

· 热点评 ·

## 大豆向热带地区发展的遗传基础

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**摘要** 大豆(*Glycine max*)是光周期敏感的植物, 该特性是决定其生育期及其生态适应区的关键因素。温带的大豆品种引种到热带地区(短日照)时, 开花期和成熟期提前、产量降低, 限制了大豆在热带地区的种植。长童期(LJ)大豆品种的发现为解决该问题的重要突破。在短日照条件下, LJ品种比温带品种开花晚、体量大、成熟晚且产量提高。前期研究发现, *J*位点是控制LJ性状的关键位点。近期, 我国科学家通过精细定位克隆了*J*基因, 发现其与拟南芥(*Arabidopsis thaliana*)早花基因(*ELF3*)同源。他们通过功能互补和近等基因系等方法验证了*J*基因的功能, 在短日照条件下, 等位基因*j*比*J*开花晚、成熟晚且产量提高。进一步研究发现, *J*蛋白与*E1*基因(豆科植物开花抑制因子)的启动子结合抑制*E1*基因的表达, 从而解除*E1*对大豆开花基因(*FT*)的抑制, 促进大豆在短日照下开花。研究还发现在大豆种质资源中存在多种*j*等位变异。该研究引领了大豆生育期遗传研究的新方向, 揭示了大豆向热带地区发展的遗传基础。

**关键词** 大豆, 生态区, 适应性, 长童期, 生育期

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近期我国科学家Lu等(2017)在*Nature Genetics*上发表了一篇关于大豆(*Glycine max*)生育期基因*J*的遗传、克隆和分子调控机制的文章。*J*的等位变异可以适应热带地区的短日照条件, 生育期延长, 大豆产量增加, 为热带地区大豆的发展提供了熟期适应的遗传解释。大豆是全球最重要的豆科经济作物, 是人类食用蛋白、植物油和动物饲料的重要来源。大豆属于短日照植物, 对光周期高度敏感, 光敏特性是决定其纬度生态区适应性的关键因素(Destro et al., 2001; Watanabe et al., 2009, 2011a)。栽培大豆由野生大豆(*G. soja*)驯化而来, 大约5000年前起源于中国温带地区(Li et al., 2008)。约2000年前引入韩国和日本, 之后扩展至东南亚和南亚地区。1765年引入北美后, 大豆在美国大量扩展, 最早有熟期组MG I–VII, 后来向北发展形成了熟期组MG 0和MG 00组, 向南发展形成了MG VIII组。20世纪后期向北又发展了MG 000特早熟组(Wilson, 2008)。但当温带地区的大豆品种引种到热带(南北纬23°26'间)或邻近地区时, 由于对热带地区的短光周期敏感, 开花和成熟期提前, 生长体量缩小, 产量很低, 限制了大豆在热带地区的种植

(Neumaier and James, 1993; Spehar, 1995; Destro et al., 2001)。因此, 光周期不敏感以延长营养生长长期的育种方向应运而生(Hartwig and Kiihl, 1979; Neumaier and James, 1993; Spehar, 1995)。在低纬度地区短日照条件下, 长童期(long-juvenile, LJ)大豆品种比温带品种开花晚、成熟晚, 从而导致其株高、主茎节数、产量及其它重要农艺性状均有所改良(Hartwig and Kiihl, 1979; Sinclair and Hinson, 1992; Carpentieri-Pipoplo et al., 2002)。LJ性状的应用使大豆在南美洲大范围发展, 熟期组延伸到MG IX和MG X, 大豆在巴西的中西部开始种植, 继而扩展到纬度15°以下甚至赤道等热带地区(Neumaier and James, 1993; Destro et al., 2001)。

以往对大豆生育期遗传的研究仅局限在温带地区。经典遗传学研究发现有11个控制大豆开花期和成熟期的基因: 分别为10个*E*系列基因, *E1*和*E2* (Bernard, 1971)、*E3* (Buzzell, 1971)、*E4* (Buzzell and Voldeng, 1980)、*E5* (Mcblain and Bernard, 1987)、*E6* (Bonato and Vello, 1999)、*E7* (Cober and Voldeng, 2001)、*E8* (Cober et al., 2010)、*E9* (Kong

