作物学报 ACTA AGRONOMICA SINICA 2011, 37(1): 1–17 http://www.chinacrops.org/zwxb/
ISSN 0496-3490; CODEN TSHPA9 E-mail: xbzw@chinajournal.net.cn

DOI: 10.3724/SP.J.1006.2011.00001

综 述

中国作物新基因发掘: 现状、挑战与展望

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摘 要: 作物新基因发掘是实现作物种质资源向基因资源转变和作物分子育种的基础。本文对中国水稻、小麦、玉米、大豆、棉花和油菜等主要作物基因发掘研究进展进行了分析和评述, 总结出近 10 年来中国科学家在作物基因发掘研究领域取得的突破性进展, 包括: (1)创制出一批具有特色的基因发掘材料, 包括基于中国作物遗传多样性的核心种质、基于优异资源的遗传分离群体和基于人工诱变的突变体等; (2)基因发掘技术和方法有所突破, 尤其是建立了针对不同基因特点整合各种技术的基因发掘技术、改进了基因/QTL 的生物统计算法等, 提高了基因发掘的效率; (3)作物重要性状基因/ QTL 的标记定位已成为作物常规遗传研究方法, 初步定位了一批抗病虫、抗逆、优质、养分高效、高产相关基因/QTL, 其中, 有 500 多个基因已精细定位; (4)以水稻为代表的作物基因克隆及功能研究在国际上受到瞩目, 在主要作物中已克隆了 300 多个基因, 其中, 在目标作物中验证的重要性状基因数超过 70 个。目前, 国际作物基因发掘正朝高效化、规模化及实用化方向发展, 中国作物基因发掘也在这些方面有所创新。然而, 与国际作物基因发掘研究相比还存在差距, 中国作物基因发掘的数量和质量还远远不能满足作物分子育种的需求, 具体表现为不同作物基因发掘研究进展不平衡、发掘基因的数量还相对有限、已发掘的基因中具有重大利用价值的基因不多等。针对中国基因发掘面临的问题和世界各国以及跨国生物技术公司争夺基因的巨大挑战, 作者提出了中国作物基因发掘应重点提高基因发掘效率, 开展重要基因克隆及基因的价值评估, 加强以生物产业发展需求为导向的基因发掘策略。

关键词: 作物; 基因; QTLs; 定位; 克隆; 发掘; 功能

Novel Gene Discovery of Crops in China: Status, Challenging, and Perspective

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Abstract: Discovery of novel genes in crops is the basis to change germplasm resources from phenotypical characterization to a gene level and hence for molecular breeding. This paper reviewed progress of novel gene discovery studies in major crops, such as rice, wheat, maize, soybean, cotton, and oilseed rape in China. In last decade, Chinese scientists have achieved a number of breakthroughs on novel gene identification in crops, including: (1) Various distinctive materials for gene discovery were created, such as core collections of germplasms based on crop genetic diversity, establishment of genetic populations based on genetic resources with favorite traits, assessment of mutants derived from mutagenesis, and so on; (2) Technology and methods of gene discovery were further developed, especially the gene-based integration of various discovery technologies with combination of biometric algorithm improvement of gene/QTLs, and therefore the efficiency of gene discovery was increased; (3) Mapping genes/QTLs related to important agronomic traits of crops has become a common method for genetic studies. A number of genes/QTLs associated with disease and insect resistance, stress tolerance, good quality, nutrient use efficiency and high yield have been mapped, of which more than 500 genes have been positioned on chromosomes precisely by fine mapping; (4) Great

本研究由国家高技术发展计划(863 计划)项目(2006AA100104), 国家重点基础研究发展计划(973 计划)项目(2004CB117213), 国家科技支撑计划项目(2006BAD13B05)和引进国际先进农业科学计划(948 计划)项目(2006-G1)资助。

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Received(收稿日期): 2010-11-28; Accepted(接受日期): 2010-12-12.

progress in cloning and functional analysis of crop genes in China, particularly in rice, has drawn world-wide attention. More than 300 genes have been cloned in the main crops, among which more than 70 genes have been functionally validated in crops. While gene discovery in crops becomes more and more efficient, large-scale and towards utilization in the world, Chinese scientists are also making new findings in this field. However, the quality and quantity of crop gene discovery in China is still far from satisfying the needs for molecular breeding and the overall level of novel gene discovery is still behind top labs/institutions in the world. Gene discovery in different crops has developed unevenly, the number of genes discovered is not large enough and the genes found to have great value for crop improvement are few. Considering weak points in gene discovery in China and the challenges both international and from biotechnology companies, the authors provided strategies in crop gene discovery in China, with focus on speeding up gene cloning and functional analysis, emphasis on identification and evaluation of the genes with utilization potential, and research activities more orientated to the biotechnology industry.
Keywords: Crops; Gene; QTLs; Mapping; Cloning; Discovery; Function

作物新基因发掘是转基因育种、分子标记育种和品种分子设计的基础[1]。众所周知，第一次绿色革命是与矮杆基因的发掘与应用分不开的。全球抗除草剂转基因大豆和中国抗虫转基因棉花的快速推广种植更是展示了基因在作物育种和农业生物产业发展中的巨大作用。

