

大豆冠层耐萎蔫的生理与遗传研究进展

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摘要: 干旱是导致大豆减产的最主要环境胁迫因子。干旱胁迫后冠层萎蔫程度是植株内部水势情况和保护调节情况的外部形态表现, 可直接反映大豆的抗旱状况。实践证明, 耐萎蔫性状的改良将是实现抗旱性与丰产性协同改良的重要途径。为了更加清晰地了解冠层耐萎蔫与抗旱性及产量的关系, 指导耐萎蔫型大豆品种的选育工作, 本文围绕着大豆耐萎蔫性状的生理机制和相关基因挖掘的研究进展进行了综述。受限于耐萎蔫优异种质资源及基因资源的匮乏, 我国大豆耐萎蔫相关育种工作相对滞后。为此, 从如何建立大豆耐萎蔫资源鉴定体系及基因挖掘等方面提出了建议, 并认为耐萎蔫基因的挖掘不仅可以为大豆抗旱育种提供基因资源, 也为深入解析大豆抗旱基因演化及调控网络奠定基础。

关键词: 大豆; 干旱; 冠层耐萎蔫; 生理机制; 基因挖掘; 分子机制

Status in Physiology and Genetics of Slow Canopy Wilting in Soybean

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Abstract: Drought is the main environmental stress factor that leads to yield reduction in soybean (*Glycine max*). The canopy wilting caused by drought stress is the external expression of the water potential status and osmotic-regulation status, which can directly reflect the drought tolerance of soybean. The improvement of drought resistance and grain yield via deploying and incorporating slow-wilting tolerance germplasm has been accepted in practical uses. This article reviews the progress on the physiological and genetic mechanisms underlying slow-wilting in soybean. Breeding for slow-wilting soybean lines/varieties in China was limited largely due to the insufficiency of elite slow-wilting germplasm resources. The suggestions on identification of elite slow-wilting germplasms and cloning of genes underlying the slow-wilting process in soybean are proposed. Thus, this article provides considerable insights to understand the interaction networks between slow canopy wilting and drought resistance and yield, and to guide the breeding of slow-wilting cultivars in soybean.

Key words: soybean; drought; slow canopy wilting; physiological mechanism; gene mining; molecular mechanisms

收稿日期: 2020-04-30 修回日期: 2020-05-29 网络出版日期: 2020-07-01

URL: <http://doi.org/10.13430/j.cnki.jpgr.20200430001>

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基金项目: 转基因重大专项 (2016ZX08004-005); 国家重点研发计划 (2016YFD0100201-01, 2017YFD0101304-2); 现代农业产业技术体系 (CARS-004-CES11)

Foundation projects: Major Genetically Modified Projects (2016ZX08004-005), National Key R&D Program of China (2016YFD0100201-01, 2017YFD0101304-2), Modern Agricultural Industry Technology System (CARS-004-CES11)

干旱胁迫对农业生产的危害极其严重,是导致作物减产的最主要环境胁迫因子^[1-2]。大豆是我国最重要的经济作物之一,在我国农业生产中占有极其重要的地位。由于大豆的蒸腾系数较高,需水量大,抗旱能力相对较弱,干旱胁迫对其产量和品质产生极大影响^[3-5]。干旱胁迫后冠层萎蔫程度是植株内部水势情况和保护调节情况的外部形态表现,可直接反映大豆的抗旱状况。在诸多抗旱相关性状中,冠层缓慢萎蔫是耐旱型大豆响应干旱胁迫的重要特征之一,该性状的遗传改良将在大豆抗旱育种中发挥重要作用^[6]。本文围绕着大豆耐萎蔫性状的生理机制和相关基因挖掘的研究进展进行了综述,为我国大豆抗旱育种工作提供指导。

