

植物NF-Y转录因子的生物学功能及其研究进展

宋秋明, 李大勇, 张慧娟, 宋凤鸣*

浙江大学生物技术研究所, 杭州310058

摘要: 核因子Y (NF-Y), 又称CCAAT盒结合因子(CBF)或亚铁血红素激活蛋白(HAP), 是一种普遍存在于酵母、哺乳动物及植物等真核生物中的转录因子, 由三种不同的亚基组成, 即NF-YA (CBF-B或HAP2)、NF-YB (CBF-A或HAP3)和NF-YC (CBF-C或HAP5)。近年来的研究发现NF-Y在植物胚胎发育、光合作用、开花时间调控、逆境胁迫响应等诸多方面起重要作用。本文简要阐述植物NF-Y的生化、互作与家族特性、基因表达调控、生物学功能等方面的研究进展。

关键词: NF-Y转录因子; 生长发育; 逆境胁迫反应

NF-Y Transcription Factors and Their Biological Functions in Plants

SONG Qiu-Ming, LI Da-Yong, ZHANG Hui-Juan, SONG Feng-Ming*

Institute of Biotechnology, Zhejiang University, Hangzhou 310058, China

Abstract: Nuclear factor Y (NF-Y), also known as CCAAT-binding factor (CBF) or Heme Activator Protein (HAP), is a conserved heterotrimeric complex composed of three subunits, NF-YA (also termed CBF-B or HAP2), NF-YB (CBF-A or HAP3) and NF-YC (CBF-C or HAP5). During the last decade, extensive studies have revealed that subunits of NF-Y complex play important roles in embryonic development, photosynthesis, flowering and stress response. This review summarizes the recent research progress on the biological function of NF-Y in plants.

Key words: NF-Y transcription factors; growth and development; stress response

核因子Y (nuclear factor Y, NF-Y), 又称CCAAT盒结合因子(CCAAT-binding factor, CBF)或亚铁血红素激活蛋白(heme activator protein, HAP), 是一类普遍存在于酵母、动物、植物等真核生物中的转录因子, 通常由三种不同亚基组成, 即NF-YA (CBF-B或HAP2)、NF-YB (CBF-A或HAP3)和NF-YC (CBF-C或HAP5) (Mantovani 1999)。但在酿酒酵母(*Saccharomyces cerevisiae*)和乳酸克鲁维酵母(*Kluyveromyces lactis*)等少数真菌中还存在第四类亚基HAP4 (Forsburg和Guarente 1989; McNabb等1997)。NF-YA、NF-YB和NF-YC通过形成异源三聚体复合物, 并与其他调控因子相互作用, 激活或抑制下游基因的表达(Coustry等1998; Wright等1995; Benatti等2008)。在酵母和哺乳动物中, 每个基因编码一个亚基(Laloum等2013), 但植物NF-Y家族在进化上不断扩张, 通常是由多个基因编码同一类亚基(Yang等2005), 因而植物NF-Y所形成的异源三聚体数目十分庞大。近年来的研究发现植物NF-Y在胚胎发育、光合作用、开花时间调控、逆境胁迫响应等诸多方面起重要作用。

用。本文简要阐述植物NF-Y的生化与家族特性及其生物学功能等方面的研究进展。

1 NF-Y转录因子

1.1 NF-Y的生化与结构特征

NF-Y分为NF-YA、NF-YB和NF-YC三个亚基, 均包含一个十分保守的区域。这些保守区域是DNA结合或蛋白-蛋白互作的功能域(Gusmaroli等2001), 其中NF-YB和NF-YC具有一段类似于组蛋白折叠元件(HFM)的保守域, 形成紧密二聚体(Luger等1997; Petroni等2012)。NF-YB在三聚体与DNA的特异性结合中起作用(Zemzoumi等1999)。

植物NF-YA蛋白在长度和结构上各不相同, 均包含一个由53个氨基酸组成的保守核心区域, 在这个核心区域中存在两个功能上保守的结构域A1和A2 (Petroni等2012)。A1位于核心区域的N端, 由20个氨基酸构成一个 α 螺旋, 主要调控同NF-

收稿 2015-04-02 修定 2015-05-09

资助 国家自然科学基金(31272028)。

* 通讯作者(E-mail: fmsong@zju.edu.cn; Tel: 0571-88982481)。

YB、NF-YC亚基的互作; A2位于核心区域的C端, 由21个氨基酸组成, 在与CCAAT盒的特异性结合中起重要作用。在植物NF-YA中, 这些保守核心区域位于蛋白的中间位置, N端通常呈酸性(Coustry等1996)。

植物NF-YB蛋白长度也各不相同, 但一般小于NF-YA, 均具有一个中心结构域, 在结构、氨基酸数目上与核心组蛋白H2B中的HFM相似(Dolfini等2012)。NF-YB由3个 α 螺旋组成, 中间被2个 β 链环域分隔, 这些结构参与蛋白-DNA及蛋白-蛋白的互作(Arents和Moudrianakis 1993)。植物NF-YB转录因子可分为LEC-1和非LEC-1两类, 其中LEC-1和L1L (LEC-1-like)同源性很高, 是植物胚胎形成的中枢调控因子(Lee等2003; Hilioti等2014)。NF-YB由N端的A结构域、中心B结构域和C端的C结构域三部分组成, 其中LEC-1和L1L类NF-YB蛋白的B结构域中存在着一段由16个氨基酸组成的特异序列(Kwong等2003; Holdsworth等2008)。这段极度保守的特异序列区分了LEC-1和非LEC-1两类NF-YB蛋白。在LEC类NF-YB蛋白的B结构域中有一个天冬氨酸Asp-55残基, 是LEC类NF-YB蛋白的功能位点, 参与调控种子的胚胎形成(Lee等2003)。拟南芥中除了L1L外, 其他NF-YB成员均不能替代LEC-1执行其生理功能(Lee等2003)。研究显示, *LEC-1*和*L1L*基因是在种子植物分化之前, 由维管植物的基因组进化而来(Cagliari等2014)。

NF-YC蛋白的大小通常介于NF-YA和NF-YB蛋白之间。和NF-YB相似, NF-YC蛋白也含有一个HFM结构域, 但该结构域与核心组蛋白H2A的关系更近(Dolfini等2012)。

NF-Y三聚体与真核生物启动子区域中一段常见的CCAAT盒结合, 从而激活或抑制基因的转录(Ceribelli等2008)。CCAAT盒是一种普遍存在于真核生物中的启动子元件, 一般位于转录起始位点上游60~100 bp的区域内(Dolfini等2009)。NF-Y复合体的转录活性位于NF-YA的N端和NF-YC的C端, 均由一段富含谷氨酰胺的疏水结构域组成(Coustry等1996)。