孟德尔的《植物杂交试验》论文于 1900 年被重新发现，开辟了作物性状遗传研究的新篇章。“基因”一词是约翰森 1909 年根据孟德尔论文中因子(Factor)一词创造的[2]。经过科学家 100 余年的努力，第一个基于遗传图谱而图位克隆(map-based cloning)的作物基因水稻抗白叶枯病基因 *Xa21* 于 1995 年问世[3]，带动了作物重要性状基因的发掘研究。随着水稻[4]和拟南芥[5]等植物基因组学研究的深入，高通量基因克隆和鉴定技术不断发展和完善，尤其是玉米(*Zea mays*)[6]、大豆(*Glycine max*)[7]、黄瓜(*Cucumis sativus*)[8]等基因组计划的相继完成，更是极大地推动了作物基因发掘的速度。在水稻基因组测序的引领下，中国水稻功能基因发掘研究在国际上一直保持领先优势，而且带动了其他作物基因的发掘研究。本文总结了中国作物基因发掘研究成果，介绍了国际作物基因发掘的发展趋势，同时也对中国基因发掘研究面临的挑战及发展进行了讨论，展示了基因发掘的前景。

1 中国作物新基因发掘的突破性进展

自“九五”以来，在国家自然科学基金、国家高技术发展计划(863 计划)、国家重点基础研究发展计划(973 计划)、国家科技攻关和支撑计划等相关项目的资助下，中国作物新基因发掘研究取得了突飞猛进的发展，通过新基因发掘材料的创制和研究方法的改进，在新基因标记和定位以及基因克隆和功能验证方面取得了可喜的成就。

1.1 创建了一批具有特色的基因发掘材料

中国保存近 40 万份的农作物种质资源，居世界第二位，这些种质资源为基因发掘奠定了坚实的物质基础。然而，如何从数以万计的种质资源中发掘出优异基因是急需解决的科学问题。Frankel 和 Brown[9]提出了核心种质的概念，为种质资源研究和利用提供了新的途径。在国家科技项目如 973 项目的资助下，我国主要农作物核心种质的系统研究远远早于国外同类研究，已构建了水稻[10-11]、小麦[12]、大豆[13-15]、玉米[16]及其他几十种农作物的核心种质和微核心种质，将种质资源的数量由上万份减少到几百份，微核心种质对总体的代表性在 75%以上，促进了种质资源的精细表型鉴定和基因型鉴定[17-18]，并在育种利用中发挥了积极作用。

在种质资源鉴定的基础上，利用具有优异性状的材料创建了一大批遗传分离群体并用于遗传图谱构建及基因定位，这些群体包括重组自交系(recombinant inbred line, RIL)群体，近等基因系(near-isogenic line, NIL)群体，F_2 群体，以及回交群体等。以不同生态区的主栽品种为受体亲本与核心种质进行杂交和回交，已经创造了一大批回交导入系(backcross introgression lines)[19]，构建基于核心种质的基因发掘研究和利用研发体系[20]。除核心种质导入系外，还构建全基因组的代换系(chromosome segment substi-tution lines, CSSL)或渐渗系，在减少遗传背景影响、克隆基因/QTL 方面发挥了重要作用[21]。

除上述的自然变异群体可用于基因发掘外，人工创制的突变体等特殊遗传材料也为基因发掘创造了条件。我国水稻基因发掘取得的显著进展是与其突变体创制分不开的，如国际上已构建的了 4 个大规模水稻插入突变体库中，中国创制了 3 个[22-24]。利用甲基磺酸乙酯(EMS)诱变[25]和同源四倍体花培[26]等技术也创制了一批水稻突变体。此外，用 ^{60}Co-γ 射线和 EMS 也筛选出大豆突变体[27-28]。利用这些不同

来源的突变体克隆了一大批水稻基因包括叶卷曲基因 *SLL1*[29], 脆秆基因 *BC10*[30], 控制分蘖数、叶夹角、植株高度的基因 *TLD1*[31], 控制早抽穗的基因 *Hd1*[32], 控制穗延伸的基因 *SP1*[33], 抗旱耐盐基因 *DST*[34]等。

1.2　基因发掘方法有所创新

现代分子生物学特别是基因组学和生物信息学的迅猛发展对基因发掘的新理论和新方法产生了巨大的促进作用, 推动了基因发掘策略与方法[35](图 1)的发展。作物基因发掘的方法主要有从表型到基因的正向遗传学方法和从基因到表型的反向遗传学方法[36]。正向遗传学中有两个代表性的方法, 一是根据目标基因在染色体上的位置进行基因克隆的图位克隆方法[37], 如我国水稻中克隆的很多控制重要性状基因如 *MOC1*、*Ghd7*、*RID1* 等[38-40]都是通过这种方法获得的。二是基于连锁不平衡(linkage disequilibrium, LD)将标记或候选基因的遗传变异(等位基因变异)与目标性状表型联系起来的关联分析(association analysis)方法[41], 包括基于全基因组扫描的关联分析和基于候选基因的关联分析, 前者如对水稻的全基因组扫描分析[42-43], 后者如对小麦光周期反应基因 *Ppd-D1*[17]的关联分析。利用反向遗传学所进行的研究中, 基因所影响的表型并不清楚, 但可通过遗传转化研究基因功能以及所引起的可能表型变异。另外, 也可以通过插入或删除、转座子标签(transposon-tagging)或 RNA 干涉(RNA interference, RNAi)[44]等产生表型变异来发掘基因。在反向遗传学方法中, 以同源基因克隆最具代表性。我国的水稻基因发掘以图位克隆为主, 而其他作物则以同源基因克隆为主。基于比较基因组学方法是克隆尚无基因组序列作物基因的一种重要方法。需要指出的是, 整合各种方法研究基因功能已成为基因发掘的主要方法。如将基因关联分析与表达分析[18]或转基因[45]相结合, 同源克隆基因与利用重组自交系群体定位[46]相结合, 以及整合连锁图谱、表达谱和功能互补分析来克隆微效抗性基因/QTL[47]等。

