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大豆光周期反应与生育期基因研究进展

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摘要: 20 世纪 20 年代, 植物学家 Garner 与 Allard 在研究大豆与烟草等植物的光反应时发现了植物光周期现象。大豆作为模式植物对光周期现象的理论形成起了重要作用。但大豆基因组的复杂性及相关功能基因的不明确性严重阻碍了学者对大豆光周期现象本质的认识。近年来, 随着控制大豆生育期主要 QTL 基因的相继克隆, 特别是对大豆生育期贡献最大的 *E1* 基因的成功破译, 学者们逐步认识到大豆光周期调控开花的独特性。遗传学及分子生物学研究表明, 大豆中具有拮抗关系的 *E1* 和 *FT* 基因位于大豆光周期调控开花主要通路的中心节点(integrator), 但两者间的作用机制及相关的调节因子尚待明晰。对大豆光周期反应及生育期基因的深入研究, 在生产实践上可为大豆品种的栽培区划、合理布局及分子育种等提供理论依据。

关键词: 大豆; 光周期反应; 开花期; 成熟期; *E1*

Research Progresses on Photoperiodic Flowering and Maturity Genes in Soybean (*Glycine max* Merr.)

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Abstract: Plant photoperiodism was discovered in 1920 when scientists studied the light response of soybean and tobacco. As a model plant, soybean made a crucial contribution towards establishment of the general concept of photoperiodism. Apart from its palaeopolyploid nature and relative bigger genome size, the unknown molecular identities of major QTL genes controlling flowering time hamper our understanding of the soybean photoperiodism. Since the successful cloning of major QTL genes controlling flowering time, especially the major QTL *E1*, the unique mechanism in soybean photoperiodic flowering has been generally revealed. Although the details of molecular mechanism of soybean photoperiodism remain unclear, genetic and molecular studies have proven that the *E1* and *GmFT* genes stand as major regulators (integrators) in the regulatory pathway of photoperiodic flowering. The advance on the mechanism of photoperiodic flowering in soybean will provide solid molecular basis for cultivar classification of maturity, proper crop arrangement and molecular breeding of new cultivars.

Keywords: Soybean; Photoperiodic response; Flowering time; Maturity time; *E1*

植物光周期现象(photoperiodism)是指植物通过感受昼夜长短而控制生理反应的现象, 其中通常研究较多的是植物通过感受昼夜长短变化而控制开花。Garner 与 Allard^[1]早在 20 世纪 20 年代通过对烟草与大豆等的光反应观察总结出植物存在着光周期现象, 如某些大豆品种即使在春季的不同时期播种, 其开花几乎在夏季的同一时期, 且与开花时的营养体大小无关。许多光周期现象(如暗期的重要性等)均是以大豆为材料而认知的, 大豆

是早期研究光周期现象的重要模式作物^[1-5]。植物根据其光周期反应的不同可分为长日、短日及日中性植物。在 24 h 昼夜周期中, 长日植物需要日照长度长于一定时数才能开花, 如大麦、小麦、黑麦、萝卜、菠菜、甘蓝、大白菜、天仙子、甜菜等^[6]。与之相反, 大豆、烟草与水稻等在日照时数超过临界日长时就不能开花, 被称之为短日植物^[6]。暗中断试验及现代分子生物学研究表明, 暗期对于光周期现象更为重要, 因而称短日植物为“长夜植物”

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或许更为准确^[7]。此外,还有一些植物为日中性植物,这类植物的开花不受日照长短的影响,在任何日照长度条件下都能正常开花,如棉花、番茄、茄子、四季豆等。

豆科植物是重要的经济作物,为人类提供了重要的蛋白质、油料及淀粉资源,在世界范围内主要种植的有大豆、鹰嘴豆、花生、蚕豆、豌豆、四季豆、扁豆和苜蓿等,其中大豆为世界上最重要的经济作物。本文首先简述模式植物拟南芥与水稻中光周期调控开花机制的最新研究进展,其后重点介绍大豆光周期反应相关的生育期基因的克隆及功能解析,最后回顾了我国在本领域所取得的主要研究进展。

1 拟南芥及水稻中光周期调控开花机制

模式植物拟南芥与水稻光周期方面的研究进展较快,特别在植物感知季节的变化如光照长度及温度的分子机制等方面^[8-9]。*CONSTANS (CO)*是一个光周期调节的重要基因,在植物的生物钟与开花之间起重要的媒介作用^[10-11]。*CO*的表达量受到 *FLAVIN-BINDING*、*KELCH REPEAT*、*F-BOX (FKF1)* 和 *GIGANTEA (GI)* 调控,而 *FKF1* 及 *GI* 的表达量亦受生物钟节律的影响^[12-13]。*FKF1* 和 *GI* 蛋白可形成一个复合体,其稳定性受蓝光调控。在长日照条件下, *FKF1* 激发 *CO* 的转录^[14]。*FT* 蛋白在拟南芥中被证实为可传导的开花素重要组分之一,它可以通过韧皮部从叶片向茎尖或侧芽的顶部输送而触发植株开花^[15-17]。因此,拟南芥在长日照条件下, *CO-FT* 调节通路在光周期调控开花中起主导作用^[12]。

这种 *CO-FT* 作用模式在不同植物种间有一定的保守性,已在水稻^[17-19]、大麦^[19]和欧洲云杉^[20]等多种植物中得到证明。近几年在水稻中研究表明,2个生物调控元件 *Ehd1* (*early heading date 1*)和 *Ghd7* (*for grain number, plant height, and heading date 7*)控制着1对 *FT (Hd3a/RFT1)* 基因的表达来实现感知关键的临界光周期长度^[17]。其中,在早晨的蓝光条件下激发 *Ehd1* 的表达进而激发 *Hd3a* 的转录量^[21]; *Ghd7* 转录产物的高积累可抑制 *Ehd1* 的表达,在短日与长日照不同条件下这种抑制高峰所出现的时段(一个昼夜内)呈现明显的差异^[17,21-22]。

