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基于多组学的苹果性状解析与分子育种研究进展

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摘要 苹果(*Malus domestica*)是全球种植最广泛的温带落叶果树之一。因其为多年生乔木、遗传背景复杂,传统育种方法效率低、遗传改良周期长。近年来,苹果组学研究取得了显著进展,逐步实现从单一参考基因组到图泛基因组的跃升,系统揭示了苹果属演化轨迹及重要性状形成机制,推动了复杂结构变异与功能区域的深度解析;表观组、代谢组与蛋白质组等多维数据的协同应用,支撑了果实品质、矮化和抗逆等性状的精准定位。在此基础上,分子标记开发、基因组选择与育种芯片加快了优异种质的早期筛选;CRISPR/Cas等基因编辑技术,则推动了功能验证与定向改良进程。本研究系统梳理了苹果组学研究的最新进展,重点聚焦于参考基因组升级、多组学数据集成、复杂性状解析及其在分子设计育种中的实践路径。同时,分析了当前在数据整合、功能识别、表型测量与基因编辑体系等方面存在的关键挑战,并展望了分子设计育种体系突破方向,为苹果种质创新与现代育种提供理论支撑与技术框架。

关键词 苹果;多组学技术;复杂性状解析;分子设计育种

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Advances in multi-omics-based elucidation of traits and molecular breeding in apple

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Abstract Apple (*Malus domestica*) is one of the most widely cultivated temperate deciduous fruit trees worldwide. However, as a perennial woody plant with a highly heterozygous and complex genetic background, traditional breeding approaches are constrained by low efficiency and long breeding cycles. In recent years, significant progress has been made in apple omics research, with a gradual transition from a single reference genome to a graph-based pan-genome. This has systematically revealed the evolutionary trajectory of the *Malus* genus and the genetic basis of important traits, while facilitating in-depth analysis of structural variations and functional genomic regions. The integrative application of epigenomics, metabolomics, and proteomics has further enhanced the precise dissection of key traits such as fruit quality, dwarfing, and stress resistance. On this basis, the development of molecular markers, genomic selection strategies, and trait-specific breeding chips has accelerated early-stage identification of elite germplasm. Meanwhile, gene-editing technologies such as CRISPR/Cas have greatly advanced functional validation and targeted trait improvement. This review provides

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a comprehensive summary of recent progress in apple multi-omics research, with a focus on reference genome upgrading, integration of multi-omics data, dissection of complex trait, and their application in molecular design breeding. Moreover, it analyzes current technical bottlenecks, such as data integration, functional identification, phenotypic measurement, genome editing system, and looks forward to the breakthrough directions of molecular design breeding systems, providing a theoretical basis and technical framework for apple germplasm innovation and modern breeding.

Keywords apple; multi-omics technologies; complex trait dissection; molecular design breeding

苹果是世界范围内种植最广泛、产业价值很高的落叶果树,其遗传改良长期面临童期长、杂合度高和倍性复杂等瓶颈问题,传统的杂交选育与表型鉴定方法在效率和精度上难以满足当前对优质、多抗、早果、熟期和矮化等综合性状快速改良的迫切需求。随着种业升级和育种目标多元化,亟需建立高效的现代育种技术体系。

近年来,随着基因组、转录组、表观组和代谢组等多组学技术的快速发展,苹果遗传研究与分子育种进入了以数据驱动和智能化分析为特征的新阶段。高质量参考基因组的不断发布、多样性群体的构建以及多维度表型数据的积累,使研究者能够从全基因组视角系统挖掘关键变异位点,并推动分子标记筛选、基因编辑与功能验证等技术路径的建立,为实现精准育种提供了坚实基础。

本研究系统梳理了苹果组学研究的主要进展,聚焦其在遗传多样性解析、复杂性状定位、核心基因挖掘及分子设计育种等方面的应用,旨在理清研究脉络、总结典型成果,并探讨未来发展趋势,以期苹果种质创新与现代育种体系构建提供理论参考与技术支持。