作物的很多重要性状都受微效多基因控制遗传, 因此, 提高这些基因/QTL 的检测效率对于基因克隆至关重要。我国科学家在国际研究方法的基础上不断创新, 提出上位性的各项主效应及基因型×环境互作效应的定位分析, 创建了发育性状条件 QTL 定位分析法[48]。同时, 还创立了 QTL 加性、显性、上位性主效应及其与环境互作的基因定位遗传模型[49-50]; 发展了数量性状基因定位及效应分析的基于混合模型的复合区间作图(MCIM)方法[51-52]; 建立了应用混合分布模型对多环境试验数据进行联合分析以及测验主基因型与环境互作及环境效应的统计方法[53]。检测作物数量性状基因与遗传标记连锁

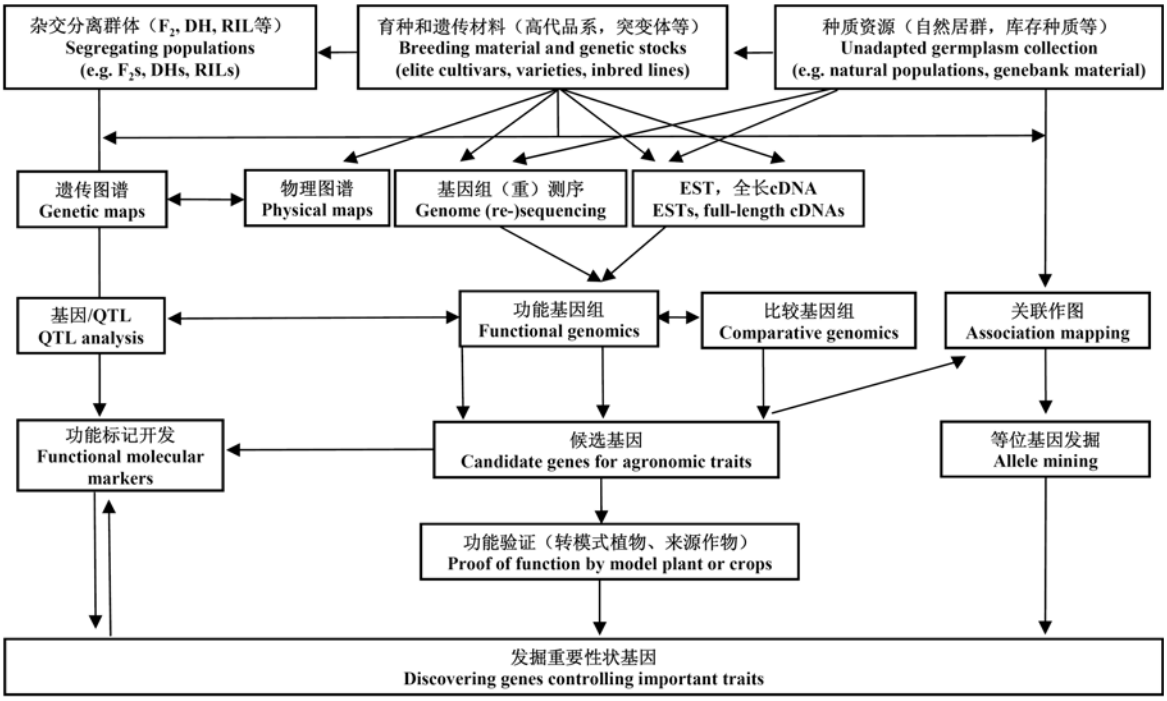

图 1　基于基因组的农作物基因发掘方法(改自文献[35])

Fig. 1　Gene discovery strategy in crops based on genome (Modified from reference[35])

关系的方差分析法[54]、四向杂交设计 QTL 分析的极大似然方法[55]以及数量性状基因的完备区间作图方法[56]先后研制成功, 从而简化了控制背景遗传变异分析过程, 提高了对 QTL 的检测功效。同时, 我国还研制了具有自主知识产权的计算机软件 QTL Ici-Mapping, 能够完成 20 种常规双亲群体中遗传连锁图谱的构建[57]、加显性效应 QTL 的完备区间作图[58-59]、2 对位点互做 QTL 的定位[60]、以及染色体片断置换系群体中的 QTL 定位[61]等功能, 为 QTL 定位研究提供了有效的计算工具。

1.3 精细定位了一批作物重要性状基因/QTLs

据不完全统计, 近 10 年我国已定位与作物性状相关的基因/QTL 超过 990 个(表 1), 定位基因的数目从 2000 年开始呈逐年急剧增加趋势。精细定位(贡献率在 10%以上, 或标记遗传距离小于 2 cM)的基因位点有 506 个, 包括产量 139 个、抗病性 86 个、抗虫 5 个、抗除草剂 1 个、抗逆 50 个、品质 93 个、形态 99 个、养分高效 4 个、育性 29 个。基因定位的精确度与构建定位群体大小密切相关, 如研究 *Xa4* 基因所用的 F_2 分离群体从 467 株、1 401 株增加到 2 800 株时, 定位范围从 400 kb、90 kb 缩小到 47 kb[62-64]。由于水稻比其他作物的基因定位群体大, 定位在 2 cM 范围内的基因相对较多, 有 61 个, 而小麦有 18 个、玉米 16 个、大豆 28 个、棉花 30 个, 油菜 46 个。只有水稻基因已精确定位在一定的物理距离范围内, 包括形态相关基因(*ibf*[65], *Cde1*(*t*)[66], *Rl9*(*t*)[67], *rl*(*t*)[68], *htd1*[69], *PAL1*[70])、育性相关基因(*S31*[71], *S32*(*t*)[72], *S33*(*t*)[73], *S-b*[74], *Sc*[75], *S-d*[76])、产量相关基因(*EP*[77], *qGL-3a*[78], *qSPP7*[79], *gpa7*[80], *psl1*[81], *rl10(t)*[82], *tms5*[83-84], *pss1*[85], *f5-Du*[86], *Rfe*[87], *OsMS-L*[88])、抗病基因(*Pigm(t)*[89], *Pi15*[90], *AvrPi7*[91], *Xa4*[62-64], *Xa10*[92], *xa13*[93], *Xa26*[94])、抗虫基因(*Bph15*[95])、抗除草剂(*Bel*[96])等。基因的精细定位为图位克隆奠定了基础。

