

大豆低聚糖种质筛选及遗传研究进展

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摘要:大豆低聚糖是重要的可溶性碳水化合物,约占大豆籽粒干重的10%,包括蔗糖、水苏糖、棉子糖等,与种子的耐储性及耐脱水性相关,还对豆制品的品质与口味产生影响。大豆种质资源中低聚糖含量存在基因型差异,积累过程除受合成途径中多种酶活性、稳定性的影响,更受到多基因调控。文章综述了特异低聚糖构成种质资源筛选、低聚糖遗传及相关QTL研究,以及代谢途径及相关酶基因的研究,初步了解大豆低聚糖的遗传机制及相关基因,利用这些基因可开发功能标记,为分子辅助育种奠定基础,为特用大豆育种提供有益信息。

关键词:大豆低聚糖;种质资源筛选;遗传;相关QTL;相关酶基因

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Research Progression Germplasm Screening and Genetic with Oligosaccharides of Soybean

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Abstract: Soy oligosaccharide is a kind of soluble carbohydrates, accounting for about 10% of the dry matter weight in soybean, mainly including stachyose, sucrose, raffinose etc. Soy oligosaccharides relate to the desiccation-tolerance and soybean storability of soybean seed, and also affect quality and taste of bean products. Oligosaccharides content is different with soybean genotypes. The oligosaccharides is regulated by enzyme activity, substrate specificity, protein stability and polygenes. This paper highlights recent advances in the studies of selecting oligosaccharides of soybean germplasm, genetic and QTL of related oligosaccharides, and metabolic pathways of oligosaccharides and related enzyme gene. Genetic mechanism and related genes of soy oligosaccharides are realized through this article. Developing functional markers for soy oligosaccharides related genes, lay a foundation for molecular assisted breeding and provide useful information for soybean breeding.

Key words: Soybean oligosaccharide; Germplasm screening; Related QTL; Related enzyme gene

大豆低聚糖是籽粒中可溶性碳水化合物的主要成分之一,约占籽粒干重的10%。主要组分为蔗糖、水苏糖和棉子糖,此外还含有少量的葡萄糖和果糖^[1]。水苏糖与棉籽糖对人体具有重要的生理功效,可促进双歧杆菌增殖,提高机体免疫力,调节脂肪代谢,降低血压等^[2]。近年来的研究表明低聚糖代谢在植物生长发育、逆境胁迫反应中也发挥重要作用。其在成熟种子中积累,与种子的发芽率、耐贮性和脱水耐性密切相关^[3],其含量与组成在种质资源中存在着显著差异,高蔗糖低水苏糖大豆适合进行豆腐加工^[4],低蔗糖高水苏糖大豆适于进行大豆低聚糖加工^[5-6]。

目前,已开展大豆低聚糖资源筛选及分子遗传机制研究^[7-8],其代谢途径已被解析,相关酶基因已被克隆^[9-11]。水苏糖合成酶(STS)基因与肌醇-1-磷

酸合成酶(MIPS1)基因是控制蔗糖、水苏糖含量的重要酶基因,STS或MIPS1的突变型都可产生高蔗糖低水苏糖、低棉子糖的表型^[10-13]。但大豆低聚糖储存在籽粒中,涉及蔗糖从“源”到“库”的运输,由多基因调控,分子遗传机制复杂^[14]。本文通过概述大豆种质资源低聚糖含量与构成研究,探讨了低聚糖遗传机制及相关QTL定位,以及代谢途径及相关酶基因的研究,旨在为大豆低聚糖相关研究提供参考。

1 大豆低聚糖种质筛选研究进展

20世纪70年代,国外学者首先开展了大豆种质低聚糖含量研究。Hymowitz等^[15]测得196份大豆种质的蔗糖含量范围为1.5%~10.2%,棉子糖含量范围为0.1%~2.1%,水苏糖含量范围为1.4%~