1.2 NF-Y家族及其特性

在酵母、动物等真核生物中, NF-Y三个亚基一般有1个或2个基因编码, 但是植物NF-Y家族则

有很大的扩张。全基因组生物信息学分析表明, 植物NF-Y组成一个基因家族, 而NF-Y的3个亚基则形成了数量不等的亚家族, 如拟南芥中有10个NF-YA亚基、13个NF-YB亚基和13个NF-YC亚基(Siefers等2009), 水稻中NF-YA、NF-YB和NF-YC分别有10、11和7个(Thirumurugan等2008), 小麦中先后鉴定了10个NF-YA、11个NF-YB和14个NF-YC(Stephenson等2007), 大豆中有20个NF-YA、39个NF-B和27个NF-YC(Laloum等2013)。在大豆、苜蓿等豆科植物中, NF-YB和NF-YC亚家族分别存在NC2 β 和NC2 α 类特殊成员, 这些特殊成员具有不同的HFM(Ripodas等2015)。

2 NF-Y在植物生长发育中的作用

2.1 在胚胎和种子发育中的作用

在很多单子叶和双子叶植物中, *LEC1*和*L1L*参与调控植株从胚胎到成熟的转变过程, *lec1*突变体表现出多效性表型, 如子叶上毛状体、胚柄的异常发育及种子在淀粉、蛋白质和油脂积累上的缺陷等(Zhang等2002; Yazawa等2004; Fambrini等2006; Alemanno等2008; Cao等2011; Tan等2011; Salvini等2012)。拟南芥中*LEC1* (*AtNF-YB9*)和*L1L* (*AtNF-YB6*)基因具有调控植物胚胎发育的功能(Kwong等2003; Junker等2012)。*AtLEC1*基因通过激活一些胚胎形成基因和细胞分化基因的转录来诱导营养细胞的胚胎发育(Lotan等1998)。染色体免疫沉淀、基因表达谱分析发现, *LEC1*是作为光信号和激素信号的一个调控枢纽从而在植物胚胎发育过程中起作用(Junker等2012)。同样, 水稻*OsHAP3E* (*OsLEC1*)在营养生长和生殖发育中具有多效性功能, *OsHAP3E*影响叶片、圆锥花序和穗粒的发育, 通过调控分生组织的形态发生在营养生长和生殖发育中起作用。*OsHAP3E*可与一些MADS转录因子互作, 当*OsHAP3E*蛋白积累水平上升时, 会干扰MADS的功能, 如在水稻中*OsHAP3E*过表达时, *OsMADS1*启动子特定区域甲基化水平升高, *OsMADS1*的表达水平下调, 最终调控叶片、花序和小穗的发育(Zhang和Xue 2013); RNAi抑制*OsHAP3E*表达或过量表达嵌合抑制子抑制*OsHAP3E*活性导致在遗传转化时细胞死亡, 无法获得转基因植株(Ito等2011)。*OsNF-YB7* (*OsL1L*)的过量表达植株则出现矮化、直立状叶片、

紧密圆锥花序、异常花轴及重瓣花等表型(Ito等2011)。此外,在玉米和油菜中分别过量表达*ZmLECI*和*ZmWR11*或*BnLECI*和*BnL1L*可以提高种子含油量。玉米*ZmWR11*是*ZmLECI*下游的一个转录因子,过表达*ZmWR11*可提高种子含油量,但不影响种子萌芽、幼苗生长和作物产量等农艺性状(Shen等2010; Tan等2011)。在拟南芥中,LECI/L1L和NF-YC2通过与种子特异性ABA响应元件结合因子bZIP67的互作,从而激活种子储藏蛋白基因*CRUCIFERIN C*的表达(Yamamoto等2009)。

除LECI外,一些其他NF-Y基因也参与了植物营养生长和生殖发育的调控。拟南芥NF-YA1/5/6/9存在功能冗余现象,因为单个基因或两个基因同时突变后并不表现出任何表型变化,但过量表达NF-YA1/5/6/9后影响雄配子发育、胚胎发育、种子形态及种子萌发等(Mu等2013)。*AtNF-YA3*和*AtNF-YA8*也存在功能冗余,并在胚胎形成的早期阶段起调控作用(Fornari等2013)。*AtNF-YB2*在拟南芥根尖部位特异性表达,过量表达*AtNF-YB2*会加快细胞分裂和伸长,促进主根伸长,这个过程可能与细胞分裂和伸长相关(Ballif等2011)。在水稻中,RNAi抑制*OsNF-YB1*表达后,细胞周期途径的一些基因表达发生变化,导致胚乳等缺陷(Sun等2014)。小麦*TaNF-YA-B1*和管涔山青杉(*Picea wilsoni*) *PwNF-YC*分别在根和花粉管中起作用,其中*PwNF-YC*的作用受Ca²⁺诱导(Yu等2011; Qu等2015)。另外,一些拟南芥NF-Y转录因子在种子萌发过程中存在相似或相反的功能,其作用可能与ABA信号途径有关(Kumimoto等2013; Siriwardana等2014)。

2.2 NF-Y在调控植物开花中的作用

在拟南芥中,AtNF-YB2和AtNF-YB3通过感受长光照来调控开花调控子*FLOWERING LOCUS T (FT)*并促进开花(Kumimoto等2008)。过表达*AtNF-YC1*和*AtNF-YC2*能提高*FT*的转录水平,加速开花进程(Hackenberg等2012a);相反,*AtHAP3b*突变体中*FT*表达水平下降,开花延迟(Chen等2007)。*AtNF-YC3/4/9*通过与AtNF-YB2/3互作,共同参与*CONSTANS (CO)*介导的开花过程(Kumimoto等2010),由此推测NF-Y复合体元件结合到*FT*基因启动子远端增强子元件,把CO引导到启动子近端的

顺式元件上,从而启动向生殖生长的转换(Cao等2014)。CO是一个关键的光诱导开花时间调控子,通过保守CCT结构域与NF-Y互作(Ben-Naim等2006; Wenkel等2006)。CCT类基因与NF-YA基因具有相似的功能。研究表明,拟南芥中CCT结构域基因CO可替代*AtNF-YA1/2*亚基,形成CO/*AtHAP3/AtHAP5*复合体,并调控开花时间(Wenkel等2006),NF-Y复合体为CO提供DNA结合位点(Tiwari等2010)。当NF-Y缺失时过表达CO会削弱或丧失其对*FT*因子的活化能力,导致不能提前开花(Kumimoto等2010);反之,当CO缺失时过表达NF-Ys则降低其调控开花的效率(Tiwari等2010)。最新研究发现,NF-Y蛋白同时与光周期途径中的CO和赤霉素途径中的DELLA互作,共同调控花器官调控因子*SOC1*基因表达,其中NF-Y复合体结合到SOC1基因启动子中特定顺式元件并调控其三甲基化H3K27水平,表明NF-Y复合体能起到表观遗传标记的关键因子作用(Hou等2014)。

在长日照条件下,水稻*OsNF-YB11 (DTH8/Ghd8/LHD1)*通过下调表达开花调控子,抑制光周期诱导开花的信号转导网络(Wei等2010; Yan等2011; Dai等2012)。过量表达*HvNF-YB1*的大麦植株能提前开花时间(Liang等2012),小麦NF-Ys通过与VRN2、CO中的CCT结构域相结合,参与春化和季节性光周期等生长发育信号和环境信号的集成,从而调控开花进程(Li等2011)。

