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转录因子NF-Y在植物生长发育和逆境胁迫响应中的作用

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摘要 核因子Y(nuclear factor-Y, NF-Y), 又名为亚铁血红素激活蛋白或CCAAT结合因子, 它是一种几乎存于所有真核生物中且进化比较保守的三聚体转录因子复合物, 该复合物由NF-YA、NF-YB和NF-YC 3个亚基所组成。在酵母和动物中, 每个亚基通常只有单个基因编码, 而在植物中每个亚甲基都有多个基因编码, 并且通常是形成三聚体复合物来发挥作用的。NF-Y在植物生长发育的多个阶段均发挥着重要的作用, 如胚胎形成、根的生长、开花年龄及果实成熟等。另外, 它也具有较强的抗逆能力。该文阐述了NF-Y单个亚基的结构和作用机制, 并综述了该转录因子在植物生长发育过程中的重要作用。最后, 对NF-Y的研究前景进行了展望。

关键词 植物; NF-Y; 生长发育; 抗逆性

Roles of Transcription Factor NF-Y in Plant Growth, Development and Response to Stress

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Abstract NF-Y (nuclear factor-Y), also known as HAP (heme activator factor) or CBFCCAAT box binding factor. The NF-Y is trimeric transcription factor complex composed of NF-YA, NF-YB, and NF-YC subunits, and it is found almost in all eukaryotes. In yeast and animals, a single gene encodes each of the three NF-Y protein subunits. However, it generally have multiple genes encode each subunit in plants, and usually form a trimer complex to function. NF-Ys play important roles in the plant growth and development. Such as, regulating embryo synthesis, root growth, flowering age and fruit ripening, etc. In addition, it also has resistance to stress. Here, we mainly describe the structure of NF-Y single subunits and regulation mechanism of NF-Y, and reviews the important role of NF-Y in plant growth and development. Finally, the research prospects of NF-Y are prospected.

Keywords plant; nuclear factor-Y; growth and development; stress tolerance

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“大哉圣人之道, 洋洋乎发育万物, 峻极於天”, “发育”一词最早出现于《礼记 · 中庸 · 大哉章》[1]。随着生命科学的发展, 在《现代汉语词典》中“发育”被解释为“生物体成熟之前, 机能和构造发生变化, 如植物的开花结果, 动物的性腺成熟”[2]。而生物体的整个生命周期是一个经历发生, 然后不断发展变化的过程。植物的生长发育被视为一系列可识别的动态事件, 最终使植株在质和量上发生变化的过程, 如根的生长、叶的发育、花的形成、果实的成熟和种子的形成等。植物的生长和发育是一个不可分离的生命过程, 并且也是一个不可逆的过程[3]。在植物体的整个生命周期中, 生长发育是一个复杂的调控过程, 受基因和外在环境因素共同调控。

转录因子是通过识别和结合靶基因启动子区域的特殊DNA元件来调节基因表达, 进而在生命生长发育中起着多种至关重要的作用[4]。核因子Y(nuclear factor-Y, NF-Y)是一种普遍存在于真核生物中的转录因子, 通常也被称为亚铁血红素激活蛋白(heme activator factor, HAP)或CCAAT结合因子(CCAAT box binding factor, CBF)。NF-Y复合物是由3个不同亚基所组成, 分别为NF-YA(HAP2/CBF-B)、NF-YB(HAP3/CBF-A)和NF-YC(HAP5/CBF-C)[5]。在动物和酵母中, NF-Y的每个亚基由单个基因编码, 而在植物中, NF-Y的各个亚基不是单独的, 而是由每个亚家族分别进化出多个成员, 并形成异源二聚体或三聚体来发挥作用, 由于形成了较多的异源二聚体或三聚体的组合, 因此在植物中的许多基因家族可能存在功能冗余或分化的现象。近年来有许多研究表明, NF-Y在植物的生长发育过程中发挥着不同的生物学功能, 比如胚胎合成[6]、参与种子萌发调控[4]、花期调控[7-9]、果实成熟[10]、响应逆境胁迫[7,11-12]等生长发育过程。NF-Y基因家族的结构特征和所有功能研究都表明它是一个强大而神秘的基因家族, 在植物生命的多个方面都有着很重要的作用。本文叙述了3个亚基的结构特征和分子机制, 并阐述了NF-Y转录因子在植物生长发育中的功能。