1.4 克隆验证了一批主要作物重要性状基因

中国主要作物的基因克隆及功能验证也取得显著进展, 尤其是水稻的研究成果令世界科学家所瞩目。据不完全统计, 我国先后克隆作物重要性状相关基因 393 个。这些已经克隆的基因包括水稻 276 个、小麦 157 个、玉米 164 个、大豆 134 个、棉花 160 个、油菜 99 个(表 1), 按作物分性状分类, 包括育性 26 个、产量 18 个、品质 63 个、抗非生物胁迫 104 个、抗病虫 48 个、资源利用 7 个、生长发育 127 个。其中, 已转入模式植物和来源作物进行功能验证的基因数分别超过 29 个[97-123]和 73 个[38-39,124-192](表 2)。

育性相关基因: 我国不仅水稻杂种优势利用在世界上处于领先水平, 其育性相关基因的克隆及功能研究也取得显著进展。在雌性育性方面, 克隆了广亲和基因 *S5*[124], 明确了籼稻 *S5* 基因(*S5-i*)和粳稻 *S5* 基因(*S5-j*)等位变异的差异源自两个氨基酸, 而广亲和等位基因(*S5-n*)的无功能特性是由于预测 S5 蛋白 N 端的基因删除导致蛋白亚细胞错误定位所致。在雄性育性方面, 籼粳杂种雄性育性基因 *Sa* 由两个相邻的基因 *SaM* 和 *SaF* 组成, 这 2 个基因构成的单倍型在籼稻和粳稻中存在差异, 从而构建了一个解释杂种雄性育性的双/三基因互作模型, 对于水稻克服亚种间不育和杂种优势利用具有重要指导意义[125]。此外, 水稻中尿苷二磷酸葡萄糖焦磷酸化酶(UDP-glucose pyrophosphorylase, UGPase)同源基因 *Ugp1* 是花粉胼胝质沉积所不可或缺的, 其共抑制形成一种新的温敏核雄性不育类型[126]。通过 *sl1* 突变体克隆到一个 C2H2 型锌指结构域的蛋白 *SL1*, 该基因参与水稻花的发育[127]; 通过对一些水稻雄性不育突变体的研究, 发现 *CSA* 参与水稻花粉发育过程中糖的分离过程[128], 而 *CYP704B2* 参与调控水稻花粉外壁的形成[129]。同时, 还发现另两个基因

表 1 主要作物近 10 年定位的重要性状的基因/QTL 位点数

Table 1 Number of gene/QTLs mapped in major crops during the past decade

作物 Crop	贡献率≥10%或遗传距离≤2 cM 位点数 Loci with contribution rate≥10% or genetic distance ≤2 cM	其他位点数 Other loci	总位点数 Total loci
水稻 Rice	196	80	276
小麦 Wheat	49	108	157
玉米 Maize	119	45	164
大豆 Soybean	59	75	134
棉花 Cotton	28	132	160
油菜 Oilseed rape	55	44	99
总计 Total	506	484	990

表 2　克隆并经遗传转化验证功能的作物基因
Table 2　Crop genes cloned and functional confirmed by transgenic study

性状 Trait	代表性基因 Representative genes	
	利用模式植物验证功能 Function confirmation in model plants	利用来源作物验证功能 Function confirmation in original crops
育性 Fertility	—	*S5*[124], *Sa*[125], *Ugp1*[126], *SL1*[127], *CSA*[128], *CYP704B2*[129], *OsC6*[130], *OsRAD21-3*[131], *PAIR3*[132], *ZEP1*[133], *RPA1a*[134]
产量 Yield	—	*MOC1*[38], *Ghd7*[39], *PROG1*[135,136], *DEP1*[137], *GIF1*[138], *GW2*[139], *GW5*[140], *GS3*[141], *LAZY1*[142], *OsLIC*[143], *TAC1*[144], *HTD1*[145], *HTD2*[146], *D27*[147], *OsMADS34*[148], *EP2*[149], *DTH8*[150], *EUI*[151], *IPA1/OsMADS34*[152]
品质 Quality	*GmDof*[97], *Zpu1*[98], *GmDGAT*[99], *ZmFDR3*[100], *ZmGS3*[101]	*OsVPE1*[153], *BADH2*[154], *Wx*[155], *OsRab5a*[156], *GhACT1*[157], *GhDET2*[158]
抗非生物逆境 Abiotic stress	*GmUBC2*[102], *GmWRKY*[103], *GmbZIP*[104], *GmAAPK*[105], *GmCAX1*[106], *GmSAMDC1*[107], *GmDREB2*[108], *GmDREB3*[109], *GmNHX2*[110], *ZmMPK7*[111], *ZmFtsH2A*[112], *ZmFtsH2B*[112], *ZmLAC1*[113], *ZmALDH22A1*[114], *TaCTR1*[115]	*SKC1*[159], *DST*[34], *OsHAL3*[160], *OsSIK1*[161], *SNAC1/2*[162-163], *DREB*[164], *OsSKIPa*[165], *DSM1*[166], *DSM2*[167], *OsMYB3R-2*[168], *MYBS3*[169], *OsbZIP23*[170], *TSRF1*[171]
抗病虫 Biotic stress	*GmHZ1*[116], *GmPti1*[117], *GmAOS*[118], *ZmRdRP1*[119]	*Xa26*[172], *Xa13*[173], *GH3-8*[174], *OsWRKY45-1/2*[175], *Pi36*[176], *Pi37*[177], *Pid2*[178], *Pid3*[179], *TaPIEP1*[180], *BPH14*[181]
资源利用 Resource utilization	*GmNMH7*[120]	*OsPTF1*[182], *OsPHR2*[183], *OsSPX1*[184-185], *OsSPX3*[186], *OsPT2*[187], *OsPT6*[187]
生长发育 Growth&development	*GmKNT1*[121], *TaCRY1a*[122], *TaCRY2*[122], *ZmGRF*[123]	*EG1*[188], *SLL1*[29], *BC10*[30], *TDR*[189], *WOX11*[190], *RID1*[40], *DRP2B*[191], *GmSERK*[192]

