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REVIEW

The Promiscuous Life of Plant NUCLEAR FACTOR Y Transcription Factors[W]

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The CCAAT box is one of the most common *cis*-elements present in eukaryotic promoters and is bound by the transcription factor NUCLEAR FACTOR Y (NF-Y). NF-Y is composed of three subunits, NF-YA, NF-YB, and NF-YC. Unlike animals and fungi, plants have significantly expanded the number of genes encoding NF-Y subunits. We provide a comprehensive classification of *NF-Y* genes, with a separation of closely related, but distinct, histone fold domain proteins. We additionally review recent experiments that have placed NF-Y at the center of many developmental stress-responsive processes in the plant lineage.

INTRODUCTION

NUCLEAR FACTOR Y (NF-Y) transcription factors (also known as Heme-associated proteins [HAPs] and CCAAT box binding factors [CBFs]) are rapidly emerging as important regulators of numerous plant developmental and stress-induced responses. NF-Ys are sequence-specific transcription factors with histone-like subunits, with the unique characteristic that they bind DNA at CCAAT sites as heterotrimeric complexes composed of single subunits from each of three protein families: NF-YA, NF-YB, and NF-YC. In the plant lineage, each subunit type is encoded by a family of ~10 genes, both in dicots and monocots, which differentiates them from animal systems, where there is typically only one or two genes encoding each subunit type. The expansion of NF-Y families in plants, combined with their heterotrimeric nature, means that many possible NF-Y complexes can form. This leads to the formation of a flexible, combinatorial system of transcription factors that may allow subtle adjustments to many different environmental conditions.

Because of overlapping functionality in the plant NF-Y families, our knowledge with respect to their functions has lagged somewhat compared with animal and fungal systems. Nevertheless, in recent years, numerous reports have emerged demonstrating the roles of individual subunits in many important processes. In this review, we comprehensively examine progress in understanding NF-Y functions in the plant lineage, providing an entrée for the nonexpert and a broad review for the aficionados. Additionally, to avoid further confusion with acronyms and the related, but functionally distinct, histone fold domain (HFD) proteins, we propose a reclassification of the plant NF-Y genes. For additional information/perspectives, we recommend the recent NF-Y review by Laloum et al. (2012).

CLASSIFICATION

NF-Ys and HAPs

The initial reports of *NF-Y* genes in plants date back to the 1990s (Li et al., 1992b; Albani and Robert, 1995; Edwards et al., 1998; Lotan et al., 1998; Kusnetsov et al., 1999). The comprehensive search for NF-Y genes in *Arabidopsis thaliana* (Gusmaroli et al., 2001, 2002; Yang et al., 2005; Siefers et al., 2009) was followed by similar ones in other plant species, including rice (*Oryza sativa*), wheat (*Triticum aestivum*), and *Brachypodium distachyon* (Stephenson et al., 2007; Thirumurugan et al., 2008; Cao et al., 2011b). It became clear that each plant *NF-Y* gene family has undergone significant amplification (e.g., seven NF-YC genes in rice [Thirumurugan et al., 2008] and 14 in wheat [Stephenson et al., 2007]).

Identification of members of each NF-Y family is based on the presence of highly conserved domains. NF-YA proteins have a conserved ~56–amino acid domain that is composed of two helices (A1 and A2) with separate functions: A1 is required for subunit interactions and A2 for sequence specificity to bind DNA at CCAAT boxes. NF-YB and NF-YC each share HFDs with the core histones H2B and H2A, respectively. Mutagenesis studies in yeast and mammals confirmed that the HFD is important for NF-Y subunit interactions and DNA binding (Romier et al., 2003 and references therein). Currently, the various NF-Y subunits of rice (and other species, although less fully adopted) are often referred to by the yeast HAP2/3/5 nomenclature (homologs of NF-YA, NF-YB, and NF-YC, respectively; Miyoshi et al., 2003; Yazawa and Kamada, 2007; Thirumurugan et al., 2008; Xie et al., 2008; Yu et al., 2011). This has created confusion and difficulty following the literature in three principal ways: (1) To the best of

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our knowledge, plants are devoid of homologs of HAP4, which is required for transcriptional activation in fungi (McNabb and Pinto, 2005; Kato, 2005), and they form a mammalian-like trimer. (2) Most genetic experiments and two thorough biochemical studies were performed on *Arabidopsis*, adhering to the NF-Y terminology (Gusmaroli et al., 2001, 2002; Siefers et al., 2009). (3) The phylogenetically unrelated *HAPLESS* mutants of *Arabidopsis* are also known as *hap* (Johnson et al., 2004), which precludes changing the *Arabidopsis* nomenclature. Thus, where the HAP terminology is used, we propose to reclassify these genes following the At-NF-Y nomenclature (Table 1).

We also propose to maintain use of the current nomenclature on *Arabidopsis* LEAFY COTYLEDON1 (At-LEC1) and LEC1-LIKE (L1L; At-NF-YB9 and At-NF-YB6, respectively). This suggestion comes from the fact that LEC1 and L1L were identified before the original *Arabidopsis* classification and many studies refer to this nomenclature (Zhang et al., 2002; Yazawa et al., 2004; Alemanno et al., 2008; Schellenbaum et al., 2008; Maillot et al., 2009; Salvini et al., 2012). We suggest that reporting on these proteins include mention of the NF-Y names to assist nonexpert readers in understanding the family connection.