1 从基因组构建到全属图谱:苹果组学研究基础的演进

1.1 从初代组装到高质量参考基因组的建立

2010年Velasco等完成的‘Golden Delicious’初版组装,奠定了苹果分子研究的基础^[1]。但由于测序技术尚处早期,组装结果存在较多片段缺失与功能注释偏差,尤其是在重复序列区域和结构复杂基因簇上表现尤为明显,难以满足复杂性状解析的需求。2017年,‘Golden Delicious’双单倍体材料GDDH13基因组发布,使得苹果基因注释的完整性与准确性得到明显提升^[2]。该基因组还整合了发育阶段DNA甲基化数据,将表观调控纳入果树基因组研究体系中,为后续表观组学研究提供了关键资

源。2019年,‘寒富’三倍体纯合材料(HFTH1)高质量参考基因组的构建进一步强化了功能导向的基因组构建思路^[3],并揭示了LTR反转座子在MYB转录因子上游的插入影响果皮着色性状,解析了结构变异在表型调控中的重要作用,也体现了苹果参考基因组在解析关键性状形成机制中的应用价值。

1.2 从单一样本到泛基因组变异的拓展

2020年,康奈尔大学首次构建了基于多个代表性样本的泛基因组图谱,揭示了苹果驯化与改良过程中基因组组成的变化规律,推动苹果从单一参考基因组研究迈向多样性时代^[4]。随后,苹果基因组研究由参考基因组构建阶段全面迈入群体多样性解析与功能图谱深化阶段,主栽品种相继完成染色体级的基因组组装^[5-15]。2023年,中国农业大学发表苹果栽培群体泛基因组研究成果,构建了系统的PAV/SV(Presence/Absence Variation)/(Structural Variation)变异图谱,识别出与果实颜色、抗病性等性状密切相关的结构变异区域^[8]。西北农林科技大学构建了涵盖74个芽变品种的高精度体细胞变异图谱,揭示了‘Fuji’芽变选种的基因组基础,解析了短枝型性状的遗传机制^[10]。

2024年,中国农业大学采用PacBio HiFi和Hi-C测序技术,对苹果砧木‘M9’‘MM106’构建了高质量单倍型基因组,系统解析了长串联重复、染色体倒位等复杂结构,为深入识别调控元件和重复基因簇提供了技术支持;该研究发现*Dw1*区域中的*DwTE*转座子能够抑制矮化砧木中*MdARF3*基因的表达,是‘M9’苹果砧木的致矮核心变异;同时,砧木特异性基因表达、砧穗mRNA传递机制等功能模块逐步与其基因组结构特征相结合,为揭示砧穗互作与非生物胁迫响应机制提供了新视角^[15]。

1.3 图形泛基因组构建及其在全属系统演化中的应用

近年来,苹果基因组研究的重心逐步从栽培种

内部的结构差异比对,拓展至整个苹果属的系统化图谱构建。2025年,中国农业大学利用PacBio HiFi和Hi-C测序技术,组装了覆盖30个苹果属物种的染色体级高质量参考基因组,并构建了图形泛基因组,首次系统呈现了苹果属的全基因组结构多样性与演化轨迹,发现苹果属起源可追溯至约5 600万年前的亚洲地区^[16]。苹果属经历的苹果族(Maleae)早期WGD(Whole-genome duplication)事件所产生的大量重复基因在后续的物种分化中被差异性地保留,影响基因组结构与功能的演变,伴随广泛的种间基因渗透,共同塑造了苹果属丰富的

遗传多样性。通过跨物种比对与结构可视化工具,鉴定出物种特异的结构变异,并开发了一套多基因组选择清除分析流程用于挖掘与驯化相关的关键基因位点,为培育抗逆苹果品种提供了重要的基因资源。多个研究团队正基于此图谱开展SV-GWAS(Genome-wide association studies)、跨物种群体分析、核心变异预测等工作,加速将演化信息转化为育种依据。