OsC6[130]和 *OsRAD21-3*[131]也参与到水稻雄蕊和花粉发育的过程。此外, *PAIR3*[132]、*ZEP1*[133]、*RPA1a*[134]三个基因通过同源染色体的配对和同源重组影响减数分裂, 进而影响水稻的育性。

产量相关基因: Li 等[38]克隆了控制水稻分蘖的基因 *MOC1*, 这是中国科学家首次克隆的作物农艺性状功能基因。转 *MOC1* 基因的水稻植株分蘖能力明显比野生型强, 表现出重要的育种应用潜力。而转 *Ghd7* 基因水稻植株表现抽穗延迟, 株高增加, 每穗颖花数显著增加, 证实该基因同时控制水稻的株高、抽穗期和穗粒数[39]。控制野生稻匍匐生长习性的基因 *PROG*[135-136], 不仅使匍匐生长变成直立生长, 株型得到改良, 更适合密植, 而且穗粒数增加, 产量大幅度提高。控制穗形态基因 *DEP1* 突变后能促进细胞分裂, 使稻穗变密、枝梗数增加、每穗籽粒数增多[137]。此外, 籽粒灌浆充实度基因 *GIF1*[138]、与粒宽和粒重性状相关的数量性状基因 *GW2*[139]、*GW5*[140]和 *GS3*[141]等都对水稻产量性状的遗传改良具有良好的应用前景。水稻的株型是影响产量的一个非常重要的因素, 近年来已经克隆出多个影响腋芽生长, 分蘖角度和叶片夹角的基因, 如 *LAZY1*[142]、*LIC*[143]、*TAC1*[144]、*HTD1*[145]、*HTD2*[146]和 *D27*[147]等。此外, 对 *OsMADS34*[148]和 *EP2*[149]等基因通过控制花序的形态和小穗数影响水稻产量; *DTH8* 基因通过抑制开花影响水稻植株高度和产量潜力[150]; 对 *EUI* 基因的研究也表明该基因通过控制水稻节间伸长影响水稻的株型[151]。控制水稻理想株型关键基因 *IPA1* 的获得, 使转基因水稻具有大穗多粒、茎秆粗壮、根系发达等特点, 产量可增加 10%[152]。

品质相关基因: 谷蛋白(glutelin)是水稻的主要贮存蛋白之一。从一个新的水稻谷蛋白突变体 *W379* 中克隆出编码半胱氨酸蛋白酶 *OsVPE1*, 该基因碱基发生点突变使维持该酶 Asn 特异切割活性的关键位点 Cys269 改变为 Gly, 虽然突变蛋白可以通过蛋白分选途径进入液泡, 但是其酶活性几乎完全丧失[153]。研究发现, 水稻一种乙醛脱氢酶基因 *BADH2* 通过抑制稻米香味成分的合成影响稻米的香味[154]。同时, 还克隆了影响直链淀粉合成的 *Wx*[155]以及影响储藏蛋白运输的 *OsRab5a*[156]等稻米品质相关基因。对于棉花肌动蛋白基因 *GmACT1* 的研究表明减低该基因的表达可以显著的影响棉纤维中细胞骨架网络的形成[157]。而克隆的另外一个基因 *GhDET2* 在棉纤维发育过程中也起非常重要的作用[158]。

抗非生物逆境基因: *SKC1* 基因是一个对水稻耐盐表型变异的贡献率达 40.1%的主效 QTL[159]。耐盐性也可以调控过氧化氢代谢相关基因的转录因子 *DST* 基因[34], 或介导与普通光受体模式不同的光控发育机制的 *OsHAL3*(*halotolerance3*)基因[160]。*HAL3* 基因的耐盐性是与一种可能参与降解细胞分裂抑制因子的 E3 泛素连接酶 HIP1 互作, 并激活后者而促