1 冠层耐萎蔫是大豆重要的抗旱性状

在漫长的进化过程中,作物以多种方式抵抗和适应干旱,形成了逃旱、避旱和耐旱等3种抗旱机制^[7]。避旱机制指作物通过增强根系吸水能力或降低冠层水分蒸腾来保持植株体内水势,而耐旱机制则指在低水势下植株耐受能力的调节^[8]。面临严重干旱时,尽管通过耐旱机制可使部分大豆植株得以存活,但仍导致大幅减产。大豆抗旱育种不仅要提高干旱胁迫下植株存活率,并且要保证产量的稳定性^[9-10]。因此,对于提高大豆稳产性而言,采取避旱策略相比于增强失水后的耐受性更加重要^[11]。

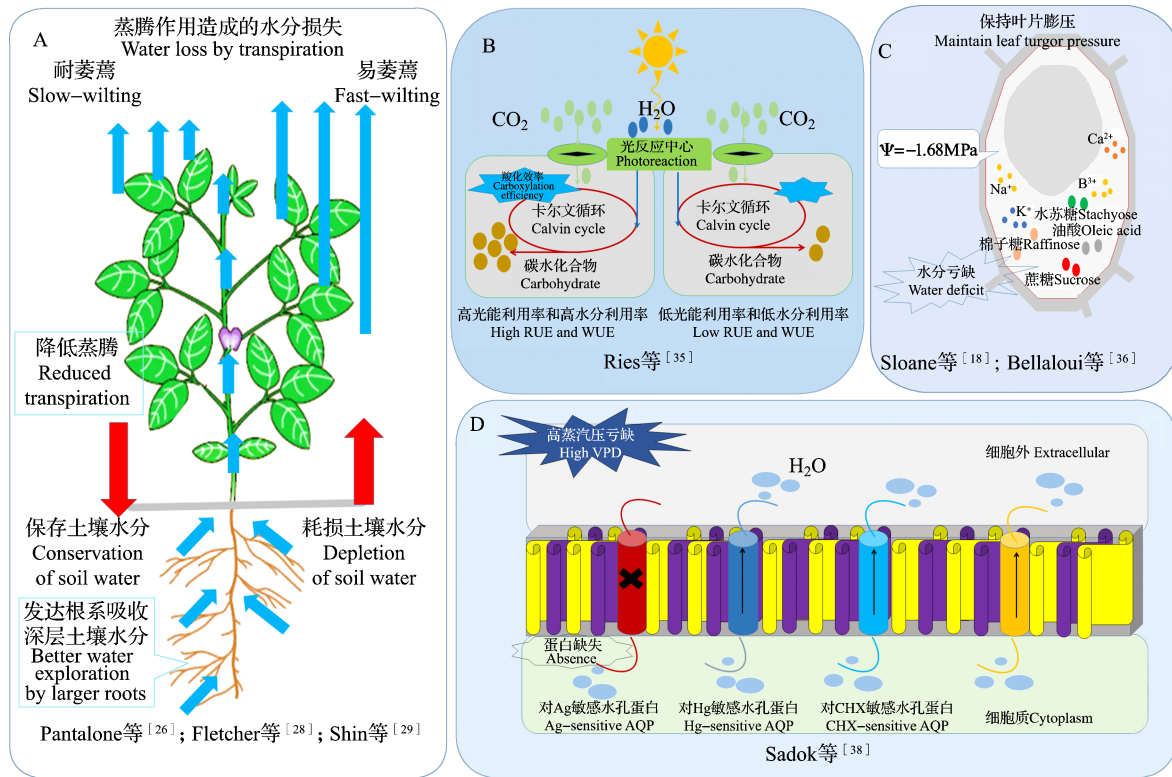
冠层萎蔫是植株失水后的第一个明显症状,萎蔫速度和程度直接反映了植株的避旱能力^[12]。前人利用冠层萎蔫指数来衡量大豆萎蔫程度,共分为5个等级,其中,0级为不萎蔫;1级为轻微萎蔫,冠层顶部叶片卷曲;2级为冠层顶部叶片严重卷曲,其余叶片中度萎蔫;3级为冠层全部叶片严重萎蔫;4级为叶柄萎蔫,大部分叶片死亡;5级为植株死亡^[13]。自耐萎蔫种质 PI 416937 和 PI 471938 获得鉴定以来,冠层耐萎蔫已成为美国大豆抗旱资源鉴定的重要指标^[13],并且利用耐萎蔫优异种质作为骨干亲本育成了诸多抗旱品种^[14-16]。通过模型预测,耐萎蔫品种的推广能使美国干旱地区大豆增产80%以上^[17]。与其他抗旱性状相比,大豆冠层耐萎蔫能力的改良不仅可避免干旱胁迫造成的大幅度减产,且不会影响正常供水下的产量潜力^[18-19]。本研究团队前期育成品种辽豆14在干旱胁迫后叶片