Table 1. Classification of Rice NF-Y Genes

Os-NF-YA Family		
NF-Y Name	Locus Name	Other Names
NF-YA1	Os03g07880	HAP2C
NF-YA2	Os03g29760	HAP2E
NF-YA3	Os03g44540	HAP2H
NF-YA4	Os03g48970	HAP2D
NF-YA5	Os07g06470	HAP2J
NF-YA6	Os07g41720	HAP2G
NF-YA7	Os08g09690	HAP2A
NF-YA8	Os10g25850	HAP2I
NF-YA9	Os12g41880	HAP2B
NF-YA10	Os12g42400	HAP2F
Os-NF-YB Family		
NF-Y Name	Locus Name	Other Names
NF-YB1	Os02g49410	HAP3K
NF-YB2	Os01g61810	HAP3A
NF-YB3	Os05g38820	HAP3B
NF-YB4	Os05g49780	HAP3C
NF-YB5	Os01g70880	HAP3J
NF-YB6	Os01g70890	HAP3G
NF-YB7	Os02g49370	HAP3E, L1L
NF-YB8	Os03g29970	HAP3I
NF-YB9	Os06g17480	HAP3D
NF-YB10	Os07g41580	HAP3F
NF-YB11	Os08g07740	HAP3H, Hd5, DTH8, Ghd8
Os-NF-YC Family		
NF-Y Name	Locus Name	Other Names
NF-YC1	Os02g07450	HAP5A
NF-YC2	Os03g14669	HAP5C
NF-YC3	Os04g58680	HAP5G
NF-YC4	Os06g45640	HAP5B
NF-YC5	Os08g10560	HAP5F
NF-YC6	Os08g38780	HAP5D
NF-YC7	Os09g30310	HAP5E

Table 2. Reclassification of Plant HFD Proteins

Former NF-Y Name	New Name	Locus ID
At-NF-YC11	At-NC2α	AT3G12480
At-NF-YB12	At-NC2β1	AT5G08190
At-NF-YB13	At-NC2β2	AT5G23090
Bd-NF-YC4	Bd-NC2α1	Bradi2g21290
Bd-NF-YC11	Bd-NC2α2	Bradi4g16840
Bd-NF-YB16	Bd-NC2β1	Bradi3g34930
Ta-NF-YC6	Ta-NC2α1	TC233433
Ta-NF-YC8	Ta-NC2α2	TC241235
Ta-Dr1A	Ta-NC2β1	AF464903_1
Ta-Dr1B	Ta-NC2β2	TC416575
At-NF-YC10	At-Dpb3-1	AT1G07980
At-NF-YC13	At-Dpb3-2	AT5G43250
At-NF-YB11	At-Dpb4	AT2G27470
Ta-NF-YC13	Ta-Dpb3-1	BJ308764
Ta-NF-YC14	Ta-Dpb3-2	TC270995
Bd-NF-YC1	Bd-Dpb3	Bradi1g01300
Bd-NF-YB3	Bd-Dpb4	Bradi1g43470

Relationship between *NF-Y*, *NC2*, and *Dpb3/4* Genes

A second level of misunderstanding has been generated by the inclusion of plant homologs of *NC2* and *Dpb3*/*Dpb4* within the *NF-Y* gene family. These genes collectively form a subfamily of H2A/H2B-like genes, with high primary sequence identity, 30/35%, reflected in structural similarities (Kamada et al., 2001; Romier et al., 2003; Hartlepp et al., 2005). It is therefore understandable that plant NC2s and Dpb3/4 might be included in a common family. In fact, these genes are more closely related to NF-Ys than other HFD proteins. Nevertheless, it has been shown that some of the classified *Arabidopsis*, wheat, and *B. distachyon* genes are outliers in the phylogenetic analyses of NF-Y proteins (Stephenson et al., 2007; Siefers et al., 2009; Cao et al., 2011b). This point is relevant, as the two related HFD groups NC2 and Dpb3/4 are not functionally overlapping with NF-Y; NC2 associates with TBP to bind TATA boxes in core eukaryotic promoters (Kamada et al., 2001), whereas Dpb3/4 are involved in complexes with DNA Pol ε and the chromatin remodeling complex Chrac (Hartlepp et al., 2005).

In summary, we propose a return to the original classification of 29 bona fide At-NF-Y proteins with the addition of At-NF-YC12 (Gusmaroli et al., 2001, 2002; Siefers et al., 2009). This nomenclature also serves to close a gap, as both NC2 and Dpb3/Dpb4 genes are highly conserved from yeast to mammals. It is now clear that At-*NC2* genes were duplicated and At-*Dpb3/4* were not expanded in plants (Table 2). Thus, plant *NF-Y* genes serve a far greater role in gene regulatory processes, leading to variable plant developmental pathways.

FUNCTIONAL STUDIES OF *NF-Y* GENES

Expression of NF-Y Subunits

The expansion of plant *NF-Y* gene families has led to the intimidating task of identifying biologically relevant NF-Y complexes.

To begin sorting through the many possible NF-Y heterotrimers, several groups have characterized *NF-Y* mRNA expression patterns for diverse plant species. Organ-specific mRNA expression patterns and phylogenetic relationships have been systematically established for *Arabidopsis*, *B. distachyon*, rice, and wheat (Gusmaroli et al., 2001, 2002; Stephenson et al., 2007; Thirumurugan et al., 2008; Cao et al., 2011b), although the *Triticum* phylogenetic classifications and database annotations require further input to make the published analyses broadly useful. Here, we developed phylogenetic trees for each NF-Y family comparing *Arabidopsis*, *B. distachyon*, and rice full-length proteins (Figure 1, Figure 2, and Figure 3; Supplemental Data Sets 1, 2, and 3 online; Laloum et al. [2012] provide trees comparing *Arabidopsis*, soybean [*Glycine max*], *Medicago truncatula*, and rice). Due to the high amino acid identity among family members, even across the dicot/monocot split, the bootstrap support for some clades is quite low (<70%); thus, these trees are not necessarily accurate for lineage inferences. Nevertheless, we opted not to collapse these branches because they provide potentially useful information for functional inferences. In fact, despite the lack of strong bootstrap support, similar trees have been useful for identifying likely NF-Y candidates involved in flowering (Kumimoto et al., 2010; Cao et al., 2011b). Based on these data, no strong patterns connecting NF-Y phylogenetics

