科学通报 2026 年 第 71 卷 第 20 期: 4782 ~ 4798
生物与信息技术赋能现代农业绿色发展专辑 评 述
《中国科学》杂志社 SCIENCE CHINA PRESS

菊属多组学与菊花分子育种研究进展

王振兴[1,2], 何彦泽[1,2], 苏江硕[1,2], 宋爱萍[1,2], 房伟民[1,2], 陈发棣[1,2*]

1. 作物遗传与种质创新利用全国重点实验室, 南京农业大学园艺学院, 南京 211800
2. 生物育种钟山实验室, 南京 210014
* 联系人, E-mail: chenfd@njau.edu.cn

2026-04-10 收稿, 2026-05-19 修回, 2026-06-10 接受, 2026-06-12 网络版发表
国家自然科学基金(32341048, 32102421, 32522095)、国家自然科学基金区域联合项目(U24A20422)和江苏省种业振兴揭榜挂帅项目(JBGS(2021)020)与国家现代农业产业技术体系项目(CARS-23-A18)资助

摘要 菊花(*Chrysanthemum* × *morifolium* Ramat.)作为菊科菊属多倍体花卉, 兼具观赏、药用、茶用与食用价值, 其基因组高度杂合且庞大的特性为遗传研究带来诸多挑战. 近年来, 基因组学技术的快速突破推动菊花研究迈入分子育种时代, 从基因组测序、功能基因挖掘到基因编辑、分子标记开发均取得显著进展. 本文系统梳理了菊花及菊属野生植物全基因组测序, 基因工程、基因编辑等分子技术在菊花重要性状调控中的研究成果, 总结了分子标记开发与全基因组选择的应用进展, 剖析了当前研究面临的关键问题, 并展望了未来发展方向, 以期为菊花分子遗传研究与精准性状改良提供理论参考.

关键词 菊花, 基因组学, 功能基因, 基因编辑, 分子育种

菊花原产于中国, 对其有文字记载的栽培历史逾1600年, 是中国十大传统名花之一, 也是全球广泛栽培的切花、盆花和园林绿化花卉, 在医药、食品、化工等领域亦具有重要应用价值[1~3]. 全球已记载的菊属植物有40余种, 其中我国分布有20余种, 为开展菊属植物的收集保存和创新利用奠定了良好的种质资源基础, 是选育菊花新品种的优异性状源头宝库[4]. 解析不同菊属植物的基因组序列, 则是整合利用多组学技术手段挖掘重要性状成因, 进一步开展分子育种的底盘. 栽培菊花多为六倍体及其非整倍体, 遗传背景极为复杂, 基因组高度杂合且基因组庞大(>8 Gb), 对解析重要性状形成的分子机制构成挑战[5]. 随着二代、三代测序技术及生物信息学的发展, 菊属植物基因组测序逐步完成, 功能基因挖掘与分子调控技术不断突破, 推动菊花研究从表型性状观察与描述, 向基因组水平的基因型解析转变, 从传统经典遗传分析, 向基于基因编辑、转录调控网络解析的精准分子调控研究方向转变[2]. 近年来, 单细胞测序、表观遗传组学、结构变异分析等新技术的应用, 进一步深化了对菊花复杂基因组的认知, 为解析其花色、花型、抗逆性等重要性状的分子调控网络奠定了基础.

1 菊属多组学研究进展

基因组学研究为菊花性状改良提供了从资源到靶标基因的关键基础, 高质量参考基因组不仅能够系统解析多倍体化、重复扩张与结构变异等菊花基因组的演化特征, 还为功能基因挖掘、优异单倍型鉴定、调控网络解析以及分子标记开发提供了框架支撑, 从而推动育种策略从传统表型选择, 向基因组信息驱动的精准育种与分子设计育种转型.

1.1 菊属植物基因组测序

2018年以来, 全球多个研究机构选用了具有代表性的菊属野生植物和栽培菊材料, 开展了菊属植物基

引用格式: 王振兴, 何彦泽, 苏江硕, 等. 菊属多组学与菊花分子育种研究进展. 科学通报, 2026, 71: 4782–4798
Wang Z, He Y, Su J, et al. Progress in multi-omics and molecular breeding of *Chrysanthemum* (in Chinese). Chin Sci Bull, 2026, 71: 4782–4798, doi: 10.1360/CSB-2026-0468

© 2026《中国科学》杂志社

因组测序，完成了从scaffold到染色体级别的基因组组装. 中国中医科学院中药研究所与南京农业大学等单位借助Nanopore纳米孔三代超读长测序结合二代Illumina测序技术，首次破译了二倍体菊花脑(*Chrysanthemum nankingense*)基因组[6]，成为菊属植物基因组研究的里程碑. 北京林业大学等单位完成了二倍体甘菊(*C. lavandulifolium*)的染色体水平基因组组装，结合功能分析深入解析了头状花序发育相关的分子调控机制, 为理解菊属花序结构多样性提供了重要线索. 日本广岛大学和荷兰瓦赫宁根大学研究团队分别完成了栽培菊花基因组潜在供体甘野菊(*C. seticuspe*)和龙脑菊(*C. makinoi*)的基因组组装，这些二倍体基因组资源在基因组结构、重复序列组成以及物种分化关系等方面为菊属比较基因组研究提供了重要补充[7~11]. 2023年, 南京农业大学菊花研究团队通过染色体涂染(oligo-painting)和高质量的PacBio三代测序技术，破译了首个栽培菊花(*C.* × *morifolium* Ramat.)基因组, 也是国际上报道的首个节段异源多倍体基因组(segmental allopolyploid)，揭示了全基因组三倍化及小规模基因重复对花发育相关基因扩展的贡献，并鉴定了与花瓣形状和花色演化相关的关键基因[5]. 2024年，广州中医药大学研究团队通过高质量的野菊基因组解析与功能验证，揭示了其关键甲基转移酶与糖基转移酶经基因复制与新功能化，协同进化形成地奥司明(Diosmin; luteolin40-methoxyl-7-O-glucosyl-rhamnoside)生物合成途径, 为植物黄酮修饰多样性的分子进化机制提供了新的案例[12]. 同年, 中国农业科学院深圳基因组所以野菊单倍型基因组为基础, 结合系统发育与功能验证, 鉴定出两种关键FOMT(flavonoid O-methyltransferase)酶催化金合欢素(Acacetin)合成机制，并解析其分化进化路径, 从而揭示了菊科黄酮甲基化合成及其基因起源的分子模型[10]. 两项研究分别解析了野菊如何通过全基因组加倍与局部串联复制驱动甲基转移酶进化，从而精确调控金合欢素与地奥司明这两大核心药效成分的生物合成, 共同构成了野菊次生代谢图谱的重要位点, 鉴定出多个新的植物类黄酮O-甲基转移酶基因，揭示了菊属药用成分合成的分子演化历程[10,12]. 东北林业大学等组装完成了神农香菊(*C. aromaticum*)基因组, 结合转录组、代谢组和成分测定，发现α-倍半萜生物合成基因簇的扩张, 是神农香菊特殊香味形成的原因[13] .

这些已解析的基因组涵盖了二倍体野生种、药用菊、芳香型菊以及六倍体栽培菊等不同类型，不仅为解析菊属植物复杂的系统发育关系、多倍体演化和种间渐渗提供了重要基础，也为研究花型、花色、芳香及药用活性成分等复杂性状的形成机制提供了关键资源(表1). 与此同时, 菊属基因组研究所采用的技术路线也经历了由二代短读长辅助组装向长读长、Hi-C以及单倍型解析组装的持续升级，组装质量显著提高，contig N50由早期不足1 Mb提升至30 Mb以上, 研究重点也逐渐由获得参考基因组草图转向解析亚基因组结构与复杂功能性状形成机制. 菊属植物已从基因组测序时代进入了多组学整合的后基因组时代. 而开展具体研究时, 还应根据具体目的, 考虑不同参考基因组的组装水平和质量, 选用合适的参考基因组, 以更好地解析科学问题.

1.2 多组学整合分析

高质量基因组为其他组学技术提供了比对参考, 基因结构注释, 调控元件信息等, 是多组学分析的基础. 近年来, 随着菊花染色体级基因组组装完成, 也得益于测序技术的日益进步和测序成本逐渐降低，使得研究人员能够以多种组学技术解析这一高倍性，复杂基因组物种的多个关键性状，比基于单一数据类型能更全面地反映潜在的生物学分子模型. 在这之中, 基因组学与转录组、代谢组、表观组、单细胞组的整合分析, 也成为解析菊花性状调控网络的重要手段.

转录组作为目前应用最广的组学手段之一，可以帮助科研人员快速筛选差异表达基因，因此也常常作为多组学分析的重要部分. 而代谢组则能够从生化功能层面反映植物生理状态，通过检测糖类、氨基酸、脂质及次生代谢物等小分子代谢物的动态变化，进一步揭示基因表达变化所导致的代谢调控. 近期, Zhao等人[15]联合转录组和代谢组，探究了高温导致菊花花瓣褪色的内在机制，发现花青素的酶促降解是主要驱动因素，筛选出的关键候选基因(*CmPRXs*和*CmOMT1*)为未来通过分子育种手段提高菊花的耐热性和花瓣色彩稳定性提供了重要靶点. 抗逆性方面, Zhao等人[16]通过整合转录组和代谢组分析，发现涝胁迫下菊花的关键代谢途径响应变化，差异基因主要富集于淀粉和蔗糖代谢、TCA循环等通路，从而揭示了菊花在淹水应激下新的转录和代谢调控关系. Jiang等人[17]借助转录组、代谢组以及DAP-seq(DNA affinity purification sequencing)分析，确立了CmVNI2-CmMYB3模块在调控菊花低温胁迫下黄酮生物合成中的关键作用，不仅鉴定出

表 1 已完成基因组测序的菊属植物

Table 1 *Chrysanthemum* species with sequenced genomes

物种	染色体数(2*n*)	组装水平	基因组大小(Gb)	重复序列含量(%)	Contig N50	基因数量	BUSCO (%)	生物学问题	参考文献
菊花脑 *C. nankingense*	18	Scaffold-scale	2.53	69.58	130.68 kb	56870	85.78	菊属起源, 次生代谢关键通路解析	[6]
	18	Chromosome-scale	2.87	–	5.98 Mb	37995	91.00	菊花起源、多倍化机制、花色和花型等重要观赏性状基因挖掘	[5]
栽培菊 *C. morifolium*	54	Chromosome-scale	8.15	83.92	1.87 Mb	138749	97.71	菊花起源、多倍化机制、花色和花型等重要观赏性状基因挖掘	[5]
甘野菊 *C. seticuspe*	18	Scaffold-scale	2.72	72.50	44.74 kb	71057	88.80	花期	[11]
	18	Chromosome-scale	3.05	81.20	–	74259	97.40	花型、正向遗传	[14]
甘菊 *C. lavandulifolium*	18	Chromosome-scale	2.60	66.15	497.00 kb	64257	89.02	花型发育	[8]
龙脑菊 *C. makinoi*	18	Chromosome-scale	3.10	80.04	258.2 kb	95074	92.10	花色进化、结构变异	[9]
野菊 *C. indicum*	18	Chromosome-scale	3.11	–	4.39 Mb	50606	91.13	功能成分关键基因发掘、结构变异	[12]
野菊 *C. indicum*	18	Chromosome-scale, Haplotype-resolved	3.08/3.09	–	12.56 Mb/ 12.40 Mb	68186	96.10	功能成分关键基因发掘、结构变异	[10]
神农香菊 *C. aromaticum*	18	Chromosome-scale	3.10	58.39	30.66 Mb	55825	98.20	花香机制解析	[13]

潜在的耐低温靶基因, 也为药用菊花次生代谢合成提供了候选基因.