2 大豆生育期及光周期反应相关基因克隆及功能验证

大豆的生育期(开花期与成熟期)特别是开花期

是大豆光周期反应的重要生态指标。经典遗传学研究发现了9个与开花期相关的基因^[23-30],除与“长童期”相关的 *J* 位点^[27]外,其余习惯称为 *E* 系列(*E1* 至 *E8*)基因;特别是 *E1*、*E3*、*E4* 和 *E7* 位点均与大豆光周期敏感性相关联^[24-26,31-33]。在长日条件下,其中 *E3* 位点在不同光质量条件下延迟开花的程度相似,说明 *E3* 位点对光质量并不敏感^[32];而 *E1*、*E4* 和 *E7* 引起的开花延迟则需要红光与远红光量子比较低的光质量条件^[29,32]。这种经光质量通路的光周期调节大豆发育在开花后仍然起作用,因而可以认为光周期对大豆生长的影响贯穿其一生。在众多的 *E* 基因中,大豆生育期基因 *E1* 对大豆的开花期及成熟期的影响最大^[23,33-36], *E1* 位点被遗传定位到连锁群 *C2* 上^[36-38]。近来的精细定位^[38]表明, *E1* 基因位于第6染色体中心粒着丝点(pericentromeric)附近。在这种异染色质区域,遗传重组率低,物理距离与遗传距离的比率较常染色质区域高^[39]。Xia等^[38]用2个含有不同 *E1* 基因型的 Harosoy 近等基因系所建立的群体,成功地实现了该基因的精细图位克隆。研究初期通过1442个个体将 *E1* 基因定位于289 kb区域内,该区域内含有40多个基因。为进一步精细定位,采用手工钻取种子内部组织提取DNA的快速方法,从13760粒种子中获得了10个极其珍贵的重组体;对这10个重组体及后代的精细解析将 *E1* 基因定位于17.4 kb区域内,在该区域内只有1个候选基因^[38]。进一步分析表明, *E1* 基因含有一个双边的(Bipartite)核定位信号(NLS)和DNA结合位点,并含有一个与B3远缘相关的结构域^[38]; *E1* 的表达在短日条件下受到明显抑制,该现象可能与大豆为短日植物关联。*E1* 基因抑制植物开花^[38,40-41], *E1* 基因的变异与开花期表型密切相关^[38]。在已发现的 *E* 系列基因型中, *E1* 基因型抑制开花的能力最强。在 Sakamotowase (坂本早生)等品种的 *E1* 基因DNA序列49核苷酸处出现单碱基缺失引致移码突变,该基因型与及 *E1* 基因整体缺失型 *e1-nl* 均表现出极早的开花及成熟期,我们可将 *e1-fs* 和 *e1-nl* 基因型统称为功能丧失型。在 *e1-as* 基因型中于 *E1* 基因的DNA序列44核苷酸处出现单碱基突变,引发了所编码的氨基酸从 *E1* 的精氨酸到 *e1-as* 的苏氨酸的转变,该位点恰好位于核定位信号区域,致使 *E1* 与 *e1* 蛋白在核及细胞的其他器官的分布呈现差异, *E1* 蛋白主要分布在细胞核中,而 *e1* 蛋白则均匀地分布在细胞核及细胞质中。*e1-as* 基因型的生育期(开花及成熟

期)表型介于 *E1* 与功能丧失型(*e1-fs* 及 *e1-nl*)之间^[38]。随着 *E1* 基因的成功克隆,对其作用机制的深入研究,可进一步揭示大豆独特的光周期反应及开花调控机制。

大豆 *E* 系列基因中, *E4* 是最先被克隆并经功能验证的基因,该基因为光敏色素 *Phytochrome A* 基因 3 个拷贝之一 *GmPHYA2*^[42]。在该基因的第 1 个外显子中插入了类似于 *Ty1/copia-like* 的转座子引致 *E4* 基因的功能缺失,形成 *e4* 基因型。*e4* 基因型需要在隐性 *e3* 基因型同时存在时,才引致光周期不敏感性^[42-43]。但隐性 *e4* 基因型中,植株去黄化现象(de-etiolation)功能没有完全消失,据此推测位于连锁群 O (第 10 染色体)上的拷贝(*GmPHYA1*)可能对植株的去黄化反应仍有部分功能,但与大豆的开花无关;而在拟南芥、豌豆及水稻等中, *PHYA* 基因发生变异可致使去黄化功能完全丧失^[44-47]。

在大豆品种 Misuzudaizu 与中国地方品种秣食豆公(Moshidogong) 503 杂交后衍生出的重组自交系(RIL)群体中,进一步鉴定获得剩余杂合体群体 RHL (residual heterozygous lines)^[48-49],其特点是要研究的 QTL 所在的区域保留着杂合特性,而基因组中的其他位点,特别是与该性状相关的其他 QTL 为纯合型。综合利用 RHL 及其自交后代群体(heterogeneous inbred family, HIF),成功地应用图位克隆法克隆了大豆生育期基因 *E2*^[49]与 *E3*^[48]。结果表明, *E2* 基因为拟南芥 *GIGANTEA* 的 1 个同源基因 *GmGla*^[49], *E3* 基因为光敏色素 *Phytochrome A* 的 3 个拷贝之一 *GmPHYA3*^[48]。*E3* 与 *E4* 同为光敏色素基因,此研究结果证实了 Cober 的推断^[32],同时, *E3* 与 *E4* 还协同调控 *E1* 基因的表达,暗示着 *E1* 基因位于光敏色素基因的下游^[38]。

在大豆的基因组中存在着多个拟南芥 *FT* 同源基因序列,其中 2 个 *FT* 同源序列 *GmFT2a* (*Glyma16g26660*)和 *GmFT5a* (*Glyma16g04830*)被证明对大豆开花起主要促进作用^[50]。转录分析表明,在短日条件下, *GmFT2a* 和 *GmFT5a* 在黎明后 3~4 h 表达量达峰值^[40-41,50],但在长日照条件下, *GmFT2a* 和 *GmFT5a* 的表达量大幅下调。*GmFT5a* 和 *GmFT2a* 在功能上出现协调分工,在长日条件下植株生长后期只有 *GmFT5a* 表达量较大而引致开花^[50]。最近, Sun 等^[51]发现 *GmFT2a* 表达受光周期所调控,且与开花的持续性有关。

3 大豆中光周期调控途径的研究进展

已有研究显示一个健全的生物钟有利于植物的生存及生物量的积累;植物利用生物钟将生物过程与外界环境如光周期相耦合,使其获得感知与预测其环境因素如日照长短的变化的能力^[52-53]。生物钟一般由输入通路、中央振荡器及输出途径等组成。这种输入通路接受环境中的相关信号,如光照及温度,经中央振荡器转换成一个生物钟固定幅频,再传至下游的输出途径来产生各种生物节律^[54-55]。