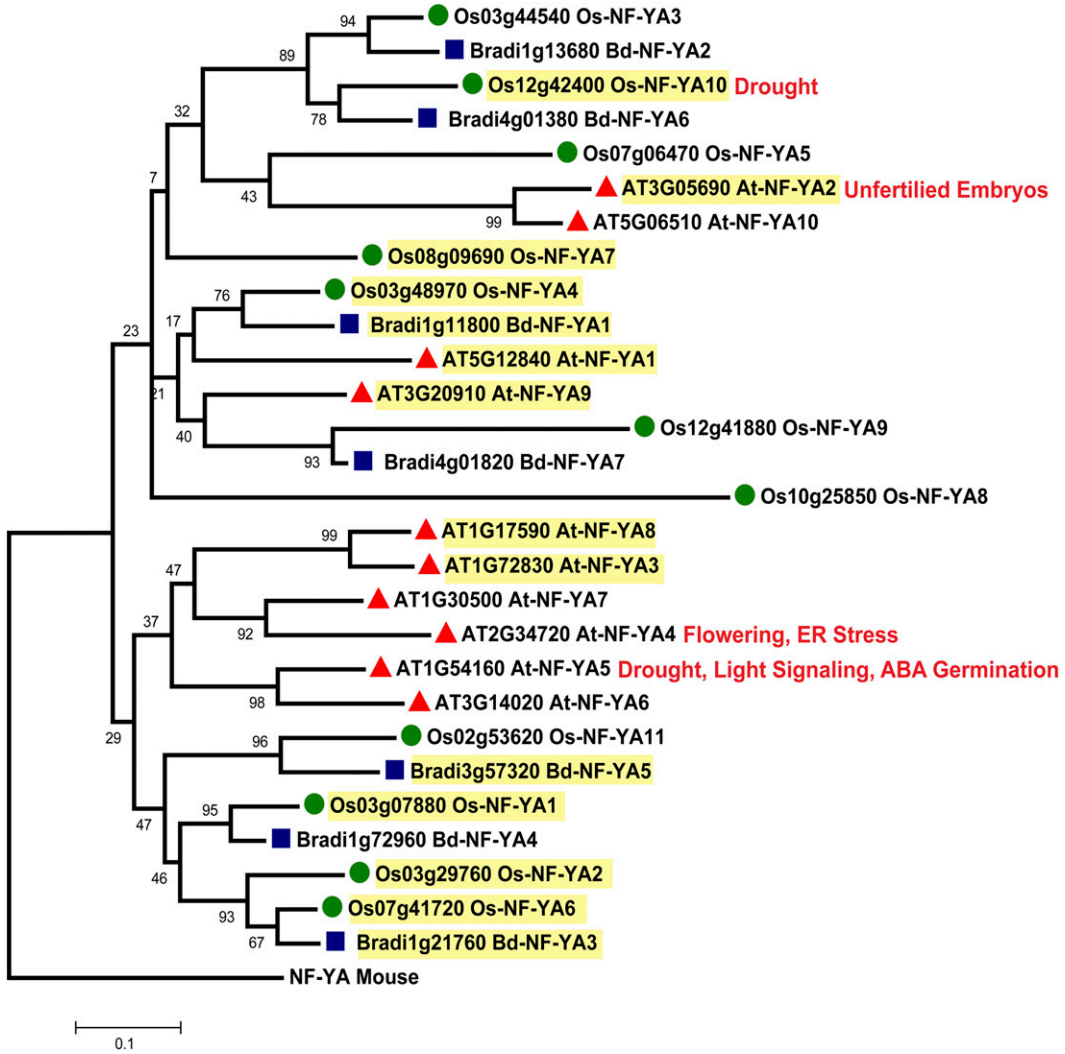

Figure 1. Phylogenetic Tree of *Arabidopsis*, *B. distachyon*, and Rice NF-YA Subunits.

For each family of NF-Y proteins, multiple sequence alignments were generated using ClustalW (Thompson et al., 2002) on full-length proteins as implemented by Molecular Evolutionary Genetics Analysis (MEGA) software, version 5.0 (Tamura et al., 2011; note that multiple alignments using MUSCLE [Edgar, 2004] generated essentially identical phylogenetic trees). Phylogenetic trees were constructed by neighbor joining with complete deletions as implemented by MEGA. Reliability values at each branch represent bootstrap samples (5000 replicates). Bootstrap values below 70% are not considered reliable for phylogenetic inferences, although trees are not collapsed at this value (see explanation in main text). The mouse NF-YA subunit was used to root the tree. Yellow highlighted genes are broadly expressed in all RT-PCR experiments. Documented phenotypes for a given gene are in red text.