由此可见,苹果基因组研究已形成了从参考基因组构建、高质量组装到泛基因组建立、物种进化与重要性状解析相融合的研究体系(图1)^[1-22]。

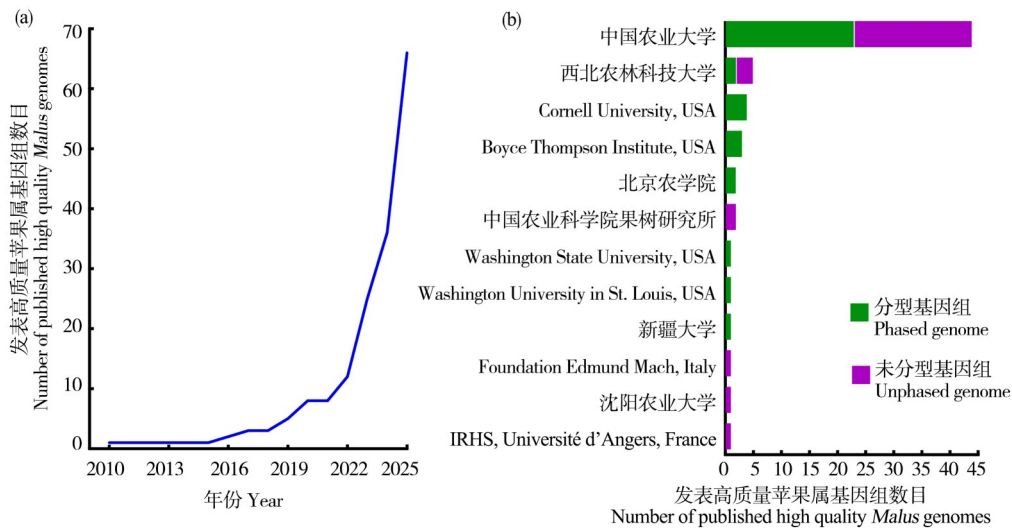


图1 苹果属高质量基因组发表年度趋势(a)及机构贡献分布(b)

Fig. 1 Annual trends of high-quality *Malus* genus genome publications (a) and distribution of institutional contributions (b)

2 多组学协同揭示苹果性状调控机制

2.1 表观组学揭示果实发育与品质调控机制

表观遗传调控作为连接基因组与表型之间的关键桥梁,正逐步显现其在苹果果实品质形成及逆境适应中的核心作用^[2,23-41]。例如,DNA甲基化可通过调控基因表达水平参与苹果果实发育、成熟及品质性状的形成^[2,23-36]。相关研究涵盖果皮色泽^[23-27]、果实大小^[2]、成熟^[28-29]、褐化^[30]及糖酸含量^[31]等多种性状,并在花芽分化^[32]、不定根发生^[33]、逆境响应^[34-36]等过程中也发挥重要作用。

在组蛋白修饰层面,Lü等^[29]发现H3K27me3在苹果乙烯生物合成基因和MADS基因区域呈现组织特异性的沉默修饰,在非成熟组织中显著富集,

而在成熟果实中则明显缺失,表明H3K27me3可能在果实成熟启动过程中发挥关键作用。组蛋白乙酰化修饰方面,Wang等^[28]报道,组蛋白乙酰转移酶(HAT)基因在成熟果实中表达显著上调,而部分组蛋白去乙酰化酶(HDAC)在未成熟果实中更为活跃,表明组蛋白乙酰化水平的变化在果实成熟过程中具有重要调控作用。同时,组蛋白修饰在抗旱等逆境响应^[36-38]过程中也具有调控功能。

此外,染色质重塑^[38-39]、m⁶A RNA甲基化^[40]等表观调控的作用亦在苹果中得到揭示。未来苹果表观组研究可进一步结合单细胞和空间组学分析、表观变异关联分析等技术手段,提升表观调控研究的时间-空间分辨率,并结合基因编辑等策略,为苹果品质提升和抗逆改良提供新手段。

2.2 代谢组学解析品质形成与胁迫应答的代谢机制

2.2.1 品质相关代谢物的动态变化与调控

代谢组技术已被广泛应用于苹果果实内在成分动态变化、采后贮藏机制等研究。例如,对‘Fuji’‘Granny Smith’等品种果实特定组织代谢谱的研究,揭示了糖类、有机酸和类黄酮等代谢物在果实发育或贮藏过程中呈现的动态积累规律及其对果实品质形成的影响^[41-44]。Kim等^[45]针对‘Fuji’等4个品种,研究了挥发性酯类、糖类、有机酸及部分醛醇等关键代谢物的差异及其对苹果风味的综合贡献。这些研究不仅揭示了苹果果实品质性状形成的代谢机制,也逐步构建起品质性状的系统代谢图谱,为精准育种和采后管理提供了数据基础和可量化指标。