1 NF-Y的蛋白结构和调控机制

1.1 NF-Y的结构特征

NF-Y转录因子分别由NF-YA、NF-YB和NF-YC3个亚基组成, 每个亚基都包含一个相对保守的结构域[13]。这些保守区域是DNA结合或蛋白–蛋白互作的功能域, NF-YB通常与NF-YC相互作用在细胞质中形成紧密的异二聚体, 其中NF-YB在异源三聚体以及DNA的特异性结合中起核心作用[14-15]。

NF-YA亚基通常定位于细胞核, 大多数NF-YA蛋白可以结合CCAAT顺式元件靶基因的启动子区域[14,16-17]。它们具有不同长度的蛋白结构, 分析发现, 它们的结构均有1个由53个氨基酸组成的蛋白核心区, 其中2个保守的α-螺旋结构域(A1和A2)存在于该核心区域, A1和A2分别由20和21个氨基酸组成, 它们之间由一个保守的连接线隔开。位于N-端结构域的A1与NF-YB和NF-YC亚基相互作用, 而C-端结构域的A2与DNA互作[14,17-18]。

NF-YB蛋白的长度通常小于NF-YA, 它的结构特征与核心组蛋白H2B中的HFM(histone-fold motif)非常相似, 该结构域由α1、α2、α3 3个α螺旋组成, 它们之间由2个β链隔开。此外, 在蛋白折叠域HFM的区域外, 还存在1个被称为αC的α螺旋[19-20]。NF-YB在蛋白–蛋白以及蛋白-DNA的互作中扮演着重要的角色。它的蛋白结构由位于N-端的A结构域、核心区B结构域和C-端的C结构域部分所组成, 由于B结构域的保守区中有1段由16个氨基酸构成的特异序列[21], 从而将NF-YB蛋白分为LEC-1(LEAFY COTYLEDON-1)和非LEC-1两类[6,22]。它们在胚胎发育, 种子分化等过程中发挥着重要的作用[11,21]。

对于NF-YC蛋白而言, 其大小通常在NF-YA和NF-YB蛋白之间, 保守域与H2A蛋白中HFM的结构类似, 并且与NF-YB相比, 它与核心组蛋白H2A更为相似。该结构域也包括由2个β链环所分隔的3个α螺旋(α1、α2、α3)。在HFM折叠区域外, 还存在1个具有7个氨基酸的αC螺旋结构。它在蛋白–蛋白与蛋白-DNA的互作中也起着重要的作用[23]。

1.2 NF-Y的作用机制

NF-Y转录因子在植物中主要是以复合物形式来发挥功能, 因此了解其具体的调控机制非常重要。研究表明, NF-Y主要通过以下两种调控机制来调节下游靶基因的表达(图1)。

(1)NF-YB和NF-YC首先在细胞质中形成异二聚体并进行组装, 然后转移到细胞核中, 进一步与NF-YA相互作用形成具有活性的异源三聚体。NF-YA/B/C复合物主要是通过NF-YA结合位于下游启动子区域的靶基因CCAAT box, 进一步使下游基因表达[24]。已有研究报道, AtNF-YA6亚基与AtNF-YB6/

YC3二聚体相互作用, 所形成的三聚体可以直接结合CCAAT顺式元件[25]。

(2)NF-YB/NF-YC先形成异二聚体, 然后与特定转录因子结合形成复合物, 再进一步与靶基因启动子的特定顺式元件结合, 进而来调节靶基因的表达。但是, 在这一调控机制中, NF-YA可能通过抑制转录因子与NF-YB-YC的结合进而抑制三聚体复合物转录因子的合成[9,26]。这一假设需要进一步的研究来进行验证。例如, AtB9-C2-bZIP67在*SUS*(sucrose synthase 2)和*CRC*(cruciferin C)的启动子区域通过bZIP67直接与ABA反应元件(ABA-response elements, ABREs)结合, 然后激活*SUS2*和*CRC*的表达进而促进种子萌发[26]。然而, NF-YA亚基通过与bZIP67结合形成NF-YA-YB9-YC2复合物而强烈抑制CRC的表达, 这表明, NF-Y亚基的不同成员在植物的生长发育中起不同作用[27]。

