

金柑属植物相关研究进展

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摘要: 柑橘是中国第一大水果, 其中金柑作为一种具有重要经济价值和科研价值的柑橘类果树, 广泛分布于广西、江西、湖南、福建和浙江等地。目前, 金柑栽培面积超 6.67 万 hm^2 。然而, 相比甜橙、蜜橘等类型而言, 对金柑的研究总体较为薄弱。近年来, 通过实生变异选种和芽变选种, 涌现了滑皮金柑、脆蜜金柑等新品种, 并成为明星品种。利用金柑无油胞突变以及野生迷你柑橘创建的 F_2 群体, 在短时间内解析了柑橘油胞形成的遗传基础和调控机制。这些新进展, 加上金柑比较耐黄龙病、树冠小以及果实连皮食用等特性, 逐渐引起人们的重视。本文梳理了金柑现有的相关文献, 旨在系统总结金柑的研究进展, 探讨未来金柑的产业发展方向。

关键词: 金柑; 演化; 遗传改良; 基因

中图分类号: S666.1

文献标志码: A

文章编号: 1009-9980(2025)10-2416-14

Research progress in kumquat

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Abstract: Citrus is the largest fruit crop in China. Kumquat, a small citrus fruit with important economic and scientific research value, is widely distributed across the Guangxi Zhuang Autonomous Region and Jiangxi, Hunan, Fujian and Zhejiang provinces of China. However, for a long time, kumquat has not received sufficient attention from researchers. Research on kumquat is generally less extensive compared to sweet orange [*Citrus sinensis* (L.) Osbeck], tangerine (*C. reticulata* Blanco) and other citrus species. The objective of this article is to review and summarize the research advance in kumquat based on published literature both domestically and internationally, systematically clarify the research achievements on kumquat and to figure out the strategic development directions for the kumquat industry. Advanced searches were conducted on China National Knowledge Infrastructure [Topic = (kumquat OR Fortunella OR Jinju) OR Title = Jindou] AND (Document Type = (Academic Journal or Dissertation)], followed by English topic searches on Web of Science (Title=Fortunella or kumquat, covering the period from 1983 to the present. Duplicate, non-accessible, or irrelevant documents were removed from the search results, which were then supplemented with additional literature from outside the databases, including previously reviewed works and those published in previous years. A total of 2524 Chinese documents and 130 English documents related to kumquat were retrieved. After screening for relevance, over 1000 documents (combining both languages) were retained. The following results were obtained through subsequent organization and analysis of these documents: (1) China is the original center of the *Fortunella*. Large-scale commercial kumquat plantations are concentrated in such regions as Rong'an and Yangshuo (Guangxi), Suichuan (Jiangxi), Liuyang (Hunan), and Youxi (Fujian). Additionally, wild

收稿日期: 2025-03-04

接受日期: 2025-05-22

基金项目: 国家现代农业(柑橘)产业技术体系(CARS-26); 中国工程院战略研究与咨询项目(2023-JB-02-02)