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et al., 2014)和*E10* (Samanfar et al., 2017), 以及与长童期相关的*J*位点(Ray et al., 1995; Cober, 2011)。*E6*、*E9*与*J*的显性等位基因促进大豆提早开花, 而其它基因的显性等位基因延迟开花和成熟。此外, 两个*FT* (*FLOWERING LOCUS T*)的同源基因*GmFT2a*和*GmFT5a*协调控制大豆开花(Kong et al., 2010)。其中, *E1*基因是一个具有核定位信号和B3远缘相关结构域的豆科植物特异性转录因子(Xia et al., 2012a, 2012b)。*E2*基因是拟南芥开花期基因*GI* (*GIGANTEA*)的同源基因(Watanabe et al., 2011a, 2011b)。*E3*和*E4*基因均是光敏色素A基因(*GmPHYA3*和*GmPHYA2*) (Liu et al., 2008; Watanabe et al., 2009)。*E9*基因是拟南芥*FT*的同源基因*FT2a* (Zhao et al., 2016), *E10*的候选基因可能是*FT*的同源基因*FT4* (Samanfar et al., 2017)。*E5-E8*与*J*基因分子基础尚有待研究。

以上重点研究的基因, 大多取材于MG I-V的材料, 所发掘的基因均与温带地区的大豆品种生育期有关。Lu等(2017)的研究与众不同, 他们利用巴西材料研究热带地区大豆长童期的分子遗传机制。研究结果为大豆向热带地区适应性理论的揭示和应用打开了一扇大门。为了对LJ性状进行遗传解析, 他们将具有LJ特性(短日照下开花期和成熟期延迟、产量提高)的PI159925和巴西品种BR121分别与温带大豆品种Harosoy杂交, 获得两个F<sub>2</sub>群体。对这两个群体在短日照条件下的开花期进行分析, 发现PI159925和BR121的LJ特性(延迟开花)主要是由位于4号染色体的隐性*j*等位基因决定; 同时发现在短日照条件下, *J*位点与*E1*位点(控制大豆成熟期的主要位点)存在上位性效应。然后对2 816个家系组成的F<sub>6</sub>群体(BR121×Harosoy)对*J*基因进行了精细定位(239 kb)。根据Williams 82的参考基因组序列, 该区间包括29个预测的基因。分别从亲本BR121和Harosoy中克隆这29个基因并测序, 发现只有1个基因(*Glyma.04G-050200.1*)在两亲本间存在序列差异, 且BR121的基因序列含有1个10 bp的缺失, 造成蛋白翻译提前终止。在另一个LJ品种PI159925中该基因的序列缺少1个胞嘧啶, 造成移码突变。这些结果表明, 该基因(*Glyma.04G050200.1*)很可能是*J*位点的候选基因。

为了验证该候选基因的功能, 他们将来自Harosoy (*J*基因型)中的*Glyma.04G050200.1*基因(自身启

动子驱动CDS)转入BR121 (*j*基因型), 发现与受体对照BR121相比, F<sub>4</sub>代转基因株系的开花期和成熟期提前、产量降低。因此, 具有完整功能的*Glyma.04G-050200.1*基因是*J*的等位变异, 而LJ品种PI159925和BR121中该基因的变异分别被命名为*j-1*和*j-2*。通过比较分别含有Harosoy *J*等位变异和BR121 *j-2*等位变异的近等基因系(NIL-*J*和NIL-*j*)的表型, 发现类似的结果, 说明*j*等位基因在短日照下延迟了大豆的开花期从而提高了产量。系统进化分析发现, *J*基因是拟南芥早花基因(*EARLY FLOWERING 3, ELF3*)的同源基因。在拟南芥中的功能互补分析同样验证了*J*基因的功能。