大豆植物光受体蛋白 *GmPHYA* 和 *GmCRY1* 可感受不同光质量(即不同光波长的光线)。在大豆的基因组中还存在另外 3 种家族成员光受体 *ZEITLUPE (ZTL)*、*FLAVIN-BINDING KELCH REPEAT F-BOX 1 (FKF1)*和 *LOV-KELCH PROTEIN2 (LKP2)*^[56-57]。在大豆的 *CRYPTOCHROME 1 (CRY1)*同源基因中,只有 *GmCRY1a* (*Glyma04g11010*)(不是 *GmCRY2a*)具有较强诱导花原基产生的能力,同时能感知不同日照长度^[58]; *GmCRY1a* 基因的表达与大豆不同生态型调控开花的光周期通路相关^[58]。然而,至今尚未观察到该基因与已知的开花期 QTL 相关联^[59],因而其调控开花的功能有待进一步验证。大豆中的 *GmPHYA3* 和 *GmPHYA2* 是由 *E3* 和 *E4* 所编码^[42,48],两者均与大豆开花及光周期反应相关联,但对不同光质量的反应存在着明显的差异,暗示两者调控开花的途径既彼此独立而又相互重叠^[60-61]。

拟南芥中与中央振荡器相关联的重要基因^[62]在大豆中均已鉴定出相应的同源基因^[40,57,63],其中中央振荡子为相互功能部分重叠的 MYB 转录因子, *LATE ELONGATED HYPOCOTYL (LHY)* 和 *CIRCADIAN CLOCK ASSOCIATED 1 (CCA1)*^[56-57]。在大豆基因组中含有 4 个 MYB 转录因子 *LHY1/CCA1-like* 基因,这些基因的表达显示了生物节律,因而推测其功能亦具有保守性^[41,63],但其与开花及日长的反应有待进一步验证。大豆中存在着 2 个或多个拷贝的 *GI*、*FLAVIN-BINDING KELCH REPEAT F-BOX1 (FKF1)*、*CYCLING OF DOF FACTOR 1 (CDF1)*、*CO* 和 *FT* 的同源基因^[40-41,56-57,63]。水稻中,在短日条件下 *CO (Hd1)*促进 *FT (Hd3)* 的表达,在长日下会转变为抑制^[64]。在蒺藜苜蓿(*Medicago truncatula*)中,一个类似于 *CO* 的同源基因所在区域存在着一个开花期 QTL^[65]。然而,在另一些植物中, *CO* 或 *CO* 同源基因被证明并不参与调控植株的开花^[66-67]。在大豆中,有较多的 *CO* 同源基因序列存在,其中

Thakare 等^[40]研究表明 Glyma08g28370 和 Glyma18g-51320 与拟南芥 COL2 蛋白同源性最高^[62,68], 但 Glyma08g28370 或 Glyma13g01290 表达无明显节律或表达量极低^[41]; GmCOL4 (Glyma20g07050) 和其他 CO 同源序列呈现昼夜节律变化^[41]。Huang 等^[69]和张清哲等^[71]亦对多个大豆中的 CO 同源基因进行了深入研究, 但其在光周期调控途径中的功能有待进一步验证。目前还没有发现已有的 QTL 与 GmCOLs 所在的位点紧密连锁。

在豌豆中, GI 同源基因(LATE BLOOMER1)调控光周期反应及开花^[72]。虽然大豆 E2 基因已被证实是 GIGANTEA 的同源序列 GmGla, 但相关的功能有待深入研究。所以, 从目前的研究结果来看, 人们还不完全清楚 GI-CO-FT 模式在大豆光周期反应或开花调控中的作用。在拟南芥与水稻中, 不同途径均在不同程度上调控开花途径的中心节点基因 FT 的表达, 其 FT 蛋白转移至茎尖生长点使其发生从营养生长向生殖生长的转变^[9,73]。虽然成花素(Florigen)在不同作物间是保守的, 但其调节机制却因植物而异^[67]。

嫁接试验所表明的诱导与抑制因素^[74-76]可能分别与近代分子生物学已明确的 GmFTs 及 E1 基因相对应。由于在拟南芥及水稻中没有 E1 的高度同源基因, 对该基因的深入研究是解析大豆开花期调控基因网络的重要一环。特别是在分子调控机制方面有待进一步解析, 如 E1 是直接还是间接调控 FT, 以及两者的相互作用是否依存 CO 蛋白等。

4 大豆中开花期相关基因的变异及功能分化

大豆为古四倍体, 拟南芥中许多与开花相关的基因在大豆中均有 2 个或 2 个以上拷贝存在^[39,56,76]。近年研究表明, 功能分化(subfunctionalization)^[77]及不等量表达^[78]是高度同源基因或多拷贝基因继续存在于基因组的重要因素^[79]。大豆中的 GmTFL2 虽然与拟南芥的 TFL 同源性最高的序列, 但两物种间其功能出现了分化, GmTFL2 对大豆生长习性没有明显的影响^[77,80]。E3 与 E4 基因虽然同为光敏色素, 但对光质量的反应既重叠又互不相同^[32,42,48]。大豆中很多拟南芥开花期基因的同源序列功能有待研究, 如 GmPHYA1^[43]及 E1 基因的 2 个拷贝^[38]。

在拟南芥与水稻中重要基因 CO、FT 和另外一些相关基因的变异会引起开花期及光周期反应发生

变化^[8,14,81-83]。除 E2 以外, 在中国、美国及日本所育成的品种及地方品种中鉴定出丰富的 E 基因及其生长习性基因的基因型, 预示着这些变异可能来源于自然变异或驯化过程中的人工选择。在已发现的与开花相关的基因中, 只有显性的 E6 和 J 基因表现出早花表型, 而隐性的 e6 和 j 显示出“长童”即极迟开花特性^[27-28], 因而使人们产生联想, 该类基因可能与 GmFTs 或关联基因的功能缺失相关, 然而这种假设有待证实。总体来看, 大豆适应于不同环境如光周期长度或不同纬度的广适应性能力来源于光周期反应相关的基因数量多、变异大及同源序列间的功能分化。