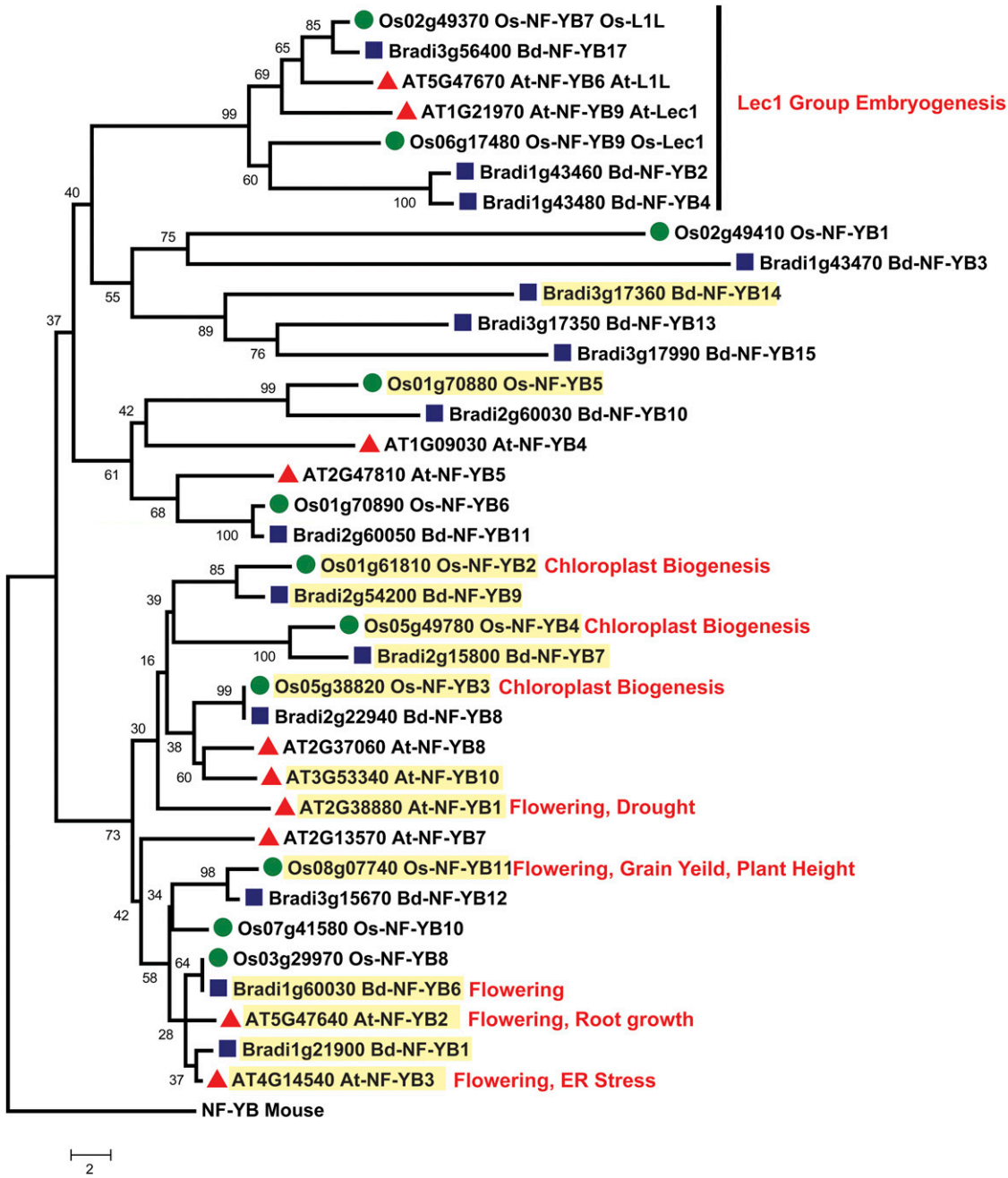

Figure 2. Phylogenetic Tree of *Arabidopsis*, *B. distachyon*, and Rice NF-YB Subunits.

See Figure 1 legend.

and reported expression patterns emerge, but *NF-Y* expression can be broken down into two very general classes: genes that are broadly expressed (found in nearly all tissues tested) and genes with more restricted or organ-specific expression patterns (see highlighting on Figure 1, Figure 2, and Figure 3). To date, most NF-Y phenotypes have been associated with the broadly expressed subunits, with a notable exception being the narrowly expressed LEC class (Figure 2).

In addition to RT-PCR data, tissue-specific expression has also been examined for each of the At-*NF-Y* genes using promoter:β-glucuronidase (*pNF-Y*:*GUS*) reporter gene fusions (Siefers et al., 2009). These tissue-specific expression patterns have proven valuable for identifying NF-Y involved in photoperiod-dependent flowering, which is regulated by interactions between NF-Y subunits and the floral promoting protein CONSTANS (CO) (Kumimoto et al., 2010). Because CO function in flowering time