遗传分析还发现, *J*位点与*E1*位点存在上位性效应, 而前期的研究表明, *E1*基因在长日照条件下延迟大豆的开花期(Watanabe et al., 2011a; Xia et al., 2012a; Cao et al., 2017)。为了进一步理解*J*与*E1*的关系, 人们利用NIL调查这两个基因的表达情况, 结果发现在短日照条件下*J*抑制*E1*基因的表达, 但*E1*却不调控*J*基因的表达, 说明在大豆开花调控网络中*J*可能位于*E1*基因的上游。进一步的ChIP-PCR等分子生物学实验表明, *J*蛋白与*E1*基因(豆科开花抑制基因)的启动子结合而使*E1*基因下调表达。Kong等(2010)和Xia等(2012a)的研究发现, 在大豆中*E1*抑制两个开花基因*FT*的同源基因*FT2a*和*FT5a*的表达。与NIL-*J*相比, 在NIL-*j*中*FT2a*和*FT5a*的表达显著降低, 这与*E1*基因的高表达相对应。因此, 在*J*基因型的大豆中, *J*蛋白与*E1*基因的启动子结合抑制*E1*基因的表达, 从而解除*E1*对大豆开花基因*FT2a*和*FT5a*的抑制, 促进大豆在短日照下开花。

对427份大豆种质资源的*Glyma.04G050200.1*基因进行测序分析, 发现这些资源中该基因的序列在40个位点上存在多态性, 包括34个SNPs和6个InDels, 共34种单倍型。其中单倍型H3和H6分别对应上述*j-1*和*j-2*等位变异, 另外4种单倍型(*j-3*到*j-6*)也属于功能丧失性等位变异(对应短日照下延迟开花的表型)。这些*j*等位变异对大豆适应低纬度地区及其在这些地区推广和生产起重要作用。此外, 虽然*j*基因是LJ性状的重要分子基础, 但是还有很多来自热带地区的LJ品种具有功能型*J*基因(具有在短日照下晚花表型), 提示人们除了*J*位点外还有其它位点决定LJ性状。对这些LJ品种进行遗传解析将有助于进一步理解大豆

在热带地区的适应性机制和大豆的推广生产。

以上揭示的11个生育期基因均是从孟德尔遗传实验中发现的,涉及的成对亲本数目有限。大豆生育期从早期的MG I-VII共7组扩展到MG 000, 00, I, II……共13组,其遗传基础必然也有很大的扩展。近年来利用分子标记分别定位到66和138个开花期和成熟期QTLs (SoyBase, www.soybase.org),说明控制生育期的基因绝不止已发现的11个。我们曾以来源于全世界13个地区的371个大豆品种为材料,通过关联分析定位到52个开花期和59个成熟期QTLs,它们分别具有241和246个等位变异。由此分别注释到110和99个与9个生物学过程有关的候选基因。Lu等(2017)的研究仅在J位点上重点说明了1个等位变异,还有大量的位点及其等位基因有待人们去揭示。例如,以上所述大豆还向高纬度地区发展形成了MG 000, 00和0等早熟品种,其新生的等位变异也需要进一步解释。故希望后续研究能继续追踪,看看除了已报道的11个决定生育期的基因外还有哪些基因与生育期有关,还有哪些基因与适应热带或寒带地区有关;以J为例,多个等位变异各有何功能,各位点又各有哪些等位变异,这些位点和等位变异如何相互配合在一个基因网络体系中决定不同品种变化多端的生育期特性。