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kumquat populations persist in the mountainous areas of Southern Fujian, Southern Jiangxi, and Southern Hunan; (2) In China's major kumquat-growing regions, the cultivars from Rong'an of Guangxi and Liuyang of Hunan both originated from Suichuan of Jiangxi. Japanese cultivated varieties trace their lineage to Ningbo of Zhejiang. The European introduction occurred through British plant hunter Robert Fortune, who collected specimens in Fujian during the 19th century, subsequently facilitating the fruit's global dissemination; (3) The genus *Fortunella* comprises of six recognized species: Hong Kong kumquat (*F. hindsii* Swingle), Luofu kumquat (*F. margarita* Swingle; syn. golden jujube), Luowen kumquat [*F. japonica* (Thunb.) Swingle; syn. round kumquat], Meiwa kumquat (*F. crassifolia* Swingle), long-leaf kumquat (*F. polyandra* Tanaka), and longevity kumquat (*F. obovata* Tanaka). Of these, the Meiwa kumquat series dominates commercial cultivation, whereas *F. hindsii* represents a basal lineage within the genus. Notably, *F. hindsii* has become a model system for citrus transgenic studies due to its diploid ($2n=18$) genome and short juvenility period; (4) Research on kumquat cultivation mainly focuses on flower and fruit protection, prevention of fruit splitting, and extension of shelf life. Additionally, significant research is conducted on germplasm innovation strategies, including hybrid breeding. New varieties such as Hua-pi, Jinquzao, Guijingan No. 1, Guijingan No. 2 and Cui-mi kumquat (*Fortunella crassifolia*) have been developed through the exploration of bud-sport and chance seedling variation; (5) The kumquat (*Fortunella* spp.) is a plant with dual applications in both culinary and medicinal contexts. It has been traditionally utilized in herbal medicine for managing conditions. Being rich in nutrients, kumquats are also widely used as key ingredients in various processed foods, including preserves, candied products, and functional beverages; (6) The taxonomic status of the *Fortunella* remains under debate; however, an increasing number of studies support its inclusion within the *Citrus*, and the classification system of the latter is gradually becoming clearer; (7) The earliest documented study on kumquat (*Fortunella* spp.) in vitro tissue culture can date to 1982. Researchers successfully cultured young stem segments of the kumquat on MS medium, achieving seedling regeneration. Concurrently, studies revealed the high embryogenic potential of the Hong Kong kumquat (*F. hindsii* Swingle), with its explants readily forming embryogenic callus. Building on these findings, Huazhong Agricultural University acquired a unique monoembryonic *F. hindsii* accession and subsequently developed its stable genetic transformation protocol. By utilizing kumquat materials with a short juvenile period, researchers assembled the kumquat genome and identified key genes involved in citrus polyembryony (*FhRWP*), self-incompatibility (*FhS2-Rnase*), and oil gland formation (*CsLMII*). The past decade has witnessed transformative developments in kumquat science, with breakthroughs in cultivation techniques, processing technologies, genomic studies, and breeding innovation. The China Modern Agricultural Citrus Industry Technology System have been studying the genetic traits of *Fortunella* (kumquat) resources for over a decade. By leveraging the small tree size, short juvenile period, and unique oil gland-free mutant materials of kumquats, combined with multi-omics technologies, they successfully identified *CsLMII*, the key gene controlling oil gland formation. This breakthrough has elevated citrus research to a new level. However, research on kumquats still faces significant challenges. Future studies should leverage modern biotechnology and digital technologies to focus on exploring key areas including genetic enhancement, environmentally-friendly cultivation techniques, functional component development, and sustainable processing methods.

Key words: Kumquat; Evolution; Genetic improvement; Gene

金柑是柑橘大家庭的一员,在广西融安、阳朔一带,以及江西遂川、湖南浏阳、福建尤溪等地有较大面积的商业种植,合计面积约6.67万hm²(国家柑橘产业技术体系调研数据,未发表)。金柑产业成为乡村振兴的重要产业,致富一方百姓。长期以来,金柑未获得研究人员足够的重视,检索金柑的国内外文献发现,金柑受到的关注度较小,文献量远不及柑橘其他类型。近年来,由于脆蜜金柑(*Fortunella crassifolia* Swingle)品种的选育和成功种植^[1],金柑这名柑橘大家庭的成员逐渐受到业界和消费者的关注;近年来,脆蜜金柑因果实品质优异,其价格居柑橘乃至众多水果之首。在国家现代农业柑橘产业技术体系的持续支持下,研究人员利用金柑树体小、童期短以及无油胞突变等材料优势,结合组学技术,经过十多年努力,成功挖掘到调控油胞的关键基因 *CsLMII*,将柑橘研究提升到一个新的水平^[2]。

在中国知网以高级检索(主题=“金桔”OR“金柑”OR“金橘”OR“金豆”,检索类型为“学术期刊”和“学位论文”),在 Web of science 以英文主题词检索(Title=‘*Fortunella*’ or ‘*kumquat*’),年限 1983 年至今,分别检索出与金柑相关的 2524 篇中文文献和 130 篇英文文献。剔除重复、无效、无关文献,并加入所阅文献中引用的数据库外往年文献,共计 1000 余篇中英文文献。本文对国内外金柑研究文献进行了梳理和综述,以供同行学者借鉴和交流。