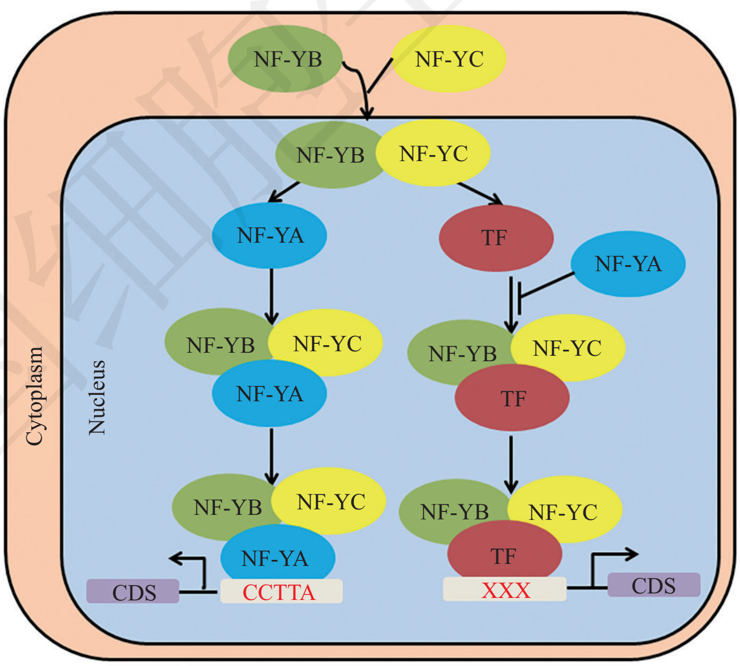
此外, 除了以上2种转录调控机制, 还存在一些其他的调控方式, 比如, *AtHAP5A*通过结合AtXTH21的CCAAT box进而调节拟南芥的抗冻应激性[28]; *At-NF-YA2*可以直接结合NFYBE顺式元件(不是CCAAT box)*SOC1*(suppresor constans1)启动子来调节*SOC1*的表达[29]。*CmNF-YB8*通过结合miRNA156来调控菊花的开花时间[8]。因此, NF-Y复合物可能与多种相关的表观遗传因素和miRNA结合来调节下游靶基因的转录, 这将有待进一步综合研究。

2 NF-Y参与植物生长发育的调控与逆境胁迫的响应

2.1 NF-Y参与植物的生长发育过程

NF-Y参与了从营养生长(种子的萌发、根的生长、叶的形成)到生殖生长(花器官的形成、果实成熟、胚胎形成以及种子的形态)整个植物的生长发育过程。下面就根据植物生命历程顺序介绍NF-Y在每个发育阶段的重要作用。

2.1.1 NF-Y调节植物胚胎形成和种子的萌发 胚胎发生是所有开花植物的关键时期, 它是由单细胞合子增殖并经过一系列的分化最终形成的。在胚胎发生的早期, 植物的极性表示为芽根轴、胚胎组织和器官系统形成; 到发育晚期阶段, 胚胎具有了抵抗干燥和积累储备的能力, 进而形成了种子[4,31]。



红、蓝、绿、黄色椭圆分别代表转录因子、NF-YA、NF-YB、NF-YC; XXX代表顺式元件; 橙色区域和浅蓝色区域分别代表细胞质区域和细胞核区域; →代表合成和调控方向, ⊤ 表示NF-YA可以抑制复合体的形成, ↱ 代表激活下游基因的表达。

Red, blue, green, and yellow oval represent transcription factors, NF-YA, NF-YB, and NF-YC; XXX represents cis-elements; orange and light blue regions represent cytoplasmic and nuclear regions, respectively; → represents the direction of synthesis and regulation, ⊤ indicates that NF-YA can inhibit the formation of complexes, and ↱ represents the Expression of downstream genes.