高质量基因组的完成为全基因组关联分析(genome-wide association study, GWAS)的应用奠定了坚实基础, 并有力推动了其与转录组、代谢组等的整合, 为复杂性状的遗传解析与分子调控网络构建提供了新的研究思路. Lu等人[18]利用RNA-seq与GWAS结合的方法, 解析了菊花抗旱性的遗传特性, 鉴定出*LPAT5*、*CYP82C4*等抗旱关键基因. 另外, Zhang等人[19]通过GWAS和加权基因共表达网络分析(weighted correlation network analysis, WGCNA)联合分析, 鉴定到*CmNRAMP3*为生根能力的负调控因子, 为培育易生根、高品质的菊花新品种提供了重要的基因储备.

解析蛋白质作为功能执行分子及其修饰与互作的调控作用, 能更直接地反映生物过程的分子机制. Wang等人[20]通过转录组学和蛋白质组学整合分析, 在菊花中筛选到了与细胞衰老和死亡以及蛋白质降解相关的关键基因和蛋白质, 它们可能在花粉败育中起着至关重要的作用. Zhang等人[21]通过转录组学和蛋白质组学探究了菊花远缘杂交胚胎败育的机制, 发现胚胎败育可能与程细胞序性死亡有关, 并且衰老或死亡相关的基因和蛋白质参与了这一过程. 进一步研究表明, 父本染色体加倍可能通过激活关键转录因子(如*AGL80*)和增强激素信号(如生长素), 促进代谢和胚胎发育基因表达, 从而一定程度缓解远缘杂交障碍, 使杂交胚胎正常发育[22]. 除经典的磷酸化等修饰外, 定量蛋白质组学的应用则为理解更多种类蛋白质翻译后修饰对菊花重要性状的调控机制提供了可能. Lin等人[23]发现, 巴豆酰化修饰(crotonylation)可能参与菊花应对冷胁迫应答. Huang等人[24]进一步研究发现, DgTIL1(temperature-induced lipocalin-1-like gene)第72位赖氨酸K72的巴豆酰化修饰调控菊花对冷胁迫的耐受性.

表观组学和单细胞组学则为菊花重要性状解析提供了全新维度的研究范式. Li等人[25]发现菊花DNA甲基化修饰参与花色调控, 通过全基因组DNA甲基化测序, 鉴定出花色基因*CmDFR*的启动子区甲基化水平与花瓣颜色深度呈负相关, 为表观修饰调控菊花花色提供了直接证据. 而Yu等人[26]通过全基因组DNA甲基化联合转录组分析筛选到了多个WRKY转录因子启动子区域的CHH位点特异性低甲基化, 从而在真菌感染时转录激活, 解析了WRKY家族应答链格孢菌侵害, 并在多倍化后提升菊属植物抗黑斑病的新机制. 同时, 该研究进一步联合DAP-seq分析, 筛选到下游*ClNPR1*和*ClPDF1.4*等受调控基因, 完善了抗病通路[26]. Yang等

人[27]则主要通过RNA甲基化测序、组蛋白修饰测序等，发现m6A和H3K4me3通过占位效应来控制菊花叶片衰老等基因表达. 单细胞测序方面，Song等人[28]通过发掘在海绵组织细胞特异发挥作用的NAC055-NAC087-ACX5模块，揭示了茉莉酸调控菊花叶片衰老的新机制，为菊花采后保鲜提供了分子育种新靶点.

综上所述，随着菊花及其近缘种属植物参考基因组的测序完成，转录组、代谢组、蛋白组、表观组、单细胞组等得以实现精准的比对、注释与整合分析，极大地促进了多组学整合在精准解析菊花关键性状中的广泛应用. 同时，南京农业大学菊花研究团队建立的菊属基因组数据平台(*Chrysanthemum* Genome Database，CGD，https://cgd.njau.edu.cn/asteraceae/homePage)集成了已发表的菊属植物基因组，并包含针对基因组数据、转录组等的多个基础在线分析工具，为菊花基因挖掘、组学分析提供了重要的数据支撑与研究平台[29]. 今后基因组信息的进一步完善，如组装完整性、注释质量提升，泛基因组构建，重复序列与着丝粒区域解析等，相信能进一步提升多组学分析手段的深度和精度，进而为全面解析菊花这一多倍体复杂遗传背景物种提供底层基础.

2 菊花分子育种研究进展

近年来，随着研究手段的进步，菊花主要观赏性状、抗性性状等调控机制已得到解析，为开展菊花分钟育种提供了关键候选位点(图1). 以基因工程、基因编辑为核心的分子调控技术，是解析菊花基因功能、实现性状定向改良的关键手段. 针对菊花多倍体基因组的特点，基因编辑体系不断优化，表观遗传编辑、多基因共调控等新技术逐步应用，实现了对菊花观赏、生物和非生物抗性重要性状的精准调控.

2.1 转基因育种

转基因育种通过导入外源基因，可在保留原有优良遗传背景的同时，对目标性状进行定向改良或引入新的性状，快速创制植物新品种(系).

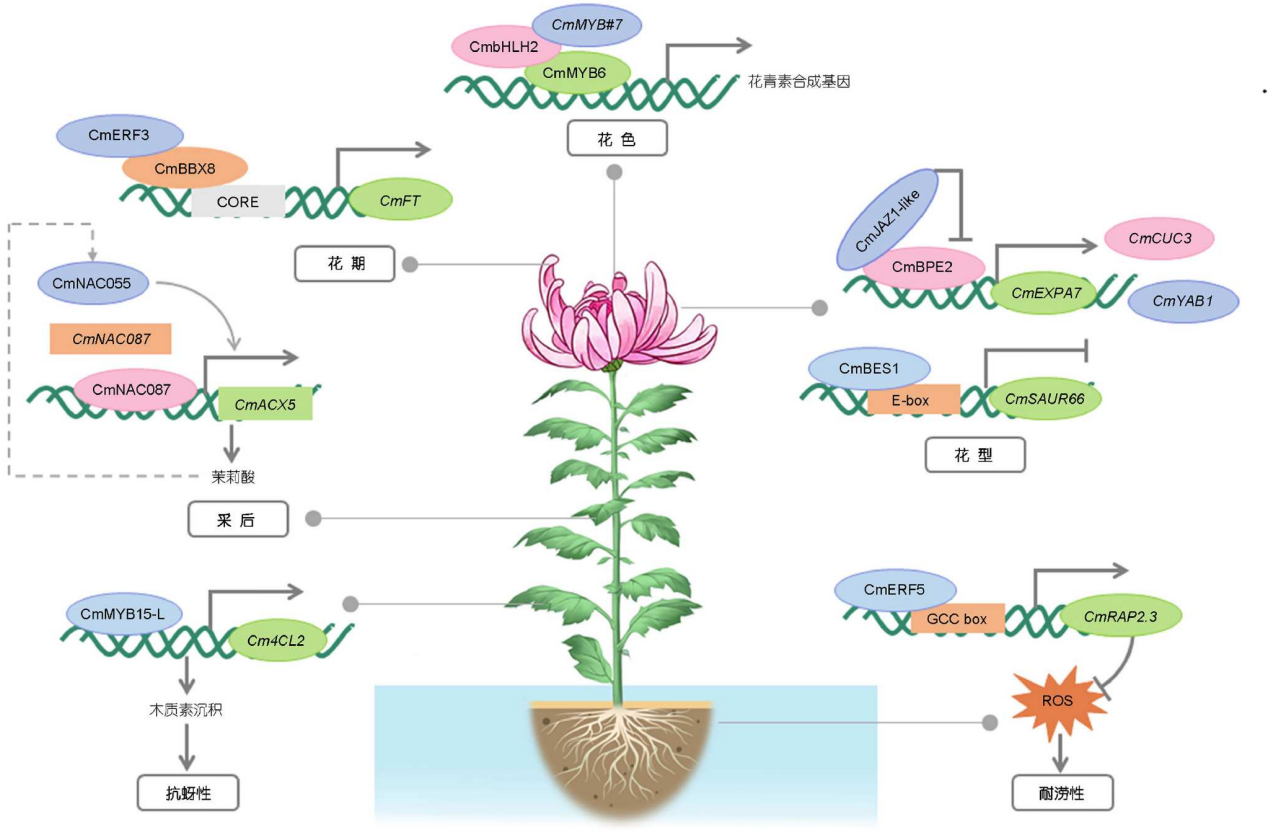

图 1 菊花重要性状形成的核心调控基因网络
Figure 1 Core regulatory gene network underlying key traits in *Chrysanthemum*

花色是重要的观赏性状之一，通过代谢工程可以精准调控花青素合成途径，在菊花中导入蝶豆花来源的*CtA3′5′GT*与风铃草来源的*F3′5′H*，可促使花瓣中积累以飞燕草素为主的花色苷并实现稳定显蓝，获得蓝色菊花[30]. 此外，南京农业大学菊花团队以‘南农粉翠’为材料，将蓝目菊来源的*OhF3′5′H*与蝶豆花*CtA3′5′GT*共转化导入菊花，获得了能够合成蓝色花色苷、呈紫罗兰色的优异种质[31]. 花型直接决定切花的商品性. 菊花头状花序中舌状花与管状花的数量与形态变化，是重瓣化、花序大小等花型差异的重要基础. 研究表明，通过过表达*CmCYC2c*可显著促进舌状花瓣伸长并增加舌状花数目，使花序更大、重瓣倾向增强，为创制饱满的重瓣花型种质提供了可行路径[32].