2.2.2 胁迫响应与养分调控中的代谢组学应用

在非生物胁迫方面,Xu等^[46]与Yu等^[47]分别对‘寒富’‘长富2号’和‘Ralls’‘Fuji’品种在冷胁迫下的代谢响应进行分析,发现多种渗透调节物质与品种抗寒能力密切相关。Li等^[48]在‘ZC9-3’‘冀砧2号’中揭示了干旱胁迫下抗逆相关代谢物的差异积累特征;Liu等^[49]通过转录组和代谢组联合分析,解析了*MdPYL9*基因在介导干旱响应中的调控机制;Yang等^[50]以‘Red Fuji’为材料,探讨了果实在遭受采后冲击损伤后的代谢变化。在应对生物胁迫及与微生物互作中的代谢调控机制方面,Jing等^[51]整合代谢组和转录组数据,系统分析了‘M26’砧木接种丛枝菌根真菌(AMF)后根与芽的发育特征,提出AMF可能通过其效应因子、RNA或代谢物等直接影响地上部的发育。Yang等^[52]针对‘Red Fuji’果实在青霉侵染下的代谢响应的系统研究,明确了病原相关代谢物的调控路径与潜在作用机制。

在养分调控方面,‘CG-935’‘M9-T337’分别在氮胁迫下表现出独特的代谢重塑能力^[53-54]。Wang等^[55]基于‘Red Fuji’‘M26’和*Malus hupehensis*的比较研究指出,高氮处理可显著降低果实可溶性糖和黄酮类物质的含量。Sun等^[56]揭示了低磷条件下‘CG-935’根系代谢的适应性调节机制。这些研究表明,苹果在应对不同胁迫及养分变化过程中具有高度动态的代谢适应能力,相关代谢产物可作为抗逆性状选择的潜在生物标志物,也为根系性状改良和高效养分管理提供了理论依据。

苹果代谢组研究在机制解析和应用转化上仍

面临挑战。首先,大多数研究仍集中于果实等特定器官的“静态采样”,难以全面揭示代谢通路的动态变化和组织特异性表达模式。未来可借助空间代谢组和多时点动态采样等手段,构建苹果不同发育阶段和逆境条件下的高分辨率代谢图谱。其次,代谢组数据与功能验证之间缺乏高效联结,需通过关键酶基因编辑等手段确认调控因果关系。此外,代谢标志物的精准育种应用仍处起步阶段,构建代谢组驱动的早期筛选平台,并与QTL定位、表型数据库深度融合,有望加速苹果改良进程。

2.3 蛋白质组学解析发育调控与环境适应机制

2.3.1 果实品质与贮藏性能相关蛋白表达调控

蛋白质作为代谢调控与表型形成的直接执行者,其时空表达动态对于苹果果实品质形成和采后生理变化具有重要调控作用。蛋白质组学的引入,为果实营养、成熟、着色、软化与贮藏品质等关键性状的调控机制解析提供了重要线索。

在果实品质方面,Guarino等^[57]在‘Annurca’苹果上鉴定出果实中参与能量代谢与果实发育调控的关键蛋白,为果实发育机制的解析提供了线索。Li等^[58]通过对‘Greensleeves’的研究,识别了参与细胞分裂、糖代谢和激素应答等过程的核心蛋白,揭示了苹果果实发育早期的蛋白调控特征。Chen等^[59]通过蛋白质组学分析发现,苹果果皮着色过程中花青素合成相关蛋白显著上调,而MAPK4和MVK等蛋白下调,表明果皮着色受多级调控。Ferrario等^[60]则比较了不同品种的果实蛋白质组特征,提出疏果期去除的幼果中富含多酚类物质,可作为重要多酚资源。