图1 NF-Y调控基因表达的分子机制示意图(根据参考文献[30]修改)

Fig.1 The molecular mechanism of NF-Y regulation of gene expression (modified by reference [30])

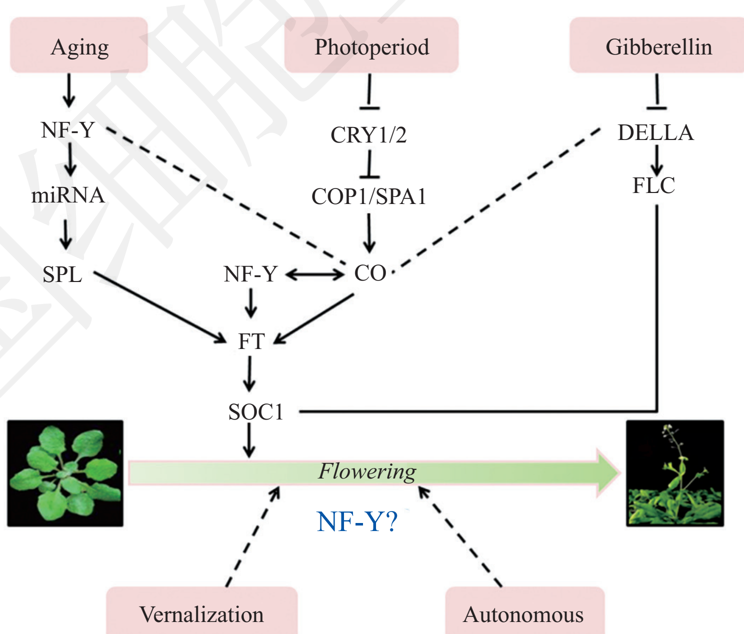
*NF-YB9*也被称作*LEC1*, 是第一个被鉴定为调节胚胎形成的关键因子, 它们可以从多方面控制胚胎的发育, 特别是在维持细胞运动以及防止未成熟的种子过早发芽起重要作用[6]。*NF-YB*转录因子成员*NF-YB6*(*LEC1-LIKE*)通过诱导与胚胎合成和细胞分化相关的基因进而调控胚胎的发育[32]。此外, 组织特异表达分析发现, 拟南芥中*AtNF-YA1*、*2*、*3*、*4*、*6*、*7*、*8*和*9*[33], 玉米中*ZmNF-YB2*、*6*、*7*、*10*、*14*和*17*[34], 蓖麻中*RcNF-YB2*和*RcNF-YB12*, 在胚胎和种子发育阶段均呈现出较高的表达水平[4], 表明它们均参与调节胚胎形成和种子发育的过程。在遗传学方面也有研究报道, 一些NF-Y成员与胚胎形成有密切的关系。例如, 拟南芥中的*NF-YA3*、*NF-YA8*的突变(双突)以及*NF-YC4*的突变都会通过调节生长素的反应进而影响早期胚胎发育[33]。在水稻中, *OsNF-YB1*的缺失突变会导致胚乳发生一些缺陷[35]。

2.1.2 NF-Y调节根的生长　根作为植物的营养器官, 位于地表以下, 负责吸收和运输水分, 并且具有支持、合成和贮存有机物质的作用。研究表明, 在拟南芥中, *NF-YA10*通过miR169调控*AtNF-YA2*, 控制植株主根的生长。此外, 在拟南芥中过量表达*AtNF-YB2*会加快植物细胞分裂和伸长, 进而加速主根的伸长[36-38]。

2.1.3 NF-Y调控叶绿体的形成和叶的发育　叶绿体的主要作用是进行光合作用并合成植物生长所需的相关物质。*NF-YA5*/*B9*/*C9*参与了叶绿素生物合成过程[39], 在水稻*OsHAP3A*缺失突变体中, 植株叶绿素降低[40], 同时*TaNF-YB3*的过表达明显增加了小麦的叶绿素含量。这些结果均表明, NF-Y在叶绿素合成过程中起重要作用[41]

2.1.4 NF-Y参与植物开花年龄的调控　开花对于被子植物从营养生长到生殖生长是一个重要的调控事件, 而开花是由外界环境和内部信号互作相结合的一个复杂的过程所决定。目前开花途经主要包括以下5个途径: 光周期途径、自主途径、春化途径、赤霉素途径和年龄途径[42-43]。这些开花途径通过相互作用最终整合到FT和SOC1, 进而参与将下游的相关开花基因激活并表达[44-45]。NF-Y一些亚基也可以与*CO*(*CONSTANS*)或miRNA互作调控FT和SOC1 2个关键整合子的转录水平, 进而使植物提前或延迟开花[8-9](图2)。