开花时间是实现花期精准调控与周年生产的关键指标. 研究表明，*CmBBX8*(*B-box*)的转录呈昼夜节律性变化，参与调控菊花由营养生长向生殖生长的成花转变，过表达*CmBBX8*可获得花期提前的新种质[33]. 此外，过表达*CmBBX7*也获得了花期提前的种质[34]，进一步说明BBX家族成员在菊花花期调控中具有重要作用. 株高是株型评价的关键指标，影响抗倒伏、运输与栽培密度等生产环节. 在菊花中，通过过表达*CmDOF6*，进而抑制菊花体内的赤霉素(gibberellic acid, GA)合成，可实现半矮杆种质的创新[35]. 分枝性状同样决定株型与生产成本，将*CmBRC1b*过表达可减少侧芽数，创制少侧芽种质，进而降低菊花生产中的抹芽人工投入[36].

近年来，菊花在生物和非生物胁迫抗性机制解析与种质创新方面取得了显著进展. 抗病性是菊花生产中的关键性状之一. 过表达*CmWD40*、*CmWRKY103*等基因能增强菊花叶片对链格孢菌的抗性，获得具有黑斑病抗性的菊花种质[26,37]. 过表达*CmMYB15*等基因则可以创制获得抗蚜性提高的菊花新种质[38]. 在抗旱研究中，沉默*CmNF-YB8*基因可显著降低叶片气孔开度并诱导表皮角质层增厚，有效限制了水分散失，从而成功创制出高耐旱菊花种质[39]. 在耐盐机制方面，过表达*CmHSFA4*能够提高CmHSFA4-CmMYBS3-CmTPL蛋白复合体的浓度. 该复合体通过介导下游基因*CmMYB121*启动子区组蛋白H3和H4的去乙酰化来抑制其表达，进而提升了植株的盐胁迫耐受性[40]. 此外，通过沉默*CmACS6*基因，可有效降低植株对水涝环境的敏感性[41]，为菊花耐涝性状的遗传改良提供了重要靶点. 优异基因的挖掘与应用将大大提高菊花观赏品质与抗逆特性，表2~4汇总了近年来利用分子生物学技术调控基因表达来改良菊花重要观赏、抗逆以及功能性成分等性状的进展.

2.2 基因编辑育种

基因编辑育种以CRISPR/Cas等系统为核心，可在不引入或尽量少引入外源遗传物质的前提下，对内源基因进行靶向敲除、精确替换或表达调控，从而实现性状的定点改良. 相较于传统转基因随机插入带来的位置效应与表达不稳定，基因编辑具有不引入外源遗传物质和周期更短等优势. 南京农业大学菊花团队依托已发表及自主测序的多种菊属植物基因组数据，结合CRISPR-P 2.0和CRISPR-Local[96,97]，自主研发了适配菊花复杂多倍体基因组的CRISPR靶位点交互式设计系统，显著提升了菊花及近缘物种基因编辑的设计效率与准确性[29]. 日本研究人员利用CRISPR/Cas9在过表达外源黄绿色荧光蛋白基因*YGFP*(*yellowish-green fluorescent protein*)菊花植株中实现了对*YGFP*基因的编辑[98]. Li等人[99]利用CRISPR/Cas9系统敲除了菊花*DgTCP1*基因，发现菊花*dgtcp1*突变体植株的耐寒性降低，而过表达*DgTCP1*菊花转基因植株的耐寒性提高. Liu等人[100]通过将荧光报告基因和CRISPR/Cas9基因编辑技术结合，在二倍体野菊中建立了基因编辑体系，并通过分别敲除*CiTFL1a*和*CiTFL1b*获得了具有早花表型的新种质. 在野菊中，敲除鼠李糖合酶*CiRHM1*可以显著提高多种黄酮苷元如芹菜素(apigenin)、木犀草素(luteolin)、去甲汉黄芩素(norwogonin)、香叶木素(diosmetin)和高车前素(hispidulin)等黄酮苷元的合成[89]. 除了直接编辑基因外，通过表观遗传编辑器可以实现花色可逆调控与新种质创制. Li等人[25]将dCas9与菊花内源性DNA甲基转移酶(CmDRM2a、CmDRM2b和CmCMT2)融合，并构建R-L和A-D双系统实现了对关键基因*CmMYB6*的双向表观遗传调控，从而调节花青素积累水平，最终获得了浅白色和深粉色的菊花种质.

2.3 分子标记辅助选择育种

分子标记是解析菊花遗传多样性、定位性状基因、实现分子辅助选择的重要工具. 随着基因组学技术的发展，分子标记从传统的AFLP(amplified fragment length polymorphism)、RAPD(random amplified polymorphic DNA)、SSR(simple sequence repeat)向高通量的SNP(single nucleotide polymorphism)、InDel(insertion and deletion)、SV(structural variation)标记转变.

表 2　调控菊花主要观赏性状形成的关键基因及其分子机制研究

Table 2　Summary of genes and mechanisms regulating major ornamental traits in *Chrysanthemum*

类型	基因	基因功能	文献
花色	*CmBBX28*, *CmMYB9a*	*CmBBX28*/*CmMYB9a*负/正调控花色苷合成	[42]
	CmMYB308	花色变浅	[43]
	CmNAC25, *CmMYB6*, *CmMYB#7*	*CmNAC25*和*CmMYB6*正调控而*CmMYB#7*负调控花色苷合成	[44]
	CmRVE2, *CmCHLI1*	绿色花色形成	[45]
	CmPUB15, *CmMYB73*	花色加深	[46]
	CmBCH1	促进花青素积累	[47]
	CmMYB6	表观遗传修饰控制花色苷合成	[25]
花型	*CmSAUR66*, *CmBES1*, *CmCYC2c*	生长素调控舌状花融合	[48]
	CmJAZ1	负调控花瓣大小	[49]
	CmDIV-like, *CmRAD1*	*CmDIV-like*增加花瓣数量, *CmRAD1*诱导不对称花瓣伸长	[50]
株型	*CmDOF6*, *CmTCP8*, *CmGA20ox1*	*CmDOF6*抑制*CmGA20ox1*转录导致矮化, *CmTCP8*相反	[35]
	CmMYC2, *CmBRC1b*	干旱胁迫下减少分枝数	[36]
	CmbZIP19, *CmDWF1*	*CmbZIP19*抑制侧芽伸长, *CmDWF1*促进侧枝伸长	[51]
	CmDWF4	增加侧芽生长速率、数量和长度	[52]
	CmAP2	促进分枝、增加腋芽数量、提高株高	[53]
	CmDRM1	抑制分枝	[54]
花期	*CmGAST1*, *CmCAM7*, *CmGAI*	*CmGAST1*促进开花, *CmCAM7*和*CmGAI*延迟开花	[55]
	CmFLC-like	延迟开花	[56]
	PRR7, *AGL24*	花序分生组织中感知短日照信号调控开花	[57]
	CmARF3, *CmTCP7*	*CmARF3*促进开花, *CmTCP7*延迟开花	[58]
	CmNLP7, *CmPP6*	延迟开花	[59]
	CmFL1	提前开花	[60]
	MIR156 (*cin-MIR156ab*)	调控营养生长向生殖生长转变	[61]
	CmTEM1	乙烯介导的开花延迟	[62]
	CmSVP	短日照或低温条件下促进开花	[63]
	CmBBX5, *CmBBX8*	延迟开花	[64]

菊花分子标记研究近年来取得了显著进展，广泛应用在种质资源鉴定、遗传多样性评价、起源进化分析、指纹图谱构建以及重要性状基因定位等方面[1,2,5]. 分子标记辅助选择MAS(molecular assisted selection)是利用与目标性状位点或基因紧密连锁的分子标记进行间接有效选择的分子育种技术. MAS不受基因表达、生长阶段和环境条件的影响，可显著减少对传统田间表型鉴定的依赖, 大幅降低育种成本, 提高选择准确性和育种效率，已成为作物遗传育种的重要工具[101]. 分子标记的类型和检测方法是决定MAS效率的关键因素. Kumare等人[1]和Su等人[2]系统总结了分子标记在菊花重要观赏和抗逆性状的遗传研究进展. 然而, 前期研究主要采用AFLP、RAPD、SRAP(sequence-related amplified polymorphism)和SSR等基于PCR的分子标记, 数量有限且难以实现高通量分型, 严重制约了QTL(quantitative trait locus)定位的精度与育种效率. 与传统分子标记相比，单核苷酸多态性(SNP)和小片段插入缺失(InDel)标记具有分布广、遗传稳定性好、共显性等特点, 更容易实现高通量和自动化检测[102].

目前，基于简化基因组测序的SNP/InDel标记已广泛应用在菊花遗传图谱构建、QTL定位、GWAS、BSA-seq(bulked segregant analysis coupled with whole-genome sequencing)等基因定位研究中. van Geest等人[103]开发了一款包含183k个SNP的基因分型芯片，系统解析了六倍体菊花的剂量遗传效应，并基于所构建的包含9条连锁群的高密度遗传图谱，对花色和花期等性状开展了多等位基因QTL分析. Song等人[104,105]利用SLAF-seq(specific-locus amplified fragment sequencing)技术开发的SNP标记，构建了一张平均图距为0.76 cM的菊花高密度遗传图谱，定位到多个与花型和花色相

表 3 调控菊花主要抗逆性状形成的关键基因及其分子机制研究

Table 3 Summary of genes and mechanisms regulating major tolerance traits in *Chrysanthemum*

类型	基因	调控性状	文献
非生物胁迫	*CmHSFA4*, *CmMYBS3*, *CmMYB121*	耐盐性	[40]
	CmDOF18	耐盐性	[65]
	CiHY5, *CiABF4*	耐盐性	[66]
	CiFNSII-1.2	耐旱性	[67]
	DgnsLTP1, *DgPIP*, *DgGPX*	耐寒性	[68]
	ClRAP2.4	耐寒性	[69]
	DgMYB, *DgATX*, *DgPOD*	耐寒性	[70]
	DgSRT2	耐寒性	[71]
	DgHDA6	耐寒性	[72]
	DgPR1	耐寒性	[73]
	CmVNI2, *CmMYB3*, *CmF3H*	低温响应黄酮醇积累	[17]
	CmERF4	耐涝性	[74]
	CmHRE2L, *CmACS6*	耐涝性	[41]
	CmASMT	耐热性	[75]
	CiMYB4, *CiPCS*	耐镉性	[76]
生物胁迫	*CmWRKY6-1*, *CmWRKY15-like*	抗枯萎病性	[77]
	CmWRKY48	抗枯萎病性	[78]
	CmNAC083	抗黑斑病性	[79]
	AaAlta1, *CmWD40*	抗黑斑病性	[37]
	ClWRKY103	抗黑斑病性	[26]
	CmCC-NB-ARC	抗白锈病性	[80]
	CmTGA1, *CmRbohD*	抗白锈病性	[81]
	CmMYC2, *CmMYBML1*	抗斜纹夜蛾	[82]
	CmMYBML1, *CmTGA1*, *CmTPS1*	抗蚜性	[83]
采后衰老	*CmbHLH63*, *CmbHLH1L*, *CmNLP6/7L*	叶片衰老	[84]
	SBPASE	叶片衰老	[27]
	NAC055, *NAC087*, *ACX5*	叶片衰老	[28]