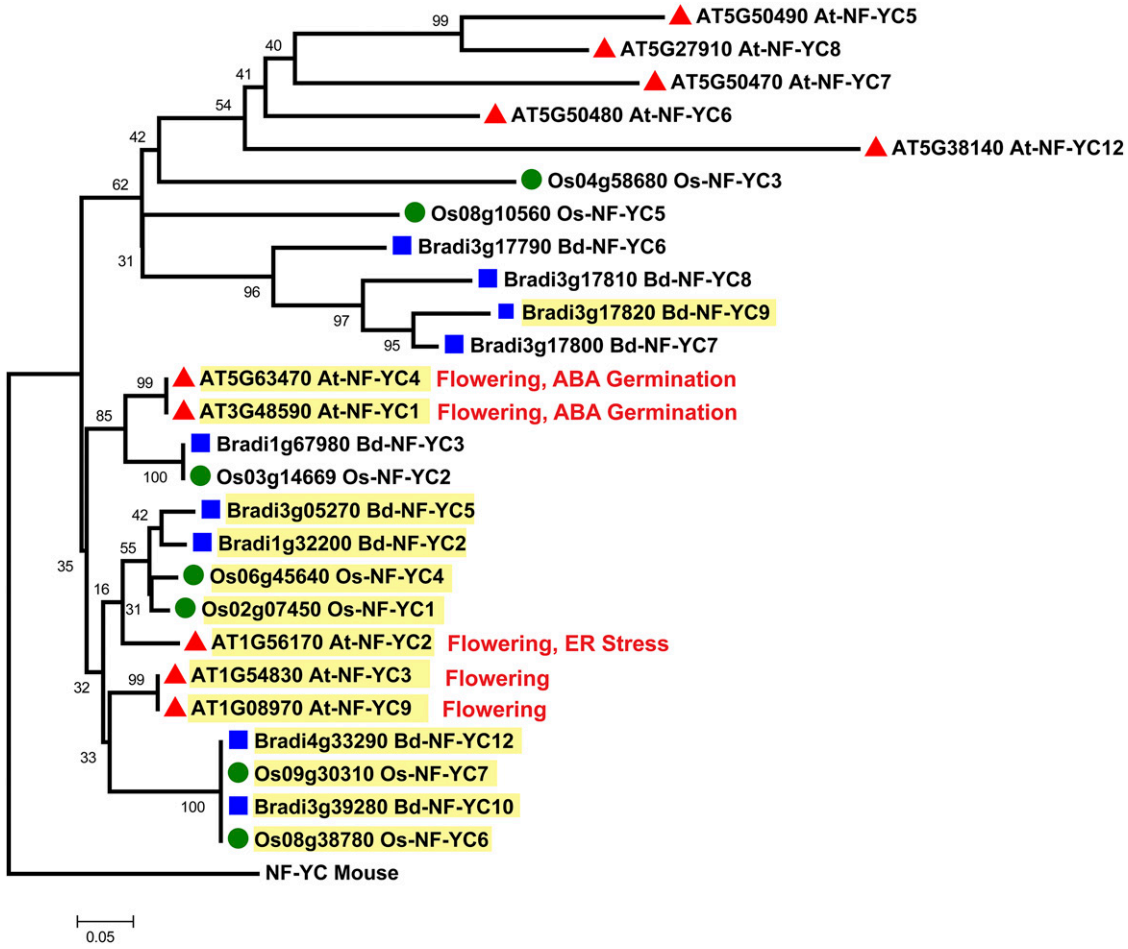

Figure 3. Phylogenetic Tree of *Arabidopsis*, *B. distachyon*, and Rice NF-YC Subunits.

See Figure 1 legend.

requires vascular expression in leaves (An et al., 2004), the *pNF-Y:GUS* reporter lines were instrumental for identifying three vascular expressed At-*NF-YC* involved in the control of photoperiod-dependent flowering (Kumimoto et al., 2010; see below).

Adding to surveys of organ- and tissue-specific expression patterns, several studies have systematically examined NF-Y responses to various environmental conditions and stresses (Stephenson et al., 2007, 2010, 2011; Hackenberg et al., 2012), and numerous studies have implicated NF-Y in regulating photosynthesis and drought responses (Kusnetsov et al., 1999; Miyoshi et al., 2003; Nelson et al., 2007; Li et al., 2008; Stephenson et al., 2010, 2011). Analysis of public microarray data also points to possible NF-Y functions related to photosynthesis, flowering time, and drought. Analysis of cell-specific transcriptome data from rice revealed the CCAAT box element is associated with cell-specific transcripts in both leaf (mesophyll, vein, and primordia) and dehydration-response data sets (Jiao et al., 2009). Finally, it was recently shown that upregulation of *Arabidopsis NF-Y* is correlated with leaf senescence (Breeze et al., 2011). Together, these expression data sets, along with publicly available microarrays, serve as a basic entrée point to *NF-Y* analyses and can be used to narrow down the number of candidates acting in a particular developmental stage or tissue type.

Embryo and Plant Development

Our initial knowledge on developmental processes regulated by *NF-Y* genes came from studies on the embryogenesis regulators At-*LEC1* and *L1L* (At-*NF-YB9* and *NF-YB6*, respectively; Meinke, 1992; West et al., 1994; Parcy et al., 1997; Lotan et al., 1998; Kwong et al., 2003; Gaj et al., 2005; Braybrook and Harada, 2008; Junker et al., 2012). Orthologs of *Arabidopsis LEC* and *L1L* have since been identified and studied in several monocot and dicot species, as well as conifers, where they consistently regulate the transition from embryo to adult status: *lec1* mutants display pleiotropic phenotypes, including abnormal development of trichomes on cotyledons, desiccation intolerance, abnormal suspensors, and seed defects in starch, protein, and lipid accumulation (Zhang et al., 2002; Yazawa et al., 2004; Fambrini et al., 2006; Alemanno et al., 2008; Mu et al., 2008; Schellenbaum et al., 2008;

Maillot et al., 2009; Shen et al., 2010; Cao et al., 2011b; Tan et al., 2011; Uddenberg et al., 2011; Salvini et al., 2012). Recent evidence suggests that LEC1 control extends beyond the embryo to etiolation responses in young seedlings (Junker et al., 2012). Furthermore, using a combination of dexamethasone-inducible *LEC1*, chromatin immunoprecipitation, and microarray analyses, these authors implicated LEC1 as a general integrator of light and hormone signaling during embryogenesis. To our knowledge, this article is also the first to show a clear enrichment for CCAAT boxes as targets of NF-Y transcriptional action in plants, a basic and long accepted expectation from the animal literature.

From an agronomic standpoint, overexpression of *LEC1* or *L1L* in various species can result in significant changes in seed lipids/oils (Mu et al., 2008; Shen et al., 2010; Tan et al., 2011). The specific genes involved are currently unknown, but there is a surprising parallel with the mammalian system, in which sterol regulatory element binding proteins, the master transcription factor regulators of fatty acids and cholesterol metabolisms, team up with NF-Y to activate hundreds of genes that fine-tune lipid levels (Reed et al., 2008). It will be interesting to assess whether these pathways are conserved in plants. Interestingly, LEC1 and L1L, but not several other tested At-NF-YB subunits, can activate seed specific promoters via interactions with the abscisic acid response element binding transcription factor bZIP67 (Yamamoto et al., 2009). Finally, in rice, Os-*NF-YB7/L1L* has roles during both vegetative and floral meristem development. Os-*NF-YB7/L1L1*–overexpressing plants have a dwarf phenotype and erected leaves, as well as a dense panicle, abnormal rachis, and double flowers (Ito et al., 2011).