1 金柑的历史起源

1.1 金柑历史起源与古籍记载

中国是金柑属植物的起源中心^[3-5]。如今,在闽南、赣南以及湘南等山岭中分布着野生金柑群落。关于金柑最早的文献记载可以追溯到3世纪,三国时期吴国人沈莹《临海水土异物志》(公元3世纪)记载“鸡橘子大如指,味甘,永宁界有之。”其中所言鸡橘子即当今的金柑,永宁位于今浙江台州、温州一带。同时期的西晋郭义恭的《广志》、张华的《博物志》等古籍中对金柑的果实形状、开花习性也有简要记述。唐宋时期,金柑栽培已较为普遍^[3]。如唐段公路《北户录》记载了金柑的风味“和皮而食,滋味绝佳”,宋韩彦直《橘录》记载了山金柑与栽培金柑的区别:“金橘(山金柑)生山径间,比金柑(栽培金柑)更小,形色颇类亦名山金柑。”明清时期的金柑相关记载则更为丰富,李时珍《本草纲目》详细记载了金柑

与山金柑的形态,还提到金柑“主治:下气快膈,止渴解醒,辟臭”的药用价值。此外,清翁长祚的《花历百咏》、高士奇的《北墅抱瓮录》、陈淦子的《花镜》都对金柑特征进行了描述。新世纪以来,华中农业大学研究团队在武夷山脉、罗霄山脉、南岭山脉等地开展了较为系统的野生金柑和农家金柑属植物的调查研究,发现和收集了一大批不同类型的材料,包括挖掘到的单胚山金柑类型^[6-7]。

1.2 金柑的传播

如今中国各大金柑主产区的栽培金柑,或自古有之,或引自他处,在历史文献记载中,同样有迹可循。宋韩彦直《橘录》“金柑出江西,北人不识,景祐(1034—1038年)中,始至汴都,因温成皇后嗜之,价遂贵重”,可见当时金柑已经在江西广泛栽培,并开始闻名京城,距今已近千年^[8]。据融安县志记载,广西融安金柑系清朝乾隆年间,1758年从江西省吉安府龙泉县(今遂川县)引进^[9],迄今已260多年历史。湖南省金柑早在200余年前即被《平江县志·艺文篇》记载为皇宫贡品“平邑瓮江金橘已贡朝上,个大籽少,味甜为之上品。”且据调查,湖南各地栽培金柑,如浏阳金柑、平江河东金柑以及桂东圆金柑都来源于江西遂川^[10]。浙江宁波地区金柑栽培历史已有400多年^[11],据史料记载,最早可追溯到明嘉靖年间(1522—1566年),《浙江通志》“宁波金豆橘形似豆,味甘香胜于大橘。”福建尤溪金柑则最早在明朝崇祯《尤溪县志》(1636年)物产篇中有记载“金橘实长曰金枣、圆曰金橘”^[12]。此外,日本广为栽培的金柑引自中国已无争议,引种时间曾存在较大争议,徐建国与林大盛对宁波金柑东渡日本进行了详细的史料考证,并确认1826年宁波金柑首先由中国的浙江宁波传至日本静冈^[13-14]。清道光年间1849年,植物猎人罗伯特·福琼(Robert Fortune)到我国浙江、福建采集植物材料,将罗浮带往欧洲^[15],这也标志着金柑作为一种重要的柑橘类水果由此开始在全球传播。

2 金柑的类型与特征

金柑是一种小型的柑橘类水果,属于芸香科(Rutaceae)柑橘亚科(Aurantioideae)柑橘族(Citreae)柑橘亚族(Citrinae)真柑橘果树组(True Citrus Fruit Trees)中的金柑属(*Fortunella*)。