萎蔫缓慢、程度低,是典型的耐萎蔫型品种。该品种不仅具有较强耐旱能力^[20],而且具有较高的产量潜力,曾创造北方春大豆超高产记录^[21-23]。由此可见,耐萎蔫品种的选育是大豆抗旱性与丰产性协同改良的重要举措^[6]。

2 大豆冠层耐萎蔫的生理机制

耐萎蔫大豆响应干旱胁迫可能存在多种生理调节机制^[12, 24-25]。研究发现,耐萎蔫种质 PI 416937 具有较大的根系表面积^[26],根系表面积的增加将扩大根系可利用的土壤体积,根系在土壤中的深扎则可利用深层土壤中的水分^[27]。本研究团队发现,耐萎蔫品种辽豆14在水分胁迫下根系具有相对较高的根系活力和根系伤流液重量,能够维持较强的根系生理活性和吸水能力,从而表现出较强的抗旱能力^[20]。冠层萎蔫虽然受根系形态及其水分吸收能力的影响,但主要由冠层蒸腾速率决定^[28]。与易萎蔫大豆相比,耐萎蔫大豆遭受干旱胁迫后主要通过降低叶片蒸腾速率和植株水分利用来保存土壤中的有限水分(图1A)^[28-29],从而缓解水分胁迫带来的不利影响,提高水分利用效率和籽粒产量^[30-34]。干旱下叶片气孔关闭是引起蒸腾速率下降的主要原因,大部分耐萎蔫品种具有较低的光能利用效率,但也存在少数品种仍然具有较高的光能利用效率(图1B),这些品种在正常水分下往往具有较高的产量潜力^[35]。耐萎蔫型大豆叶肉细胞中K、Ca、B、Na等矿质元素和蔗糖等有机物的大量积累^[18, 36],有利于叶片保持较高的细胞膨压和水势,以实现渗透调节作用(图1C)^[37]。Sadok等^[38]研究发现,水孔蛋白的分布与表达、维管束与保卫细胞间的水力导度是限制大豆叶片蒸腾作用的关键因素,一种对AgNO₃敏感的水孔蛋白(Ag-sensitive AQP)的缺失能够使叶片在高蒸汽压亏缺下保持稳定的蒸腾速率(图1D)。

我国研究者普遍将冠层萎蔫指数作为抗旱指标对大豆种质资源进行鉴定,但针对耐萎蔫生理机制的研究则较少^[39-40]。本研究团队研究表明,辽豆14叶片气孔对干旱响应敏感,能通过气孔关闭来降低植株水分蒸腾,并且在较低胞间CO₂浓度下具有较高的核酮糖-1,5-二磷酸羧化酶(Rubisco)羧化活性和光系统II(PSII)活性,从而能够维持相对较高的光合速率^[20]。然而,关于辽豆14耐萎蔫的生理机制仍需深入研究。



A: 耐萎蔫大豆的根系吸水能力和冠层蒸腾速率; B: 耐萎蔫大豆的光能利用效率 (RUE) 和水分利用效率 (WUE);

C: 耐萎蔫大豆叶片的渗透调节机制; D: 耐萎蔫大豆水孔蛋白活性调控叶片蒸腾速率的机制

A: Water uptake capacity and canopy transpiration rate of slow-wilting soybeans, B: Radiation use efficiency (RUE) and water use efficiency (WUE) of slow-wilting soybeans, C: Osmotic regulation mechanism of leaves in slow-wilting soybeans,