进细胞分裂的结果[160]。*OsSIK1* 编码一个受体类蛋白激酶，过量表达该基因使转基因水稻表现出更高的耐盐和耐旱性[161]。*SNAC1/2* 编码 NAC 类转录因子，其表达受干旱、高盐、低温和 ABA 的诱导，过量表达 *SNAC2* 的转基因植株虽然与野生型植株没有任何形态差异，但其在苗期和成株期的抗旱性明显增强[162-163]。小麦的转录因子 DREB 也参与小麦的抗旱过程[164]。过量表达 *OsSKIPa* 可以通过调控细胞的活力提高水稻在缺水条件下的生存能力，降低干旱引起的产量损失[165]。对于水稻中两个干旱超敏感突变体 *dsm1* 和 *dsm2* 的研究表明 *DSM1* 和 *DSM2* 基因都参与到水稻的抗旱过程[166-167]。水稻 MYB 转录因子基因 *OsMYB3R-2* 通过对有丝分裂进程的调节来调控植物的耐低温反应[168]，而在水稻中通过对另一个 MYB 类转录因子 *MYBS3* 过量表达和缺失功能分析表明该基因可以调控水稻耐冷反应[169]。水稻中另外两个转录因子 *OsbZIP23*[170]和 *TSRF1*[171]的研究表明，它们和水稻的抗旱性有关。综上所述，抗非生物逆境基因克隆以转录因子居多。

抗病虫基因：水稻白叶枯抗病(*Xanthomonas oryzae* pv. *oryzae*)是世界上最严重的细菌性病害之一。水稻抗白叶枯病基因 *Xa26*[172]是中国和日本等地粳稻育种中的主要抗白叶枯病主效基因，编码一个受体激酶类蛋白质，最近克隆的抗白叶枯病基因 *Xa13* 除与抗病有关外还参与花粉的发育过程[173]。*GH3-8* 编码 IAA 酰胺合成酶，催化 IAA-氨基酸的合成从而抑制生长素的作用，研究表明，*GH3-8* 的过量表达可以提高水稻对白叶枯病的抗性[174]。*OsWRKY45-1* 和 *OsWRKY45-2* 是抗水稻抗细菌病害白叶枯病菌变种 *Xoo* 和 *Xoc* 的一对等位基因，他们在调控水稻和白叶枯病菌相互作用的过程中起着相反的调控作用[175]。水稻稻瘟病(*Magnaporthe grisea*)是最严重的真菌性病害之一。到目前为止，全世界已克隆了 10 个水稻的稻瘟病抗性基因，中国科学家克隆了其中 4 个基因，包括 *Pi36*[176]、*Pi37*[177]、*Pid2*[178]和 *Pid3*[179]。*TaPIEP1* 基因的过量表达则可以提高小麦对纹枯病的抗性[180]。中国科学家还克隆了第一个水稻抗虫基因 *BPH14*[181]。

资源利用相关基因：作物高效吸收、利用养分促进产量的生物学过程受到包含多个关键基因在内的互作基因网络的调控，中国在养分吸收特别是磷吸收的调控过程中做了大量的工作。转录因子 *OsPTF1* 是国际上第一个在植物中明确了提高磷效率功能，它参与植物磷的利用过程，过量表达的转基因植株耐磷饥饿能力高于野生型植株[182]。*OsPHR2* 参与磷饥饿信号途径，调节磷饥饿诱导基因的表达，在低磷条件下，*OsPHR2* 的增强表达可以引起植物地上部有效磷的大量积累[183]。水稻 *OsSPX1* 和 *OsSPX3* 基因参与调控水稻的磷酸盐平衡，*OsSPX1*-RNAi 植株中磷的过度积累是由于磷转运增加所致。相反，过量表达 *OsSPX1* 则对所检测的所有 10 个基因的磷饥饿诱导表达产生抑制。因此，*OsSPX1* 形成了一个负反馈，使植物在磷缺乏的条件下能够达成适度的生长[184-186]。同时，通过对 *OsPT2* 和 *OsPT6* RNAi 转基因水稻的分析也表明这两个基因在植物体内长距离磷运输的过程中起重要作用[187]。

生长发育相关基因：作物的生长发育过程与作物的品质和产量密切相关，对作物生长发育机理的研究也是作物基因发掘研究的重点。在阐明水稻生长发育的调控机理方面，克隆了控制水稻颖片形成和小穗发育的脂酶基因—水稻额外颖基因 *EXTRA GLUME1*(*EG1*) [188]，该基因不但决定水稻颖片形成，而且还可控制小花的发育。此外，还克隆了一些生长发育基因包括叶卷曲基因 *SLL1*[29]，脆秆基因 *BC10*[30]，控制水稻绒毡层程序性死亡关键调控因子 *TDR* 基因[189]，控制不定根生长发育的关键调节因子基因 *WOX11*[190]，控制水稻成花转换的分子开关基因 *RID1*[40]，控制细胞次生壁纤维素生物合成的基因 *DRP2B*[191]等。同时，在大豆中克隆了控制大豆叶片衰老的受体类蛋白激酶基因 *GmSERK1* [192]。

2 国际作物基因发掘的发展趋势

2.1 基因组序列测定技术更新换代为基因高效化发掘奠定了基础

基因组测序技术由基于凝胶板测定、毛细管测序仪测序[193-194]发展到基于纳米孔(nanopore)的单分子读取技术，数据读取速度从以年计到按天计算，从而使作物的测序和重测序成为可能。海量数据的获得无疑使基因发掘研究的易操作、低成本、高效益和高价值回报成为现实。由于人类基因组学的发展引领了整个生物界的研究，从其利用超过 310 万个单核苷酸多态性(single nucleotide polymorphism, SNP)绘制第二代单倍型图谱[195]可以预测，基于全基因组扫描的植物基因发掘将为时不远。随着测序技术的进一步发展，全基因组重测序的方法将成为