金柑的类型通常包括6个种,分别是山金柑(*F. hindsii* Swingle)、罗浮(金枣)(*F. margarita* Swing-

le)、罗纹(圆金柑)(*F. japonica* (Thunb.) Swingle)、金弹(*F. crassifolia* Swingle)、长叶金柑(*F. polyandra* Tanaka)和长寿金柑(*F. obovata* Tanaka)^[3,11]。此外,还有山金柑的一个变种,名为金豆(*F. venosa*),其与山金柑在中国湖南、浙江、广东、江西、福建等地的山野中仍有野生分布^[6,16]。罗浮金柑和罗纹金柑作为少有的栽培类型,在福建长汀有少量分布^[17]。金弹包括了目前中国主要的金柑栽培类型,遍布全国各大金柑产区,如众所周知的融安金柑和阳朔金柑等^[18]。栽培金柑果实外观橙色或黄色,外形小巧,直径2~5 cm。果皮光滑,分为含油胞与无油胞2种类型,香气浓郁,全果可食,果肉酸甜可口。除鲜食外,金柑常被用于果脯、果酱、果酒等原料,在生活中受到广泛欢迎。山金柑则是金柑中的一个较为原始类型,相比栽培金柑植株更矮,果型更小,果实颜色更深。值得一提的是,山金柑由于突出的早花、矮化和短童期等生物学特点,近些年备受关注^[6,19-20],尤其是单胚山金柑的发现,因其具有易于自交和杂交的特点,已作为柑橘模式材料投入实践^[7,21]。此外,有关不同金柑类型详细特征的描述,在不少文献与著作中已有详细记载^[16,22]。

3 金柑主栽类型分布及品种选育

3.1 我国主栽金柑类型及分布

各类型金柑中除长叶金柑分布在海南岛等热带地区外,其余主要分布在亚热带地区^[3-4],包括江西的遂川县,浙江的北仑区(原镇海县),湖南的浏阳县,广西的融安县、阳朔县,福建的尤溪县等^[23]。中国金柑主产区包括广西的融安、阳朔,江西的遂川,湖南的浏阳、蓝山,福建的尤溪及浙江的宁波等地,均以金弹类型为主。由于历史原因与地域差异,在各大产区的金柑形成了具有各自地域色彩的名字,如融安金柑、遂川金柑、宁波金柑、尤溪金柑、浏阳金柑、蓝山金柑^[24]等。

3.2 新品种选育

随着地方实生变异选种、芽变选种等工作的开展,近年来不少金柑资源新类型得到挖掘,涌现出了滑皮金柑^[25]、金秋早^[26]、桂金柑1号^[27]、脆蜜金柑^[1]等新型品种,我国的栽培金柑品种类型愈加丰富。因果皮光滑、油胞稀少、全果可食等特点而出众的滑皮金柑,是1981年科技人员在融安县大将镇发现的融安金柑实生变异,也是根据已有记载的最早审定的

金柑新品种^[28-29]。同样是融安县大将镇的金柑实生变异优株还有富圆金柑^[30],表型与滑皮金柑近似。继而在滑皮金柑优良资源的基础上进一步定向筛选,获得一自然芽变突变体,相比于滑皮金柑表现出果实体积更大、单位面积油胞数更少、无核、多汁,风味浓郁,可食率更高等特性,命名为脆蜜金柑^[31-32]。华中农业大学研究团队通过正向与反向遗传学方法,揭示了滑皮金柑无油胞表型源于一段89 kb基因组片段的缺失。该缺失片段含有*CsLMII*基因,其缺失影响油胞的形成。无油胞属于隐性突变,与有油胞(油皮)的金柑杂交后代 F_1 表现为有油胞,自交后代 F_2 油胞有无呈典型的孟德尔性状分离比^[2]。油胞减少后,果实可溶性固形物含量(TSS)增加2°(白令度)^[25,32]。最近,随着对脆蜜金柑栽培技术的掌握,特别是坐果技术的突破,其产量显著提升,并已实现批量上市。因其独特的风味深受市场的青睐,价格位居柑橘品种之首,田间收购价可达40元·kg⁻¹,出口海外市场,每磅售价接近20美元。油胞数量的大幅度减少导致植株抗虫性能减弱,害虫更喜欢取食其叶片,果实也引来蜗牛和鸟类取食,成为栽培管理中的一个难点。通过实生选育,培育出若干不同熟期的金柑新品种,早熟金柑品种桂金柑1号和晚熟金柑品种桂金柑2号均于广西的阳朔县金柑果园选育^[27,33],福建省尤溪县选育出早熟金柑金秋早^[26]。同时,无核金柑新品种的选育工作也在进行^[34-35]。