5 我国大豆光周期研究历史回顾

几乎在人们发现光周期现象的同时, 1917 年我国诞生了一位著名的大豆光周期研究先驱者——王金陵教授。从 20 世纪 40 年代起, 王金陵教授就对我国大豆光周期现象进行了观察, 分别于 1942 年和 1956 年先后发表了《大豆之光期性》^[84]和《中国南北地区大豆光照生态类型的分布点》^[85]等重要研究论文。在 20 世纪 60 年代, 我国大豆光周期研究重点集中在野生大豆及栽培大豆的光照生态类型、大豆主要形态和产量性状的形成等方面。研究明确了适应北方高纬度地区种植的大豆品种, 短日性均弱; 而在光照时数渐短的低纬度地区, 品种的短日性愈强, 这些特性是源于长期自然选择和人工选择的结果。这些结果为我国科研人员最早结合大豆生产实际而明确大豆光周期反应的规律, 成为国内大豆引种、资源保存、栽培区划和确定合理播期等技术措施的理论依据^[86]。在 60 余年的大豆育种生涯中, 王金陵教授育成的东农 44、东农 49、东大 1 号和东大 2 号等早熟大豆品种, 适宜于在北部高寒长日照有效积温低地区推广种植, 将我国大豆种植的北界向前推进了 100 多千米。我国其他研究学者如盖钧镒院士等^[87]以美洲一套不同熟期组代表品种为对照, 将中国大豆品种熟期组的划分与国际一般分类法相接轨。许多研究者对我国不同区域来源的大豆主栽品种及野生资源的光周期特性进行了有关试验, 证实了光周期不敏感性的强弱排序是北方春豆>南方春豆和江淮春豆>黄淮夏豆>南方夏豆>南方秋豆^[88-89], 并总结出了异地引种的一般原则。宁慧霞等^[90]利用国外引进的多组不同生育期近等基因系, 分析其基因型与分子标记间的连锁关系, 并根据品种的分

标记预测了大豆品种的生育期基因的基因型。王金陵教授培养的学生常汝镇、杨庆凯、韩天富和邱丽娟等在大豆光周期及生育期相关研究领域亦做出了的重要贡献^[88,90]。近年来,中国科学院东北地理与农业生态研究所的夏正俊等^[38,48-49]、刘宝辉等^[42,77]及孔凡江等^[50]等与日本科学家原田久也及阿部纯领导的研究小组进行了长期密切的合作,对成功破译与大豆光周期反应相关 *E1*、*E2*、*E3*、*E4* 及 *GmFTs* 等生育期基因做出了突出的贡献。

6 大豆生育期基因与其他重要农艺性状间的关系

遗传控制大豆生育期的研究成果对于大豆生产实践及育种尤为重要,大豆生育期基因对大豆产量与品种的适宜种植范围密切相关^[85-87]。大豆在开花后顶端生长点继续保持营养生长称之为无限生长习性;相反,在植株开花后顶端生长点迅速转化为花序,植株停止营养生长,称之为有限生长习性。控制大豆生长习性的主要基因位点为 *Dt1*,由 *GmTFL1* 基因所控制^[77,87]。同时,另一个尚未明确的基因位点 *Dt2* 亦协同 *Dt1* 调控大豆的生长习性,具 *Dt1Dt2* 基因型的品种其表现型介于有限与无限生长习性之间并被称之为亚有限生长习性^[77]。一般而言野生大豆具无限生长习性,而栽培大豆大多为有限生长习性或亚有限生长习性。生长习性与植株高度及结荚数直接相关,因而又称为结荚习性,是联系大豆开花期与产量性状的桥梁性状。相同产量的有限生长习性品种总比无限生长习性品种的株高低^[77,91]。近年来的研究表明,生育期基因或位点还直接影响大豆的产量性状如单株的分枝数,定位结果表明 *E1* 及 *E3* 基因位点均存在着影响分枝数的主要 QTL^[92]。相关近等基因系^[93-94]研究发现, *E* 基因系列还与多种其他生理效应相关联^[95],如植株的产量^[37,96],大豆的闭花授粉性(cleistogamy)^[97]及冷害的耐受性^[98-99]等。因而,在克隆控制大豆产量或其他性状的基因时,有必要明确大豆生育期基因的基因型以排除其干扰。随着研究的深入,生育期基因与大豆重要农艺性状间的互作分子机制将会越来越清楚。

7 大豆光周期研究未来发展趋势

自 Woodworth^[100]报道了大豆中具有能影响其成熟的基因以来,科学家陆续检测出多个影响大豆开花期及成熟期的 QTL 基因。迄今已明确 *E1*、*E2*、

E3、*E4*、*GmFT2a/GmFT5a* 和 *Dt1* 等位点的功能基因,并进行了相关的功能验证。但人们尚不知晓 *E5*、*E6*、*E7*、*E8*、*J* 及新近发现的 QTL 的分子基础,虽然已有研究者根据基因组信息对相关位点进行了一些推测,但尚未得到实验数据的证实。适应于不同纬度即不同光周期长度的大豆品种,需要具有不同程度的光周期不敏感性。现代分子生物学解析表明,这种光周期不敏感性源于大豆的主要生育期基因或与之相关的调控基因的变异及组合。同时,人们尚不明确众多拟南芥开花期同源基因在大豆中的生理功能。目前随着大豆基因组信息量迅速积累,单碱基突变多态性(SNP)可大大提高图位法克隆或全基因组关联分析克隆 QTL 基因的效率^[101-106]。随着大豆中生育期基因 *E1*、*E2*、*E3* 和 *E4* 主要功能基因及相互关系的明确,有理由相信在大豆光周期现象发现的百年大典之际,人们有望对该现象的本质有更深层次的认识。

References

- [1] Garner W W, Allard H A. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *J Agric Res*, 1920, 18: 553-606
- [2] Owen F V. Inheritance studies in soybeans: II. Glabrousness, color of pubescence, time of maturity, and linkage relations. *Genetics*, 1927, 12: 519-523
- [3] Garner W W, Allard H A. Comparative responses of long-day and short-day plants to relative length of day and night. *Plant Physiol*, 1933, 8: 347-356
- [4] Heinze P H, Parker M W, Borthwick H A. Floral initiation in Biloxi soybean as influenced by grafting. *Bot Gaz*, 1942, 103: 518-530
- [5] Coulter M W, Hamner K C. Photoperiodic flowering response of Biloxi soybean in 72-hour cycles. *Plant Physiol*, 1964, 39: 848-856
- [6] Mauseth J D. Botany: an Introduction to Plant Biology, 3rd edn. Sudbury, MA: Jones and Bartlett Learning, 2003. pp 422-427
- [7] Hamner K C. Interrelation of light and darkness in photoperiodic induction. *Bot Gaz*, 1940, 101: 658-687
- [8] Hayama R, Coupland G. The molecular basis of diversity in the photoperiodic flowering responses of *Arabidopsis* and rice. *Plant Physiol*, 2004, 135: 677-684
- [9] Tsuji H, Taoka K, Shimamoto K. Regulation of flowering in rice: two florigen genes, a complex gene network, and natural variation. *Curr Opin Plant Biol*, 2011, 14: 45-52