在采后生理调控方面,Zheng等^[61]和Shi等^[62]分别对‘Golden Delicious’果实在乙烯处理和贮藏过程中的蛋白质组变化进行分析,识别出一批与细胞壁重塑、能量代谢及抗氧化相关的差异蛋白,强调了成熟诱导与贮藏过程中蛋白动态调控的重要性。Du等^[63]以‘Cortland’‘Red Delicious’为材料,解析果实虎皮病的蛋白质调控基础,发现该病害与抗氧化/氧化还原系统紊乱、苯丙素代谢异常密切相关。Xu等^[64]探讨了钙处理对‘Golden Delicious’苹果贮藏期果肉软化的影响,结果表明钙离子可通过调控细胞壁相关蛋白的表达,有效延缓果肉软化进程。这些研究揭示了苹果果实在不同成熟阶段与贮藏环境下抗氧化蛋白及激素调控蛋白的表达变化,为

品质提升和贮藏管理提供了重要蛋白质标志物与功能靶点。

2.3.2 发育过程与胁迫响应中的蛋白质组调控网络

蛋白质组学亦被用于探索苹果树体发育及其对生物、非生物胁迫的应答机制。Niu等^[65]对‘长富2号’花芽分化过程的蛋白质组分析,揭示了糖代谢在花芽启动中的关键作用。Zheng等^[66]通过蛋白质组学分析,发现BR通过调控能量代谢、细胞壁修饰及信号转导等过程,促进‘M9-T337’砧木的生长发育。Daniëls^[67]对‘M9’砧木的蛋白质组分析,发现多个与防御、细胞壁强化和信号转导相关的蛋白在对苹果黑星病的应答中起到关键作用。Luo等^[68]与Xu等^[69]则分别研究了‘Ambrosia’果实对低温冷藏和‘Red Fuji’果实对青霉侵染的蛋白质响应机制,指出应激环境下果实通过调节热激蛋白、病程相关蛋白及代谢相关酶类,实现对不良环境的缓冲与自我修复。

苹果蛋白质组研究的深入转化应用仍面临多重挑战。首先,蛋白翻译后修饰(如磷酸化、乙酰化、泛素化等)在调控蛋白稳定性与活性中的作用尚缺乏系统解析。其次,蛋白互作网络仍不完善,需结合信号转导通路分析,构建关键调控模块以揭示核心功能网络。此外,果树基因功能验证体系效率偏低,可借助瞬时表达系统与AI辅助的蛋白结构预测等手段,探索快速验证机制与精准干预路径,为苹果性状定向改良与分子设计育种提供有力支撑。

3 从性状挖掘到品种改良:组学赋能苹果分子设计育种

苹果传统育种存在效率低、周期长、过程不可控等突出问题。随着图形泛基因组和多组学技术的发展,苹果复杂性状的分子基础正在被系统揭示,为实现高效、定向且可预测的分子设计育种提供了理论依据和技术路径。

3.1 全基因组关联分析(GWAS)与多组学融合提升复杂性状定位效率

GWAS凭借其在自然群体中高分辨率定位变异的优势,已成为挖掘农艺性状关键基因的重要手段。然而,GWAS定位往往难以直接明确功能基因。为实现从“变异定位”向“功能解析”的有效转

化,研究者逐步引入多组学数据,通过数据整合与功能验证,系统揭示表型形成的分子机制。

3.1.1 GWAS在核心基因挖掘中的应用进展

近年来,基于大规模群体遗传变异数据,GWAS在苹果中已广泛应用于解析表型变异的遗传基础(图2)^[70-93]。Watson等^[70]在239份样本中鉴定出与萌芽期相关的*MdPRX10*基因。Urrestarazu等^[71]在1168份二倍体苹果材料中定位了开花期和成熟期相关位点,发现了位于第3、9、10和16染色体上的候选基因。在果实外观和质地性状方面,*MdLEA*、*MdERECTA*、*MdOFP4*和*MdOFP17*被证实与果形和果实大小密切相关^[73-74,78];多个MYB类转录因子,以及*MdNAP*、*MdABCG25*和*MdUGT*等基因则参与调控果重、果皮与果肉颜色以及褐变过程^[73,75-76,78-80,89];而果肉硬度主要与*MdNAC18.1*显著相关^[72,77-79]。果实酚类化合物、酸、糖和芳香物的GWAS研究揭示了包括*MdUGT*、*MdPAL*、*MdLAR1*、*MdMA1*、*MdTDT*、*MdSOT2*、*MdAAT1*和*MdLOX8b*等多个关键代谢基因^[75-76,80-84,90-91]。在抗逆性状方面,GWAS定位了与叶片蜡质相关的*MdHDG5*、*MdSHN1*和*MdRDR1*等基因^[85-86],并在苹果褐斑病、火疫病、黑星病和水心病等抗性研究中鉴定了多个关键调控位点和候选基因,包括*MdSWEET12a*等^[87-89,92-93]。这些研究构建了苹果复杂性状遗传调控的初步图谱,并为后续的功能验证、优异等位基因聚合和分子设计育种提供了候选基因资源和理论依据。