4 金柑的栽培与育种研究

金柑在中国栽培历史已超过1600年,林大盛等^[15]在金柑栽培史考一文中对我国金柑的栽培历史进行了详细的考证。如早在公元15世纪,明朱权撰写的《暇仙神隐》记录了金柑的栽培过程,包括播种、栽植、用肥等技术。随着时代发展与科技进步,相关研究更加细致全面,涉及生长特性、栽培模式与种质创新等诸多方面。

生长特性上,崔德珍^[36]利用石蜡切片染色观察,将金柑花芽形态分化分为了叶芽期至子房形成期等7个阶段,后人在此基础上加深了花芽分化机制及分化过程与营养成分等关系的研究^[29,37-38]。基于大量田间观测数据,结果显示,结果母枝上以第一次花所形成的果实坐果率最高,但同时其落果、裂果量也最大^[39-41]。因此通过栽培模式保花保果与防治裂果成了近年研究的重点。覆膜避雨栽培技术防裂果效

果显著,最早应用于阳朔金柑产区,其后推广至全国并逐步形成配套的综合栽培技术^[42]。此后又探索出结合留树保鲜的避雨栽培技术,在保持较高营养品质的同时,将果实采收期延长2~3个月^[43-45]。相较于这些易操作的管理方式,一些较高投入的管理模式则在部分产区实施,如通过花前施肥提高首批花的质量,疏除其余批次花来提高坐果率,这在脆蜜金柑生产栽培中尤为常见^[40-41]。随着消费者对果实品质要求的不断提高,果实套袋、弯枝技术等更加精细化管理的栽培方法也正在被应用^[46-47]。同时新技术与大数据结合的遥感技术,也通过物种分布模型预测金柑气候适宜区,助力金橘栽培的发展^[48-49]。

在栽培金柑种质创新方面,受限于以多胚为主难以杂交的生物学特性,除金柑杂种四季橘与长寿金柑属于偶然的自然杂交外^[50-51],当前金柑新品种主要来源于自然芽变与实生变异。芽变新品种脆蜜金柑属于混合多倍体变异,其染色体倍性具有不稳定性,因而容易产生变异^[52]。因此,还需发掘可用于人工杂交的金柑材料。除已知单胚山金柑外,对主要栽培金柑材料的胚性研究表明,罗纹金柑表现出较强的单胚性,或能作为杂交母本应用^[53]。同时发现,金柑在去雄不授粉条件下仍能坐果,表现出单性结实特性^[38],使其在不利气候发生时,也能在一定程度上保证坐果量;此外,金柑的杂交亲和性比自交亲和性更强,有利于金柑杂交育种^[54]。

5 金柑采后与加工研究

金柑果实的采后与加工研究主要集中在果实的分级、贮藏保鲜和产品加工三个方面。目前我国金橘主要用于鲜食和食品加工^[55]两大领域。金柑果实分级仍然以人工分选为主,运用机器视觉提取图像进行自动分选的研究正在推进^[56-57]。在融安金橘产区,已实现了从分拣到包装的自动化分选系统落地,大大提高了效率。分级后的贮藏保鲜研究聚焦在保鲜方法的改进,表现为新型保鲜剂配方的开发,如将山苍籽精油^[58]、龙蒿精油^[59]与壳聚糖复配以降低水分流失量,并结合生长调节剂^[60]、次氯酸钙^[61]和鞣花酸溶液^[62]浸泡处理,均可延缓品质下降^[63-64]。再结合单果包装和纳米复合膜等新型包装材料的应用,又进一步延长了保鲜期^[65]。此外,金橘加工已不限于传统的金橘果脯、果汁、果酒等食品的开发^[66-67],精油的提取也成为提高经济效益的重要途径。在不断地

探索中,金橘精油提取工艺得到了逐步改善,主要集中在传统水蒸气蒸馏法的优化、亚临界萃取技术的应用以及提取产物的分析与应用等方面^[68-70]。这些技术的综合应用为金橘的长期保鲜提供了有力支持,同时也吸引了更多研究者对其果实品质和营养成分的探索。