关的关键位点. Su等人[106]以‘南农雪峰’×‘蒙白’为作图群体(n=167), 通过GBS(genotyping by sequencing)测序开发的SNP标记, 构建了一张包含27条连锁群、总图距2967.76 cM、平均图距0.26 cM、双亲整合的高密度遗传图谱, 检测出34个菊花耐涝性QTL簇, 并对主效基因*CmWAT6.1*进行了功能验证. Sumitomo等人[107]采用ddRAD-seq(double digest restriction-site associated DNA sequencing)技术开发的SNP标记开展GWAS, 成功定位到与菊花白锈病抗性相关的重要基因座*Phr2*. 南京农业大学菊花团队对包含346份菊花及近缘种属的核心种质开发了高密度SNP标记, 通过GWAS先后定位了叶夹角[108]、株高[109]、花期[110]、花色[111]、功能性成分[112]、扦插生根能力[19]以及花型[48]等性状显著关联遗传位点和候选基因, 为MAS育种奠定了重要基础. 整合多组学数据的GWAS, 能够直接建立基因型与多维表型的因果关系, 实现从“关联”到“机制”的深入解析. Luo等人[89]通过代谢组GWAS(mGWAS)挖掘出控制野菊主要黄酮苷元芹菜素合成的候选基因*CiRHM1*, 并发现其表达与黄酮苷元积累呈显著负相关.

在MAS实际育种应用中, 对于菊花等基因组庞大的物种来说, SNP和InDel难以直接实现大规模群体基因分型, 通常需将其转化为其他类型的分子标记. 例如, 研究人员将GWAS分析检测到的菊花耐涝性、花径大小和开花时间关联SNP转化成与目标性状共分离的dCAPS(derived cleaved amplified polymorphic sequences)标记, 选择效率分别为80%、87.2%和82.7%[113,114]. 以菊花白锈病基因*CmPLD*α1在抗病和感病品种之间的碱基差异位点开发的CAPS分子标记, 检测效率达到

表 4 调控菊花主要功能性成分形成的关键基因及其分子机制研究

Table 4 Summary of genes and mechanisms regulating key functional metabolites in *Chrysanthemum*

类型	基因	调控性状	文献
黄酮/酚酸	*CmHY5*, *CmFNSII-1*	芹菜素积累	[85]
	CmMYB3a, *CmMYB3b*, *CmCHI*, *CmFLS*	黄酮醇积累	[86]
	CmMYB11	黄酮积累	[87]
	CmBBX20, *CmPAL*, *CmCHS1/2*, *CmF3'H*, *CmFNS*, *CmHQT*	黄酮和绿原酸积累	[88]
	CiFNSII-1.2	黄酮积累	[67]
	CiRHM1	黄酮苷元积累	[89]
	CmVNI2, *CmMYB3*, *CmF3H*	黄酮醇积累	[17]
萜类/香气	*CiGPS*, *CiFPS*	萜类积累	[90]
	CiMYC2	萜类积累	[91]
	CiTPS	芳香萜类合成	[92]
	CiTPSs	挥发性萜类合成	[93]
	CmWRKY41, *CmHMGR2*, *CmFPPS2*	倍半萜合成	[94]
	CaTPSs	香气形成	[95]

81.25%[115]. Yang等人[116]利用BSA在菊花F_1群体中开发了一个可有效区分托桂和非托桂花型的SCAR(sequence characterized amplified regions)标记, 选择效率在开发群体和验证群体中分别可达92.5%和87.9%, 为菊花托桂花型的早期选择提供了可能. dCAPS和SCAR标记的检测依赖凝胶电泳进行片段分离, 费时费力、通量较低, 且dCAPS标记开发还受限于限制性内切酶的价格, 进一步限制了其实际应用. KASP(kompetitive allele specific PCR)标记是一种基于荧光检测的基因分型新方法. 该技术基于引物末端碱基的特异匹配来对SNP或InDel位点进行精准的双等位基因判定, 具有简便灵活、准确性高、成本低、高通量等明显优势, 可实现高通量育种平台检测[117]. 在菊花上, KASP标记已成功应用于花型[118]和光周期反应[119]的基因分型, 展现出广阔的育种应用前景. 新近, Luo等人[89,120]通过基于结构变异的SV-GWAS鉴定出一个黄酮含量显著关联位点, 开发了与黄酮合酶II基因*CiFNSII-1.2*紧密连锁的SV标记(418 bp), 可用于早期高效筛选高黄酮含量野菊种质, 并将该片段成功导入栽培菊花, 实现了功能菊花高黄酮性状的定向选择和聚合.

2.4 全基因组选择研究进展

全基因组选择(genomic selection, GS)是由挪威生命科学大学Meuwissen等人[121]于2001年率先提出的一种育种策略. 该方法利用覆盖全基因组的分子标记信息, 通过统计模型预测个体基因组估计育种值, 从而实现优良个体的早期选择. 与传统关注主效位点的MAS相比, GS对微效多基因控制、遗传力偏低的复杂数量性状具有更高的预测准确度, 且不依赖QTL定位和表型测量, 支持多性状同步预测, 可大幅度缩短育种周期[122,123]. 目前, GS育种技术已从早期在家畜奶牛选育中的成功应用[124], 逐步拓展至水稻[125]、玉米[126]、大豆[127]等主要农作物的育种实践, 成为基因组指导育种体系中的革命性工具. 影响GS预测准确度的因素有很多, 主要包括目标性状的遗传特性、训练群体规模、标记及统计模型选择、训练群体与验证群体间的亲缘关系等. 构建高效的GS预测模型, 已成为当前国内外植物分子育种领域的研究热点.

菊花基因组图谱的公布以及测序成本的下降为菊花全基因组选择提供了丰富的遗传变异信息. Su等人[110]利用200个代表性品种和330710个GBS-SNP标记, 对菊花花期性状进行了GS预测. 该研究采用5折交叉验证, 以80%的个体为训练集, 系统评估了统计模型、标记密度、标记类型等因素对预测精度的影响. 研究发现, 经典机器学习模型支持向量机SVM以及GWAS鉴定获得的显著关联位点可以快速高效预测菊花动态花期, 准确度可达89.7%~95.0%[110]. Zhang等人[109]利用岭回归最佳线性无偏预测rrBLUP模型对菊花株高相关性状进行了GS分析. 结果表明, 随着标记位点数目的增加, 其预测准确度呈现先上升后平缓趋势, 由GWAS检测得到的前1000个显著关联SNPs构成的子集预测准确度最高, 分别为相同规模随机SNPs集合的2.16倍, 以及

全基因组所有可用标记集合的1.94倍. 此外, 还有研究利用性状关联位点建立了耐盐性[128]的GS育种体系, 其预测准确度为82.3%. 综合比较发现, 在菊花多个复杂性状的预测中, rrBLUP和SVM模型普遍展现出较高且稳定的准确性, 而随机森林RF模型的预测性能相对有限. 由此可见, GS技术在菊花育种中具有巨大的应用潜力. 然而, 现有研究多局限于同一遗传群体内部的验证, 缺乏跨群体的系统性评估, 加之菊花基因组庞大导致的基因分型成本高昂、计算资源需求大等问题, 共同制约了该技术在菊花育种实践中的规模化应用.

3 菊花分子育种的挑战与前景

近年来, 多种重要花卉的基因组测序相继完成, 极大推动了花卉多组学与分子育种研究. 以月季为例, 得益于染色体水平基因组[129,130]、单倍型图谱[131]及泛基因组[132]的解析, 研究人员得以系统揭示花香合成[133]等重要性状的遗传调控网络, 从而显著推进了分子设计育种进程. 而菊花、百合[134,135]等物种由于其基因组庞大, 多组学研究和分子育种仍存在挑战.

3.1 分子育种挑战

首先, 栽培菊花复杂的节段异源六倍体与高度杂合的基因组背景, 以及栽培种间极大的遗传变异, 构成了分子育种的底层障碍. 这种复杂的遗传基础不仅严重迟滞了高质量参考基因组的破译, 也为后续的分子育种带来了巨大挑战. 其次, 菊花的遗传转化与植株再生体系具有强烈的基因型依赖性且整体效率偏低, 这已成为制约传统转基因育种及新型基因组编辑技术落地的核心瓶颈. 此外, 相较于农作物, 观赏植物的基础生物学研究仍相对滞后, 缺乏系统性的多组学数据支撑, 且内源高效的转录调控元件(如启动子与终止子)尚未得到充分挖掘, 这从根本上限制了优异抗逆基因的快速鉴定及其在分子改良中的工程化应用.

在功能基因组学与分子育种研究中, 多倍体同源拷贝间的序列多态性往往预示着基因功能的分化. 因此, 若对等位基因的解析仅局限于单一拷贝, 不仅难以反映基因家族真实的全局表达贡献, 更极易掩盖同源拷贝在多倍化进程中衍生出的新功能或特异的亚功能分化. 此外, 在处理转录组等高通量测序数据时, 由于短读长难以精确区分高度相似的同源序列, 常导致比对时reads错误地富集于单一参考拷贝上. 这种生信分析偏差掩盖了同源基因间的表达差异, 极大增加了菊花等复杂多倍体植物中真实功能基因挖掘与精准定量的难度.

在基因编辑育种方面, 单倍型间的显著序列差异反映了进化过程中的亚基因组优势或特定单倍型的丢失, 这为多倍体观赏植物的靶点设计带来了严峻挑战. 首先, 基因冗余现象使得单一等位基因的敲除极易被其他同源拷贝的功能所代偿, 难以呈现典型的表型突变; 其次, 同源拷贝间普遍存在亚功能化与表达偏好性. 例如, 普通小麦(*Triticum aestivum*)平均约30%的同源三联体(A、B和D亚基因组)呈现出表达偏好, 印证了同源基因功能的分化[136]. 因此, 仅针对单一拷贝的靶向编辑难以准确评估其对全局表型的贡献权重, 这显著提升了菊花遗传改良的不可预见性.

菊花分子标记开发的主要挑战源于其基因组冗余性、同源序列相似性及等位基因剂量效应. 由于存在多套基因组(AAA'A'BB), 开发特异性标记时, 引物极易在多个同源位点非特异性结合, 导致扩增产物复杂、背景噪音高. 此外, 传统的基于二倍体的基因分型模型难以准确区分和量化不同等位基因组合及其剂量, 严重制约了标记的开发效率与遗传定位的精度.