D: Regulation mechanism of transpiration rate by aquaporins activity in slow-wilting soybeans

图 1 大豆冠层耐萎蔫的主要生理机制

Fig. 1 Physiological mechanism of slow canopy wilting in soybean

3 大豆冠层耐萎蔫的分子机制

3.1 连锁分析

为了加速耐萎蔫型大豆品种的选育,国内外研究者利用连锁作图对耐萎蔫相关性状 QTLs 进行研究。大豆耐萎蔫及其相关性状均由多基因控制,遗传机制极为复杂。吕彩霞等^[39]以 PI 471938 与普通大豆品种 Dare 和丰收黄杂交构建的 F₂ 群体对与耐萎蔫相关地上部与根系性状进行了遗传分析,并且定位了 5 个 QTLs。Du 等^[41]利用科丰 1 号与南农 1138-2 构建的重组自交系群体对抗旱相关指标进行了 QTL 分析,于 A2 和 H 连锁群上检测出 2 个与叶片水分状况相关的 QTL。Charlson 等^[13]利用 KS4895 与 Jackson 杂交构建的重组自交系群体对大豆冠层萎蔫指数进行了 QTL 分析,于 A2、B2、D2 和 F 连锁群上检测了 4 个相关 QTL,表型贡献率达 16%~44%。Abdel-Haleem 等^[11]以 PI 416937 与 Benning 构建的重组自交系作为作图

群体,通过 5 个不同环境下联合分析检测出 7 个 QTL,共解释了 75% 的表型变异,其中 5 个增效等位基因来源于 PI 416937,这些 QTL 在图谱中位置均与其他抗旱 QTL 重合,说明耐萎蔫 QTL 还控制其他与抗旱相关的形态或生理性状。Hwang 等^[42]利用 93705KS4895 × Jackson、08705KS4895 × Jackson、KS4895 × PI 424140、A5959 × PI 416937、Benning × PI 416937 等 5 个重组自交系群体在 15 个环境下对耐萎蔫 QTL 进行了检测,共检测出 8 个在至少 2 个环境下表达的 QTL。Ye 等^[43]研究发现,新鉴定的早熟耐萎蔫种质 PI 567690 和 PI 567731 的作用机制与 PI 416937 不同,其蒸腾速率对水孔蛋白抑制剂响应敏感,通过构建重组自交系群体分别于第 3 和第 6 染色体上定位了 2 个多环境下稳定表达的 QTLs,贡献率达 20%~30%。目前,在大豆基因组数据库 (www.soybase.org) 中共登记了 39 个耐萎蔫 QTL (表 1),但这些 QTL 均未实现精细定位与基因克隆。