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6.7%。Kerr^[16]和Neus^[17]通过测定数千份种质的低聚糖含量,筛选到2份高蔗糖、低水苏糖的材料PI200508和VS99-5098,蔗糖含量分别高达9.4%和11.2%,水苏糖含量为0.64%和0.14%。PI200508现已成为提高蔗糖含量,降低水苏糖含量特用大豆选育的骨干亲本。VS99-5098是加工豆腐专用的优质品种。Hou等^[18]测得引自28个国家241份种质的蔗糖含量范围为0.16%~9.54%,水苏糖含量范围为0.02%~6.96%,获得7份特异大豆低聚糖组分种质。其中PI243545为高蔗糖种质,Jack为高葡萄糖、果糖种质,V97-3000为高水苏糖种质,PI200508、V99-5089、PI424061B及PI424089为低水苏糖种质。

王曙明等^[19]分析了181份吉林省不同地区大豆种质的低聚糖含量,低聚糖、棉子糖和水苏糖含量的变异范围分别为2.6%~6.7%、0.3%~1.8%和2.1%~5.1%。研究同时表明,不同地区种质间低聚糖含量差异没有明显的规律性,低聚糖含量的高低与产地无关。宋志峰等^[20]测得500份吉林省种质的低聚糖含量,低聚糖总量范围为7.73%~13.46%,超过12%的品种(系)有49个,蔗糖含量范围为3.42%~8.27%,棉子糖含量范围为0.41%~1.37%,水苏糖含量范围为3.23%~4.87%。与国外学者测得种质低聚糖含量相比,国内已鉴定种质的蔗糖、水苏糖含量变幅较小,未筛选到高蔗糖、低水苏糖含量的种质。

近年来对专用大豆营养组成的研究不断深入。Rao等^[21]测得台湾地区采用大豆葡萄糖含量变幅为0.74%~1.37%,其中菜用大豆品种Hutcheson葡萄糖含量最高,但其百粒重、产量相对较低,还需进一步品种改良。Li等^[22]对30份菜用大豆进行营养品质分析,蔗糖含量均值为4.30%,变幅2.11%~9.37%,遗传变异187%。Yoshikawa等^[23]研究了15个纳豆品种,包括3个优质、9个中等、3个劣质纳豆品种的低聚糖含量,优质纳豆组的低聚糖含量显著高于其他两组。Sharma等^[24]分析了百粒重8.7~11.1g小粒大豆的营养组成,蔗糖含量变幅为5.6%~11.8%。与常规大豆相比小粒大豆蔗糖含量相对较高。Yuan等^[25]对大豆低植酸突变体进行营养品种分析,发现突变型较野生型蔗糖含量增高47.4%~86.1%、棉子糖含量减少74.2%~84.3%。

2 大豆低聚糖遗传及相关 QTL 研究进展

Clevinger^[26]利用V99-5089×PI200508构建的F₂群体研究水苏糖的遗传机制,结果表明水苏糖含量受2对隐性等位基因控制。Skoneczka等^[27]利用

PI87013×PI200508和PI243545×PI200508构建的F₂群体,将PI200508内低水苏糖含量基因定位在C2连锁群上,可解释88.0%~94.0%的水苏糖含量遗传变异。利用已公布大豆基因组数据库Phytozome(<http://www.phytozome.org>)在此位点发掘到低水苏糖基因(*rsm*),与水苏糖合成酶基因(*STS*)高度同源。序列比对分析鉴定到6个SNP其中4个为有义突变。Saghai等^[28]将V99-5089内低水苏糖基因定位在G连锁群上,可解释87.6%水苏糖含量遗传变异;此位点发掘到的低水苏糖基因与肌醇-1-磷酸合成酶基因(*MIPS1*)高度同源。*MIPS1*基因的低水苏糖等位基因同时控制棉子糖和植酸含量降低。

Maughan等^[29]利用V71-370×PI407162构建的F_{4:2}群体定位蔗糖含量相关QTL,共得到17个QTL,分别位于A1、A2、E、F、I、L和M连锁群上,遗传效应值6.1%~12.4%,其中I连锁群上的QTL效应值最大,临近标记为A144_1。Kim等^[30]利用Keunolkong×Iksan 10构建的F₁₀重组自交系群体(RIL)研究蔗糖含量相关QTL,定位了4个QTL,分别位于B1、D1b和L连锁群上,遗传效应值6.5%~10.8%。Kim等^[31]又利用Keunolkong×Shinpaldalkong构建的F_{2:10}RIL群体继续鉴定蔗糖含量相关的QTL,定位了6个QTL,分别位于B2、D1b、E、H和J连锁群上,遗传效应值3.9%~14.8%,其中E连锁群上的QTL效应值最大,临近标记为Satt483。Feng等^[32]定位了2个棉子糖含量相关QTL,分别位于K和B1连锁群上,可解释表型变异率分别为16.0%和25.0%;并在O连锁群上定位到1个水苏糖相关的QTL,可解释表型变异率18.8%。Stombaugh等^[33]利用Minsoy×Archer构建的重组自交系群体定位了1个葡萄糖含量相关QTL,位于O连锁群,遗传效应值为13.0,临近标记Satt153。