- [10] Samach A, Onouchi H, Gold S E, Ditta G S, Schwarz-Sommer Z, Yanofsky M F, Coupland G. Distinct roles of CONSTANS target genes in reproductive development of *Arabidopsis*. *Science*, 2000, 288: 1613–1616
- [11] Valverde F, Mouradov A, Soppe W, Ravenscroft D, Samach A, Coupland G. Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. *Science*, 2004, 303: 1003–1006
- [12] Fornara F, de Montaigu A, Coupland G. SnapShot: control of flowering in *Arabidopsis*. *Cell*, 2010, 141: 550. e1–2
- [13] Imaizumi T, Schultz T F, Harmon F G, Ho L A, Kay S A. FKF1 F-box protein mediates cyclic degradation of a repressor of CONSTANS in *Arabidopsis*. *Science*, 2005, 309: 293–297
- [14] Sawa M, Nusinow D A, Kay S A, Imaizumi T. FKF1 and GIGANTEA complex formation is required for day-length measurement in *Arabidopsis*. *Science*, 2007, 318: 261–265
- [15] Mathieu J, Warthmann N, Küttner F, Schmid M. Export of FT protein from phloem companion cells is sufficient for floral induction in *Arabidopsis*. *Curr Biol*, 2007, 17: 1055–1060
- [16] Tamaki S, Matsuo S, Wong H L, Yokoi S, Shimamoto K. Hd3a protein is a mobile flowering signal in rice. *Science*, 2007, 316: 1033–1036
- [17] Itoh H, Nonoue Y, Yano M, Izawa T. A pair of floral regulators sets critical day length for *Hd3a* florigen expression in rice. *Nat Genet*, 2010, 42: 635–638
- [18] Notaguchi M, Abe M, Kimura T, Daimon Y, Kobayashi T, Yamaguchi A, Tomita Y, Dohi K, Mori M, Araki T. Long-distance, graft-transmissible action of *Arabidopsis* FLOWERING LOCUS T protein to promote flowering. *Plant Cell Physiol*, 2008, 49: 1645–1658
- [19] Griffiths S, Dunford R P, Coupland G, Laurie D A. The evolution of *CONSTANS-Like* gene families in barley, rice, and *Arabidopsis*. *Plant Physiol*, 2003, 131: 1855–1867
- [20] Gyllenstrand N, Clapham D, Källman T, Lagercrantz U. A Norway spruce *FLOWERING LOCUS T* homolog is implicated in control of growth rhythm in conifers. *Plant Physiol*, 2007, 144: 248–257
- [21] Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M. Hd3a, a rice ortholog of the *Arabidopsis* FT gene, promotes transition to flowering downstream of *Hd1* under short-day conditions. *Plant Cell Physiol*, 2002, 43: 1096–1105
- [22] Xue W, Xing Y, Weng X, Zhao Y, Tang W, Wang L, Zhou H, Yu S, Xu C, Li X, Zhang Q. Natural variation in *Ghd7* is an important regulator of heading date and yield potential in rice. *Nat Genet*, 2008, 40: 761–767
- [23] Bernard R L. Two major genes for time of flowering and maturity in soybeans. *Crop Sci*, 1971, 11: 242–244
- [24] Buzzell R I. Inheritance of a soybean flowering response to fluorescent-daylength conditions. *Can J Genet Cytol*, 1971, 13: 703–707
- [25] Buzzell R I, Voldeng H D. Inheritance of insensitivity to long day length. *Soybean Genet Newsl*, 1980, 7: 26–29
- [26] McBlain B A, Bernard R L, Cremeens C R, Korczak J F. A procedure to identify genes affecting maturity using soybean isoline testers. *Crop Sci*, 1987, 27: 1127–1132
- [27] Ray J D, Hinson K, Mankono J E B. Genetic control of a long-juvenile trait in soybean. *Crop Sci*, 1995, 35: 1001–1006
- [28] Bonato E R, Vello N A. *E6*, a dominant gene conditioning early flowering and maturity in soybeans. *Genet Mol Biol*, 1999, 22: 229–232
- [29] Cober E R, Voldeng H D. A new soybean maturity and photoperiod-sensitivity locus linked to *E1* and *T*. *Crop Sci*, 2001, 41: 698–701
- [30] Cober E R, Molnar S J, Charette M, Voldeng H D. A new locus for early maturity in soybean. *Crop Sci*, 2010, 50: 524–527
- [31] Cober E R, Tanner J W, Voldeng H D. Genetic control of photoperiod response in early-maturing near-isogenic soybean lines. *Crop Sci*, 1996, 36: 601–605
- [32] Cober E R, Tanner J W, Voldeng H D. Soybean photoperiod-sensitivity loci respond differentially to light quality. *Crop Sci*, 1996b, 36: 606–610
- [33] Abe J, Xu D H, Miyano A, Komatsu K, Kanazawa A, Shimamoto Y. Photoperiod-insensitive Japanese soybean landraces differ at two maturity loci. *Crop Sci*, 2003, 43: 1300–1304
- [34] Stewart D W, Cober E R, Bernard R L. Modeling genetic effects on the photothermal response of soybean phenological development. *Agron J*, 2003, 95: 65–70
- [35] Yamanaka N, Ninomiya S, Hoshi M, Tsubokura Y, Yano M, Nagamura Y, Sasaki T, Harada K. An informative linkage map of soybean reveals QTLs for flowering time, leaflet morphology and regions of segregation distortion. *DNA Res*, 2001, 8: 61–72
- [36] Yamanaka N, Watanabe S, Toda K, Hayashi M, Fuchigami H, Takahashi R, Harada K. Fine mapping of the *FT1* locus for soybean flowering time using a residual heterozygous line derived from a recombinant inbred line. *Theor Appl Genet*, 2005, 110: 634–639
- [37] Mansur L M, Orf J H, Chase K, Jarvik T, Cregan P B, Lark K G. Genetic mapping of agronomic traits using recombinant inbred lines of soybean. *Crop Sci*, 1996, 36: 1327–1336
- [38] Xia Z, Watanabe S, Yamada T, Tsubokura Y, Nakashima H, Zhai H, Anai T, Sato S, Yamazaki T, Lü S, Wu H, Tabata S, Harada K.