In addition to At-*LEC1/NF-YB9* and At-*L1L/NF-YB6*, other *NF-Y* genes play roles in vegetative and reproductive development (Table 3). Recent evidence suggests overlapping roles for At-*NF-YA1*, *5*, *6*, and *9* during numerous stages of embryogenesis (Mu et al., 2012), and NF-YA loss of function can be embryo lethal (Pagnussat et al., 2005). Overexpression of At-*NF-YB2* enhances primary root elongation due to a faster cell division and/or elongation (Ballif et al., 2011). In the model legume *Medicago truncatula*, Mt-*HAP2-1* is expressed in the root nodule meristematic zone and is essential for the differentiation of root nodule cells (Combier et al., 2006). Spatial and temporal expression of this gene (and NF-YA subunits in general across plant lineages) is controlled by microRNA 169 (miR169; Jones-Rhoades and Bartel, 2004) as well as a small peptide encoded by its own 5′ leader sequence (Combier et al., 2008). In *Arabidopsis*, miR169 is also strongly downregulated in response to nitrogen starvation, and this is correlated with the concomitant induction of multiple NF-YA family members, changes that are at least correlated to nitrogen sensitivity through the analysis of transgenic plants overexpressing miR169 (Zhao et al., 2011). Studies of Pv-*NF-YC1* overexpression and RNA silencing further implicate *NF-Ys* in nodule organogenesis for the legume *Phaseolus vulgaris* (Zanetti et al., 2010). Additionally, overexpression of Pv-*NF-YC1* is linked to the selection of *Rhizobium etli* strains during nodulation. An *NF-YA* from *Brassica napus* (Bn-*CBF-B*) has a function in reproductive tissues: Plants expressing an antisense Bn-*CBF-B* (*NF-YA*) in the anthers show reduced quantity of viable pollen due to degeneration of the tapetal cell layer and reduced female fertility (Lévesque-Lemay et al., 2003). Finally, Yu et al. (2011) showed a novel function of an NF-YC gene from *Picea wilsonii* that has a role in regulation of pollen tube growth orientation.

Flowering Time

An important discovery is the involvement of *NF-Y* genes in the control of photoperiod-dependent flowering time (Ben-Naim et al., 2006; Wenkel et al., 2006). At-*NF-YB2* and At-*NF-YB3* are necessary for the promotion of flowering in response to inductive long-day photoperiodic conditions (Cai et al., 2007; Kumimoto et al., 2008). At-*NF-YB2* and At-*NF-YB3* act through the activation of the key floral regulator *FLOWERING LOCUS T* (*FT*), a gene responsible for the vegetative to floral meristem conversion (Samach et al., 2000; Corbesier et al., 2007; Jaeger and Wigge, 2007; Mathieu et al., 2007; Tamaki et al., 2007). At-NF-YB2 and At-NF-YB3 interact in vivo with At-NF-YC3, At-NF-YC4, and At-NF-YC9, which are also required for flowering (Kumimoto et al., 2010). Additionally, At-*NF-YC1* and At-*NF-YC2* can activate flowering when overexpressed, which is additionally correlated with increased *FT* transcript levels (Hackenberg et al., 2012). Importantly, NF-YB and NF-YC subunits physically interact with CO, a key regulator of photoperiod-induced flowering time, via the conserved CCT (for CO, CO-Like, and TOC1) domain (Ben-Naim et al., 2006; Wenkel et al., 2006; see section 3). The interaction between NF-YC and CO-like proteins is conserved in tomato (*Solanum lycopersicum*), and overexpression of *THAP5a* (an NF-YC protein) in *Arabidopsis* accelerates flowering time (Ben-Naim et al., 2006).

In the absence of NF-Y, overexpressed *CO* is either unable or strongly reduced in its ability to activate *FT* and drive early flowering (Kumimoto et al., 2010). The converse is also true; in the absence of *CO*, overexpressed *NF-Y*s do not effectively activate flowering (Tiwari et al., 2010), but recent work showed that overexpression of At-*NF-YB2* fused to a novel activation domain can activate flowering in a *co* null mutant (Tiwari et al., 2012). These data support a model in which NF-Y complexes provide a DNA binding component to CO, although this simple interpretation does not address the recent finding that CO can bind DNA directly at TGTG(N^{2-3})ATG sites (Tiwari et al., 2010). Blackman and Michaels (2010) proposed a mixed model where CO can interact with the *FT* promoter via direct DNA interactions and/or through interactions with NF-Y complexes (i.e., NF-Ys act as a binding platform). These possibilities are supported by the presence of multiple CCAAT and TGTG(N^{2-3})ATG sites throughout the functionally defined minimal *FT* promoter (Adrian et al., 2010).

NF-Y function in flowering time has also been reported in monocots. In particular, rice NF-YB11 (also called *DTH8*/*Ghd8*/*LHD1*) probably plays a suppressive role in the signal network of photoperiodic flowering by downregulating the expression of several floral regulators during noninductive long-day conditions (rice is a short day flowering plant; Wei et al., 2010; Yan et al., 2011; Dai et al., 2012). It was also demonstrated that overexpression of *B. distachyon NF-YB6* (Cao et al., 2011b) and barley (*Hordeum vulgare*) *NF-YB1* (Liang et al., 2012), orthologs of At-*NF-YB2/3*, resulted in significantly earlier flowering in *Arabidopsis*. Furthermore, Bd-*NF-YB6* could rescue late-flowering *nf-yb2 nf-yb3* mutants