## 参考文献

- Bernard R** (1971). Two major genes for time of flowering and maturity in soybeans. *Crop Sci* **11**, 242–244.
- Bonato ER, Vello NA** (1999). *E-6*, a dominant gene conditioning early flowering and maturity in soybeans. *Genet Mol Biol* **22**, 229–232.
- Buzzell R** (1971). Inheritance of a soybean flowering response to fluorescent-daylength conditions. *Can J Genet Cytol* **13**, 703–707.
- Buzzell R, Voldeng H** (1980). Inheritance of insensitivity to long daylength. *Soyb Genet Newsl* **7**, 26–29.
- Cao D, Takeshima R, Zhao C, Liu BH, Jun A, Kong FJ** (2017). Molecular bases of flowering under long days and stem growth habit in soybean. *J Exp Bot* **68**, 1873–1884.
- Carpentieri-Pipoplo V, Almeida LAD, Kiihl RAS** (2002). Inheritance of a long juvenile period under short-day conditions in soybean. *Genet Mol Biol* **25**, 463–469.
- Cober ER** (2011). Long juvenile soybean flowering responses under very short photoperiods. *Crop Sci* **51**, 140–145.
- Cober ER, Molnar SJ, Charette M, Voldeng HD** (2010). A new locus for early maturity in soybean. *Crop Sci* **50**, 524–527.
- Cober ER, Voldeng HD** (2001). A new soybean maturity and photoperiod-sensitivity locus linked to *E1* and *T*. *Crop Sci* **41**, 698–701.
- Destro D, Carpentieri-Pipoplo V, Kiihl RAS, Almeida LA** (2001). Photoperiodism and genetic control of the long juvenile period in soybean: a review. *Crop Breed Appl Biotechnol* **1**, 72–92.
- Hartwig EE, Kiihl RAS** (1979). Identification and utilization of a delayed flowering character in soybeans for short-day conditions. *Field Crops Res* **2**, 145–151.
- Kong FJ, Liu BH, Xia ZJ, Sato S, Kim BM, Watanabe S, Yamada T, Tabata S, Kanazawa A, Harada K, Abe J** (2010). Two coordinately regulated homologs of *FLOWERING LOCUS T* are involved in the control of photoperiodic flowering in soybean. *Plant Physiol* **154**, 1220–1231.
- Kong FJ, Nan HY, Cao D, Li Y, Wu FF, Wang JL, Lu SJ, Yuan XH, Cober ER, Abe J, Liu BH** (2014). A new dominant gene *E9* conditions early flowering and maturity in soybean. *Crop Sci* **54**, 2529–2535.
- Li YH, Guan RX, Liu ZX, Ma YS, Wang LX, Li LH, Lin FY, Luan WJ, Chen PY, Yan Z, Guan Y, Zhu L, Ning XC, Smulders MJM, Li W, Piao RH, Cui YH, Yu ZM, Guan M, Chang RZ, Hou AF, Shi AN, Zhang B, Zhu SL, Qiu LJ** (2008). Genetic structure and diversity of cultivated soybean (*Glycine max* (L.) Merr.) landraces in China. *Theor Appl Genet* **117**, 857–871.
- Liu B, Kanazawa A, Matsumura H, Takahashi R, Harada K, Abe J** (2008). Genetic redundancy in soybean photoresponses associated with duplication of the phytochrome A gene. *Genetics* **180**, 995–1007.
- Lu SJ, Zhao XH, Hu YL, Liu SL, Nan HY, Li XM, Fang C, Cao D, Shi XY, Kong LP, Su T, Zhang FG, Li SC, Wang Z, Yuan XH, Cober ER, Weller JL, Liu BH, Hou XL, Tian ZX, Kong FJ** (2017). Natural variation at the soybean *J* locus improves adaptation to the tropics and enhances yield. *Nat Genet* **49**, 773–779.
- Mcblain BA, Bernard RL** (1987). A new gene affecting the time of flowering and maturity in soybeans. *J Hered* **78**, 160–162.
- Neumaier N, James AT** (1993). Exploiting the long-juvenile trait to improve adaptation of soybeans to the tropics. *Food Legume Newsl* **8**, 12–14.
- Ray JD, Hinson K, Mankono JEB, Malo MF** (1995). Gene-

