUC)达0.907, 含10个特征代谢物, 这些代谢途径标志物的预测性在不同环境和杂交群体中均得到了验证.

全基因组选择(genomic selection, GS)是一种基于全基因组高密度分子标记的育种方法，通过构建预测模型, 依据基因组估计育种值(genomic estimated breeding value, GEBV)实现早期个体的精准预测与选择, 加速育种进程. Xu等人[102]利用基因组最佳线性无偏预测(genomic best linear unbiased prediction, GBLUP)模型, 以210个水稻重组自交系产生的278个随机杂交种为训练集，并基于25万个SNP标记预测了21,945个潜在杂交种的表现. 结果显示，前100个优选杂交种的平均产量较全体杂交种提高了16%，验证了GBLUP模型在预测杂交种产量上的高效性. 近期，Gu等人[41]汇集了最大规模的杂交稻种质资源，含2,839份杂交稻与9,839个分离个体，利用88,909个SNP及表型数据，构建了基因组选择模型. 该模型精准预测了单株产量等7项农艺性状, 准确度高达0.95. 为实现多性状优选，研究还根据表型分布设定最优值范围，对符合条件GEBV给予高分，并基于此评估了58,353个潜在组合, 发现少数高分组合育种潜力巨大.

虽然GS技术在水稻等作物中前景广阔，但仍面临以下关键挑战[103]：模型局限性. 现有方法以加性效应为主, 显性及上位性效应建模精度不足; 多维复杂性缺失. 单性状、单环境研究方式占主导，缺乏多性状协同调控机制解析及基因型-环境互作整合；多组学整合不足. 基因组数据孤立应用, 未有效融合转录组、表观组等跨组学信息; 技术体系不完善. 专用基因芯片、分析平台及数据共享机制缺位, 制约技术标准化; 应用转化滞后. 多数研究停留于方法学验证阶段, 尚未实现规模化育种应用.

4 讨论与展望

大量水稻杂种优势位点的定位与优势基因的克隆数量并不匹配, 除性状自身复杂性外, 高质量参考基因组的获取及QTL定位技术的突破也是重要因素. Shang等人[104]构建包含251份高质量水稻基因组的超级泛基因组，这也是植物界规模最大、注释最全的基因组资源，能精确解析包括复杂结构变异在内的各类基因组变异. 近期，Hamilton等人[105]完成了水稻基因组注释项目(rice genome annotation project, RGAP)的更新, 涉及基因组数据扩展、基因表达数据等内容，旨在为研究者提供更加全面和高质量的水稻基因组数据资源. 相较于传统的数量性状克隆技术, Wei等人[106]利用18K超大规模水稻遗传群体，开发了一种水稻GWAS到基因(rice genome-wide association study to gene, RiceG2G)的QTL基因快速发掘方法. 通过收集基因注释、在18个水稻组织的时空表达模式等信息，对每个性状的候选基因赋分，将分数最高的3个基因作为目标基因. 基于此法, 研究高效发掘了16个农艺性状的1207个QTLs, 并对其中2个候选基因进行了验证. 科学家们在水稻功能基因组学的这些最新进展，将加快推进杂种优势QTL的克隆与验证工作，为深入解析杂种优势遗传调控机制提供有力支撑.

随着种植环境的持续恶化，作物生产面临的非生

物胁迫(如洪涝、干旱、高温、冷害和高盐碱等)日益频繁且严重. 因此, 作物抗逆性杂种优势(包括抗旱耐涝、耐盐碱、抗冷耐热等)的有效利用, 以及产量杂种优势相关位点与逆境互作效应的解析, 已成为作物杂种优势研究的重要方向之一[81]. 当前水稻杂种优势研究主要还是聚焦于产量性状, 虽偶有涉及盐胁迫[92,107,108]、微生物[109,110]及激素[111]等外界因素的报道, 但分子机制尚不清晰. 此外, 水稻还将面对稻瘟病、稻飞虱、白叶枯等多种病虫害的生物胁迫, 虽然抗性品种可有效防控病害, 但增强防御反应往往以牺牲产量为代价[112]. 值得注意的是, 拟南芥核心昼夜节律基因*CCA1*能在不影响生长的前提下, 赋予杂交种的细菌抗性杂种优势. *CCA1*于病原菌入侵的第一天黎明在F_1中超高亲表达, 导致水杨酸合成基因超高亲激活, 水杨