6 金柑的主要营养及功能成分研究

金柑果实富含维生素、氨基酸、矿物质等多种营养成分,以及大量贮存于果皮中的芳香油^[71-72],其果实品质的研究主要集中在营养成分的品种差异及功能特性等方面。不同品种金柑在果实品质和营养成分上存在显著差异^[32,73],传统金柑果皮较软,油胞密集,味微苦;而滑皮金柑和脆蜜金柑因果皮较硬、油胞少、辛辣味弱等特点,具有易贮藏、口感佳等优势,深受消费者青睐,成为金柑品种的新宠^[73]。值得一提的是,金柑果皮上的油胞会带来苦味,其分泌的精油中化合物种类丰富,有百余种,以柠檬烯为主,富含黄酮类功能性物质^[74],但其精油所含化合物的种类和含量受到品种和提取方法的影响^[75-78]。基于有油胞和无油胞金柑的杂交材料,最近关于油胞形成的两个关键基因 *CsDRNL* 和 *CsLMII* 被挖掘,并发现其下游的 *CsMYC5* 基因调控了油胞的后期成熟与其内精油的生成^[2],这为提升金柑类果实鲜食品质和增加甜橙、柠檬等精油产值提供了重要理论依据。

在功能特性研究方面,《本草纲目》记载金橘为药食同源植物,具有下气、止渴、解醒等功效,具体功能物质并不清楚。近现代研究中,金柑中的柠檬苦素^[79]、多糖类^[80]、酚类^[81]与类黄酮^[82]等物质获得越来越多的关注,并被认为其在抑菌抗氧化、降血脂、抗癌和抗病毒等方面具有重要作用。因此在临床中,金柑也作为药材用于治疗消化、泌尿和呼吸系统疾病,可单独使用或与其他药材组成复方制剂^[83-85]。金橘药材图谱绘制完成后,对其质量控制也有了一定的参考^[86]。此外,在化妆品、植物药和食品工业中,金柑具有的潜在应用价值亟待探索^[78,87]。

7 金柑属系统地位与属内分类研究

7.1 金柑属系统地位的争议

金柑属与柑橘属(*Citrus*)亲缘关系较近,二者杂交亲和性高,导致金柑属的分类困难,其分类地位和系统进化一直是植物分类学中的热点问题^[88-89]。早

期研究中, Swingle^[90]在1915年首次将金柑确立为独立于柑橘属的果树,这一观点也得到了田中和曾勉等学者的认可,并在《中国果树志-柑橘卷》中被引用^[91]。而在《中国植物志》(*The Flora Reipublicae Popularis Sinicae*)中编者则将金柑属纳入柑橘属,并将传统金柑视为柑橘属下的一个种,命名为 *Citrus japonica* (Thunb.) Swingle^[92]。近年来,随着分子生物学技术的发展,叶绿体基因组和核基因组的研究为金柑属的分类提供了新的视角。基于叶绿体基因组 cpSSR 标记与基于核基因组的分子标记得到了不同的结果,一方面许多学者坚持认为金柑属应被视为独立的属^[93-96],而另一方面则将金柑属归入柑橘属的一个种^[88,97],近年来,中国科学院武汉植物园的研究进一步认可了这一观点^[98]。直至最新的全基因组遗传关系和杂交生育力评估,表明金柑属与柑橘属在基因层面具有一定的相似性和同源性^[99]。