3.1.2 多组学整合驱动性状解析与功能转化

基于图形泛基因组与多组学数据的整合应用,研究人员正在逐步提升复杂性状解析的系统性与精度。如在苹果抗病研究中,通过整合图谱中的SV注释,识别出特异结构片段SCAB-R,定位于经典抗病基因*Rvi6*区域,证实其为由*M. floribunda*单倍型贡献的抗黑星病核心变异^[16];通过比较矮化砧木‘M9’与半矮化砧木‘MM106’基因组结构变异,结合RNA-seq与遗传分析,定位到调控株高的关键激素响应基因*MdARF3*^[15]。这种多组学联动的策略不仅提升了定位精度,也增强了对复杂性状调控机制的系统理解。

3.2 分子标记开发与精准聚合促进早期筛选

在苹果复杂性状解析不断深入的基础上,以分子标记为核心的辅助选择体系已成为推动早期筛

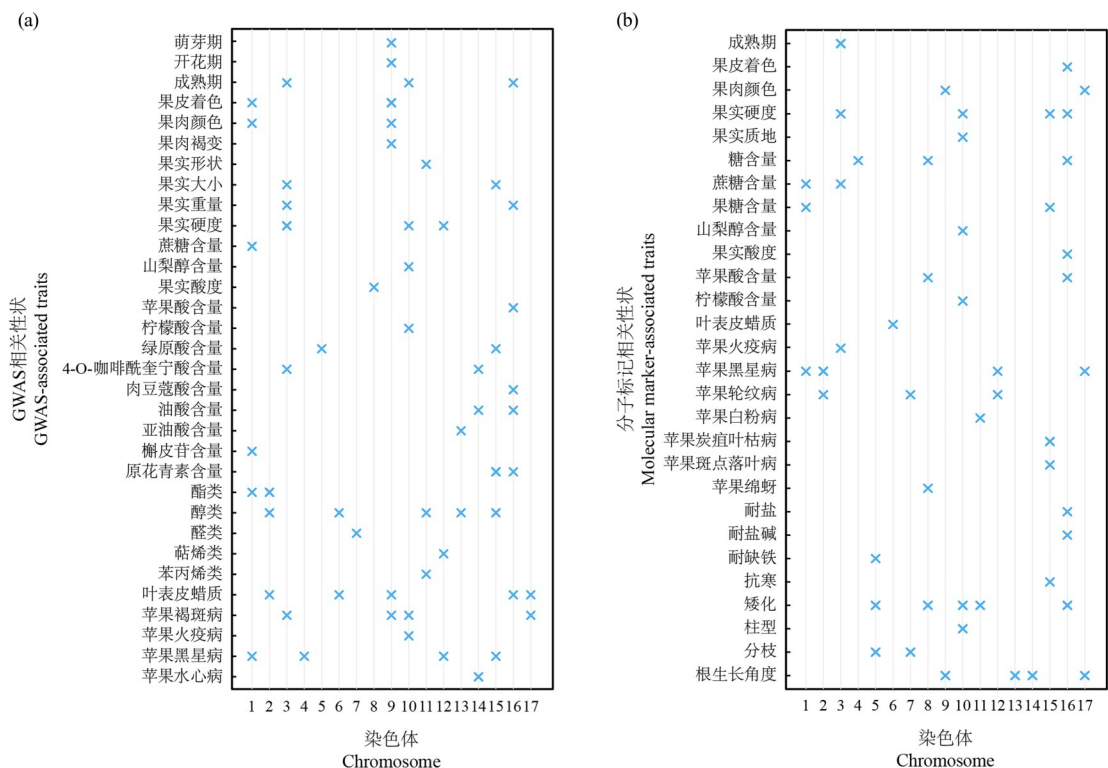


图2 苹果属GWAS(a)及分子标记(b)分析相关性状的染色体定位

Fig. 2 Chromosomal mapping of GWAS-associated traits (a) and molecular marker-associated traits (b) in *Malus* species