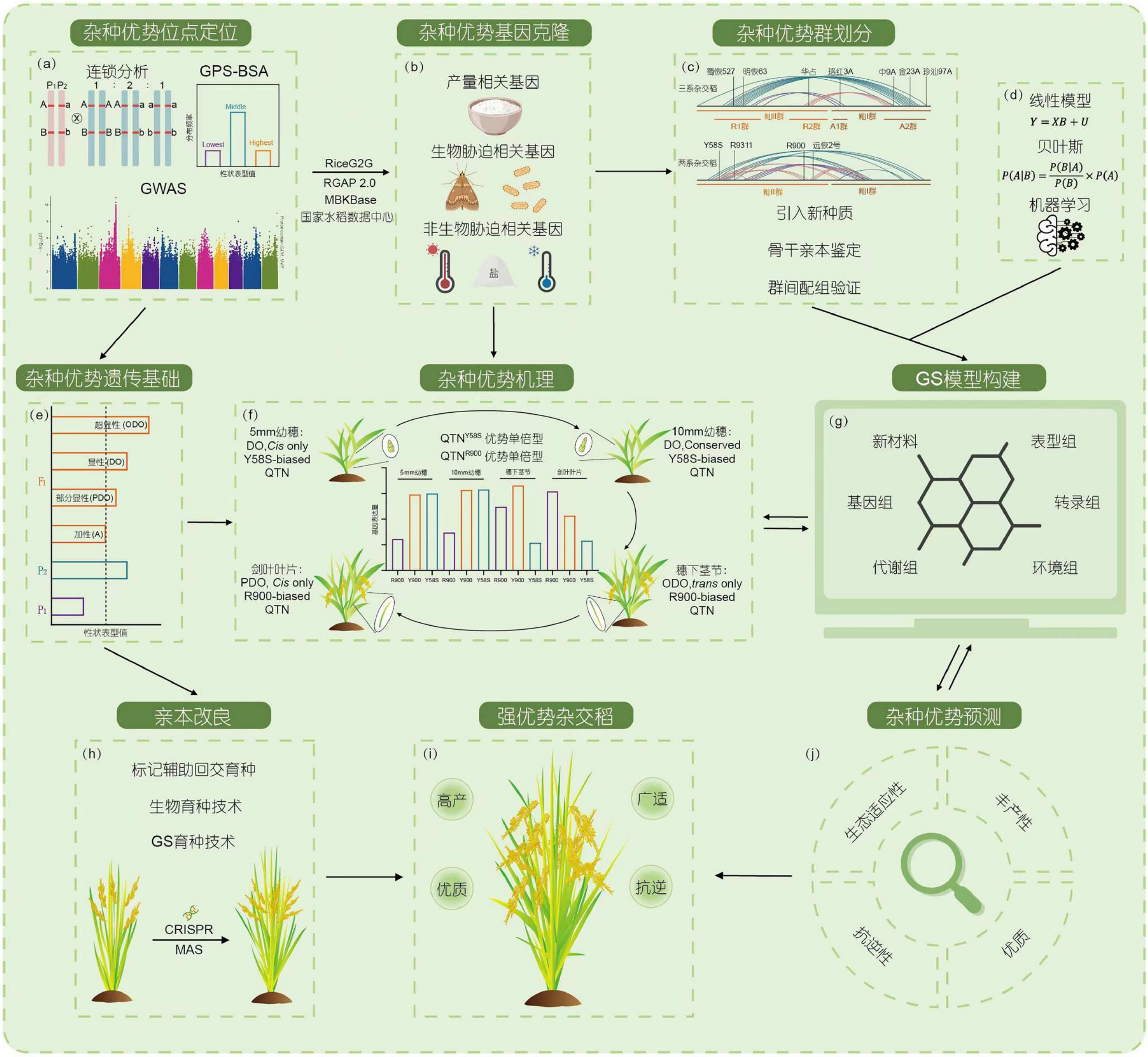

图 2 (网络版彩色)水稻杂种优势遗传机理及分子预测研究示意图. 图中部分图片元素由BioRender创建. (a) 杂种优势位点定位; (b) 杂种优势基因克隆; (c) 杂种优势群划分; (d) 全基因组选择方法; (e) 杂种优势遗传基础; (f) 杂种优势机理; (g) 全基因组选择模型构建; (h) 亲本改良; (i) 强优势杂交稻; (j) 杂种优势预测

Figure 2 (Color online) Schematic diagram of the genetic mechanisms and molecular prediction of heterosis in rice (Created by Biorender, Y, W. (2025) https://BioRender.com/e71k166). (a) Mapping of heterosis loci; (b) cloning of heterosis genes; (c) classification of heterotic groups; (d) genomic selection methods; (e) genetic basis of heterosis; (f) mechanisms of heterosis; (g) construction of genomic selection models; (h) improvement of parental lines; (i) high-yielding hybrid rice with strong heterosis; (j) prediction of heterosis