2.3 NF-Y在叶绿体形成和光合作用中的作用

在拟南芥中,AtNF-YA5、AtNF-YB9和AtNF-YC9形成的复合体与GCR1 (G蛋白偶联受体)、GPA1 (G蛋白α亚基)和Pirin1 (一个cupin家族成员)组成一个信号传递链,参与拟南芥黄化苗植株中叶绿素A/B结合蛋白基因的表达(Warpeha等2007)。水稻*OsHAP3A*丧失功能突变体中,叶绿素含量降低,叶绿体退化,说明水稻*OsHAP3A*参与叶绿体的发育(Kusnetsov等1999);水稻*OsNF-YB2/3/4 (OsHAP3A/B/C)*调控许多编码核酮糖-1,5-二磷酸羧化酶/氧合酶小亚基和叶绿素a/b结合蛋白的光合相关基因(Miyoshi等2003)。在小麦中,过量表达*TaNF-YB3*后显著提高叶绿素含量、光合速率及早期生长率(Stephenson等2011),*TaNF-YC11*受光照调控,且参与光合作用相关基因表达

的调控(Stephenson等2010)。

3 NF-Y在非生物胁迫反应中的作用

3.1 在干旱胁迫响应中的作用

有学者系统研究了拟南芥和小麦NF-Y基因在干旱胁迫下的表达变化,发现在拟南芥中大多NF-YA基因呈上调表达,但在小麦中NF-YA基因的表达则相反(Stephenson等2007; Hackenberg等2012a)。转基因研究表明,过表达*AtNF-YB1*和*ZmNF-YB2*的转基因拟南芥和玉米植株显著提高干旱抗性(Nelson等2007)。同样,在拟南芥中过表达大豆*GmNF-YA3*或白杨*PdNF-YB7*可以减少叶片水分损失,提高植株抗旱性(Ni等2013; Han等2013)。NF-Y调控植物抗旱性的机制可能比较复杂,一般通过影响叶绿素含量、气孔电导率、叶面温度、蒸腾效率及光合作用等几个因素进行调控。过表达*AtNF-YB1*的转基因拟南芥中大批干旱反应相关基因如DREB和ABA途径基因的表达并无显著变化,因此*AtNF-YB1*可能通过其他未知信号途径来调控抗旱反应(Nelson等2007)。同时,小RNA可能通过影响NF-Y基因转录本丰度来调控NF-Y在抗旱反应中的作用。干旱胁迫下,拟南芥*AtNF-YA5*在维管组织和保卫细胞中的表达水平显著上调,其表达受ABA途径调控,但在转录后则受miR169调控,在气孔保卫细胞中*AtNF-YA5*的上调表达改变气孔的孔径等,而在非保卫细胞中*AtNF-YA5*可以激活一些胁迫响应基因的表达(Li等2008);利用人工miRNA方法抑制*ERF (NF-YA5 Enhancing RING FINGER)*基因表达后增加miR169丰度,但显著降低NF-YA5的转录本积累水平(Gao等2015)。

3.2 在高盐胁迫响应中的作用

在拟南芥芽后生长的早期阶段,*AtNF-YA1*过表达植株增加对高盐胁迫和ABA的敏感性(Li等2013)。过量表达小麦*TaNF-YA10-1*的拟南芥植株显著增加对盐胁迫的敏感性,降低ABA敏感性,同时*AtRAB18*、*AtRD29B*、*AtABI5*、*AtCBF1*和*AtCBF3*等胁迫相关基因的表达水平显著下降(Ma等2015)。但过表达百慕大草*CdtNF-YC1*的转基因水稻植株增强抗盐性。研究表明,ABA、H₂O₂和NO参与盐胁迫诱导*CdtNF-YC1*基因的转录表达,当抑制ABA合成或去除H₂O₂、NO分子时*Cdt-*

*NF-YC1*的转录表达就会终止(Chen等2014)。高盐胁迫下,水稻miR169首先上调表达,然后选择性降解NF-YA基因,抑制其表达(Zhao等2009)。

3.3 在其他胁迫响应中的作用

在拟南芥中,研究发现*AtNF-YC2*、*AtNF-YA4*、*AtNF-YB3*和*AtbZIP28*形成转录复合体,从而诱导内质网胁迫响应基因的上调表达(Liu和Howell 2010)。拟南芥*AtHAP5A*通过结合*AtXTH21*的CCAAT元件来正调控抗冷性,抑制活性氧积累,激活ABA途径基因的表达(Shi等2014)。*AtNF-YC10*能与DREB2A互作,在热胁迫中*AtNF-YC10*与*AtNF-YA2*、*AtNF-YB3*形成三聚体复合物,并与DREB2A协同调控热胁迫诱导基因的启动子,从而提高植株的耐热性(Sato等2014)。

4 NF-Y在植物-微生物互作中的作用

研究表明NF-Y在豆科植物-根瘤菌互作中起重要作用。在菜豆-*Rhizobium etli*互作中,RNAi沉默*PvNF-YC1*基因表达后导致根瘤菌不能侵染、抑制根瘤形成,而过量表达后则显著提高结瘤效率,表明*PvNF-YC1*在根瘤菌侵染和根瘤形成中起重要作用(Zanetti等2010)。在蒺藜状苜蓿中,*MtNF-YA1*和*MtNF-YA2*存在功能冗余,在豆科植物-根瘤菌共生系统形成的早期阶段起作用(Laloum等2014)。*MtNF-YA1*在共生关系建立时上调表达,其转录本丰度受miRNA169调控(Reynoso等2013),进一步研究表明,*MtNF-YA1*通过影响侵染索的形成来调控根瘤菌的侵染(Laporte等2014)。NF-YC1和一个GRAS转录因子SIN1间的互作在根瘤形成发挥重要作用。NF-Y三聚体中的NF-YC1与SIN1发生互作,并特异性结合到CCAAT框序列上,激活细胞周期相关基因及其下游基因的表达,最终调控根瘤菌的侵染和根瘤的形成(Soyano等2013; Battaglia等2014; Rípodas等2014)。

NF-Y在植物抗病反应中的作用鲜有研究。最近发现,过量表达*OsHAP2E*的水稻植株显著提高对稻瘟病和白叶枯病的抗病性,芯片表达谱分析显示在过量表达*OsHAP2E*的植株中大量防卫基因表达上调(Alam等2015)。因此,NF-Y在植物抗病反应中起重要作用,但其作用机制有待研究阐明。