3.2 应对策略

首先, 构建高质量的泛基因组(pan-genome)图谱是破解序列多态性与参考基因组偏差的基础. 全面的基因组信息对于等位基因挖掘、靶点设计、突变体鉴定及脱靶评估至关重要[137]. 泛基因组通过整合多个代表性栽培种的完整序列信息, 能够系统解析单核苷酸多态性与结构变异, 有效克服单一参考基因组带来的分析局限. 这不仅为重要性状的靶基因挖掘提供了广阔的变异资源库, 更为设计广谱或等位基因特异性的sgRNA提供了高精度的数据支撑. 此外, 引入长读长测序技术是实现多倍体基因精准解析的关键策略. 依托等位基因间微小的SNPs与SVs, 可实现同源序列的高精度拆分与无偏差比对. 这不仅从根本上纠正了短读长reads错误富集造成的定量偏差, 更为等位基因特异性表达分析提供了坚实的方法学支撑.

其次, 依托多组学技术系统挖掘顺式作用元件(*cis*-regulatory elements, CREs). 在菊花中, 综合运用全长转录组、ATAC-seq以及CUT&Tag等前沿组学技术, 可以在全基因组水平高效、精准地锚定顺式作用元件与关键调控区. 这不仅有助于开发菊花内源的高效表达元

件(如特异性启动子), 更为利用CRISPR技术重建调控网络、创制连续的表型变异提供理想靶点.

最后, 开发无组培递送体系以解除基因型限制. 当前菊花遗传转化对特定品种(如‘神马’)的依赖, 阻碍了基因编辑技术在优异品种中的应用. 未来, 基于病毒诱导的基因编辑(virus-induced gene editing, VIGE)或新型纳米材料介导的核糖核蛋白(ribonucleoproteins, RNP)直接递送技术将展现出巨大潜力. 这些新兴策略有望绕过繁琐且高度依赖基因型的组织培养与植株再生环节, 直接在菊花中实现稳定的遗传修饰.

此外, 菊花复杂的多倍体背景及其丰富的同源拷贝, 为创制连续的表型变异提供了可能. 通过精准靶向编辑不同数量的同源拷贝, 研究者能够从头创制多梯度的等位基因变异库. 该策略有望实现对靶基因转录丰度的连续剂量调控, 有效克服传统单基因敲除中“非开即关”的二元局限. 这种基于等位基因剂量的精细微调机制, 在改良菊花株高、分枝结构、花期及抗逆性等多基因控制的复杂数量性状中, 具有极高的分子育种应用潜力.

而针对菊花复杂多倍体带来的技术困难, 综合利用HiFi、ONT等高保真长读长测序及单倍型分型技术, 构建菊花复杂单倍型的端粒到端粒(T2T)级别高质量参考基因组, 是突破高特异性分子标记开发瓶颈、实现菊花重要性状精准遗传解析的核心前提. 其次, 开发适配菊花特殊遗传背景的生物信息学工具与统计模型, 如准确定量等位基因剂量的基因分型流程、专门针对其节段异源多倍体基因组结构优化的GWAS模型, 从而有效解析多套基因组背景下复杂的剂量-表型关系. 此外, 在标记类型上, 相较于传统SNP和InDel变异, 开发基于序列结构变异或表观遗传修饰的标记, 往往能展现出更高的多态性与位点特异性.

3.3 未来重点发展方向

水稻等主粮作物已向育种5.0迈进[138], 而随着多组学、基因编辑、人工智能等技术的快速发展, 菊花基因组学与分子研究也将朝着精准化、系统化、智能化的方向发展(图2), 未来重点发展方向如下.

(1) 完善菊属植物泛基因组与单倍型图谱: 整合代表性菊花栽培种和野生近缘种, 构建高质量的分型T2T超级泛基因组, 深入挖掘隐藏的结构变异, 解析剂量效应和等位基因调控机制, 为复杂性状的遗传解析提供基础.

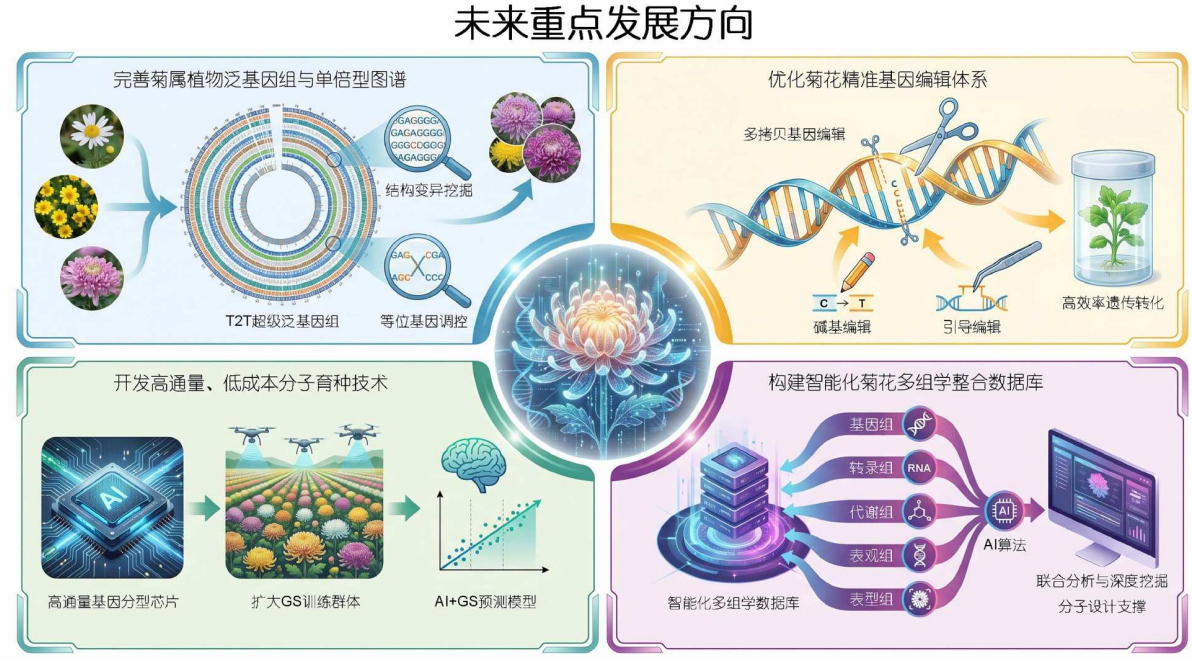

图 2 菊花未来分子育种工作的系统性框架. 本图借助Nano Banana Pro工具辅助制作, 并结合人工手绘完成, 作者对图表内容的科学性进行了审查

Figure 2 A systematic framework for future molecular breeding of *Chrysanthemum*. This figure was produced with the aid of Nano Banana Pro and further refined by manual modifications, and the authors have verified the scientific validity of the figure

(2) 优化菊花精准基因编辑体系: 针对多倍体基因组特点, 开发高效的多拷贝基因编辑技术, 优化碱基编辑、引导编辑、表观遗传编辑等精准改造工具, 建立低嵌合、高效率的菊花遗传转化体系, 实现基因的定点敲除、替换与表达调控.

(3) 开发高通量、低成本分子育种技术: 研发适用于菊花的高通量基因分型芯片, 建立标准化的功能型分子标记开发与验证体系; 扩大GS技术的训练群体规模, 结合人工智能构建高效的多性状GS预测模型, 提升跨群体、跨环境的预测准确度, 降低基因分型成本.

(4) 构建智能化菊花多组学整合数据库: 基于人工智能算法, 整合菊花基因组、转录组、代谢组、表观组、表型组等数据, 建立标准化、开放的菊花多组学数据库, 开发生物信息学分析工具, 实现多组学数据的联合分析与深度挖掘, 为功能基因挖掘与分子设计提供平台支撑.

参考文献

1 Kumar M, Chaudhary V, Sirohi U, et al. Biochemical and molecular markers for characterization of *Chrysanthemum* germplasm: a review. J Pharmacogn Phytochem, 2018, 7: 2641–2652

2 Su J, Jiang J, Zhang F, et al. Current achievements and future prospects in the genetic breeding of *Chrysanthemum*: a review. Hortic Res, 2019, 6: 109

3 Anderson N O. Conventional breeding of *Chrysanthemum*. In: SharathKumar M, Heuvelink E, eds. Chrysanthemum. Wallingford, UK: CABI, 2026. 21–83

4 Li X L, Chen F D. Advances of genetic improvement and germplasm resources for *Chrysanthemum* (in Chinese). Chin Bull Bot, 2004, 21: 392–401 [李辛雷, 陈发棣. 菊花种质资源与遗传改良研究进展. 植物学通报, 2004, 21: 392–401]

5 Song A, Su J, Wang H, et al. Analyses of a chromosome-scale genome assembly reveal the origin and evolution of cultivated *Chrysanthemum*. Nat Commun, 2023, 14: 2021

6 Song C, Liu Y, Song A, et al. The *Chrysanthemum nankingense* genome provides insights into the evolution and diversification of *Chrysanthemum* flowers and medicinal traits. Mol Plant, 2018, 11: 1482–1491

7 Nakano M, Taniguchi K, Masuda Y, et al. A pure line derived from a self-compatible *Chrysanthemum seticuspe* mutant as a model strain in the genus *Chrysanthemum*. Plant Sci, 2019, 287: 110174

8 Wen X, Li J, Wang L, et al. The *Chrysanthemum lavandulifolium* genome and the molecular mechanism underlying diverse capitulum types. Hortic Res, 2022, 9: uhab022

9 van Lieshout N, van Kaauwen M, Kodde L, et al. *De novo* whole-genome assembly of *Chrysanthemum makinoi*, a key wild *Chrysanthemum*. G3 (Bethesda), 2022, 12: jkab358

10 Hou Z, Yang S, He W, et al. The haplotype-resolved genome of diploid *Chrysanthemum indicum* unveils new acacetin synthases genes and their evolutionary history. Plant J, 2024, 119: 1336–1352

11 Hirakawa H, Sumitomo K, Hisamatsu T, et al. *De novo* whole-genome assembly in *Chrysanthemum seticuspe*, a model species of *Chrysanthemum*s, and its application to genetic and gene discovery analysis. DNA Res, 2019, 26: 195–203

12 Deng Y, Yang P, Zhang Q, et al. Genomic insights into the evolution of flavonoid biosynthesis and O-methyltransferase and glucosyltransferase in *Chrysanthemum indicum*. Cell Rep, 2024, 43: 113725