王跃强等^[34]利用V97-3000×V99-5089构建的F₂群体定位了11个大豆低聚糖组分QTL,在E连锁群上定位到1个葡萄糖含量QTL,相关标记为Satt598,遗传效应值为6.2%;在E、D2和G连锁群上分别定位到1个果糖含量QTL,相关分子标记为Satt598、Satt372和Satt324,遗传效应值分别为5.7%、5.1%和7.3%;在M、I连锁群上各定位到1个蔗糖含量QTL,相关标记分别为Satt680和Satt270,遗传效应值为4.6%和5.2%;在M和O连锁群上各定位到1个棉子糖含量QTL,相关标记分别为Satt150与Satt478和Satt282,遗传效应值为5.3%和5.4%;在O连锁群上定位到1个水苏糖含量QTL,相关标记为Satt635和Satt353,遗传效应值

为 10.5% ;在 M 和 L 连锁群上各定位到 1 个总糖含量 QTL,相关标记为 Satt150 和 Satt313,遗传效应值

为 6.5% 和 4.5%。综上研究结果,大豆低聚糖组分 QTL 研究概况见表 1。

表 1 大豆低聚糖组分 QTL 研究概况

Table 1 Research on QTL of oligosaccharide in soybean

性状 Trait	QTL 数量 QTL No.	连锁群 LG	遗传效应值 Genetic effect/%	标记数量 Marker No.	文献来源 Literature resources
葡萄糖含量 Glucose content	2	E、O	6.2 ~ 13.0	2	王跃强,2012 Stombaugh, et al,2004
果糖含量 Fructose content	3	E、D2、G	5.1 ~ 7.3	3	王跃强,2012
蔗糖含量 Sucrose content	29	A1、A2、E、F、I、L、M、B1、D1b、B2、H、J	3.9 ~ 14.8	29	王跃强,2012 Maughan, et al,2002 Kim, et al,2005;2006
棉子糖含量 Raffinose content	4	M、O、K、B1	5.3 ~ 25.0	9	王跃强,2012 Feng, et al,2004
水苏糖含量 Stachyose content	4	G、O、C2	10.8 ~ 94.0	6	王跃强,2012 Feng, et al,2004 Skoneczka, et al,2009 Saghai,2008
合计 Total	42			49	

由表 1 可知,已报道 42 个低聚糖组分 QTL,分别位于 E、D2、G、L、M、A2、A1、B1、D1b、F、O、K、C2、I、B2、H、J 连锁群上,相关标记 49 个,含有 19 个 RFLP 标记,30 个 SSR 标记。Skoneczka 等与 Saghai 等定位到主效水苏糖含量 QTL,并在 QTL 位点内挖掘到相关酶基因。同时,王跃强与 Feng 等在 O 连锁群上均鉴定到水苏糖含量相关 QTL,遗传效应值分别为 10.5%、18.8%,表明此位点可能含有水苏糖合成的相关调控基因,还需进一步验证。