酸含量显著超亲，杂种表现出抗病杂种优势. 在病原菌入侵后的每一天中午，*CCA1*节律性在F_1中超低亲表达，从而解除其对下游生长相关基因的抑制，使F_1具有更强的光合作用和淀粉利用效率，表现出显著的生长杂种优势[113]. 目前，水稻抗病杂种优势研究仅局限于少数位点的定位分析[25]，其抗病虫杂种优势的分子机制尚未阐明. 未来研究应着重拓展两个方向：一方面需深化水稻耐盐碱等非生物胁迫性状的杂种优势研究；另一方面应加强抗病虫等生物胁迫性状杂种优势位点的发掘与功能鉴定. 通过系统解析杂种优势位点与外界环境的互作机制，为培育具有环境适应性的优质水稻新种质提供理论基础.

杂种优势利用是农作物育种的核心技术，是显著提升农作物产量和增强适应性的主要途径，其进一步突破依赖于杂种优势机理的全面解析及优势类群的高效应用. 玉米作为最早发现杂种优势[114]并利用最为彻底的农作物，其清晰优势机理仍有待完善，但在杂种优势群的精准划分及改良利用上取得了突破，提高了传统育种效率. 杂种优势群理论源于玉米杂种优势利用的长期实践，很多具有影响力的组合均源于Reid和Lancaster两个自交系群间的杂交，由这对杂种优势类群组成一套杂种优势利用模式[115]. 杂种优势群蕴含的丰富变异和优势基因为性状改良提供了重要资源，这些基因在杂种后代中通过显性、超显性及上位性等遗传效应相互作用，从而赋予杂种显著的竞争优势. 当前结合高通量测序技术划分水稻杂种优势群已经成为热点[116]，可以从全基因组角度剖析遗传变异，使分群更精准并具代表性. 基于1143份我国不同稻区的籼型杂交稻亲本重测序数据[33]，所有材料被初分为IndI与IndII两大亚群，进一步细分发现，三系恢复系/保持系与三系不育系界限分明，而两系恢复系与不育系因遗传成分高度杂糅，难以独立成群，凸显了两系杂交稻育种中杂种优势利用同质化现象. 研究还依据组合审定信息，解析了三系、两系杂交稻亲本配组规律，初步确立了杂种优势利用模式.