基因型鉴定的主要方法之一, 从而为大规模的基因发掘和许多不同生物问题的解决提供了强有力的研究工具[42]。基于重测序的基因发掘研究已在中国水稻[43]、玉米[196]和大豆[197]研究中开始应用。

2.2　作物自然群体的系统鉴定为基因规模化发掘创造了条件

在基因组序列测定的基础上, 开发 SNPs 标记及其芯片, 为基因型的规模化分子鉴定创造了条件。整合基因型与作物群体表型开展关联分析, 促进了基因发掘规模化的进程, 也将促进基因发掘由单基因向基因网络方向发展。例如, 人类[198]、拟南芥[199]、玉米[200-202]和大豆的 1536 SNPs 基因型鉴定[203]等等, 已在鉴定重要经济性状功能基因方面产生了效果[204], 并将产生更深远的影响。中国水稻地方品种的关联分析[43], 已发掘出与水稻 14 个重要农艺性状相关的分子标记。此外, 中国科学家还开展了基于代谢途径[45]或调控网络基因[205]及基因类别[179]等的关联分析, 提高了基因发掘效率。

2.3　基因发掘更加注重实用及其知识产权保护

随着基因发掘研究的深入, 关于克隆基因的分析, 已不仅仅局限于基因位点。科学家们在克隆基因的同时, 也在探索其等位基因的分布, 并鉴定出优异的等位基因类型, 这对于基因的利用具有重要的指导意义。众所周知的“绿色革命”矮秆基因就是由株高基因的等位基因差异所致, 因为矮秆基因与高秆基因的差异仅在于编码区的一个碱基的不同[206]。在克隆出目标基因后, 对种质资源中等位基因的多样性、等位基因在植物基因组中的分布以及基因的进化等进行深入鉴定, 将大大加速作物中新基因的发掘和利用进程[207]。自 20 世纪 90 年代以来, 拥有“基因专利”已成为发达国家及其跨国公司垄断生物技术产业的集中表现。美国、日本和澳大利亚等发达国家拥有全球 70%以上的水稻基因专利, 90%以上的玉米基因专利, 80%以上的小麦基因和 75%以上的棉花基因的专利。孟山都、杜邦等五大跨国公司利用其基因专利和品种, 控制了国际种业市场 70%的份额。因此, 基因的知识产权之争是今后生物产业发展的焦点[207]。中国科学家也在通过挖掘作物种质资源中的优异基因并对其实施知识产权保护, 将种质资源优势逐渐转变为基因优势, 避免“种中国豆侵美国权”。

3　中国作物基因发掘面临的挑战与发展对策

中国作物基因发掘取得了长足的进步, 以水稻基因发掘为代表的作物基因规模化、高效化发掘取得了显著进展。然而, 由于中国相关研究起步较晚, 资金投入不足, 与发达国家总体研究水平相比还存在一定差距, 尤其在跨国公司为抢占市场而争夺基因知识产权的情况下, 中国作物分子育种及生物产业的发展面临严峻的考验。

目前, 中国作物基因发掘研究存在“三多三少”: 一是作物预测的基因数目多、但定位和克隆的基因还很少, 二是与水稻发掘的基因相比, 其他作物发掘的特性基因还很少, 不同作物之间的基因发掘研究不平衡, 三是与已发掘基因数量相比, 具有重要利用价值的基因还不多。针对这三个问题, 作者提出了以生物产业发展需求为导向, 提高基因发掘效率, 加强特异基因克隆及重视基因价值评估的基因发掘策略。

3.1　加强材料及方法研究, 提高基因发掘效率

作物基因组都比较复杂和庞大, 通过对已经测序完成的水稻、玉米、大豆等作物基因组分析, 预测的基因数目都在上万个之多。作物的基因数目不仅多, 而且基因与性状之间的关系也很复杂。如水稻育性, 据不完全统计, 与其相关的基因有 80 多个, 分布在水稻核基因组的 12 个连锁群, 个别基因位于线粒体基因组上, 还有一些基因如杂种劣势 *W-2*、杂种不育 *S-D(t)*和双子房 *TOR* 尚未被定位。在这些定位的基因中, 约有 50%基因已被克隆, 除广亲和(*S5*)和杂种不育(*Sn*)基因外, 控制育性的基因功能类型很多, 如同源染色体配对、复制蛋白、减数分裂、姐妹染色单体粘连和分离关键因子、细胞色素 P450 基因、MADS 盒基因等。作为模式作物的水稻尚且如此, 其他基因组比较大作物的性状和基因复杂性可想而知。因此, 材料的创制和技术方法的改进是提高作物基因发掘效率的前提。

在基因发掘材料的准备方面, 虽然已定位了一批与重要性状相关的基因/QTL, 但精细定位和克隆这些基因还需要构建更大的群体。利用同一个组合, 如果增加个体数, 定位的区间会缩小, 但不同组合需要的群体大小的规模则不能一概而论。对不同组合定位基因的物理距离统计表明, 群体规模越大, 基因定位的物理区间越小, 在 17 个小于 2 000 个单株的群体中, 基因被定位的物理距离范围为 7.5~912.4 kb, 平均为 157.5 kb, 而用 12 个大于 2 000 个单株(2 068~9 472 个单株)的较大群体, 基因被定