- Positional cloning and characterization reveal the molecular basis for soybean maturity locus *E1* that regulates photoperiodic flowering. *Proc Natl Acad Sci USA*, 2012, DOI: 10.1073/pnas.1117982109
- [39] Schmutz J, Cannon S B, Schlueter J, Ma J, Mitros T, Nelson W, Hyten D L, Song Q, Thelen J J, Cheng J, Xu D, Hellsten U, May G D, Yu Y, Sakurai T, Umezawa T, Bhattacharyya M K, Sandhu D, Valliyodan B, Lindquist E, Peto M, Grant D, Shu S, Goodstein D, Barry K, Futrell-Griggs M, Abernathy B, Du J, Tian Z, Zhu L, Gill N, Joshi T, Libault M, Sethuraman A, Zhang X C, Shinozaki K, Nguyen H T, Wing R A, Cregan P, Specht J, Grimwood J, Rokhsar D, Stacey G, Shoemaker R C, Jackson S A. Genome sequence of the palaeopolyploid soybean. *Nature*, 2010, 463: 178–183
- [40] Thakare D, Kumudini A, Dinkins R D. Expression of flowering-time genes in soybean *E1* near-isogenic lines under short and long day conditions. *Planta*, 2010, 231: 951–963
- [41] Thakare D, Kumudini A, Dinkins R D. The alleles at the *E1* locus impact the expression pattern of two soybean *FT*-like genes shown to induce flowering in *Arabidopsis*. *Planta*, 2011, 234: 933–943
- [42] Liu B, Kanazawa A, Matsumura H, Takahashi R, Harada K, Abe J. Genetic redundancy in soybean photoresponses associated with duplication of the *phytochrome A* gene. *Genetics*, 2008, 180: 995–1007
- [43] Kanazawa A, Liu B, Kong F, Arase S, Abe J. Adaptive evolution involving gene duplication and insertion of a novel *Ty1/copia*-like retrotransposon in soybean. *J Mol Evol*, 2009, 69: 164–175
- [44] Neff M M, Chory J. Genetic interactions between phytochrome A, phytochrome B, and cryptochrome 1 during *Arabidopsis* development. *Plant Physiol*, 1998, 118: 27–35
- [45] Weller J L, Murfet I C, Reid J B. Pea mutants with reduced sensitivity to far-red light define an important role for phytochrome A in day-length detection. *Plant Physiol*, 1997, 114: 1225–1236
- [46] Weller J L, Beauchamp N, Kerckhoffs L H, Platten J D, Reid J B. Interaction of phytochromes A and B in the control of deetiolation and flowering in pea. *Plant J*, 2001, 26: 283–294
- [47] Takano M, Inagaki N, Xie X, Yuzurihara N, Hihara F, Ishizuka T, Yano M, Nishimura M, Miyao A, Hirochika H, Shinomura T. Distinct and cooperative functions of phytochromes A, B, and C in the control of deetiolation and flowering in rice. *Plant Cell*, 2005, 17: 3311–3325
- [48] Watanabe S, Hideshima R, Xia Z, Tsubokura Y, Sato S, Nakamoto Y, Yamanaka N, Takahashi R, Ishimoto M, Anai T, Tabata S, Harada K. Map-based cloning of the gene associated with the soybean maturity locus *E3*. *Genetics*, 2009, 182: 1251–1262
- [49] Watanabe S, Xia Z, Hideshima R, Tsubokura Y, Sato S, Yamanaka N, Takahashi R, Anai T, Tabata S, Kitamura K, Harada K. A map-based cloning strategy employing a residual heterozygous line reveals that the *GIGANTEA* gene is involved in soybean maturity and flowering. *Genetics*, 2011, 188: 395–407
- [50] Kong F, Liu B, Xia Z, Sato S, Kim B M, Watanabe S, Yamada T, Tabata S, Kanazawa A, Harada K, Abe J. Two Coordinately regulated homologs of *FLOWERING LOCUS T* are involved in the control of photoperiodic flowering in soybean. *Plant Physiol*, 2010, 154: 1220–1231
- [51] Sun H, Jia Z, Cao D, Jiang B, Wu C, Hou W, Liu Y, Fei Z, Zhao D, Han T. *GmFT2a*, a soybean homolog of *FLOWERING LOCUS T*, is involved in flowering transition and maintenance. *PLoS One*, 2011, 6: e29238
- [52] Harmer S L. The circadian system in higher plants. *Annu Rev Plant Biol*, 2009, 60: 357–377
- [53] McClung C R, Gutierrez R A. Network news: prime time for systems biology of the plant circadian clock. *Curr Opin Genet Dev*, 2010, 20: 588–598
- [54] Bell-Pedersen D, Cassone V M, Earnest D J, Golden S S, Hardin P E, Thomas T L, Zoran M J. Circadian rhythms from multiple oscillators: lessons from diverse organisms. *Nat Rev Gene*, 2005, 6: 544–556
- [55] Más P. Circadian clock function in *Arabidopsis thaliana*: time beyond transcription. *Trends Cell Biol*, 2008, 18: 273–81
- [56] Hecht V, Foucher F, Ferrandiz C, Macknight R, Navarro C, Morin J, Vardy M E, Ellis N, Beltran J P, Rameau C, Weller J L. Conservation of *Arabidopsis* flowering genes in model legumes. *Plant Physiol*, 2005, 137: 1420–1434
- [57] Quecini V, Zucchi M I, Baldin J, Vello N A. Identification of soybean genes involved in circadian clock mechanism and photoperiodic control of flowering time by *in silico* analyses. *J Integr Plant Biol*, 2007, 49: 1640–1653
- [58] Zhang Q, Li H, Li R, Hu R, Fan C, Chen F, Wang Z, Liu X, Fu Y, Lin C. Association of the circadian rhythmic expression of *GmCRY1a* with a latitudinal cline in photoperiodic flowering of soybean. *Proc Natl Acad Sci USA*, 2008, 105: 21028–21033
- [59] Matsumura H, Kitajima H, Akada S, Abe J, Minaka N, Takahashi R. Molecular cloning and linkage mapping of cryptochrome multigene family in soybean. *Plant Genome*, 2009, 2: 271–281
- [60] Cerdán P D, Chory J. Regulation of flowering time by light quality. *Nature*, 2003, 423: 881–885
- [61] Xia Z J, Zhai H, Liu B H, Kong F J, Yuan X H, Wu H Y, Cober E, Harada K. Molecular identification of genes controlling flower-