13 Kim C, Wang X, Xue W, et al. Integrated genomic, transcriptomic, and metabolomic analyses of *Chrysanthemum aromaticum* provide insights into the volatile terpene biosynthesis. Plant J, 2025, 123: e70327

14 Nakano M, Hirakawa H, Fukai E, et al. A chromosome-level genome sequence of *Chrysanthemum seticuspe*, a model species for hexaploid cultivated *Chrysanthemum*. Commun Biol, 2021, 4: 1167

15 Zhao G, Li Y, Peng J, et al. Anthocyanin degradation drives heat-induced petal fading in *Chrysanthemum morifolium* at full bloom: a multi-omics analysis. Agriculture, 2025, 15: 950

16 Zhao N, Yang F, Niu S, et al. Metabolome-transcriptome integration reveals waterlogging tolerance pathways in *Chrysanthemum morifolium*. Chem Biol Technol Agric, 2026, 13: 29

17 Jiang T, Sun Y, Wang Y, et al. CmVNI2 *CmMYB3* module regulates flavonol biosynthesis in response to low temperature in *Chrysanthemum* flower. Mol Horticulture, 2025, 5: 53

18 Lu Z, Su J, Xiang Y, et al. Integrative linkage mapping, GWAS, and RNA-Seq analysis unravel the genetic architecture and candidate genes for drought tolerance in *Chrysanthemum* interspecific F_1 progeny. Hortic Res, 2025, 12: uhaf169

19 Zhang X, Sun W, Su J, et al. Elucidation of the genetic basis underlying rooting ability in vegetatively propagated *Chrysanthemum*. Hortic Res,

2026, 13: uhaf289
20 Wang F, Zhong X, Huang L, et al. Cellular and molecular characteristics of pollen abortion in *Chrysanthemum* cv. Kingfisher. Plant Mol Biol, 2018, 98: 233–247
21 Zhang F, Wang Z, Dong W, et al. Transcriptomic and proteomic analysis reveals mechanisms of embryo abortion during *Chrysanthemum* cross breeding. Sci Rep, 2014, 4: 6536
22 Zhang F, Hua L, Fei J, et al. Chromosome doubling to overcome the *Chrysanthemum* cross barrier based on insight from transcriptomic and proteomic analyses. BMC Genomics, 2016, 17: 585
23 Lin P, Bai H, He L, et al. Proteome-wide and lysine crotonylation profiling reveals the importance of crotonylation in *Chrysanthemum* (*Dendranthema grandiforum*) under low-temperature. BMC Genomics, 2021, 22: 51
24 Huang Q, Liao X, Yang X, et al. Lysine crotonylation of DgTIL1 at K72 modulates cold tolerance by enhancing DgnsLTP stability in *Chrysanthemum*. Plant Biotechnol J, 2021, 19: 1125–1140
25 Li X, Bu F, Zhang M, et al. Enhancing nature's palette through the epigenetic breeding of flower color in *Chrysanthemum*. New Phytol, 2025, 245: 2117–2132
26 Yu Z, Ci H, Jing R, et al. Polyploidization enhances plant resistance to *Alternaria alternata* via DNA hypomethylation activated WRKYs. Hortic Res, 2026, 13: uhag050
27 Yang Y, Huang Y, Wang T, et al. mRNA m6A regulates gene expression via H3K4me3 shift in 5′ UTR. Genome Biol, 2025, 26: 54
28 Song J, Zhang Y, Hu X, et al. Spongy mesophyll cell death is induced by jasmonic acid during leaf senescence in *Chrysanthemum*. Plant Cell, 2026, 38: koag095
29 Ye J, Wang C, Liu Y, et al. CGD: a multi-omics database for *Chrysanthemum* genomic and biological research. Hortic Res, 2024, 11: uhae238
30 Noda N, Yoshioka S, Kishimoto S, et al. Generation of blue *Chrysanthemum*s by anthocyanin B-ring hydroxylation and glucosylation and its coloration mechanism. Sci Adv, 2017, 3: e1602785
31 Han X Y, Luo Y T, Lin J Y, et al. Generation of purple-violet *Chrysanthemum*s via anthocyanin B-ring hydroxylation and glucosylation introduced from *Osteospermum hybrid F3'5'H* and *Clitoria ternatea A3'5'GT*. Ornam Plant Res, 2021, 1: 4
32 Huang D, Li X, Sun M, et al. Identification and characterization of CYC-like genes in regulation of ray floret development in *Chrysanthemum morifolium*. Front Plant Sci, 2016, 7: 1633
33 Wang L, Sun J, Ren L, et al. CmBBX8 accelerates flowering by targeting *CmFTL1* directly in summer *Chrysanthemum*. Plant Biotechnol J, 2020, 18: 1562–1572
34 Zhai Y, Zhu Y, Wang Q, et al. BBX7 interacts with BBX8 to accelerate flowering in *Chrysanthemum*. Mol Horticulture, 2023, 3: 7
35 Tang J, Liu P, Yu Q, et al. The CmDOF6 transcription factor controls *Chrysanthemum* plant height by repressing *CmGA20ox1* via CmTCP8. Plant Physiol, 2025, 199: kiaf509
36 Jin J, Zhu Y, Li S, et al. Jasmonic acid signaling inhibits axillary bud development under drought stress via the CmMYC2–CmBRC1b module. Plant Physiol, 2025, 199: kiaf505
37 Zhang S, Liu L, Li W, et al. *Alternaria alternata* effector AaAlta1 targets CmWD40 and participates in regulating disease resistance in *Chrysanthemum morifolium*. PLoS Pathog, 2025, 21: e1012942
38 Li F, Zhang Y, Tian C, et al. Molecular module of CmMYB15-like-Cm4CL2 regulating lignin biosynthesis of *Chrysanthemum* (*Chrysanthemum morifolium*) in response to aphid (*Macrosiphoniella sanborni*) feeding. New Phytol, 2023, 237: 1776–1793
39 Wang T, Wei Q, Wang Z, et al. CmNF-YB8 affects drought resistance in *Chrysanthemum* by altering stomatal status and leaf cuticle thickness. J Integr Plant Biol, 2022, 64: 741–755
40 Wang X, Wang Y, Jiang Y, et al. Transcription factor CmHSFA4–CmMYBS3 complex enhances salt tolerance in *Chrysanthemum* by repressing *CmMYB121* expression. Plant Physiol, 2024, 195: 3119–3135
41 Yan Y, Zhang W, Wang Y, et al. CmHRE2L-CmACS6 transcriptional cascade negatively regulates waterlogging tolerance in *Chrysanthemum*. Mol Horticulture, 2025, 5: 15
42 Zhou L, Peng J, Chen C, et al. CmBBX28-CmMYB9a module regulates petal anthocyanin accumulation in response to light in *Chrysanthemum*. Plant Cell Environ, 2025, 48: 3750–3765
43 Geng Z, liu M, Wang Y, et al. Transcriptomic and metabolomic analyses reveal CmMYB308 as a key regulator in the pink flower color variation of 'Dante Purple' *Chrysanthemum*. Plant Cell Rep, 2024, 43: 157
44 Wang Y, Wang Y, Zhou L J, et al. CmNAC25 targets *CmMYB6* to positively regulate anthocyanin biosynthesis during the post-flowering stage in *Chrysanthemum*. BMC Biol, 2023, 21: 211
45 Fang J, Liu S, Chen S, et al. A R1-type MYB CmREVEILLE2 regulates light-mediated chlorophyll biosynthesis and green color formation in *Chrysanthemum* flowers. Hortic Adv, 2025, 3: 17
46 Geng Z, Zhou L, Wang Y, et al. A U-box E3 ubiquitin ligase CmPUB 15 targets CmMYB 73 to regulate anthocyanin biosynthesis in response to

low temperatures in *Chrysanthemum*. New Phytol, 2025, 248: 1304–1320
47 Han S, Li S, Li Y, et al. The *Chrysanthemum morifolium* β-carotene hydroxylase gene *CmBCH1* promotes tolerance to high light by enhancement of the xanthophyll cycle. Environ Exp Bot, 2024, 217: 105545
48 Jia D, Zhang Y, Su J, et al. An auxin-induced transcriptional cascade CmBES1–CmSAUR66 orchestrates the ray floret development in *Chrysanthemum morifolium*. Proc Natl Acad Sci USA, 2026, 123: e2527961123
49 Guan Y, Ding L, Jiang J, et al. The TIFY family protein CmJAZ1-like negatively regulates petal size via interaction with the bHLH transcription factor CmBPE2 in *Chrysanthemum morifolium*. Plant J, 2022, 112: 1489–1506
50 Ma Y, Zhang H, Zou Q, et al. Transcriptome-based identification, cloning and functional characterization of the MYB-related transcription factor genes CmDIV-like and CmRAD1 in *Chrysanthemum morifolium* cv. 'Hangju'. Plant Sci, 2026, 362: 112749
51 Zhang L, Fu X, Ye J, et al. CmbZIP19 inhibits lateral bud elongation via the brassinolide pathway in *Chrysanthemum*. Plant J, 2025, 121: e70080
52 Fu X, Song A, Peng B, et al. Brassinosteroid biosynthetic gene CmDWF4 regulates bud outgrowth in *Chrysanthemum morifolium*. Phyton, 2023, 92: 1681–1694
53 Ling Q, Mei P, Tang S, et al. CmAP2 interacts with CmRAX2 and promotes branching by affecting the cytokinin pathway in *Chrysanthemum*. Plant Physiol Biochem, 2026, 231: 111012
54 Zhang Y, Liu W, Peng B, et al. *CmDRM1* negatively regulates lateral bud break in *Chrysanthemum*. Sci Horticulturae, 2024, 335: 113359
55 Liu W, Li J, Zhang H, et al. The peptide CmGAST1 integrates calcium and gibberellin signaling to regulate flowering in *Chrysanthemum*. Plant Cell, 2025, 37: koaf269
56 Hu Q, Yin M, Gao Z, et al. Late flowering in *Chrysanthemum* induced by low ambient temperature is mediated by *FLOWERING LOCUS C- like*. J Exp Bot, 2025, 76: 2192–2206
57 Liu X, Han M, Jiang T, et al. AGAMOUS-LIKE 24 senses continuous inductive photoperiod in the inflorescence meristem to promote anthesis in *Chrysanthemum*. Plant Cell, 2024, 36: 4658–4671
58 Tian C, Zhai L, Wang J, et al. *CmARF3–CmTCP7* module regulates flowering time in *Chrysanthemum* (*Chrysanthemum morifolium*). Hortic Res, 2025, 12: uhaf095
59 Wang G, Wang J, Yin M, et al. CmNLP7 interacts with CmPP6 to suppress flowering time in *Chrysanthemum*. Horticultural Plant J, 2025, 11: 865–876
60 Zhao K, Jia D, Zhang X, et al. *FUL* homologous gene *CmFL1* is involved in regulating flowering time and floret numbers in *Chrysanthemum morifolium*. Plant Sci, 2023, 336: 111863
61 Gao X, Liu L, Wang T, et al. Aging-dependent temporal regulation of *MIR156* epigenetic silencing by CiLDL1 and CiNFYB8 in *Chrysanthemum*. New Phytol, 2025, 245: 2309–2321
62 Cheng H, Wang Q, Zhang Z, et al. The RAV transcription factor TEMPRANILLO1 involved in ethylene-mediated delay of *Chrysanthemum* flowering. Plant J, 2023, 116: 1652–1666
63 Zhang Z, Hu Q, Gao Z, et al. Flowering repressor CmSVP recruits the TOPLESS corepressor to control flowering in *Chrysanthemum*. Plant Physiol, 2023, 193: 2413–2429
64 Wang Q, Wang L, Cheng H, et al. Two B-box proteins orchestrate vegetative and reproductive growth in summer *Chrysanthemum*. Plant Cell Environ, 2024, 47: 2923–2935
65 Li P, Fang T, Chong X, et al. CmDOF18 positively regulates salinity tolerance in *Chrysanthemum morifolium* by activating the oxidoreductase system. BMC Plant Biol, 2024, 24: 232
66 Xia B, Li Z, Liu X, et al. Functional characterization of *CiHY5* in salt tolerance of *Chrysanthemum indicum* and conserved role of *HY5* under stress in *Chrysanthemum*. Plant Physiol Biochem, 2025, 223: 109797
67 Luo J, Luo C, Han M, et al. A natural variation of flavone synthase II gene enhances flavone accumulation and confers drought adaptation in *Chrysanthemum*. New Phytol, 2025, 247: 1445–1459
68 Liao X, Zhang X, Li X, et al. Lysine malonylation of DgnsLIPID TRANSFER PROTEIN1 at the K81 site improves cold resistance in *Chrysanthemum*. Plant Physiol, 2023, 192: 3152–3169
69 Ren M, Yang W, Zhang J, et al. Overexpression of ClRAP2.4 in *Chrysanthemum* enhances tolerance to cold stress. Funct Plant Biol, 2023, 50: 470–481
70 Luo Y, Wang Y, Li X, et al. Transcription factor DgMYB recruits H3K4me3 methylase to *DgPEROXIDASE* to enhance *Chrysanthemum* cold tolerance. Plant Physiol, 2024, 194: 1104–1119
71 Wang Y, Zeng Q, Tian Y, et al. The histone deacetylase SRT2 enhances the tolerance of *Chrysanthemum* to low temperatures through the ROS scavenging system. Plant Physiol Biochem, 2024, 207: 108405
72 Zhang X, Zeng Q, Yang Q, et al. DgHDA6 enhances the cold tolerance in *Chrysanthemum* by improving ROS scavenging capacity. Ecotoxicol Environ Saf, 2024, 269: 115737