表 1 大豆中已发现的冠层耐萎蔫 QTL

Table 1 QTL identified for slow canopy wilting in soybean

QTL	连锁群 Linkage group	定位区间 (cM) Interval	区间标记 Flanking marker	亲本 Parents	参考文献 References
CW1-2	D1b	5.51~16.61	BARC-020103-04462~BARC-050661-09809	93705KS4895 × Jackson	[42]
CW1-3	D1b	5.51~19.87	BARC-020103-04462~BARC-065787-19749	93705KS4895 × Jackson	[42]
CW2-1	D1b	0~20.61	Sat_096~Sat_351	Benning × PI 416937	[42]
CW1-4	D1b	5.51~20.61	BARC-032525-08992~Sat_351	93705KS4895 × Jackson	[42]
CW2-3	D1b	39.34~57.50	Satt372~Sat_092	Benning × PI 416937	[42]
CW1-1	D1b	41.29~63.93	Sat254~Satt266	Benning × PI 416937	[11]
CW2-2	D1b	76.27~100.88	Sat_089~Satt172	Benning × PI 416937	[42]
CW2-5	C1	0~47.11	Satt565~BARC-044521-08714	93705KS4895 × Jackson	[42]
CW2-4	C1	64.99~76.03	Sat_646~Satt139	Benning × PI 416937	[11]
CW2-7	A1	3.21~15.78	BARC-062429-17772~BARC-019415-03923	93705KS4895 × Jackson	[42]
CW2-6	A1	0~22.08	Satt684~Satt276	Benning × PI 416937	[11]
CW3-1	A1	14.43~51.95	BARC-021573-04148~Satt717	93705KS4895 × Jackson	[42]
CW3-2	C2	3.12~3.15	Satt681~BARC-054349-12493	93705KS4895 × Jackson	[42]
CW3-3	C2	121.26~126.23	Satt307~Satt202	93705KS4895 × Jackson	[42]
CW3-4	A2	27.90~36.77	Sat319~Satt177	KS4895 × Jackson	[13]
CW3-5	A2	26.56~35.60	BARC-065591-19578~BARC-045199-08906	93705KS4895 × Jackson	[42]
CW3-6	K	51.26~56.93	BARC-050815-09887~BARC-056323-14257	93705KS4895 × Jackson	[42]
CW3-9	B1	54.55~82.04	BARC-042473-08271~BARC-059773-16088	KS4895 × PI 424140	[42]
CW3-8	B1	46.38~67.05	Satt197~BARC-059851-16137	93705KS4895 × Jackson	[42]
CW3-7	B1	54.77~67.05	BARC-032817-09052~BARC-059851-16137	93705KS4895 × Jackson	[42]
CW3-10	H	68.90~81.04	Satt302~Satt676	Benning × PI 416937	[11]
CW3-11	H	84.22~108.15	BARC-049209-10821~BARC-039237-07479	93705KS4895 × Jackson	[42]
CW3-12	F	82.83~87.01	Satt362~Satt072	KS4895 × Jackson	[13]
CW3-13	B2	6.05~31.87	Satt577~Sat_287	KS4895 × Jackson	[13]
CW4-2	B2	30.30~40.34	BARC-031281-07037~BARC-055975-13947	93705KS4895 × Jackson	[42]
CW4-1	B2	67.92~90.00	Sat_189~Sct_064	Benning × PI 416937	[11]
CW4-4	D2	11.69~26.04	Sct_192~Satt135	Benning × PI 416937	[11]
CW5-2	D2	34.06~47.77	BARC-058841-15463~BARC-024449-04894	93705KS4895 × Jackson	[42]
CW4-5	D2	47.74~47.77	BARC-035383-07190~BARC-024449-04894	93705KS4895 × Jackson	[42]
CW4-3	D2	39.34~57.07	Satt154~Satt372	KS4895 × Jackson	[13]
CW4-6	D2	39.34~57.07	Satt372~Satt154	93705KS4895 × Jackson	[42]
CW4-7	D2	47.74~57.07	BARC-035383-07190~Satt154	93705KS4895 × Jackson	[42]
CW5-1	D2	114.89~133.62	BARC-011591-00299~BARC-039151-07458	93705KS4895 × Jackson	[42]
CW5-3	D2	115.69~134.02	Satt031~BARC-039151-07458	KS4895 × PI 424140	[42]
CW5-4	L	40.00~65.39	Satt462~Satt076	Benning × PI 416937	[11]
CW6-2	L	81.77~86.13	BARC-065769-19741~BARC-024345-04854	KS4895 × PI 424140	[42]
CW6-1	L	86.13~97.46	BARC-024345-04854~BARC-064609-18739	93705KS4895 × Jackson	[42]
CW6-3	L	81.77~102.53	BARC-065769-19741~BARC-029051-06057	KS4895 × PI 424140	[42]
CW6-4	L	78.23~106.37	Sat_099~Satt513	Benning × PI 416937	[42]