选与多性状聚合的重要手段,其技术路径正由单一标记辅助选择逐步拓展至基因组选择和育种芯片集成应用,构建起高效、智能的性状识别平台。

3.2.1 分子标记辅助选择(MAS)的应用拓展

MAS仍是当前苹果分子育种中应用最广泛、最直接的手段,特别适用于主效基因控制的性状,如抗病性等(图2)^[3,15-16,81,86,94-133]。组学数据支撑下的分子标记开发为苹果品种早期选择提供了技术工具^[15-16]。除了传统的单碱基核苷酸多态性(SNP)与插入或缺失(InDel)标记外,功能性结构变异(SV)正在成为分子标记的新资源。例如,针对果实着色^[3]、糖酸平衡^[98-101]等性状区域的SV位点,开发了KASP/CAPS等高通量分型标记,实现快速筛选与亲本配置,在苹果品质改良中展现出良好效果。

3.2.2 基因组选择(GS)在多性状聚合中的价值

GS正在成为复杂性状聚合的有效手段,通过整合全基因组标记信息,构建表型预测模型,即可对早期世代个体进行遗传潜力评估。研究已针对果实风味、成熟期和抗性性状建立GS模型^[134],结合组学数据中的PAV、SV变异,实现育种“前移”。GS与MAS的融合,已初步在苹果复杂性状的聚合

育种中得到应用。

3.2.3 育种芯片开发与集成应用

为提升标记应用效率与通量,结合多样性数据,研究人员已构建多套苹果专用育种芯片平台,并在实际育种流程中实现应用,有效支撑了育种群体的大规模基因型分析与早期精准选择,加快了优质多抗品种的创制进程。代表性进展主要有:(1)苹果全基因组SNP芯片,如“Apple480K”平台,整合高质量SNP位点,广泛应用于群体构建、GS模型训练与种质遗传分析^[135-136];(2)目标性状芯片,聚焦果实风味、抗病等关键性状,整合SNP、SV等多类型变异,已在多个育种群体中用于高通量基因型检测与材料筛选^[99]。

通过构建以功能标记为基础、GS建模为核心和芯片检测为工具的分子识别体系,苹果分子育种有望形成从基因定位、标记开发到高通量筛选的一体化体系,支撑复杂性状的高效聚合与定向选育。

3.3 基因编辑推动功能验证与定向改良

引入CRISPR/Cas系统极大加快了苹果基因功能验证与性状改良的速度,尤其适用于复杂背景下的单基因突变效应确认与精细调控区编辑。

目前已有多个苹果目标基因实现编辑并获得突变体(表 1)^[137-149]。例如,敲除 *MdPDS* 基因创制白化突变体,为基因编辑体系建立提供可视化标记^[137-140,144,147-149];敲除 *MdTFL1.1* 促进早花,加快育种世代推进^[137];编辑 *MdSPL6* 促进不定芽再生,有望解决遗传转化中组织再生难的问题^[145];

敲除 *MdDIPM* 能够降低火疫病感病性,有望减少病害产量损失^[141-142];敲除 *MdPGT1* 在不影响植物生长和叶片形态的同时降低根皮苷含量^[143]。未来,基因编辑的靶标可以逐步扩展至调控元件、增强子和可变剪接位点,实现对表型形成的精细调控。