7.2 金柑属属内起源与分类的争议

金柑属内部种类划分经历过较大争议,主要在于部分种的定位问题以及杂种的认定。早期, Tanaka^[100]根据金柑的形态特征,提出将金柑属进一步划分为金柑亚属(包括罗浮 *F. margarita*、金弹 *F. crassifolia*、罗纹 *F. japonica*) 和山金柑 (*F. hindsii*)。Swingle^[101]推测金弹起源于罗浮和罗纹的杂交或与柑橘属的回交,不具有种的地位。但是这得到了 Zhu 等^[18]的否定,并重新证明罗纹具有罗浮和金弹的杂交遗传背景。另有学者基于 RAPD 和细胞质分析,提出了金柑混杂物 (*F. margarita complex*) 的概念,认为金柑属只包含山金柑和 *F. margarita complex* 两个真实物种^[51],其后基于 CMA 核型分析结果也提供了支持^[102]。Zhu 等^[18]利用叶绿体位点、核微卫星 (nSSR) 和基因组单核苷酸多态性 (SNP) 数据进行系统发育和群体分析,否定了 *F. margarita complex* 的概念,并视栽培金柑(罗浮、罗纹、金弹)为独立物种,这也是学界对金柑的主流认识。此外,被认为是金柑近亲的四季橘与长寿金柑,已被证实是金柑与橘的杂交后代^[50-51, 102]。而金豆作为山金柑的变种^[16],在形态上与山金柑有显著差异,如株高更矮、果实更小,分布范围更靠北,且与罗纹存在显著差异^[103],不断有研究从孢粉学、分子生物学的角度为金豆作为独立种地位提供了新的支持^[98, 104]。

尽管金柑属的分类地位存在争议,但随着分子生物学技术的发展,越来越多的研究证实了金柑属

与柑橘属具有较近的亲缘关系,因此金柑属的研究对柑橘属其他物种研究具有重要的参考价值,这在基因功能分子机制研究中有具体表现。

8 金柑在转基因与基因挖掘中的利用

金柑最早于1982年用于离体培养,利用金柑嫩茎诱导出金柑幼苗^[105],山金柑十分容易诱导胚性愈伤组织^[9]。后续研究在再生体系建立、再生效率提升等方面有了更多的尝试^[106-108]。2007年金柑转基因首次被报道,转化效率达到3.6%^[109]。然而,直到单胚山金柑种质资源被发现,金柑转基因研究才真正迎来了浪潮。

自2009年以来,华中农业大学收集了闽南、赣南以及湘南等地野生山金柑种质资源,包括珍贵资源单胚山金柑^[6, 20]。后续研究在此基础上,构建了山金柑遗传转化体系并开展了大量功能基因挖掘工作。通过山金柑单多胚杂交群体,定位到多胚性关键基因 *FhRWP*。多胚品种中,转录因子 *FhARID* 能特异性地结合 *FhRWP* 基因启动子区域的 MITE (微型反向重复转座元件) 片段,使其高表达而表现多胚性状。基于此开发了与多胚性状完全连锁的分子标记 *mite_p1*, 该标记可有效区分柑橘单胚和多胚品种^[110-111]。最新研究进一步揭示了多胚品种 *FhRWP* 基因启动子 MITE 区域的染色质开放水平发生改变,其上游转录调控可能需要 *FhARID* 和其他调节因子的协同参与^[112-113]。同时,从单胚山金柑连续自交获得的 S3 代群体中筛选出高纯合材料 S3y-45^[21],进而测序成功组装了山金柑基因组 1.0,并基于 CRISPR/Cas9 系统将山金柑作为模式材料使用,可对目标基因进行 1 bp 的插入或缺失,显著提高了转化效率^[114]。得益于此,山金柑高转化株系得以筛选^[115],并尝试通过利用山金柑内源启动子 U6 来提高基因编辑效率^[116]。

随着基因组测序技术的不断进步和组学研究的深入,山金柑的染色体水平基因组成功组装^[117],更多未解的机制解析有了更高质量的参考。柑橘自交亲和性机制的研究,基于山金柑自交亲和 (SC) 与自交不亲和 (SI) 杂交群体,发现 SC 关键位点位于 1 号染色体 286.6 kb 区间,其内 *FhS2-RNase* 基因启动子上游存在一个 786 bp 的 MITE 转座子插入,导致 SI 转向了 SC,去除 MITE 后,SI 表型也随之恢复^[118],揭示了自交不亲和丧失的内在机制。此外,还有大量

研究聚焦在金柑花器发育^[119-121]、果实转色^[122-123]、果形形成^[124]、蔗糖合成通路解析^[125-126]、类黄酮积累模式解析^[127]以及金柑的抗病性^[128-129]、抗冻性^[130-131]与耐盐性^[132]等机制解析方面。这些基础性研究将有力推动金柑这一宝贵资源在产业中的广泛应用。