5 miR169对NF-YA转录本丰度的转录后调控

研究发现,miR169在转录后水平上调控

*NF-YA*基因转录本的积累水平(Jones-Rhoades和Bartel 2004)。在干旱胁迫响应中, 水稻miR169成员上调表达(Zhao等2007, 2009), 而拟南芥中miR169则多数下调表达(Li等2008)。在干旱、盐胁迫及缺乏氮素条件下, 拟南芥miR169表达上调, 而一些*NF-YA*基因转录本的积累水平则显著下降(Zhao等2011; Leyva-González等2012); miR169a比miR169c对*AtNF-YA5*转录本积累的抑制作用更为显著, 导致*AtNF-YA5*转录本水平下降, 使得植株对干旱胁迫更为敏感(Li等2008)。这与番茄中的结果相反, 过量表达SlymiR169c后*SINP-YA1/2/3*等基因转录本的积累水平显著下调, 却提高抗旱性(Zhang等2011)。在短期干旱、盐胁迫中, 大部分玉米*ZmNF-YA*基因转录本积累量增加, 但在长期胁迫时其转录本积累量下降; 相应的miR169在干旱胁迫中下调表达, 在盐胁迫中先上调后下调表达(Luan等2015)。在氮素缺乏时, 拟南芥miR169强烈下调, 而其靶标*AtNF-YA*的转录本积累水平则显著上调, 过量表达miR169a的拟南芥植株中*AtNF-YA*的转录本积累水平显著下降, 导致植株对氮素胁迫更为敏感(Zhao等2011)。此外, 拟南芥*AtNF-YA2*、蒺藜状苜蓿*MtNF-YA1*和*MtHAP2-1*、白杨*PtrHAP2*及矮牵牛和金鱼草*NF-YA*等在根系发育、根瘤形成、叶芽休眠、花器官形态等的作用均受到miRNA169的调控(Combier等2006; Cartolano等2007; Liu和Howell 2010; Potkar等2013; Sorin等2014)。

6 NF-Y亚基间的互作及其复合体

NF-Y的功能需要NF-YA/B/C形成异源三聚体复合体, 但是NF-Y亚基间的互作十分复杂, 且NF-Y亚基间的互作存在一定的特异性。最近, 采用酵母双杂交技术分析拟南芥中NF-YB成员和NF-YC成员的互作关系, 除*AtNF-YB9* (LEC1)不与任何一个*AtNF-YC*成员发生互作外, 两个家族间绝大部分成员均存在一定的互作关系, 其中*AtNF-YB/AtNF-YC*间均存在较强的互作关系(Calvenzani等2012)。胡萝卜一个NF-YB (LEC1)和两个NF-YC间具有互作关系(Yazawa和Kamada 2007); 水稻OsHAP3A与2个OsHAP2、6个OsHAP5s间具有互作关系(Thirumurugan等2008)。酵

母三杂交实验结果表明, 在*AtNF-YB2/3/4/5*存在时, *AtNF-YA4*与*AtNF-YC2*存在互作(Liu和Howell 2010)。

在作用上, NF-YB和NF-YC最初在细胞质中形成异源二聚体, 后穿梭至细胞核中并与NF-YA结合, 形成成熟的异源三聚体复合体(Kahle等2005)。研究证明, 拟南芥*AtNF-YB*、*AtNF-YC*亚基间形成异源二聚体, 但不能形成同源二聚体; *AtNF-YA*只能与含HFD亚基形成的二聚体组装成异源三聚体复合体, 但是不能与单个*AtNF-YA*或*AtNF-YB*亚基相结合(Hackenberg等2012b)。

7 小结和展望

自在油菜中第一次报道植物NF-YA以来(Albani和Robert 1995), 有关植物NF-Y及其生物学功能的研究已经取得显著进展。研究显示, NF-Y的生物学功能十分多样, 涉及胚胎形成、光合作用、开花时间调控及各种胁迫响应等重要生理过程(表1)。相比而言, NF-Y在植物抗病反应中的作用尚需研究阐明。目前NF-Y的研究主要集中在拟南芥等少数模式植物中, 其他植物特别是农作物中NF-Y的功能鉴定和作用研究尚有待深入。已有研究证明, 改变NF-Y亚基基因的表达水平可以提高植物种子含油量及对各种逆境胁迫的抗逆性。因此, NF-Y在作物农艺性状的改良及分子育种中具有巨大的潜力。

在体内, NF-Y组装形成异源三聚体复合体, 从而发挥其调控胚胎发育、开花时间、光合效率及逆境胁迫响应等方面的功能。NF-Y在植物生长发育和各种逆境胁迫反应中的作用机制极为复杂, 今后有关NF-Y作用机制的研究包括: (1) NF-Y不同亚基之间的互作形成的异源三聚体组成与特异性及其在不同生物学过程中的功能; (2) NF-Y异源三聚体与其他调控因子(如转录因子)互作形成的转录复合体及其协同作用; (3) miR169等小RNA调控*NF-YA*基因转录本积累及其对NF-Y异源三聚体组成与功能的影响; (4)分离鉴定上游调控NF-Y基因表达和异源三聚体形成的因子、NF-Y异源三聚体所调控的下游靶标基因及其功能。这些研究将有助于全面认识NF-Y的生物学功能、作用机制及其调控网络。

表1 已知功能的植物NF-Y亚基及其生物学功能
Table 1 Plant NF-Y subunits with known biological functions

基因	植物	功能分析方法	生物学性状	参考文献
<i>AtNF-YA1</i>	拟南芥	过量表达	胚胎发育; 盐胁迫相关	Li等2013; Mu等2012
<i>AtNF-YA3</i>	拟南芥	RNAi	胚胎发育	Fornari等2013
<i>AtNF-YA4</i>	拟南芥	T-DNA插入突变体	内质网逆境胁迫	Liu和Howell 2010
<i>AtNF-YA5</i>	拟南芥	T-DNA插入突变体	胚胎发育; 干旱胁迫	Warpeha等2007; Li等2008; Mu等2013
<i>AtNF-YA8</i>	拟南芥	T-DNA插入突变体; RNAi	胚胎发育	Fornari等2013
<i>AtNF-YB1</i>	拟南芥	过量表达	干旱胁迫耐受性	Nelson等2007
<i>AtNF-YB2</i>	拟南芥	过量表达	促进主根伸长; 调控花期	Ballif等2011; Kumimoto等2008
<i>AtNF-YB3</i>	拟南芥	过量表达; T-DNA插入突变体	调控花期; 内质网逆境胁迫	Kumimoto等2008; Liu和Howell 2010
<i>AtNF-YB6</i>	拟南芥	RNAi	胚胎发育	Kwong等 2003
<i>AtNF-YB9</i>	拟南芥	T-DNA插入突变体	胚胎发育	Junker等2012; Warpeha等2007
<i>AtHAP3b</i>	拟南芥	T-DNA插入突变体	调控花期	Chen等2007
<i>AtHAP5A</i>	拟南芥	过量表达	冷胁迫耐受性	Shi和Chan 2014
<i>AtNF-YC1</i>	拟南芥	过量表达	调控花期	Hackenberg等2012a
<i>AtNF-YC2</i>	拟南芥	过量表达	调控花期; 内质网逆境胁迫	Hackenberg等2012a; Liu和Howell 2010
<i>AtNF-YC10</i>	拟南芥	过量表达	热胁迫耐受性	Sato等2014
<i>OsHAP2E</i>	水稻	过量表达	抗病性	Alam等2015
<i>OsHAP3E</i>	水稻	过量表达	营养和生殖发育	Zhang和Xue 2013
<i>OsNF-YB1</i>	水稻	过量表达; RNAi	胚乳发育; 调控细胞周期	Sun等2014
<i>OsNF-YB2</i>	水稻	RNAi	叶绿素合成与叶绿体发育	Kusnetsov等1999
<i>OsNF-YB7</i>	水稻	过量表达	营养和生殖发育	Ito等2011
<i>OsNF-YB11</i>	水稻	QTL位点	抑制开花	Wei等2010; Yan等2011; Dai等2012
<i>TaNF-YA10-1</i>	小麦	过量表达	盐胁迫相关	Ma等2015
<i>TaNF-YB3</i>	小麦	过量表达	叶绿素含量; 光合作用	Stephenson等2011
<i>BnLEC1</i>	油菜	过量表达	脂肪酸生物合成	Tan等2011
<i>BnL1L</i>	油菜	过量表达	脂肪酸生物合成	Tan等2011
<i>BdNF-YB6</i>	二穗短柄草	过量表达	提前开花	Cao等2011
<i>ZmLEC1</i>	玉米	过量表达	脂肪酸生物合成	Shen等2010
<i>ZmNF-YB2</i>	玉米	过量表达	干旱胁迫耐受性	Nelson等2007
<i>PvNF-YC1</i>	菜豆	过量表达; RNAi	根瘤发育	Zanetti等2010
<i>PwNF-YCs</i>	管涔山青扦	过量表达; RNAi	花粉管发育	Yu等2011
<i>GmNF-YA3</i>	大豆	过量表达	干旱胁迫耐受性	Ni等2013
<i>PdNF-YB7</i>	白杨	过量表达	干旱胁迫耐受性	Han等2013
<i>CdtNF-YC1</i>	百慕大草	过量表达	耐盐性; 耐旱性	Chen等2014
<i>HvNF-YB1</i>	大麦	过量表达	提前开花	Liang等2012
<i>MtHAP2-1</i>	蒺藜状苜蓿	RNAi	促进根瘤发育	Combier等2006