表 1 苹果属基因编辑研究进展
Table 1 Genome editing advances in *Malus*

苹果属植物样本 <i>Malus</i> accession	目标基因 Target gene	目标性状 Target trait	参考文献 Reference
<i>Malus domestica</i> ‘Gala’	<i>MdPDS</i>	白化	[137-140]
	<i>MdTFL1.1</i>	早花	[137]
	<i>MdALS</i>	氯磺隆抗性	[138]
	<i>MdDIPM1</i>	苹果火疫病	[141]
	<i>MdDIPM4</i>	苹果火疫病	[141-142]
<i>Malus domestica</i> ‘Golden Delicious’	<i>MdDIPM4</i>	苹果火疫病	[141-142]
	<i>MdPGT1</i>	根皮苷含量	[143]
GL-3	<i>MdPDS</i>	白化	[144]
	<i>miR171i</i>	耐旱性	[144]
	<i>MdSPL6</i>	不定芽再生	[145]
‘M26’	<i>MdMADS15</i>	花发育	[146]
	<i>MdMADS221</i>	花发育	[146]
‘JM2’	<i>MdPDS</i>	白化	[147-148]
<i>Malus sieversii</i>	<i>MsPDS</i>	白化	[149]

4 挑战与未来展望

尽管苹果组学研究在图泛基因组、多组学整合、关键性状解析与分子设计育种方面取得了显著进展,但要真正实现“从基因发现到优异品种创制”的高效转化,仍面临多方面技术瓶颈与挑战。

4.1 当前面临的挑战

多组学数据整合难度大。不同苹果组学层次之间,如基因组、表观组、蛋白质组和代谢组,因数据格式、分析角度和时空动态特征存在较大差异,导致整合分析面临较高技术门槛。目前尚缺乏统一的分析流程和可通用的数据模型,难以实现面向复杂性状的系统解析与育种应用支撑。

组学数据与功能研究衔接不足。尽管苹果已积累了大量基因组、转录组、代谢组以及结构变异等数据资源,但真正进入功能验证并应用于性状改

良的基因仍属少数。复杂农艺性状往往受多基因协同调控网络的影响,同时又受环境因素干扰,使得从遗传变异到性状表达的因果关系难以明确建立,限制了关键基因的精准挖掘与利用。

表型数据获取能力仍显薄弱。相较于近年来快速增长的组学数据,表型信息的采集仍处于低通量、低标准化水平。诸如果实风味、质地和抗病性等关键性状,往往测量过程复杂、成本高且重复性差,尚未形成统一规范。这一短板严重制约了大规模材料的性状精准评估与关联分析,影响育种效率的提升。

基因编辑技术受限于转化体系瓶颈。目前苹果仅在少数品种和材料中实现遗传转化,且效率普遍偏低^[150],成为限制基因功能验证与基因编辑育种应用的关键障碍。缺乏稳定、高效、适用于多品种背景的基因编辑体系,以及可规模化推广的无外源

基因编辑策略,使得组学成果难以高效应用于新种质创制。

4.2 技术融合趋势与突破方向

人工智能赋能多组学整合与表型预测。针对组学数据来源多样且异质性强等整合难题,以及高通量、精准表型获取能力不足的瓶颈,人工智能(AI)和机器学习正展现出重要突破口,有望在整合图形泛基因组所提供的结构变异、基因表达和表观修饰等多维数据的基础上,构建高精度的表型预测模型,并用于复杂性状的遗传解析与后代筛选。特别是在缺乏精准表型测定的情况下,AI可通过图像识别、数据建模等手段提升表型数据获取效率,增强复杂性状的解析深度和分子设计育种的精准性与可操作性。

空间组学与单细胞技术研究拓展。空间转录组、单细胞转录组及染色质三维结构分析等前沿技术,正推动苹果研究从器官层面深入到细胞亚群和发育动态层面。引入时空维度分析,将有助于揭示果实发育、砧木致矮等过程中的关键细胞类型和调控网络,为复杂性状的精准调控与分子育种策略的制定提供新的技术支撑。

建立高效遗传转化平台与无外源基因编辑体系。亟需构建适用于‘Fuji’‘Gala’等主栽品种及‘M9’等主流砧木的高效、稳定遗传转化体系,为苹果基因功能研究和分子育种提供技术支撑。为克服外源DNA整合带来的产业化障碍,可探索多种无外源DNA编辑策略,如农杆菌介导的瞬时表达系统,操作简便,适合结合高通量突变体筛选平台使用;或采用RNP(核糖核蛋白)复合物直接递送策略,通常依赖原生质体等方式实现。上述策略的逐步完善与集成,将有助于推动基因编辑技术在苹果中的规模化应用。

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