- ing time, maturity, and photoperiod response in soybean. *Plant Syst Evol*, 2012, 298: 1217–1227
- [62] Hayama R, Coupland G. Shedding light on the circadian clock and the photoperiodic control of flowering. *Curr Opin Plant Biol*, 2003, 6: 13–19
- [63] Liu H, Wang H, Gao P, Xü J, Xü T, Wang J, Wang B, Lin C, Fu Y F. Analysis of clock gene homologs using unifoliolates as target organs in soybean (*Glycine max*). *J Plant Physiol*, 2009, 166: 278–289
- [64] Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y, Sasaki T. *Hd1*, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the *Arabidopsis* flowering time gene *CONSTANS*. *Plant Cell*, 2000, 12: 2473–2484
- [65] Pierre J B, Bogard M, Herrmann D, Huyghe C, Julier B. A *CONSTANS-like* gene candidate that could explain most of the genetic variation for flowering date in *Medicago truncatula*. *Mol Breed*, 2011, 28: 25–35
- [66] Ben-Naim O, Eshed R, Parnis A, Teper-Bamnolker P, Shalit A, Coupland G, Samach A, Lifschitz E. The CCAAT binding factor can mediate interactions between *CONSTANS*-like proteins and DNA. *Plant J*, 2006, 46: 462–476
- [67] Hayama R, Agashe B, Luley E, King R, Coupland G. A circadian rhythm set by dusk determines the expression of *FT* homologs and the short-day photoperiodic flowering response in *Pharbitis*. *Plant Cell*, 2007, 19: 2988–3000
- [68] Suárez-López P, Wheatley K, Robson F, Onouchi H, Valverde F, Coupland G. *CONSTANS* mediates between the circadian clock and the control of flowering in *Arabidopsis*. *Nature*, 2001, 410: 1116–1120
- [69] Huang G W, Ma J H, Han Y Z, Chen X J, Fu Y F. Cloning and expression analysis of the soybean *CO-like* gene *GmCOL9*. *Plant Mol Bio Rep*, 2011, 29: 352–359
- [70] Liu L, Ma J, Han Y, Chen X, Fu Y F. The isolation and analysis of a soybean *CO* homologue *GmCOL10*. *Russian J Plant Physiol*, 2011, 58: 330–336
- [71] Zhang Q-Z(张清哲), Ma J-H(马锦花), Chen X-J(陈新建), Fu Y-F(傅永福). Cloning and analysis of *GmCOL4* gene in *Glycine max* L. *Acta Agron Sin* (作物学报), 2010, 36(4): 539–548 (in Chinese with English abstract)
- [72] Hecht V, Knowles C L, Vander Schoor J K, Liew L C, Jones S E, Lambert M J, Weller J L. Pea *LATE BLOOMER1* is a *GIGANTEA* ortholog with roles in photoperiodic flowering, deetiolation, and transcriptional regulation of circadian clock gene homologs. *Plant Physiol*, 2007, 144: 648–661
- [73] Castillejo C, Pelaz S. The balance between *CONSTANS* and *TEMPRANILLO* activities determines *FT* expression to trigger flowering. *Curr Biol*, 2008, 18: 1338–1343
- [74] Cober E R, Curtis D F. Both promoters and inhibitors affected flowering time in grafted soybean flowering-time isolines. *Crop Sci*, 2003, 43: 886–891
- [75] Przepiorkowski T, Martin S K S. The effect of grafting on the flowering of near-isogenic lines of soybean. *Crop Sci*, 2003, 43: 1760–1763
- [76] Shoemaker R C, Polzin K, Labate J, Specht J, Brummer E C, Olson T, Young N, Concibido V, Wilcox J, Tamulonis J P, Kochert G, Boerma H R. Genome duplication in soybean (*Glycine* subgenus *soja*). *Genetics*, 1996, 144: 329–338
- [77] Tian Z, Wang X, Lee R, Li Y, Specht J E, Nelson RL, McClean P E, Qiu L, Ma J. Artificial selection for determinate growth habit in soybean. *Proc Natl Acad Sci USA*, 2010, 107: 8563–8568
- [78] Schlueter J A, Scheffler B E, Schlueter S D, Shoemaker R C. Sequence conservation of homoeologous bacterial artificial chromosomes and transcription of homoeologous genes in soybean (*Glycine max* L. Merr). *Genetics*, 2006, 174: 1017–1028
- [79] Du J, Tian Z, Sui Y, Zhao M, Song Q, Cannon S B, Cregan P, Ma J. Pericentromeric effects shape the patterns of divergence, retention, and expression of duplicated genes in the paleopolyploid soybean. *Plant Cell*, 2012, 24: 21–32
- [80] Liu B, Watanabe S, Uchiyama T, Kong F, Kanazawa A, Xia Z, Nagamatsu A, Arai M, Yamada T, Kitamura K, Masuta C, Harada K, Abe J. The soybean stem growth habit gene *Dt1* is an ortholog of *Arabidopsis* *TERMINAL FLOWER1*. *Plant Physiol*, 2010, 153: 198–210
- [81] Le Corre V, Roux F, Reboud F. DNA polymorphism at the *FRIGIDA* gene in *Arabidopsis thaliana*: Extensive nonsynonymous variation is consistent with local selection for flowering time. *Mol Biol Evol*, 2002, 19: 1261–1271
- [82] Doi K, Izawa T, Fuse T, Yamanouchi U, Kubo T, Shimatani Z, Yano M, Yoshimura A. *Ehd1*, a B-type response regulator in rice, confers short-day promotion of flowering and controls *FT-like* gene expression independently of *Hd1*. *Genes Dev*, 2004, 18: 926–936
- [83] Takahashi Y, Teshima K M, Yokoi S, Innan H, Shimamoto K. Variations in *Hd1* proteins, *Hd3a* promoters, and *Ehd1* expression levels contribute to diversity of flowering time in cultivated rice. *Proc Natl Acad Sci USA*, 2009, 106: 4555–4560
- [84] Wang J-L(王金陵). Photoperiodic response in soybean. *Agric-Forest Gazeta* (农林新报), 1942, 19–30 (in Chinese)
- [85] Wang J-L(王金陵), Wu Y-X(武镛祥), Wu H-L(吴和礼), Sun S-C(孙善澄). Analysis on photoperiod ecotypes of cultivated