Table 3. Summary of Genotype/Phenotype Correlations

Gene	Other Name	Organism	Function	References
Dicots				
At-*NF-YA5*		*Arabidopsis*	Drought resistance	Li et al. (2008)
At-*NF-YB1*		*Arabidopsis*	Drought-related stress tolerance	Nelson et al. (2007)
At-*NF-YB2*	At-*HAP3b*	*Arabidopsis*	Promotion of flowering, root growth	Chen et al. (2007); Kumimoto et al. (2008); Ballif et al. (2011)
At-*NF-YB3*		*Arabidopsis*	Promotion of flowering	Chen et al. (2007); Kumimoto et al. (2008)
At-*L1L*	At-*NF-YB6*	*Arabidopsis*	Embryo development	Kwong et al. (2003); Lee et al. (2003); Yamamoto et al. (2009); Le et al. (2010)
Vv-*L1L*		*Vitis vinifera*	Somatic embryogenesis	Schellenbaum et al. (2008); Maillot et al. (2009)
Tc-*L1L*		*Theobroma cacao*	Partial rescue of *lec1* mutant	Alemanno et al. (2008)
Ha-*L1L*		*Helianthus annuus*	Zygotic and in somatic embryogenesis	Fambrini et al. (2006); Chiappetta et al. (2009); Salvini et al. (2012)
At-*LEC1*	At-*NF-YB9*	*Arabidopsis*	Early and late embryogenesis	Meinke et al. (1992); Kagaya et al. (2005); Casson et al. (2006); Mu et al. (2008); Junker et al. (2012)
Dc-*C-LEC1*		*Daucus carota*	Embryo development; complements *lec1* mutant	Yazawa et al. (2004); Yazawa and Kamada. (2007)
Bn-*LEC1* Bn-*L1L*		*B. napus*	Seed oil production	Tan et al. (2011)
At-*NF-YC1*		*Arabidopsis*	Floral induction	Hackenberg et al. (2012)
At-*NF-YC2*		*Arabidopsis*	Floral induction, ER stress	Liu and Howell (2010); Hackenberg et al. (2012);
At-*NF-YC4*		*Arabidopsis*	Germination	Warpeha et al. (2007 Liu and Howell (2010)
At-*NF-YC3* At-*NF-YC4* At-*NF-YC9*		*Arabidopsis*	Flowering	Kumimoto et al. (2010 Liu and Howell (2010)
	Mt-*HAP2-1*	*M. truncatula*	Root nodule development	Combier et al. (2006); Liu and Howell (2010)
	Bn-*CBF-B*	*B. napus*	Development of tapetal cell layer of anthers and female fertility	Lévesque-Lemay et al. (2003); Liu and Howell (2010)
	Sl-*THAP5a*	*S. lycopersicum*	Flowering	Ben-Naim et al. (2006)
Pv-*NF-YC1*		*P. vulgaris*	Root nodule development	Zanetti et al. (2010)
Monocots				
Zm-*NF-YB2*		*Z. mays*	Drought tolerance in maize	Nelson et al. (2007)
Zm-*LEC1*		*Z. mays*	Embryogenesis and seed oil production	Zhang et al. (2002); Shen et al. (2010)
Os-*NF-YB2*	Os-*HAP3A*	*O. sativa*	Chloroplast biogenesis	Miyoshi et al. (2003)
Os-*NF-YB3*	Os-*HAP3B*			
Os-*NF-YB4*	Os-*HAP3C*			
Os-*NF-YB11*	Os-*HAP3H, DTH8, Ghd8*	*O. sativa*	Photoperiodic flowering	Wei et al. (2010)
Os-*L1L*	Os-*HAP3E*	*O. sativa*	Floral meristem identity	Ito et al. (2011)
Ta-*NF-YB2*		*T. aestivum*	Drought adaptation	Stephenson et al. (2007)
Ta-*NF-YB3*		*T. aestivum*	Positive regulation of photosynthesis genes	Stephenson et al. (2011)
Hv-*NF-YB1*		*H. vulgare*	Overexpression results in earlier flowering in *Arabidopsis*	Liang et al. (2012)
Bd-*NF-YB6*		*B. distachyon*	Overexpression results in earlier flowering in *Arabidopsis* and rescue of the late-flowering phenotype in *nf-yb2 nf-yb3* mutants	Cao et al. (2011b)
Conifers				
	Pw-*HAP5*	*P. wilsonii*	Pollen tube development and control of tube orientation	Yu et al. (2011)
	Pa/Ps-*HAP3A, HAP3B*	*Picea abies*, *Pinus silvestris*	Embryogenesis	Uddenberg et al. (2011)

(Cao et al., 2011b). Finally, in wheat, interactions between the CCT domains of VRN2 and CO with NF-Ys integrate seasonal vernalization and photoperiod signals, providing a flexible combinatorial system to connect multiple developmental and environmental signals in the regulation of flowering initiation in cereals (Li et al., 2011).

Plant–Environment Interactions

NF-Ys have been identified as regulators of drought tolerance in different plant species. Transgenic *Arabidopsis* and maize (*Zea mays*) plants overexpressing At-*NF-YB1* and the maize ortholog Zm-*NF-YB2*, respectively, have improved performance and survival under drought conditions (Nelson et al., 2007). Microarray data suggest At-*NF-YB1* does not transcriptionally regulate the dehydration-responsive element binding proteins or the abscisic acid (ABA)–dependent drought tolerance pathway, suggesting it may act through a novel drought resistance pathway. Nevertheless, no alternative mechanism has been proposed, and we note increasing evidence for NF-Y/bZIP interactions and the fact that bZIP proteins are well known to be involved in ABA signaling.

At-*NF-YA5* is also involved in drought resistance; its expression is strongly induced by drought, as well as osmotic and salt stresses. At-*NF-YA5* is transcriptionally regulated through an ABA-dependent mechanism and posttranscriptionally regulated by miR169. miR169 is downregulated by drought stress through an ABA-dependent pathway. This dual regulation is consistent with the critical importance of At-*NF-YA5* for drought resistance. In stomatal guard cells, At-*NF-YA5* expression regulates aperture size. In nonguard cells, At-*NF-YA5* is likely important for dehydration tolerance via activating stress-responsive genes, such as genes involved in oxidative stress responses (Li et al., 2008). In rice, an NF-YA gene (Os-*HAP2E*) has been identified as a target gene of miR169, which is induced by high salinity and is probably regulated by an ABA-dependent pathway, since ABA response elements have been found in its promoter (Zhao et al., 2009).

Drought-related expression has been systematically examined for *NF-Y* from wheat and *Arabidopsis* (Stephenson et al., 2007; Hackenberg et al., 2012), as well a more limited study of five *NF-YB* genes in barley (Liang et al., 2012). Furthermore, in addition to its role in flowering time, At-*NF-YB2* is also upregulated by osmotic stress (Chen et al., 2007). While many At-*NF-Ys* were upregulated by drought stress, none were downregulated (Hackenberg et al., 2012). The opposite is true in wheat (Stephenson et al., 2007), pointing to a possible functional divergence between monocots and dicots. The NF-YA family is targeted by the stress-responsive miR169 (Reinhart et al., 2002; Kidner and Martienssen, 2005; Jones-Rhoades et al., 2006; Reynoso et al., 2012; Leyva-González et al., 2012). In rice, miR169 family members were shown to be upregulated under drought and salt stress conditions (Zhao et al., 2007, 2009). This was in contrast with *Arabidopsis*, where miR169 members were downregulated (Li et al., 2008), further supporting the possible functional divergence of NF-Y in monocots and dicot during stress responses.