在光周期调控途径中, NF-Y的复合体可与CO



单箭头代表正向调节; 双箭头代表两个因子互作调控下游基因; ┬表示抑制下游基因的表达; 虚线(虚线箭头)代表调控机制未知。

Single arrows represent positive regulation; double arrows represent two factors interacting to regulate downstream genes; ┬ indicates inhibition of downstream gene expression, and dotted lines (dotted arrows) indicate that regulatory mechanisms are unknown.

图2　植物NF-Y调控开花时间网络

Fig.2　Nuclear factor Y of plants regulation flowering time network

蛋白结合，激活光周期途径进而促进下游开花转录因子的表达。例如，在NF-YA中，*CO*替代了拟南芥NF-YA亚基，形成了CO/AtHAP3/AtHAP5复合体来调控开花时间，并且通过交替过表达和缺失*CO*和NF-Y，进一步验证了它们是通过复合体进一步调控开花。在NF-YB中，拟南芥中AtNF-YC3/4/9与AtNF-YB2/3互作，来共同调控*constans*从而影响开花过程[9]。此外，在长日照条件下，水稻*OsNF-YB11*通过下调开花调控子的表达，抑制了光周期从而诱导开花[46]。此外，小麦中的*TaNF-YC5*、*TaNF-YC8*、*TaNF-YC9*、*TaNF-YC11*和*TaNF-YC12*也受光信号调控[41]。

年龄调控途径也是近年来人们关注的焦点，miRNA156是控制植物年龄途径的非编码RNA[43]。目前研究表明，菊花*CmNF-YB8*与cmo-MIR156基因的启动子结合，*CmNF-YB8*通过调节年龄路径中cmo-MIR156的表达进而提早菊花的开花时间[8]。

在赤霉素调控途径中，NF-Y通过与GA依赖性途径中的蛋白质DELLA相互作用影响开花时间。研究表明，在拟南芥中，*NF-YA2*/B2/*C9*复合物可以与CO和DELLA相互作用，其中*NF-YA2*与SOC1启动子中的NFYBE顺式元件结合，然后NF-Y复合物通过对H3K27水平去甲基化，促进SOC1表达并导致早花，这也表明NF-Y复合体在表观遗传修饰中具有关键的作用[29]。

除此之外，NF-Y转录因子还参与花粉管发育，进而来调节开花。如管涔山青扦(*Picea wilsoni*) *PwNF-YC*的过表达可以促进花粉管的发育[47]。

2.1.5 NF-Y参与果实成熟的调控　果实成熟是一个复杂的动态过程，在此过程中，许多转录因子通过调控成熟相关基因的表达，在果实成熟过程中发挥着重要作用[48]。众所周知，转录因子RIN是果实成熟的关键调控因子，研究表明，转录因子RIN对4个*NF-Y*基因(*Solyc10g079150*、*Solyc10g081840*、*Solyc12g009050*、*Solyc03g111460*)具有直接结合能力，表明番茄NF-Y转录因子在果实成熟中发挥作用[10]。

2.1.6 NF-Y调控种子粒的大小　种子粒形状(粒长、宽度和厚度)是决定一些农作物产量和品质的重要因素。粒度和形状受到小穗壳生长的限制。最新研究发现，通过基因编辑得到的*osnf-yc10*突变体和OsNF-YC10 RNAi株系宽度和粒重均表现出减少。进一步研究发现，*OsNF-YC10*在颗粒宽度方向上影响细胞数。同时，在*osnf-yc10*和OsNF-YC10 RNAi转基因系中检测到相关的细胞周期基因的表达水平显着降低。因此，这也表明，*OsNF-YC10*通过影响细胞增殖来调节谷粒宽度和粒重[49]。