与玉米杂种优势群的成熟应用相比，水稻杂种优势群的精准划分及利用仍面临许多挑战[117]. 在现有籼型杂交稻亲本优势群初步划分的基础上，根据稻区骨干亲本的亲缘关系进一步细分杂种优势类群. 结合稻区特定需求，如长江中下游的中大穗型、上游的重穗型及华南稻区的多穗型等，引入新种质资源，综合水稻产量与品质等的分子互作网络[118]，深入挖掘水稻高产、优质、抗逆等性状的优良基因或单倍型，鉴定新型不育系和恢复系基因，创新水稻杂种优势利用的核心种质，拓展杂种优势利用模式. 通过鉴定杂种优势群，旨在为骨干亲本构建精确的电子图谱，明确各自交系所属的杂种优势类群，从而有针对性地进行组配，避免同类群内的冗余配种[81]. 在此基础上，广泛收集各优势类群的新增改良自交系基因型和表型数据，利用机器学习及组学大数据(包括基因组、代谢组、蛋白质组等)，构建基于杂交稻亲本的迭代基因组选择模型(图2). 对预测杂交种进行多年、多点的丰产性试验，将农艺性状、生态环境等表型数据反馈至模型，不断优化提升，预期将提高水稻杂交种的配组效率和杂种优势预测的准确性，丰富杂种优势形成的遗传理论基础.

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Summary for “水稻杂种优势遗传基础及机理解析研究进展”

Research progress on the genetic basis and mechanistic elucidation of heterosis in rice

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Heterosis, or hybrid vigor, refers to the phenomenon where F_1 hybrids exhibit superior performance in yield, stress tolerance, and other agronomic traits compared to their parental lines. As a foundational principle in modern crop breeding, heterosis has been widely applied. In China, over six decades of research have led to the development of three-line and two-line hybrid rice technologies and the breeding of super hybrid rice, securing global leadership in this field. With rapid advances in genomics and biotechnology, substantial progress has been made in elucidating the molecular basis of heterosis and guiding more efficient breeding practices. This review summarizes key progress in three areas of rice heterosis research: genetic basis, molecular mechanisms, and breeding applications, while offering perspectives for future research. At the genetic level, classical hypotheses—including dominance complementation, overdominance, and epistasis—have been broadly validated and explain most heterosis phenomena. Additive effects, as core components of trait inheritance, also contribute significantly. The paper further reviews major heterotic loci that have been cloned and analyzes their regulatory mechanisms. At the molecular level, heterosis is shown to arise from complex, multilayered processes. Mechanisms such as genomic complementation, allele-specific expression, and enhanced activation of metabolic pathways are explored. These findings highlight the importance of integrating population genetics, molecular biology, and bioinformatics to unravel the underlying mechanisms. In breeding applications, achievements include the systematic assembly of heterotic loci across different genetic backgrounds and the construction of predictive molecular models. Challenges in genome-wide selection are discussed, including issues of model accuracy, integration of multi-omics data, technical standardization, and application scalability. Notably, limited research exists on heterotic loci related to resistance against abiotic and biotic stresses. Future studies should expand investigations into heterosis for traits such as salt and alkali tolerance, and deepen the identification and functional analysis of loci associated with pest and disease resistance. An in-depth understanding of heterotic locus-environment interactions is also essential. Based on the preliminary classification of indica hybrid rice heterotic groups, the paper proposes refined grouping based on genetic relationships among elite parental lines in specific rice-growing regions. Considering regional breeding goals—such as large-panicle types in the middle and lower Yangtze River basin, heavy-panicle types in the upper reaches, and multi-panicle types in South China—introducing new germplasm and identifying favorable alleles for yield, quality, and stress tolerance is vital. The discovery of novel male-sterile and restorer genes will further drive innovation in core germplasm and heterosis application models. Finally, this study recommends collecting newly improved inbred lines and integrating their genotypic and phenotypic data. Using machine learning and multi-omics platforms—including genomics, metabolomics, and proteomics—an iterative genomic selection model can be developed. Multi-location trials of predicted hybrids, coupled with agronomic and ecological data, will improve hybrid selection efficiency and heterosis prediction, supporting the development of broadly adaptable, high-performing hybrid rice varieties.

hybrid rice, heterosis, genetic basis, molecular mechanism, utilization of heterosis

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