73 Tian Y, Feng Y, Wang Y, et al. The overexpression of *DgPR1* enhances *Chrysanthemum* cold tolerance through the ROS-mediated pathway. Plant Sci, 2025, 356: 112493

74 Li C, Wang L, Su J, et al. A group VIIIa ethylene-responsive factor, CmERF4, negatively regulates waterlogging tolerance in *Chrysanthemum*. J Exp Bot, 2024, 75: 1479–1492

75 Meng H, Luo B Y, Lu Z Y, et al. Cloning of *CmASMT* and its role in thermotolerance of *Chrysanthemum*. Sci Agric Sin, 2025, 58: 1617–1626

76 Chen S, Yue L, Yang X, et al. *CiPCS* regulated by *CiMYB4* enhances the tolerance of *Chrysanthemum indicum* to cadmium stress. Plant Cell Rep, 2025, 45: 2

77 Miao W, Xiao X, Wang Y, et al. CmWRKY6–1–CmWRKY15-like transcriptional cascade negatively regulates the resistance to *Fusarium oxysporum* infection in *Chrysanthemum morifolium*. Hortic Res, 2023, 10: uhad101

78 Li W, Wang M, Liu Y, et al. A pattern for the early, middle, and late phase of tea *Chrysanthemum* response to *Fusarium oxysporum*. Physiol Plant, 2024, 176: e14373

79 Huang C G, Dong C B, Jiang C J, et al. *CmNAC083* regulates resistance to *Alternaria alternata via* reactive oxygen species and jasmonic acid signaling pathways in *Chrysanthemum morifolium*. OPR, 2023, 3: 0

80 Jiang C L, Feng C X, Chen C X, et al. Cloning and identification of *CmCCNBARC*, a *Chrysanthemum* white rust resistance gene. OPR, 2023, 3: 0

81 Chen Q, Jin R, Liu D, et al. The CmTGA1–CmRbohD cascade confers resistance against *Chrysanthemum* white rust by promoting reactive oxygen species generation. Plant Cell Environ, 2025, 48: 3459–3470

82 Guan Y, Jiang L, Wang Y, et al. CmMYC2–CmMYBML1 module orchestrates the resistance to herbivory by synchronously regulating the trichome development and constitutive terpene biosynthesis in *Chrysanthemum*. New Phytol, 2024, 244: 914–933

83 Wang Y, Guan Y, Hong C, et al. CmMYBML1 CmTGA1 *CmTPS1* module regulates *Chrysanthemum* (*Chrysanthemum morifolium*) resistance to the aphid *Macrosiphoniella sanbourni*. New Phytol, 2025, 248: 2564–2582

84 Yang Y, Qian Z, Li Y, et al. Competition binding of CmbHLH1L and CmNLP6 7L to CmbHLH63 modulates leaf senescence in *Chrysanthemum*. Plant Biotechnol J, 2025, 23: 5456–5473

85 Luo C, Liu L, Zhao J, et al. CmHY5 functions in apigenin biosynthesis by regulating flavone synthase II expression in *Chrysanthemum* flowers. Planta, 2022, 257: 7

86 Yang F, Wang T, Guo Q, et al. The CmMYB3 transcription factors isolated from the *Chrysanthemum morifolium* regulate flavonol biosynthesis in *Arabidopsis thaliana*. Plant Cell Rep, 2023, 42: 791–803

87 Wang Y, Zhou L J, Song A, et al. Comparative transcriptome analysis and flavonoid profiling of floral mutants reveals CmMYB11 regulating flavonoid biosynthesis in *Chrysanthemum*. Plant Sci, 2023, 336: 111837

88 Lu C, Liu Y, Yan X, et al. Multiplex approach of metabolomic and transcriptomic reveals the biosynthetic mechanism of light-induced flavonoids and CGA in *Chrysanthemum*. Industrial Crops Products, 2024, 221: 119420

89 Luo C, Luo J, Han M, et al. Identification and knockout of rhamnose synthase *CiRHM1* enhances accumulation of flavone aglycones in *Chrysanthemum* flower. Plant Biotechnol J, 2025, 23: 1002–1004

90 Gao W, Meng Q, Wang X, et al. Overexpression of *GPS* and *FPS* from *Chrysanthemum indicum* var. *aromaticum* resulted in modified trichome formation and terpenoid biosynthesis in tobacco. Plant Growth Regul, 2023, 99: 553–566

91 Gao W, Meng Q, Wang X, et al. Overexpression of *CiMYC2* transcription factor from *Chrysanthemum indicum* var. *aromaticum* resulted in modified trichome formation and terpenoid biosynthesis in transgenic tobacco. J Plant Growth Regul, 2023, 42: 4161–4175

92 Liu Y, Ji W, Wang X, et al. Identification and functional characterization of a new terpene synthase gene from *Chrysanthemum indicum* var. *aromaticum*. Hortic Sci, 2023, 50: 61–71

93 Feng Y, Zhang X, Xu X, et al. *DgbHLH2* positively regulates cold tolerance by activating *DgGST* expression to mediate ROS scavenging in *Chrysanthemum*. Industrial Crops Products, 2026, 245: 123234

94 Hu Y, Song A, Guan Z, et al. CmWRKY41 activates *CmHMGR2* and *CmFPPS2* to positively regulate sesquiterpenes synthesis in *Chrysanthemum morifolium*. Plant Physiol Biochem, 2023, 196: 821–829

95 Zhong J, Chen Y, Shi H, et al. Identification and functional analysis of terpene synthases revealing the secrets of aroma formation in *Chrysanthemum aromaticum*. Int J Biol Macromol, 2024, 279: 135377

96 Liu H, Ding Y, Zhou Y, et al. CRISPR-P 2.0: an improved CRISPR-Cas9 tool for genome editing in plants. Mol Plant, 2017, 10: 530–532

97 Sun J, Liu H, Liu J, et al. CRISPR-Local: a local single-guide RNA (sgRNA) design tool for non-reference plant genomes. Bioinformatics, 2019, 35: 2501–2503

98 Kishi-Kaboshi M, Aida R, Sasaki K. Generation of gene-edited *Chrysanthemum morifolium* using multi-copy transgenes as targets and markers. Plant Cell Physiol, 2017, pcw222

99 Li X, Yang Q, Liao X, et al. A natural antisense RNA improves *Chrysanthemum* cold tolerance by regulating the transcription factor *DgTCP1*. Plant Physiol, 2022, 190: 605–620

100 Liu L, Xue Y, Luo J, et al. Developing a UV-visible reporter-assisted CRISPR/Cas9 gene editing system to alter flowering time in *Chrysanthemum indicum*. Plant Biotechnol J, 2023, 21: 1519–1521

101 Singh A, Prasad S S, Ingle K P, et al. Molecular marker-assisted selection in plant breeding. In: Al-Khayri J M, Ingle K P, Jain S M, et al., eds. Plant Molecular Breeding in Genomics Era. Switzerland: Springer Nature, 2024. 95–111

102 Panahi B, Mohammadzadeh Jalaly H, Hamid R. Using next-generation sequencing approach for discovery and characterization of plant molecular markers. Curr Plant Biol, 2024, 40: 100412

103 van Geest G, Bourke P M, Voorrips R E, et al. An ultra-dense integrated linkage map for hexaploid *Chrysanthemum* enables multi-allelic QTL analysis. Theor Appl Genet, 2017, 130: 2527–2541

104 Song X, Xu Y, Gao K, et al. High-density genetic map construction and identification of loci controlling flower-type traits in *Chrysanthemum* (*Chrysanthemum* × *morifolium* Ramat.). Hortic Res, 2020, 7: 108

105 Song C X, Tian C Y, Gao C K, et al. Genetic and QTL analysis of flower color and pigments in small-flowered *Chrysanthemum* based on high-density genetic map. OPR, 2023, 3: 17