3 低聚糖代谢途径及相关酶基因研究

3.1 低聚糖代谢研究

大豆成熟期间,棉子糖和水苏糖的合成发生在细胞溶质中。大豆胚轴中,可溶性糖的含量为干重的 28%,其中低聚糖占 50% 以上。大豆低聚糖的合成是由几种 α -半乳糖苷转移酶的顺序反应完成的,葡萄糖是蔗糖、棉子糖、水苏糖的碳骨架来源^[35]。葡萄糖在己糖激酶的作用下生成磷酸-6-葡萄糖,活化的葡萄糖可在肌醇-1-磷酸合酶(myoinositol-1-phosphate synthase, MIPS)与肌醇-1-磷酸磷酸酶的作用下生成肌醇,也可在 UDP-葡萄糖焦磷酸化酶、UDP-葡萄糖表型异构酶与肌醇半乳糖苷合成酶(galactinol synthase, GS)作用下合成半乳糖苷肌醇,更可在葡萄糖-6-磷酸异构酶与己糖激酶作用下生成果糖。果糖与 UDP-葡萄糖在蔗糖合成酶作用下生成蔗糖。蔗糖与半乳糖苷肌醇在棉子糖合成酶(raffinose synthase, RS)作用下生成棉子糖。棉子糖与半乳糖苷肌醇在水苏糖合成酶(stachyose synthase, STS)作用下生成水苏糖^[36]。

此合成过程中主要的调控酶包括有肌醇-1-磷酸合成酶、棉子糖合成酶、肌醇半乳糖苷合成酶和水苏糖合成酶,半乳糖苷合成酶和棉子糖合成酶是蔗糖到棉子糖半乳糖苷系列寡糖生物合成途径中的关键酶^[37]。低聚糖合成是一个复杂的代谢网络系统,其在植物中受多因素影响,由多个代谢途径综合调控。此外,蔗糖多在叶片中合成,其运输机制也影响籽粒中低聚糖的积累^[38]。这些酶都是细胞核基因编码的产物,亚细胞定位于高等植物的胞质和质体中,表明了低聚糖合成部位。目前,已开展对这几种酶基因的研究,为阐述棉子糖系列寡糖合成途径的分子遗传机制提供有益信息。

3.2 相关代谢酶基因研究

Hitz 等^[39]利用大豆 MIPS1 基因缺失突变种对低聚糖合成途径进行研究,发现突变种中肌醇含量下降,同时引起半乳糖苷肌醇和棉子糖含量下降,表明肌醇-1-磷酸合酶基因是低聚糖合成的关键酶基因。Keller 等^[40]利用转基因的马铃薯(*Solanum tuberosum*)块茎进行研究也得到相同的结果。上述研究表明 MIPS1 基因编码的酶受底物浓度调控。Song 等^[41]在拟南芥(*Arabidopsis thaliana*)中对 MIPS 基因进行克隆与表达分析,研究表明 *AtMIPS1* 编码的氨基酸序列中含有保守结构域“SYNHLGNDG”,与其他植物的 MIPS 基因编码的氨基酸保守结构域相同,进一步表明 MIPS 基因在物种进化过程中具有较高的保守性。

Sprenger 等^[42]在匍匐筋骨草(*Ajuga reptans* cv.)中对编码肌醇半乳糖苷合成酶(GS)基因进行研究,克隆到 2 个 GS 基因 GS-1 和 GS-2,其中 GS-1

参与储存型棉子糖系列寡糖的合成,而 *GS-2* 涉及到运输型低聚糖的合成。水苏糖是多种农作物种子中重要的可溶性糖类之一,研究表明水苏糖与棉子糖都和植物抗冷性密切相关。水苏糖合成酶(*STS*)催化水苏糖合成,并参与毛蕊花糖合成,在棉子糖系列寡糖代谢中,可调控低聚糖含量的变化^[43]。Peterbauer 等^[44]在小豆(*Vigna umbellata*)中对 *STS* 基因进行表达分析研究,结果表明在种子发育过程中,*STS* 基因的 mRNA 会瞬间高水平表达,并在种子成熟后及发芽过程中高水平累积。

4 展 望

关于大豆低聚糖种质筛选及分子遗传机制研究已取得很大的进展,但国内大豆低聚糖种质筛选及遗传机制相关研究报道较少。目前已明确低聚糖组分构成与专用特用大豆品种密切相关。我国虽育成了很多专用大豆品种,但其营养品质鉴定较少。而且,国内种质资源低聚糖含量测定数据量不足,不利于特用大豆育种的发展。

前人研究表明,可利用低聚糖表型值及已有大豆低聚糖相关 SSR 标记筛选更多国内大豆种质,鉴定低聚糖组成特异种质,构建低聚糖含量相关基因变异丰富的应用核心群体。利用该应用核心群体采用关联分析开发功能标记,为分子辅助育种奠定技术基础,为特用大豆育种提供优异种质。

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