位的物理距离范围及平均物理距离均呈缩小趋势，分别为 19~400 kb 和 92.8 kb。突变体库等遗传材料已在模式作物水稻的基因发掘研究中发挥了重要作用，但由于外源基因插入位点的非随机性[41-43]，导致标记的基因不能覆盖整个基因组的功能基因，因此，应该构建不同类型的突变体库，以增加对全基因组基因的标记。需要特别强调指出的是，在材料准备方面，当基因型鉴定高通量成为可能时，由于作物生长发育周期长，表型易受环境条件影响，限制基因发掘速度的则是表型数据的积累，因此，在建立基因发掘材料的同时，应加强表型的多年多点鉴定或精准鉴定。

在技术和方法方面，与科技发达国家相比，中国基因发掘速度较慢与研究起步相对较晚、基因发掘技术平台不完备有关。我国近年来投资建立了一批“中心”、“实验室”，但因设施条件的配套程度存在很大差异，其使用效率还不同程度地有待提高。不容忽视的是，中国基因发掘所用的仪器设备和技术方法基本都源自国外，导致同类研究跟踪较多、创新较少。加之，技术创新促使仪器设备的更新换代速度加快，而这些新设备国产化低、造价高、也在某种程度上制约了我国基因发掘研究的进展。因此，通过农业与工业等学科的协作，加强作物基因研究技术创新是引领作物基因发掘研究的重要措施。

3.2 建立基因功能研究平台，加强特异基因克隆

无论是作物基因定位还是克隆，均以水稻为最多，而其他作物则较少。从基因的功能验证研究来看，水稻基因转水稻进行功能验证的数量较多，而其他作物则进行转基因功能验证的基因屈指可数。尽管不同作物的基因可通过转化模式植物如拟南芥、蒺藜苜蓿、烟草等进行功能验证，如大豆特有的结瘤特性尽管在拟南芥中不能进行验证，也可以转结瘤作物的模式植物蒺藜苜蓿(*Medicago truncatula*)[208]和百脉根(*Lotus japonicus*)[209]。但是需要指出的是，在模式植物中的功能验证并不都能完全代表其在来源作物中的直接验证。如水稻的候选基因与拟南芥基因的直系同源性在很多情况下都是可行的[4]，但水稻与拟南芥的共线性也是有限的。构建不同作物的高效转化系统[211]是检验基因功能不容忽视的技术平台，水稻基因发掘研究所取得的成就就是与技术平台的建立分不开的。除重复序列及微共线性关系外，不同作物都各有其特点，如玉米特有的蛋白质是拟南芥的 2 倍[210]。因此，我国不同作物应加强其特有基因的发掘，以水稻功能基因组学研究为榜样，借鉴其新理论、新技术和新方法，从而促进我国不同作物特异基因发掘的快速发展。

3.3 加强重要价值基因的克隆与应用，促进生物产业的发展

我国作物的基因发掘研究进展比较快，但这些基因的发掘多处在理论研究的层面。在本文统计的 300 多个已克隆基因中，只有约 18%的基因转入来源作物进行功能检测，表现出应用潜力，但在育种中进行利用价值评估的基因数目却寥寥无几，存在基因发掘研究与实际利用相脱节的现象。无论是中国还是世界，与预测的作物基因数目相比[6-7,211-214]，已克隆出的基因数目还只是沧海一粟，由于主要农作物的系统分化发生在距今至少 300 多万年前，无论是单子叶作物玉米、水稻和小麦，还是双子叶植物大豆、棉花和油菜以及模式植物蒺藜苜蓿和拟南芥，在进化过程中都经历了多倍化，普遍存在复制基因[215]，加之，基因在基因组中的分布不均匀[216]，导致基因发掘的难度较大[217]。与基因组体积相比，作物中预测的基因数目所占比例很小，但预测基因的数目仍然上万个之多，在如此浩瀚的基因海洋中，基因发掘研究不能面面俱到，建议中国作物基因发掘应以中国作物育种和生物产业发展为目标，加强不同学科和专业的分工协作，将研究与应用紧密结合，有目的、有计划地克隆作物重要经济性状基因，明确其等位基因的应用价值，为分子育种和生物种业发展奠定基础。

综上所述，如果以 1900 年的经典遗传学为前基因组时代起始标志，以基因组序列公布为结束标志，则前基因组时代至少经历了 100 多年的历史。这一时期主要是对性状进行描述，对种内性状的认识具有同质性。例如，孟德尔 1865 年发表的关于豌豆花色性状的关键基因，在 150 年后被克隆出来并证明该基因是一种控制花青素生物合成途径的转录因子[218]。这表明从前基因组时代的仅仅认识性状到基因组时代的发掘基因经历了一个漫长的阶段。在基因组时代，通过对基因的克隆及作用机制的阐述，认识到对种内性状的异质性，实现了对目标性状的基因改良。由于国际作物基因发掘的高效化、规模化及实用化，作物基因的发掘将进入快速发展阶段。自水稻功能基因组 2005 年公布[219]以来的短短五年中，基因发掘的速度比前基因组时代有了飞速的发展。到目前为止，人们对基因的了解还很有限，从模式作物水稻看，已经鉴定抗稻瘟病基因 84 个及大量的数量抗性遗传位点(QTL)，但仅克隆出 9 个主效抗性基因及 1 个隐性部分抗性基因[220]，同时关于这些基因的相互关系尚不清楚。因此，基因发掘研究尚无止

境。在着科学技术发展的带动下，作物基因发掘的速度和数量大幅度提高，促进了后基因组时代的到来，从而加深对基因互作的了解，揭开作物重要性状的基因网络调控途径。通过基因的定向组装达到性状的协调改良，突破传统育种的瓶颈，实现作物品种的精准分子设计育种[221-222]。

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