106 Su J, Li C, Ou X, et al. *CmWAT6.1*, mined by high-density genetic map-based QTL mapping, enhances waterlogging tolerance in *Chrysanthemum*. Environ Exp Bot, 2024, 219: 105612

107 Sumitomo K, Shirasawa K, Isobe S, et al. A genome-wide association and fine-mapping study of white rust resistance in hexaploid *Chrysanthemum* cultivars with a wild diploid reference genome. Hortic Res, 2022, 9: uhac170

108 Lou L, Su J, Ou X, et al. Multi-locus genome-wide association studies reveal genetic loci and candidate genes for leaf angle traits in cut *Chrysanthemum*. Sci Horticulturae, 2023, 322: 112406

109 Zhang X, Su J, Jia F, et al. Genetic architecture and genomic prediction of plant height-related traits in *Chrysanthemum*. Hortic Res, 2024, 11: uhad236

110 Su J, Lu Z, Zeng J, et al. Multi-locus genome-wide association study and genomic prediction for flowering time in *Chrysanthemum*. Planta, 2024, 259: 13

111 Wan W, Jia F, Liu Z, et al. Quantitative evaluation and genome-wide association studies of *Chrysanthemum* flower color. Sci Horticulturae, 2024, 338: 113561

112 Zhang X, Ning X, He Y, et al. GWAS reveals the genetic basis and genomic regions underlying four active compounds in *Chrysanthemum*. Horticultural Plant J, 2025, 11: 2211–2224

113 Su J, Zhang F, Chong X, et al. Genome-wide association study identifies favorable SNP alleles and candidate genes for waterlogging tolerance in *Chrysanthemum*s. Hortic Res, 2019, 6: 21

114 Chong X, Su J, Wang F, et al. Identification of favorable SNP alleles and candidate genes responsible for inflorescence-related traits via GWAS in *Chrysanthemum*. Plant Mol Biol, 2019, 99: 407–420

115 Cao X Y. Functional verification of *CmPLDα1* against *Chrysanthemum* white rust and development and application of CAPS molecular markers (in Chinese). Master Thesis. Shenyang: Shenyang Agricultural University, 2025 [曹馨予. *CmPLDα1*抗菊花白色锈病的功能验证及CAPS分子标记开发应用. 硕士学位论文. 沈阳: 沈阳农业大学, 2025]

116 Yang X, Wu Y, Su J, et al. Genetic variation and development of a SCAR marker of anemone-type flower in *Chrysanthemum*. Mol Breeding, 2019, 39: 48

117 Dipta B, Sood S, Mangal V, et al. KASP: a high-throughput genotyping system and its applications in major crop plants for biotic and abiotic stress tolerance. Mol Biol Rep, 2024, 51: 508

118 Su J, Zhang H, Yang Y, et al. BSA-seq identified candidate genes and diagnostic KASP markers for anemone type flower in *Chrysanthemum*. Sci Horticulturae, 2024, 327: 112790

119 Zeng J W. Association loci mining and molecular marker development for flowering time of cut *Chrysanthemum* varieties (in Chinese). Master Thesis. Nanjing: Nanjing Agricultural University, 2024 [曾俊未. 切花菊花期关联位点挖掘及分子标记开发. 硕士学位论文. 南京: 南京农业大学, 2024]

120 Luo J, Song Z, Jiang T, et al. A molecular marker developed for high linarin *Chrysanthemum* breeding. Horticultural Plant J, 2026, 12: 493–496

121 Meuwissen T H E, Hayes B J, Goddard M E. Prediction of total genetic value using genome-wide dense marker maps. Genetics, 2001, 157: 1819–1829

122 Alemu A, Åstrand J, Montesinos-López O A, et al. Genomic selection in plant breeding: key factors shaping two decades of progress. Mol Plant, 2024, 17: 552–578

123 Kumar R, Das S P, Choudhury B U, et al. Advances in genomic tools for plant breeding: harnessing DNA molecular markers, genomic selection, and genome editing. Biol Res, 2024, 57: 80

124 Hayes B J, Bowman P J, Chamberlain A J, et al. Invited review: genomic selection in dairy cattle: progress and challenges. J Dairy Sci, 2009, 92: 433–443

125 Spindel J, Begum H, Akdemir D, et al. Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite, tropical rice breeding lines. PLoS Genet, 2015, 11: e1004982
126 Millet E J, Kruijer W, Coupel-Ledru A, et al. Genomic prediction of maize yield across European environmental conditions. Nat Genet, 2019, 51: 952–956
127 Xu S, Zhu D, Zhang Q. Predicting hybrid performance in rice using genomic best linear unbiased prediction. Proc Natl Acad Sci USA, 2014, 111: 12456–12461
128 Zhou Y X. Genome-wide association analysis and genomic selection for salt tolerance of cut *Chrysanthemum* (in Chinese). Master Thesis. Nanjing: Nanjing Agricultural University, 2023 [周迎雪. 切花菊耐盐性的关联分析和基因组选择. 硕士学位论文. 南京: 南京农业大学, 2023]
129 Hibrand Saint-Oyant L, Ruttink T, Hamama L, et al. A high-quality genome sequence of Rosa chinensis to elucidate ornamental traits. Nat Plants, 2018, 4: 473–484
130 Raymond O, Gouzy J, Just J, et al. The Rosa genome provides new insights into the domestication of modern roses. Nat Genet, 2018, 50: 772–777
131 Zhang Z, Yang T, Liu Y, et al. Haplotype-resolved genome assembly and resequencing provide insights into the origin and breeding of modern rose. Nat Plants, 2024, 10: 1659–1671
132 Zhang X, Lan L, Yang Y, et al. Pangenomic analyses of rose uncover widespread structure variation and empower genomics-directed breeding. Nat Genet, 2026, 58: 1164–1175
133 Li Y, Li R, Shang J, et al. A *de novo*-originated gene drives rose scent diversification. Cell, 2025, 188: 6121–6137.e24
134 Xu S, Chen R, Zhang X, et al. The evolutionary tale of lilies: giant genomes derived from transposon insertions and polyploidization. Innovation, 2024, 5: 100726
135 Liang Y, Gao Q, Li F, et al. The giant genome of lily provides insights into the hybridization of cultivated lilies. Nat Commun, 2025, 16: 45
136 Ramírez-González R H, Borrill P, Lang D, et al. The transcriptional landscape of polyploid wheat. Science, 2018, 361
137 Xu Z, Wang G, Zhu X, et al. Genome assembly of two allotetraploid cotton germplasms reveals mechanisms of somatic embryogenesis and enables precise genome editing. Nat Genet, 2025, 57: 2028–2039
138 Yu H, Bai S, Li J. Towards Breeding 5.0: smart variety by intelligent breeding (in Chinese). Chin Sci Bull, 2024, 69: 4687–4690 [余泓, 白世伟, 李家洋. 迈向育种5.0: 智能品种的智能培育. 科学通报, 2024, 69: 4687–4690]

Summary for “菊属多组学与菊花分子育种研究进展”

Progress in multi-omics and molecular breeding of *Chrysanthemum*

Zhenxing Wang[1,2], Yanze He[1,2], Jiangshuo Su[1,2], Aiping Song[1,2], Weimin Fang[1,2] & Fadi Chen[1,2*]

[1] *State Key Laboratory of Crop Genetics & Germplasm Enhancement and Utilization, College of Horticulture, Nanjing Agricultural University, Nanjing 211800, China*
[2] *Zhongshan Biological Breeding Laboratory, Nanjing 210014, China*
* Corresponding author, E-mail: chenfd@njau.edu.cn

Chrysanthemum×morifolium Ramat., a polyploid ornamental plant of the genus *Chrysanthemum* in the family Asteraceae, possesses ornamental, medicinal and economic values. As segmental allopolyploid hexaploids, cultivated *Chrysanthemum* s possess an enormous and highly heterozygous genome, which has long been a major obstacle to genetic dissection and targeted varietal improvement. Benefiting from the rapid evolution of next-generation sequencing and long-read sequencing technologies, multi-omics research on the genus *Chrysanthemum* has witnessed tremendous progress over recent years. The rapid breakthroughs in genomics technologies have propelled *Chrysanthemum* research into the era of molecular precision, with remarkable achievements made in genome sequencing, functional gene mining, gene editing and molecular marker development.

To date, high-quality chromosome-scale genome assemblies have been completed for a wide range of *Chrysanthemum* species, including diploid wild relatives, aromatic varieties, medicinal germplasms and commercial hexaploid cultivars. These genomic resources reveal the evolutionary characteristics of polyploidization, genome expansion and structural variation within the genus, and lay a fundamental framework for functional gene mining and molecular mechanism analysis. Integrated multi-omics strategies combining transcriptomics, metabolomics, proteomics, epigenomics and single-cell transcriptomics have been widely adopted to dissect complex agronomic traits. A large number of core genes and regulatory modules related to flower color, flower shape, flowering time, plant architecture, biotic and abiotic stress tolerance, postharvest senescence and biosynthesis of active ingredients have been identified and functionally verified. These findings clarify the molecular regulatory networks of key traits and provide abundant candidate genes for precise genetic improvement.

Currently, a comprehensive molecular breeding system has been established for *Chrysanthemum*. Transgenic technology enables directional modification of important traits such as ornamental and stress-related traits by regulating critical metabolic and signaling pathways. Optimized CRISPR/Cas and epigenetic editing systems support accurate manipulation of endogenous genes, overcoming the limitations of conventional breeding methods. Meanwhile, a full range of molecular markers, from traditional PCR-based markers to high-throughput SNP, InDel and SV markers, have been widely applied in germplasm identification, genetic map construction, QTL mapping and genome-wide association studies. Genomic selection has also shown prominent application value in predicting complex quantitative traits such as plant height and flowering time, displaying broad application potential in practical breeding programs in *Chrysanthemum*.

Despite substantial progress, multiple bottlenecks still restrict the large-scale application of *Chrysanthemum* molecular breeding. The complex polyploid genetic background leads to widespread gene redundancy and functional differentiation of homologous genes. Additionally, genotype-dependent transformation systems, ambiguous allelic dosage effects and high costs of high-throughput genotyping remain major obstacles. To address these issues, future research will prioritize constructing high-quality pan-genomes and haplotype maps, developing efficient multi-gene editing tools and novel genotype-independent delivery systems. It is also essential to build low-cost high-throughput genotyping platforms and intelligent multi-omics databases for data sharing and deep mining. Collectively, these technological advancements will fully promote the transformation of *Chrysanthemum* breeding from conventional breeding to modern precise and intelligent molecular design breeding in the future.

***Chrysanthemum×morifolium* Ramat., genomics, functional gene, gene editing, molecular breeding**

doi: 10.1360/CSB-2026-0468