参考文献

- Alam MM, Tanaka T, Nakamura H, Ichikawa H, Kobayashi K, Yaeno T, Yamaoka N, Shimomoto K, Takayama K, Nishina H et al (2015). Overexpression of a rice *heme activator protein* gene (*OsHAP2E*) confers resistance to pathogens, salinity and drought, and increases photosynthesis and tiller number. *Plant Biotechnol J*, 13: 85~96
- Albani D, Robert LS (1995). Cloning and characterization of a *Brassica napus* gene encoding a homologue of the B subunit of a heteromeric CCAAT-binding factor. *Gene*, 167: 209~213
- Alemanno L, Devic M, Niemenak N, Sanier C, Guilleminot J, Rio M, Verdeil JL, Montoro P (2008). Characterization of *leafy cotyledon1-like* during embryogenesis in *Theobroma cacao* L.. *Planta*,

- 227: 853~866
- Arents G, Moudrianakis EN (1993). Topography of the histone octamer surface: repeating structural motifs utilized in the docking of nucleosomal DNA. *Proc Natl Acad Sci USA*, 90: 10489~10493
- Ballif J, Endo S, Kotani M, MacAdam J, Wu Y (2011). Over-expression of *HAP3b* enhances primary root elongation in *Arabidopsis*. *Plant Physiol Biochem*, 49: 579~583
- Battaglia M, Ripodas C, Clúa J, Baudin M, Aguilar OM, Niebel A, Zanetti ME, Blanco FA (2014). A nuclear factor Y interacting protein of the GRAS family is required for nodule organogenesis, infection thread progression, and lateral root growth. *Plant Physiol*, 164: 1430~1442
- Benatti P, Basile V, Merico D, Fantoni LI, Tagliafico E, Imbriano C (2008). A balance between NF-Y and p53 governs the pro- and anti-apoptotic transcriptional response. *Nucleic Acids Res*, 36: 1415~1428
- Ben-Naim O, Eshed R, Parnis A, Teper-Bamnolker P, Shalit A, Coupland G, Samach A, Lifschitz E (2006). The CCAAT binding factor can mediate interactions between CONSTANS-like proteins and DNA. *Plant J*, 46: 462~476
- Cagliari A, Turchetto-Zolet AC, Korbes AP, dos Santos Maraschin F, Margis R, Margis-Pinheiro M (2014). New insights on the evolution of LEAFY COTYLEDON1 (LEC1) type genes in vascular plants. *Genomics*, 103: 380~387
- Calvenzani V, Testoni B, Gusmaroli G, Lorenzo M, Gnesutta N, Petroni K, Mantovani R, Tonelli C (2012). Interactions and CCAAT-binding of *Arabidopsis thaliana* NF-Y subunits. *PLoS ONE*, 7: e42902
- Cao S, Kumimoto RW, Gnesutta N, Calogero AM, Mantovani R, Holt BF (2014). A distal CCAAT/NUCLEAR FACTOR Y complex promotes chromatin looping at the *FLOWERING LOCUS T* promoter and regulates the timing of flowering in *Arabidopsis*. *Plant Cell*, 26: 1009~1017
- Cao S, Kumimoto RW, Siriwardana CL, Risinger JR, Holt III BF (2011). Identification and characterization of NF-Y transcription factor families in the monocot model plant *Brachypodium distachyon*. *PLoS ONE*, 6: e21805
- Cartolano M, Castillo R, Efreanova N, Kuckenberger M, Zethof J, Gerats T, Schwarz-Sommer Z, Vandenbussche M (2007). A conserved microRNA module exerts homeotic control over *Petunia hybrida* and *Antirrhinum majus* floral organ identity. *Nat Genet*, 39: 901~905
- Ceribelli M, Dolfini D, Merico D, Gatta R, Viganò AM, Pavesi G, Mantovani R (2008). The histone-like NF-Y is a bifunctional transcription factor. *Mol Cell Biol*, 28: 2047~2058
- Chen M, Zhao Y, Zhuo C, Lu S, Guo Z (2014). Overexpression of a NF-YC transcription factor from bermudagrass confers tolerance to drought and salinity in transgenic rice. *Plant Biotechnol J*, doi: 10.1111/pbi.12270
- Chen NZ, Zhang XQ, Wei PC, Chen QJ, Ren F, Chen J, Wang XC (2007). *AtHAP3b* plays a crucial role in the regulation of flowering time in *Arabidopsis* during osmotic stress. *J Biochem Mol Biol*, 40: 1083~1089
- Combier JP, Frugier F, De Billy F, Boualem A, El-Yahyaoui F, Moreau S, Vernié T, Ott T, Gamas P, Crespi M et al (2006). *MtHAP2-1* is a key transcriptional regulator of symbiotic nodule development regulated by microRNA169 in *Medicago truncatula*. *Genes Dev*, 20: 3084~3088
- Coustry F, Maity SN, Sinha S, de Crombrughe B (1996). The transcriptional activity of the CCAAT-binding factor CBF is mediated by two distinct activation domains, one in the CBF-B subunit and the other in the CBF-C subunit. *J Biol Chem*, 271: 14485~14491
- Coustry F, Sinha S, Maity S, Crombrughe BD (1998). The two activation domains of the CCAAT-binding factor CBF interact with the dTAF(II)110 component of the Drosophila TFIID complex. *Biochem J*, 331: 291~297
- Dai X, Ding Y, Tan L, Fu Y, Liu F, Zhu Z, Sun X, Gu P, Cai H, Sun C (2012). *LHD1*, an allele of *DTH8/Ghd8*, controls late heading date in common wild rice (*Oryza rufipogon*). *J Integr Plant Biol*, 54: 790~799
- Dolfini D, Gatta R, Mantovani R (2012). NF-Y and the transcriptional activation of CCAAT promoters. *Crit Rev Biochem Mol Biol*, 47: 29~49
- Dolfini D, Zambelli F, Pavesi G, Mantovani R (2009). A perspective of promoter architecture from the CCAAT box. *Cell Cycle*, 8: 4127~4137
- Fambrini M, Durante C, Cionini G, Geri C, Giorgetti L, Michelotti V, Salvini M, Pugliesi C (2006). Characterization of *LEAFY COTYLEDON1-LIKE* gene in *Helianthus annuus* and its relationship with zygotic and somatic embryogenesis. *Dev Genes Evol*, 216: 253~264
- Fornari M, Calvenzani V, Masiero S, Tonelli C, Petroni K (2013). The *Arabidopsis NF-YA3* and *NF-YA8* genes are functionally redundant and are required in early embryogenesis. *PLoS ONE*, 8: e82043
- Forsburg SL, Guarente L (1989). Identification and characterization of HAP4: a third component of the CCAAT-bound HAP2/HAP3 heteromer. *Genes Dev*, 3: 1166~1178
- Gao W, Liu W, Zhao M, Li WX (2015). *NERF* encodes a RING E3 ligase important for drought resistance and enhances the expression of its antisense gene *NFYA5* in *Arabidopsis*. *Nucleic Acids Res*, 43: 607~617
- Gusmaroli G, Tonelli C, Mantovani R (2001). Regulation of the CCAAT-binding NF-Y subunits in *Arabidopsis thaliana*. *Gene*, 264: 173~185
- Hackenberg D, Keetman U, Grimm B (2012a). Homologous NF-YC2 subunit from *Arabidopsis* and tobacco is activated by photooxidative stress and induces flowering. *Int J Mol Sci*, 13: 3458~3477
- Hackenberg D, Wu Y, Voigt A, Adams R, Schramm P, Grimm B (2012b). Studies on differential nuclear translocation mechanism and assembly of the three subunits of the *Arabidopsis thaliana* transcription factor NF-Y. *Mol Plant*, 5: 876~888
- Han X, Tang S, An Y, Zheng DC, Xia XL, Yin WL (2013). Overexpression of the poplar *NF-YB7* transcription factor confers drought tolerance and improves water-use efficiency in *Arabidopsis*. *J Exp Bot*, 64: 4589~4601