总而言之，NF-Y因子参与植物的生长和发育，如胚胎形成、种子萌发、开花、果实成熟等，见表1。

2.2 NF-Y参与植物响应胁迫反应

2.2.1 响应干旱胁迫　植物生长于一个复杂多变的自然环境中，通常会遭受多种外界环境胁迫，其中干旱胁迫是最为普遍的一种，*NF-Y*作为响应干旱胁迫的重要转录因子[50-51]，主要通过miR169、ABA交叉的信号以及光合作用等途径进行调控。研究表明，*At-miR169a*过表达，可进一步调控*AtNF-YA5*使得拟南芥植株具有较强的抗旱能力[50]。同时，在番茄中过表达*miR169c*，也使得植株的抗旱性显著提高[52]。光合作用调控方面，干旱的条件下，过表达玉米*NF-YB2*基因，转基因植株与野生型比较，叶片窄小，叶绿素含量增加，光合速率、气孔电导率等指数均增强[7]。同样，小麦过量表达*TaNF-YB3*也会导致植株的光合速率、叶绿素含量提高，使小麦的抗旱性增强[41]。在拟南芥中过表达杨树*PtNF-YA9*也能够增强植株对干旱胁迫的敏感性[11]。拟南芥*AtNF-YA5*参与了蓝光与ABA相结合的信号转导途径，促进黄化幼苗中叶绿素a和b的结合蛋白表达[53]。此外，在拟南芥中*LEC1*和*L1L*的突变体对ABA表现超敏感[53]。将*PdNF-YB7*在拟南芥中过表达，植株表现出较长的初生根和较大的叶片面积，并且其光合速率提高，这一研究进一步表明，*PdNF-YB*是通过参与ABA依赖途径来增强干旱胁迫的耐性[54]。玉米*ZmNF-YA3*还可通过JA和ABA信号传导，提高旱胁迫耐受性[7]。除以上调节途径，过表达*AtNF-YB1*的转基因拟南芥植株具有较强的抗旱能力，但是检测其抗旱相关基因和ABA相关途径的基因均无明显变化，推测其可能通过其他的途径来抵御干旱胁迫，但这一作用机制还有待研究阐明[51]。

2.2.2 响应其他胁迫　除了响应干旱胁迫外，许多研究表明，NF-Y转录因子还参与高盐、冷冻以及高温等逆境胁迫响应。对于响应高盐胁迫，在拟南芥中，过表达*AtNF-YA1*、*HvNF-Y*和*TaNF-YA10*-1均可以提高对植株的耐盐能力[55-56]。在水稻中，将百慕大草*CdtNF-YC1*在水稻中过表达，会增强植株对盐胁迫的敏感性[57]。对于内质网逆境胁迫，研究表明，bZIP28可通过水解蛋白并与*AtNF-Y*亚基形成转录