在 QTL 定位中,尽可能缩小 QTL 定位区间是决定基因发掘效率的关键。一方面,耐萎蔫基因发掘效率受连锁图谱标记密度影响,但目前广泛采用的高通量 SNP 标记可以避免 SSR、InDel、RFLP、AFLP 等传统分子标记存在标记数量少、分布不均、覆盖密度低等缺陷^[44]。另一方面,群体规模的限制会使染色体部分区段的重组率较低,仍需通过精细定位进一步明确候选基因^[43]。在 QTL 初步定位的基础上,通过构建次级定位群体进行基因精细定位仍然是主要策略,但构建大规模 F₂、回交及近等基因系等群体耗时长,将严重影响着基因发掘效率。另外,在前人定位的耐萎蔫 QTL 中,等位基因仅来自于作图群体双亲,其结果往往在其他遗传背景和环境下无法适用,将制约着分子标记辅助选择育种的效率。

3.2 全基因组关联分析

全基因组关联分析是对多个个体在全基因组范围的遗传变异多态性进行检测,获得基因型,进而将基因型与表型进行群体水平的统计学分析。Kaler 等^[45]基于高密度 SoySNP50K 芯片(42000 个 SNP)对 4 个不同环境下 373 份 IV 熟期组大豆种质资源耐萎蔫表型进行了全基因组关联分析,共检测到 61 个 SNP 与耐萎蔫表型存在显著关联,其中 21 个 SNP 在多环境下得到重复检测,这些 SNP 分别位于 23 个耐萎蔫 QTLs 内,其中 6 个 QTL 位于前期连锁定位区间内,另外一些 SNP 位于已知与蒸腾速率或水分运输相关基因区域内。Steketee 等^[46]利用 SoySNP50K 芯片对 4 个不同环境下 162 份 VI-VIII 熟期组大豆耐萎蔫表型进行了全基因组关联分析,检测出 45 个 SNP 与耐萎蔫表型存在显著关联,分别位于 44 个 QTL 区间内。

在开展大豆种质资源耐萎蔫表型分析的同时,结合高通量测序,利用基于连锁不平衡的关联分析可以在自然群体中检测耐萎蔫基因,发掘优异等位变异和单倍型,这些研究成果将有助于大豆耐萎蔫分子标记辅助选择与基因聚合奠定重要基础。但关联分析易受群体遗传结构的影响,对低频率等位基因检测效率低。

3.3 转录组测序分析

随着后基因组时代的到来,转录组测序技术得到了迅猛发展。通过对比耐萎蔫型与易萎蔫型大豆在干旱胁迫下的差异表达基因,不仅有助于破解耐萎蔫大豆干旱响应机制,同时还有助于发掘调控耐萎蔫的关键基因,从而为分子育种奠定基础。Vidal

等^[47]利用 RNA-seq 比较了干旱胁迫下敏感型品种 BR16 和耐旱型品种 Embrapa48 叶片的基因的差异表达,共发现 2222 个表达量上调的基因,以此鉴定出的 165 个 SNPs 可用于分子标记辅助选择育种。Prince 等^[48]通过干旱胁迫下转录组测序分析发现,耐萎蔫大豆 PI 567690 特异表达上调的基因主要涉及蛋白质结合、水解酶活性、碳水化合物/脂质代谢、与细胞壁、质外体和叶绿素 a/b 结合蛋白等,而特异表达下调的基因主要涉及非生物胁迫应答、离子结合与转运、氧化还原反应和电子载体活性等,其中,UDP 葡萄糖醛酸转移酶活性编码基因是耐萎蔫大豆重要的差异表达基因。通过降低叶片的蒸腾速率来维持植株正常生长是耐萎蔫大豆响应高蒸汽压亏缺的重要特征,研究表明,在高蒸汽压亏缺胁迫下,易萎蔫品种 Hutcheson 仅 1 个基因得到差异表达,而耐萎蔫种质 PI 416937 存在 944 个基因得到差异表达,这些基因主要富集于碳代谢、转录调控、脂类代谢、氧化反应和细胞壁修饰等生理过程^[49]。Gallino 等^[50]通过转录组测序分析发现, *Gmelfiso4G-1a* 作为编码真核翻译起始因子的基因在耐萎蔫大豆 N7001 中得到特异表达,过表达转化拟南芥能够提高植株对渗透胁迫、盐胁迫、干旱胁迫和高温胁迫的抗性,说明该基因是关键的耐萎蔫基因。另外,将转录组测序技术应用于传统图位克隆也是提高基因发掘效率的重要手段^[51-52]。Shin 等^[29]对耐萎蔫种质 PI 416937 和易萎蔫品种 Benning 受水分胁迫后不同时间的基因表达进行分析,在已知的耐萎蔫 QTL 区间内发现了 5 个关键的差异表达基因。