9 讨论和展望

21世纪以来,中国柑橘产业发展迅速,金柑作为一种具有重要经济价值和科研价值的果树,在起源传播、种质创新和基因挖掘等多个领域取得了显著进展。高品质金柑新品种脆蜜和早熟金柑金秋早的选育,拓宽了金柑市场;避雨栽培和留树保鲜管理模式的应用,延长了金柑果实的鲜果期;金橘酒、金橘片和金橘精油的开发,增加了金柑产业的附加值;分子生物学和基因组学的发展,让金柑属系统地位和属内分类越来越清晰。尤其是单胚山金柑材料的发现及其作为柑橘转基因模式材料的使用,为金柑乃至柑橘的分子育种和功能基因挖掘提供了新的工具和思路。总体而言,比起甜橙和蜜橘等其他柑橘类型,金柑不论在基础研究还是基因功能研究方面,广度和深度仍不足,今后可从以下几方面进一步研究。

其一,充实金柑地理起源与演化路径的科学证据。关于金柑的起源与传播,史料记载之详细,表明了中国南方地区悠久的金柑栽培历史,也提供了金柑属植物可能最早起源于中国的历史证据。然而,更多的科学证据还需要进一步挖掘,今后可加强野生金柑资源的调查与收集,进一步确定金柑的原始分布区域,通过整合现代分子生物学技术与历史证据深入探索金柑在中国的传播路径。

其二,加强金柑的功能成分和药用价值研究。在金柑的种质资源利用领域,现有研究多集中在保鲜和加工技术的改进上,附加产品也主要局限于金橘类食品。虽然大量研究表明金柑中富含功能性物质类黄酮、柠檬苦素等,并可用于临床研究,但是现有研究局限于果实的利用,且当前技术还无法对其内功能性物质进行大批量高纯度提取。民间中医将山金柑的根、叶、果作为药材治疗感冒、胃痛及黄疸型肝炎等多种疾病,但目前尚未有山金柑根部药用价值的相关报道。金柑作为药食同源植物,其潜在的药用价值有待进一步开发。未来可对金柑中功能性成分高效提取方式进行改进,还可通过与食品科

学、营养学和医学等多学科的交叉融合,深入挖掘金柑在健康食品和药用领域的潜在价值,这不仅能够显著提升金柑的附加值,更能为现代医药和健康产业开辟新的资源和发展方向。

其三,推进金柑种质资源创新。金柑的童期短、抗冻性强和耐黄龙病等是其重要特征,在新品种选育和优质功能基因挖掘上具有较大潜力。尽管CRISPR/Cas9基因编辑技术在金柑中的成功应用为分子育种提供了新的思路,并揭示了金柑多胚性状的关键基因,但金柑的多胚性、单性结实等生物学特性限制了杂交育种的效率,且现有的基因组资源和转化技术仍处于发展阶段,难以满足快速育种和功能基因验证的需求。在滑皮金柑与脆蜜金柑这两个品种选育和种植推广之前,我国主栽金柑果型较为单一,且普遍偏大。而山金柑虽属小果型金柑种质,但其果肉或酸涩,或可食率低,并不适宜鲜食。未来的研究可着重关注栽培金柑的果型与口感品质的创新,这不仅能丰富鲜食金柑的种类,还能借助其植株矮小等特点,推动柑橘省力化的栽培模式发展。此外,在现有材料基础上,探索更高效的转化材料和转化模式的同时,还应进一步加强金柑野生资源的收集保存,以丰富金柑种质资源库,并利用金柑材料进行属间杂交和远缘杂交创制新型品种和优良砧木类型。

综上所述,金柑的研究近年来取得了快速进展,但仍面临诸多挑战。未来研究需要利用现代生物技术和数字技术,在遗传改良、绿色栽培、加工工艺和金柑功能成分等方面进行深入探索,以加快研究进程。由于金柑特殊的生物学特性,即个体较小、新梢容易成花,以及比较耐黄龙病等,是未来柑橘产业实现产品优质功能化、生产省力化、智慧化和绿色化发展的理想类型。

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