表1 植物中*NF-Y*基因的功能

Table 1 Plant *NF-Y* genes with biological functions

基因名 Gene name	植物 Plant	生物学功能 Biological function
AtNF-YA1	*Arabidopsis thaliana*	Regulate flowering time and embryonic development
AtNF-YA2	*Arabidopsis thaliana*	Regulate flowering time; regulate root development
AtNF-YA3	*Arabidopsis thaliana*	Regulate embryonic development
AtNF-YA4	*Arabidopsis thaliana*	Regulate flowering time; regulate ER stress
AtNF-YA5	*Arabidopsis thaliana*	Drought response; regulate embryonic development
AtNF-YA6	*Arabidopsis thaliana*	Regulate seed germination and root development
AtNF-YA8	*Arabidopsis thaliana*	Regulate embryonic development
AtNF-YA10	*Arabidopsis thaliana*	Regulate root development
AtNF-YB1	*Arabidopsis thaliana*	Regulate flowering time; drought response
AtNF-YB2	*Arabidopsis thaliana*	Regulate flowering time and root development
AtNF-YB3	*Arabidopsis thaliana*	Regulate flowering time; regulate ER and heat stress
AtNF-YB6	*Arabidopsis thaliana*	Embryonic developmental regulation
AtNF-YB9	*Arabidopsis thaliana*	Regulate embryonic synthesis and hypocotyl growth
AtNF-YC1	*Arabidopsis thaliana*	Regulate flowering time; cold response
AtNF-YC2	*Arabidopsis thaliana*	Regulate flowering time; regulate ER stress
AtNF-YC3	*Arabidopsis thaliana*	Regulate flowering time
AtNF-YC4	*Arabidopsis thaliana*	Regulate flowering time
AtNF-YC9	*Arabidopsis thaliana*	Regulate flowering time and chlorophyll synthesis
AtNF-YC10	*Arabidopsis thaliana*	Heat response
OsHAP2E	Rice	Disease resistance
OsHAP3E	Rice	Regulate reproductive development
OsNF-YB1	Rice	Regulate the development of endosperm
OsNF-YB2	Rice	Regulation of chlorophyll synthesis
OsNF-YB7	Rice	Regulate reproductive development
OsNF-YC10	Rice	Regulation of rice granule width
OsNF-YB11	Rice	Regulate flowering time
GmNF-YA3	Soybean	Drought response
TaNF-YA10	Wheat	Salt response
TaNF-YB3	Wheat	Regulation of photosynthesis and chlorophyll synthesis
SiNF-YA1	Foxtail millet	Salt and drought response
SiNF-YA8	Foxtail millet	Drought and osmotic response
Solyc06g069310	Tomato	Regulation of fruit ripening
Solyc07g065500	Tomato	Regulation of fruit ripening
Solyc08g062210	Tomato	Regulation of fruit ripening
Solyc11g065700	Tomato	Regulation of fruit ripening
Solyc01g087240	Tomato	Regulation of fruit ripening
MtHAP2-1	Medicago	Regulate the development of nodules
RcNF-YB2	Castor bean	Regulate seed germination
RcNF-YB12	Castor bean	Regulate seed germination
CsNF-YA5	Citrus	Drought response
PtNF-YA9	Poplar	Regulate flowering time; salt and drought response; regulate flowering time
CmNF-YB8	*Chrysanthemum*	
VvNF-YA1	Grape	Regulate fructose and glucose synthesis
VvNF-YB7	Grape	Regulate fructose and glucose synthesis
BnLEC1	*Brassica napus L.*	Regulate fatty acid synthesis
BnL1L	*Brassica napus L.*	Regulate fatty acid synthesis

复合物, 进而上调响应内质网诱导基因的表达[58]。此外, 过表达*AtNF-YC1*和*AtNF-YC10*分别可以提高对拟南芥植株对冷冻和高温的耐受性[28]。在蓖麻中*RcNF-YB6*、*RcNF-YB11*、*RcNF-YC2*、*RcNF-YC12*等多个基因也参与了冷冻和高温的逆境响应过程[4], 最近研究发现, *AtNF-YB2*和*AtNF-YB3*的过表达可以增强拟南芥植株的干旱和热胁迫耐受性[59]。

总的说来, NF-Y参与干旱、高盐、冷冻以及高温等逆境胁迫响应, 见表1。

3 展望

相比动物和酵母, NF-Y在植物中的功能更加多样, NF-Y因子不仅参与植物的生长和发育(如胚胎形成、种子萌发、开花、果实成熟等), 同时在逆境胁迫响应(如抗旱、抗盐、高温、冷胁迫等)中也扮演着重要的角色。在生长发育过程中, 尤其是调控开花过程中的研究, 目前主要集中在光周期和赤霉素途径。*CmNF-YB*参与年龄开花途径, 但是NF-Y是否通过春化途径和自主途径来调控开花仍然未知, 因此还需科研工作者的进一步探索。关于NF-Y的生物学功能的深入研究仅限于在模式植物拟南芥和少数草本植物中, 对于多年生的木本植物仅有一些基础的研究, 而对于其是如何调控靶基因进而发挥功能仍未知。因此, 研究NF-Y在木本植物中是如何调控下游靶基因发挥作用也具有重要的意义。

此外, 任何生命活动的进行都需要多种因子相互调控协作来完成, NF-Y包括3个亚基, 它们在发挥作用时通常通过形成三聚体作用, 而目前除模式植物外, 其他植物中的分子作用机制还有待进一步研究。最近研究也表明, miR156等小RNA调控*NF-YB*基因进而来调控开花时间。因此, 关于NF-Y从转录调控和翻译后修饰来解析NF-Y因子是如何工作的, 以及与microRNA之间是如何调控互作的, 这都值得更多科研工作者关注。

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