4 总结与展望

自耐萎蔫种质 PI 416937 和 PI 471938 获得鉴定以来,冠层耐萎蔫已成为美国大豆抗旱资源鉴定的重要指标,利用耐萎蔫优异种质作为骨干亲本育成了诸多抗旱品种,并通过实践证明了耐萎蔫性状的改良将是实现抗旱性与丰产性协同改良的重要途径。耐萎蔫大豆遭受干旱胁迫后可通过气孔调控、渗透调节和水孔蛋白活性等途径降低叶片蒸腾作用,从而保持植株体内的水势,但该过程可能涉及多种未知的生理机制,仍需进一步深入研究。大豆耐萎蔫性状由多基因控制,遗传机制极为复杂。前人分别通过连锁分析、关联分析和转录组测序分析开展了大豆耐萎蔫基因挖掘工作,取得一定进展,但仍未实现耐萎蔫基因的克隆。然而,受限于耐萎蔫优异种质资源及基因资源的匮乏,我国大豆耐萎蔫相

关育种工作相对滞后。因此,亟待大豆耐萎蔫基因发掘与功能解析等工作的开展,服务于大豆抗旱分子育种。

4.1 建立大豆耐萎蔫种质资源鉴定体系

国外研究者前期主要通过多环境田间条件下对大豆冠层耐萎蔫进行鉴定,而通过人工控水盆栽、PEG6000 模拟干旱胁迫、高蒸汽压亏缺等进行相关研究则较少。未来研究中应该联合上述研究方法,建立稳定、高效的鉴定体系,实现对大豆冠层耐萎蔫的精准鉴定。另外,不同生育阶段遭受干旱胁迫对大豆生长发育的影响不同。因此,应全面对大豆苗期、花期、结荚期和鼓粒期冠层耐萎蔫开展鉴定研究。

4.2 开展大豆耐萎蔫基因挖掘工作

在开展大豆种质资源耐萎蔫表型分析的同时,结合高通量测序,利用基于连锁不平衡的关联分析可以在自然群体中检测耐萎蔫基因,发掘优异等位变异和单倍型,从而可为该基因的利用及分子标记辅助选择创造有利条件。同时,利用特异的耐萎蔫种质资源(例如辽豆 14 等)构建重组自交系等作图群体,开展耐萎蔫相关性状的 QTL 分析,发掘多环境稳定表达的主效 QTL。联合连锁分析与关联分析,使彼此优缺点得到互补,同时借助转录组测序、QTL 测序等技术,提高目标基因发掘效率。

4.3 大豆耐萎蔫基因的应用前景

目前,我国研究者已经克隆了 *GmUBC46*、*GmAIRP1* 和 *GmMYB174* 等基因,功能涉及大豆抗旱性的调控^[53-55]。然而,通过将耐旱基因引入到作物中增强耐旱性的同时,作物通常又表现出生长较弱。如何做到作物只耐旱又不影响正常生长是作物抗旱性育种的策略需求。鉴于目前已知耐萎蔫基因的供体材料不仅抗旱能力强,并且综合表现突出,从中分离的耐萎蔫基因将对大豆抗旱育种和高产育种均具有重要的应用价值。此外,大豆耐萎蔫基因的挖掘,还将为深入解析耐萎蔫基因功能、基因演化以及基因间调控网络奠定基础。

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