- Hilioti Z, Ganopoulos I, Bossis I, Tsaftaris A (2014). LEC1-LIKE paralog transcription factor: how to survive extinction and fit in NF-Y protein complex. *Gene*, 543: 220~233
- Holdsworth MJ, Bentsink L, Soppe WJ (2008). Molecular networks regulating *Arabidopsis* seed maturation, after-ripening, dormancy and germination. *New Phytol*, 179: 33~54
- Hou X, Zhou J, Liu C, Liu L, Shen L, Yu H (2014). Nuclear factor Y-mediated H3K27me3 demethylation of the *SOCl* locus orchestrates flowering responses of *Arabidopsis*. *Nat Commun*, 5: 4601
- Ito Y, Thirumurugan T, Serizawa A, Hiratsu K, Ohme-Takagi M, Kurata N (2011). Aberrant vegetative and reproductive development by overexpression and lethality by silencing of *OsHAP3E* in rice. *Plant Sci*, 181: 105~110
- Jones-Rhoades MW, Bartel DP (2004). Computational identification of plant microRNAs and their targets, including a stress-induced miRNA. *Mol Cell*, 14: 787~799
- Junker A, Mönke G, Rutten T, Keilwagen J, Seifert M, Thi TMN, Renou JP, Balzergue S, Viehöver P, Hähnel U et al (2012). Elongation-related functions of *LEAFY COTYLEDON1* during the development of *Arabidopsis thaliana*. *Plant J*, 71: 427~442
- Kahle J, Baake M, Doenecke D, Albig W (2005). Subunits of the heterotrimeric transcription factor NF-Y are imported into the nucleus by distinct pathways involving importin β and importin 13. *Mol Cell Biol*, 25: 5339~5354
- Kumimoto RW, Adam L, Hymus GJ, Repetti PP, Reuber TL, Marion CM, Hempel FD, Ratchliffe OJ (2008). The Nuclear Factor Y subunits *NF-YB2* and *NF-YB3* play additive roles in the promotion of flowering by inductive long-day photoperiods in *Arabidopsis*. *Planta*, 228: 709~723
- Kumimoto RW, Siriwardana CL, Gayler KK, Risinger JR, Siefers N, Holt BF (2013). NUCLEAR FACTOR Y transcription factors have both opposing and additive roles in ABA-mediated seed germination. *PLoS ONE*, 8: e59481
- Kumimoto RW, Zhang Y, Siefers N, Holt BF (2010). NF-YC3, NF-YC4 and NF-YC9 are required for CONSTANS-mediated, photoperiod-dependent flowering in *Arabidopsis thaliana*. *Plant J*, 63: 379~391
- Kusnetsov V, Landsberger M, Meurer J, Oelmüller R (1999). The assembly of the CAAT-box binding complex at a photosynthesis gene promoter is regulated by light, cytokinin, and the stage of the plastids. *J Biol Chem*, 274: 36009~36014
- Kwong RW, Bui AQ, Lee H, Kwong LW, Fischer RL, Goldberg RB, Harada JJ (2003). LEAFY COTYLEDON1-LIKE defines a class of regulators essential for embryo development. *Plant Cell*, 15: 5~18
- Laloum T, Baudin M, Frances L, Lepage A, Billault-Penneteau B, Cerri MR, Ariel F, Jardinaud MF, Gamas P, de Carvalho-Niebel F et al (2014). Two CCAAT-box-binding transcription factors redundantly regulate early steps of the legume-rhizobia endosymbiosis. *Plant J*, 79: 757~768
- Laloum T, De Mita S, Gamas P, Baudin M, Niebel A (2013). CCAAT-box binding transcription factors in plants: Y so many? *Trends Plant Sci*, 18: 157~166
- Laporte P, Lepage A, Fournier J, Catrice O, Moreau S, Jardinaud MF, Mun JH, Larrainzar E, Cook DR, Niebel A et al (2014). The CCAAT box-binding transcription factor NF-YA1 controls rhizobial infection. *J Exp Bot*, 65: 481~694
- Lee H, Fischer RL, Goldberg RB, Harada JJ (2003). *Arabidopsis* LEAFY COTYLEDON1 represents a functionally specialized subunit of the CCAAT binding transcription factor. *Proc Natl Acad Sci USA*, 100: 2152~2156
- Leyva-González MA, Ibarra-Laclette E, Cruz-Ramírez A, Herrera-Estrella L (2012). Functional and transcriptome analysis reveals an acclimatization strategy for abiotic stress tolerance mediated by *Arabidopsis* NF-YA family members. *PLoS ONE*, 7: e48138
- Li C, Distelfeld A, Comis A, Dubcovsky J (2011). Wheat flowering repressor VRN2 and promoter CO2 compete for interactions with NUCLEAR FACTOR-Y complexes. *Plant J*, 67: 763~773
- Li WX, Oono Y, Zhu J, He XJ, Wu JM, Iida K, Lu XY, Cui X, Jin H, Zhu JK (2008). The *Arabidopsis* NFYA5 transcription factor is regulated transcriptionally and posttranscriptionally to promote drought resistance. *Plant Cell*, 20: 2238~2251
- Li YJ, Fang Y, Fu YR, Huang JG, Wu CA, Zheng CC (2013). *NFYA1* is involved in regulation of postgermination growth arrest under salt stress in *Arabidopsis*. *PLoS ONE*, 8: e61289
- Liang M, Hole D, Wu J, Blake T, Wu Y (2012). Expression and functional analysis of *NUCLEAR FACTOR-Y*, subunit B genes in barley. *Planta*, 235: 779~791
- Liu JX, Howell SH (2010). bZIP28 and NF-Y transcription factors are activated by ER stress and assemble into a transcriptional complex to regulate stress response genes in *Arabidopsis*. *Plant Cell*, 22: 782~796
- Lotan T, Ohto M, Yee KM, West MAL, Lo R, Kwong RW, Yamagishi K, Fischer RL, Goldberg RB, Harada JJ (1998). *Arabidopsis* LEAFY COTYLEDON1 is sufficient to induce embryo development in vegetative cells. *Cell*, 93: 1195~1205
- Luan M, Xu M, Lu Y, Zhang L, Fan Y, Wang L (2015). Expression of zma-miR169 miRNAs and their target *ZmNF-YA* genes in response to abiotic stress in maize leaves. *Gene*, 555: 178~185
- Luger K, Mader AW, Richmond RK, Sargent DF, Richmond TJ (1997). Crystal structure of the nucleosome core particle at 2.8 Å resolution. *Nature*, 389: 251~260
- Ma X, Zhu X, Li C, Song Y, Zhang W, Xia G, Wang M (2015). Overexpression of wheat *NF-YA10* gene regulates the salinity stress response in *Arabidopsis thaliana*. *Plant Physiol Biochem*, 86: 34~43
- Mantovani R (1999). The molecular biology of the CCAAT-binding factor NF-Y. *Gene*, 239: 15~27
- McNabb DS, Tseng KA, Guarente L (1997). The *Saccharomyces cerevisiae* Hap5p homologue from fission yeast reveals two conserved domains that are essential for assembly of heterotetrameric CCAAT binding factor. *Mol Cell Biol*, 17: 7008~7018
- Miyoshi K, Ito Y, Serizawa A, Kurata N (2003). *OsHAP3* genes regulate chloroplast biogenesis in rice. *Plant J*, 36: 532~540
- Mu J, Tan H, Hong S, Liang Y, Zuo J (2013). *Arabidopsis* transcription factor genes *NF-YA1*, 5, 6 and 9 play redundant roles in male gametogenesis, embryogenesis, and seed development.