- tic-control of a long-juvenile trait in soybean. *Crop Sci* **35**, 1001–1006.
- Samanfar B, Molnar SJ, Charette M, Schoenrock A, Dehne F, Golshani A, Belzile F, Cober ER** (2017). Mapping and identification of a potential candidate gene for a novel maturity locus, *E10*, in soybean. *Theor Appl Genet* **130**, 377–390.
- Sinclair TR, Hinson K** (1992). Soybean flowering in response to the long-juvenile trait. *Crop Sci* **32**, 1242–1248.
- Spehar CR** (1995). Impact of strategic genes in soybean on agricultural development in the Brazilian tropical savannah. *Field Crops Res* **41**, 141–146.
- Watanabe S, Harada K, Abe J** (2011a). Genetic and molecular bases of photoperiod responses of flowering in soybean. *Breed Sci* **61**, 531–543.
- Watanabe S, Hideshima R, Xia ZJ, Tsubokura Y, Sato S, Nakamoto Y, Yamanaka N, Takahashi R, Ishimoto M, Anai T, Tabata S, Harada K** (2009). Map-based cloning of the gene associated with the soybean maturity locus *E3*. *Genetics* **182**, 1251–1262.
- Watanabe S, Xia ZJ, Hideshima R, Tsubokura Y, Sato S, Yamanaka N, Takahashi R, Anai T, Tabata S, Kitamura K, Harada K** (2011b). A map-based cloning strategy employing a residual heterozygous line reveals that the *GIGANTEA* gene is involved in soybean maturity and flowering. *Genetics* **188**, 395–U260.
- Wilson RF** (2008). Soybean: Market Driven Research Needs in Genetics and Genomics of Soybean. New York: Springer-Verlag.
- Xia ZJ, Watanabe S, Yamada T, Tsubokura Y, Nakashima H, Zhai H, Anai T, Sato S, Yamazaki T, Lu SX, Wu HY, Tabata S, Harada K** (2012a). Positional cloning and characterization reveal the molecular basis for soybean maturity locus *E1* that regulates photoperiodic flowering. *Proc Natl Acad Sci USA* **109**, E2155–E2164.
- Xia ZJ, Zhai H, Liu BH, Kong FJ, Yuan XH, Wu HY, Cober ER, Harada K** (2012b). Molecular identification of genes controlling flowering time, maturity, and photoperiod response in soybean. *Plant Syst Evol* **298**, 1217–1227.
- Zhao C, Takeshima R, Zhu JH, Xu ML, Sato M, Watanabe S, Kanazawa A, Liu BH, Kong FJ, Yamada T, Abe J** (2016). A recessive allele for delayed flowering at the soybean maturity locus *E9* is a leaky allele of *FT2a*, a *FLOWERING LOCUS T* ortholog. *BMC Plant Biol* **16**, 20.

# The Genetic Basis of Soybean Extended to Tropical Regions

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**Abstract** Soybean (*Glycine max*) is a plant sensitive to photoperiod, which determines its maturity date and therefore its adaptation to respective eco-regions. The soybean varieties from temperate regions flower and mature very early in tropical regions (short photoperiod), which leads to low yields and limits the commercial cultivation of soybean in these regions. The discovery of long-juvenile (LJ) soybean varieties is a major breakthrough to overcome this problem. Under short photoperiod, the LJ soybean varieties show delayed flowering and maturity time, enhanced growth and therefore, higher yields than temperate varieties. Previous studies found that locus *J* had a major contribution to the LJ trait. Recently, Chinese scientists cloned the *J* gene by fine-mapping and found it as an ortholog of *Arabidopsis thaliana* *EARLY FLOWERING 3 (ELF3)*. The functions of *J* gene were confirmed by transgenic complementation and near-isogenic lines: the *j* genotype showed later flowering and maturity date and more yield potential than the *J* genotype. Further studies showed that the *J* protein bound to the promoter of the *E1* gene (a legume-specific flowering repressor) to downregulate *E1* expression, thereby relieving the suppression of *E1* on soybean *FLOWERING LOCUS T (FT)* genes, which leads to early flowering under short photoperiod. In addition, multiple *j* alleles and haplotypes were identified from soybean germplasm. The study leads to a new direction in genetic research of growth periods for the expansion of soybean to tropical regions.

**Key words** soybean, eco-region, adaptation, long-juvenile, maturity

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