- soybean originating from different locations of China. *Acta Agric Sin* (农业学报), 1956, 7(3): 169–180 (in Chinese)
- [86] Wang J-L(王金陵), Zhu Q-C(祝其昌). Preliminary study on the inheritance of soybean maturity. *Acta Agron Sin* (作物学报), 1963, 2(3): 333–336 (in Chinese with English abstract)
- [87] Gai J-Y(盖钧镒), Wang Y-S(汪越胜), Zhang M-C(张孟臣), Wang J-A(王继安), Chang R-Z(常汝镇). Studies on the classification of maturity groups of soybeans in China. *Acta Agron Sin* (作物学报), 2001, 27(3): 286–292 (in Chinese with English abstract)
- [88] Wang Y(王英), Wu C-X(吴存祥), Zhang X-M(张学明), Wang Y-P(王云鹏), Han T-F(韩天富). Effects of soybean major maturity genes under different photoperiods. *Acta Agron Sin* (作物学报), 2008, 34: 1160–1168 (in Chinese with English abstract)
- [89] Han T-F(韩天富), Wang J-L(王金陵). A study on the responses of different ecotypes of Chinese soybean to post-flowering photoperiod. *Acta Agron Sin* (作物学报), 1996, 22: 20–26 (in Chinese with English abstract)
- [90] Ning H-X(宁慧霞), Li Y-H(李英慧), Liu Z-X(刘章雄), Chang R-Z(常汝镇), Guan R-X(关荣霞), Luo S-P(罗淑萍), Qiu L-J(邱丽娟). Deducing maturity genotype of the Chinese soybean varieties. *Acta Agron Sin* (作物学报) 2008, 34(3): 382–388 (in Chinese with English abstract)
- [91] Cober E R, Morrison M J. Regulation of seed yield and agronomic characters by photoperiod sensitivity and growth habit genes in soybean. *Theor Appl Genet*, 2010, 120: 1005–1012
- [92] Sayama T, Hwang T Y, Yamazaki H, Yamaguchi N, Komatsu K, Takahashi M, Suzuki C, Miyoshi T, Tanaka Y, Xia Z, Tsukubura Y, Watanabe S, Harada K, Funatsuki H, Ishimoto M. Mapping and comparison of quantitative trait loci for soybean branching phenotype in two locations. *Breed Sci*, 2010, 60: 380–389
- [93] Upadhyay A P, Asumadu H, Ellis R H. A Characterization of photothermal flowering responses in maturity isolines of soybean [*Glycine max* (L.) Merrill] cv. Clark. *Ann Bot*, 1994, 74: 87–96
- [94] Upadhyay A P, Summerfield R H, Ellis R H, Roberts E H, Qi A. Variation in the durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering among eight maturity isolines of soybean [*Glycine max* (L.) Merrill]. *Ann Bot*, 1994, 74: 97–101
- [95] Curtis D F, Tanner J W, Luzzi B M, Hume D J. Agronomic and phenological differences of soybean isolines differing in maturity and growth habit. *Crop Sci*, 2000, 40: 1624–1629
- [96] Saindon G, Beversdorf W D, Voldeng H D. Adjustment of the soybean phenology using the *E4* locus. *Crop Sci*, 1989, 29: 1361–1365
- [97] Khan N A, Githiri S M, Benitez E R, Abe J, Kawasaki S, Hayashi T, Takahashi R. QTL analysis of cleistogamy in soybean. *Theor Appl Genet*, 2008, 117: 479–487
- [98] Takahashi R, Abe J. Soybean maturity genes associated with seed coat pigmentation and cracking in response to low temperatures. *Crop Sci*, 1999, 39: 1657–1662
- [99] Githiri S M, Yang D, Khan N A, Xu D, Komatsuda T, Takahashi R. QTL analysis of low temperature induced browning in soybean seed coats. *J Hered*, 2007, 98: 360–366
- [100] Woodworth C M. Inheritance of growth habit, pod color, and flowering color in soybean. *J Am Soc Agron*, 1923, 15: 485–495
- [101] Kim M Y, Lee S, Van K, Kim T H, Jeong S C, Choi I Y, Kim D S, Lee Y S, Park D, Ma J, Kim W Y, Kim B C, Park S, Lee K A, Kim D H, Kim K H, Shin J H, Jang Y E, Kim K D, Liu W X, Chaisan T, Kang Y J, Lee Y H, Kim K H, Moon J K, Schmutz J, Jackson S A, Bhak J, Lee S H. Whole-genome sequencing and intensive analysis of the undomesticated soybean (*Glycine soja* Sieb. and Zucc.) genome. *Proc Natl Acad Sci USA*, 2010, 107: 22032–22037
- [102] Lam H M, Xu X, Liu X, Chen W, Yang G, Wong F L, Li M W, He W, Qin N, Wang B, Li J, Jian M, Wang J, Shao G, Wang J, Sun S S, Zhang G. Resequencing of 31 wild and cultivated soybean genomes identifies patterns of genetic diversity and selection. *Nat Genet*, 2010, 42: 1053–1059
- [103] Choi I Y, Hyten D L, Matukumalli L K, Song Q, Chaky J M, Quigley C V, Chase K, Lark K G, Reiter R S, Yoon M S, Hwang E Y, Yi S I, Young N D, Shoemaker R C, van Tassell C P, Specht J E, Cregan P B. A soybean transcript map: gene distribution, haplotype and single-nucleotide polymorphism analysis. *Genetics*, 2007, 176: 685–696
- [104] Haun W J, Hyten D L, Xu W W, Gerhardt D J, Albert T J, Richmond T, Jeddeloh J A, Jia G, Springer N M, Vance C P, Stupar R M. The composition and origins of genomic variation among individuals of the soybean reference cultivar Williams 82. *Plant Physiol*, 2011, 155: 645–655
- [105] Libault M, Farmer A, Joshi T, Takahashi K, Langley R J, Franklin L D, He J, Xu D, May G, Stacey G. An integrated transcriptome atlas of the crop model *Glycine max*, and its use in comparative analyses in plants. *Plant J*, 2010, 63: 86–99
- [106] Wong C E, Singh M B, Bhalla P L. Molecular processes underlying the floral transition in the soybean shoot apical meristem. *Plant J*, 2009, 57: 832–845