- Mol Plant, 6: 188~201
- Nelson DE, Repetti PP, Adams TR, Creelman RA, Wu J, Warner DC, Anstrom DC, Bensen RJ, Castiglioni PP, Heard JE et al (2007). Plant nuclear factor Y (NF-Y) B subunits confer drought tolerance and lead to improved corn yields on water-limited acres. Proc Natl Acad Sci USA, 104: 16450~16455
- Ni Z, Hu Z, Jiang Q, Zhang H (2013). *GmNFYA3*, a target gene of miR169, is a positive regulator of plant tolerance to drought stress. Plant Mol Biol, 82: 113~129
- Petroni K, Kumimoto RW, Gnesutta N, Calvenzani V, Fornari M, Tonelli C, Holt BF, Mantovani R (2012). The promiscuous life of plant NUCLEAR FACTOR Y transcription factors. Plant Cell, 24: 4777~4792
- Potkar R, Recla J, Busov V (2013). ptr-MIR169 is a posttranscriptional repressor of *PtrHAP2* during vegetative bud dormancy period of aspen (*Populus tremuloides*) trees. Biochem Biophys Res Commun, 431: 512~518
- Qu B, He X, Wang J, Zhao Y, Teng W, Shao A, Zhao X, Ma W, Wang J, Li B et al (2015). A wheat CCAAT box-binding transcription factor increases the grain yield of wheat with less fertilizer input. Plant Physiol, 167: 411~423
- Reynoso MA, Blanco FA, Bailey-Serres J, Crespi M, Zanetti ME (2013). Selective recruitment of mRNAs and miRNAs to polyribosomes in response to rhizobia infection in *Medicago truncatula*. Plant J, 73: 289~301
- Ripodas C, Castaingts M, Clúa J, Blanco F, Zanetti ME (2015). Annotation, phylogeny and expression analysis of the nuclear factor Y gene families in common bean (*Phaseolus vulgaris*). Front Plant Sci, doi: 10.3389/fpls
- Ripodas C, Clúa J, Battaglia M, Baudin M, Niebel A, Zanetti ME, Blanco F (2014). Transcriptional regulators of legume-rhizobia symbiosis: Nuclear Factors Ys and GRAS are two for tango. Plant Signal Behav, 9: e28847
- Salvini M, Sani E, Fambrini M, Pistelli L, Pucciariello C, Pugliesi C (2012). Molecular analysis of a sunflower gene encoding an homologous of the B subunit of a CAAT binding factor. Mol Biol Rep, 39: 6449~6465
- Sato H, Mizoi J, Tanaka H, Maruyama K, Qin F, Osakabe Y, Morimoto K, Ohoria T, Kusakabe K, Nagata M et al (2014). *Arabidopsis* DPB3-1, a DREB2A interactor, specifically enhances heat stress-induced gene expression by forming a heat stress-specific transcriptional complex with NF-Y subunits. Plant Cell, 26: 4954~4973
- Shen B, Allen WB, Zheng P, Li C, Glassman K, Ranch J, Nubel D, Tarczynski MC (2010). Expression of *ZmLECI* and *ZmWRII* increases seed oil production in maize. Plant Physiol, 153 (3): 980~987
- Shi H, Ye T, Zhong B, Liu X, Jin R, Chan Z (2014). AtHAP5A modulates freezing stress resistance in *Arabidopsis* through binding to CCAAT motif of AtXTH21. New Phytol, 203: 554~567
- Sieffers N, Dang KK, Kumimoto RW, Bynum WE, Tayrose G, Holt BF (2009). Tissue-specific expression patterns of *Arabidopsis* NF-Y transcription factors suggest potential for extensive combinatorial complexity. Plant Physiol, 149: 625~641
- Siriwardana CL, Kumimoto RW, Jones DS, Holt BF (2014). Gene family analysis of the *Arabidopsis* NF-YA transcription factors reveals opposing abscisic acid responses during seed germination. Plant Mol Biol Rep, 32:971~986
- Sorin C, Declerck M, Christ A, Blein T, Ma L, Lelandais-Brière C, Njo MF, Beeckman T, Crespi M, Hartmann C (2014). A miR169 isoform regulates specific NF-YA targets and root architecture in *Arabidopsis*. New Phytol, 202: 1197~1211
- Soyano T, Kouchi H, Hirota A, Hayashi M (2013). Nodule inception directly targets NF-Y subunit genes to regulate essential processes of root nodule development in *Lotus japonicus*. PLoS Genet, 9: e1003352
- Stephenson TJ, McIntyre CL, Collet C, Xue GP (2007). Genome-wide identification and expression analysis of the NF-Y family of transcription factors in *Triticum aestivum*. Plant Mol Biol, 65: 77~92
- Stephenson TJ, McIntyre CL, Collet C, Xue GP (2010). *TaNf-YC11*, one of the light-upregulated NF-YC members in *Triticum aestivum*, is co-regulated with photosynthesis-related genes. Funct Integr Genomics, 10: 265~276
- Stephenson TJ, McIntyre CL, Collet C, Xue GP (2011). *TaNf-YB3* is involved in the regulation of photosynthesis genes in *Triticum aestivum*. Funct Integr Genomics, 11: 327~340
- Sun X, Ling S, Lu Z, Ouyang Y, Liu S, Yao J (2014). *OsNF-YB1*, a rice endosperm-specific gene, is essential for cell proliferation in endosperm development. Gene, 551: 214~221
- Tan H, Yang X, Zhang F, Zheng X, Qu C, Mu J, Fu F, Li J, Guan R, Zhang H et al (2011). Enhanced seed oil production in canola by conditional expression of *Brassica napus* LEAFY COTYLEDON1 and LEC1-LIKE in developing seeds. Plant Physiol, 156: 1577~1588
- Thirumurugan T, Ito Y, Kubo T, Serizawa A, Kurata N (2008). Identification, characterization and interaction of HAP family genes in rice. Mol Genet Genomics, 279: 279~289
- Tiwari SB, Shen Y, Chang HC, Hou Y, Harris A, Ma SF, McPartland M, Hymus GJ, Adam L, Marion C et al (2010). The flowering time regulator CONSTANS is recruited to the FLOWERING LOCUS T promoter via a unique cis-element. New Phytol, 187: 57~66
- Warpeha KM, Upadhyay S, Yeh J, Adamiak J, Hawkins SI, Lapik YR, Anderson MB, Kaufman LS (2007). The GCR1, GPA1, PRN1, NF-Y signal chain mediates both blue light and abscisic acid responses in *Arabidopsis*. Plant Physiol, 143: 1590~1600
- Wei X, Xu J, Guo H, Jiang L, Chen S, Yu C, Zhou Z, Hu P, Zhai H, Wan J (2010). *DTH8* suppresses flowering in rice, influencing plant height and yield potential simultaneously. Plant Physiol, 153: 1747~1758
- Wenkel S, Turck F, Singer K, Gissot L, Le Gourrierec J, Samach A, Coupland G (2006). CONSTANS and the CCAAT box binding complex share a functionally important domain and interact to regulate flowering of *Arabidopsis*. Plant Cell, 18: 2971~2984
- Wright KL, Moore TL, Vilen BJ, Brown AM, Ting JPY (1995). Major histocompatibility complex class II-associated invariant chain gene expression is up-regulated by cooperative interactions of Sp1 and NF-Y. J Biol Chem, 270: 20978~20986

- Yamamoto A, Kagaya Y, Toyoshima R, Kagaya M, Takeda S, Hattori T (2009). *Arabidopsis* NF-YB subunits LEC1 and LEC1-LIKE activate transcription by interacting with seed-specific ABRE-binding factors. *Plant J*, 58: 843~856
- Yan WH, Wang P, Chen HX, Zhou HJ, Li QP, Wang CR, Ding ZH, Zhang YS, Yu SB, Zhang QF et al (2011). A major QTL, *Ghd8*, plays pleiotropic roles in regulating grain productivity, plant height, and heading date in rice. *Mol Plant*, 4: 319~330
- Yang J, Xie Z, Glover BJ (2005). Asymmetric evolution of duplicate genes encoding the CCAAT-binding factor NF-Y in plant genomes. *New Phytol*, 165: 623~631
- Yazawa K, Kamada H (2007). Identification and characterization of carrot HAP factors that form a complex with the *embryo*-specific transcription factor C-LEC1. *J Exp Bot*, 58: 3819~3828
- Yazawa K, Takahata K, Kamada H (2004). Isolation of the gene encoding carrot LEAFY COTYLEDON1 and expression analysis during somatic and zygotic embryogenesis. *Plant Physiol Biochem*, 42: 215~223
- Yu Y, Li Y, Huang G, Meng Z, Zhang D, Wei J, Yan K, Zheng C, Zhang L (2011). PwHAP5, a CCAAT-binding transcription factor, interacts with PwFKBP12 and plays a role in pollen tube growth orientation in *Picea wilsonii*. *J Exp Bot*, 62: 4805~4817
- Zanetti ME, Blanco FA, Beker MP, Battaglia M, Aguilar OM (2010). A C subunit of the plant nuclear factor NF-Y required for rhizobial infection and nodule development affects partner selection in the common bean-*Rhizobium etli* symbiosis. *Plant Cell*, 22: 4142~4157
- Zemzoumi K, Frontini M, Bellorini M, Mantovani R (1999). NF-Y histone fold α 1 helices help impart CCAAT specificity. *J Mol Biol*, 286: 327~337
- Zhang JJ, Xue HW (2013). *OsLEC1/OsHAP3E* participates in the determination of meristem identity in both vegetative and reproductive developments of rice. *J Integr Plant Biol*, 55: 232~249
- Zhang S, Wong L, Meng L, Lemaux PG (2002). Similarity of expression patterns of *knotted1* and *ZmLEC1* during somatic and zygotic embryogenesis in maize (*Zea mays* L.). *Planta*, 215: 191~194
- Zhang X, Zou Z, Gong P, Zhang J, Ziaf K, Li H, Xiao F, Ye Z (2011). Over-expression of microRNA169 confers enhanced drought tolerance to tomato. *Biotechnol Lett*, 33: 403~409
- Zhao B, Ge L, Liang R, Li W, Ruan K, Lin H, Jin Y (2009). Members of miR-169 family are induced by high salinity and transiently inhibit the NF-YA transcription factor. *BMC Mol Biol*, 10: 29
- Zhao B, Liang R, Ge L, Li W, Xiao H, Lin H, Ruan K, Jin Y (2007). Identification of drought-induced microRNAs in rice. *Biochem Biophys Res Commun*, 354: 585~590
- Zhao M, Ding H, Zhu JK, Zhang F, Li WX (2011). Involvement of miR169 in the nitrogen-starvation responses in *Arabidopsis*. *New Phytol*, 190: 906~915