The endoplasmic reticulum (ER) stress response is phylogenetically conserved. In mammals, gene expression programs are promoted by several transcription factors, including ATF6 (Bailey and O'Hare, 2007; Yoshida, 2007), a bZIP transcription factor that binds to ER stress–responsive elements. ATF6 recruitment requires previous binding of NF-Y to a nearby CCAAT box (Kabe et al., 2005). In *Arabidopsis*, NF-YC2, NF-YA4, and NF-YB3 form a transcriptional complex with bZIP28 that upregulates ER stress-induced genes (Liu and Howell, 2010). At-*NF-YC2* is also strongly induced in response to photodynamic, light, oxidative, heat, and drought stresses, and a tobacco (*Nicotiana tabacum*) *NF-YC* was found to be inducible by photooxidative stress. Despite the stress induction, At-*nf-yc2* mutants and At-*NF-YC2* overexpressors did not show phenotypic differences compared with wild-type seedlings in response to photooxidative stress, possibly due to the compensatory potential of other members of the At-*NF-YC* family (Hackenberg et al., 2012).

Several studies have suggested that the NF-Y family is involved in light-mediated gene regulation (Kusnetsov et al., 1999; Miyoshi et al., 2003; Warpeha et al., 2007). Kusnetsov et al. (1999) demonstrated that assembly of the NF-Y complex at the CCAAT box in the spinach (*Spinacia oleracea*) AtpC promoter is regulated by light and rice plants with antisense or RNA interference constructs of Os-HAP3A (Os-NF-YB2) have reduced leaf chlorophyll content and degenerated chloroplasts. Furthermore, three NF-YB proteins (Os-HAP3A-C/Os-NF-YB2/3/4) regulate a number of photosynthesis genes, including chlorophyll *a*/*b* binding protein (CAB) and the ribulose-1,5-bisphosphate carboxylase/oxygenase small subunit (Miyoshi et al., 2003). In *Arabidopsis*, NF-YA5 and LEC1 (NF-YB9) are also involved in the regulation of CAB expression in response to blue light and ABA (Warpeha et al., 2007). Transgenic wheat lines constitutively overexpressing Ta-*NF-YB3* have a significant increase in leaf chlorophyll content, photosynthesis rate, and early growth rate (Stephenson et al., 2011). Additionally, many Ta-*NF-YCs* are regulated by light (Ta-*NF-YC3*,Ta-*NF-YC5*, Ta-*NF-YC8*, Ta-*NF-YC9*, Ta-*NF-YC11*, and Ta-*NF-YC12*), and Ta-*NF-YC11* is important in the regulation of photosynthesis-related genes (Stephenson et al., 2010).

In summary, in addition to the original role in embryogenesis discovered for the LEC1/L1L branch of NF-YBs, genetic experiments are pinpointing several other *NF-Y* genes specifically involved in single pathways. In parallel, biochemical work is starting to unveil the possible molecular mechanisms.

BIOCHEMISTRY

Interactions of NF-Y Subunits

The presence of 30 *NF-Y* genes in the *Arabidopsis* genome could result in the formation of ~1000 alternative heterotrimeric combinations, and an obvious question is whether there is specificity in those interactions and in DNA binding.

A first important concept is that NF-YA binds only to a preformed HFD dimer: Selected HFD interactions have been initially reported (Warpeha et al., 2007; Yazawa and Kamada, 2007; Thirumurugan et al., 2008; Kumimoto et al., 2010; Liu and Howell, 2010), and two recent systematic studies employed yeast two-hybrid (Y2H) assays (Hackenberg et al., 2011; Calvenzani et al., 2012). These studies agreed on most interactions, with some limited

preferences and reduced affinities for some of the heterodimers. In general, yeast assays should be interpreted with great caution, particularly because of the presence of endogenous yeast HAPs, shown to be able to interact with mammalian and plant NF-Ys (Chodosh et al., 1988; Hooft van Huijsduijnen et al., 1990; Ben-Naim et al., 2006; Yazawa and Kamada, 2007; Kumimoto et al., 2008).

Importantly, in accordance with the new classification proposed here, At-NF-YC12 interacts with all At-NF-YBs, but not with At-Dpb4 (formerly NF-YB11), while At-Dpb3-2 (formerly At-NF-YC13) does not interact with any of the At-NF-YBs (Hackenberg et al., 2011). Note that At-NC2α (formerly At-NF-YC11) shows interactions with At-NF-YB2/3 (Hackenberg et al., 2011), and Y2H library screens using At-NF-YB2 and At-NF-YB3 as bait occasionally isolate At-NC2α1/2 (B.F. Holt and R.W. Kumimoto, unpublished data), so there may remain some potential for cross-reactivity between families.

It is safe to conclude that At-NF-YBs and At-NF-YCs can interact promiscuously with each other, a result expected from our knowledge of the mouse HFD dimer crystal structure (Romier et al., 2003). Important hydrophobic amino acid contacts in helices α2 of the two HFDs are well conserved, as is the α1 helix of NF-YBs, whose hydrophobic interactions are stacked against the perfectly conserved Trp-85 of NF-YC helix α2 (Figure 4, Figure 5, and Figure 6). Additionally, bidentate salt bridges between Arg-108 and Asp-115 of NF-YB and Arg-93 and Asp-100 of NF-YC, which are perfectly conserved in all plant genes, are absent in the other HFDs (Figure 4, Figure 5, and Figure 6). The HFD side of the trimerization surface relies on selected residues in the α2 helix of NF-YB and in the αC helix of NF-YC. Glu-90 and Glu-98 of mouse NF-YB are important for NF-YA binding and conserved in all At-NF-YBs. In NF-YC, some members have notable modifications in the crucial αC helix, such as Arg-109 (At-NF-YC5), two Asp residues at 111-112 and Ile-113 (At-NF-YC8); At-NF-YC7 has a four

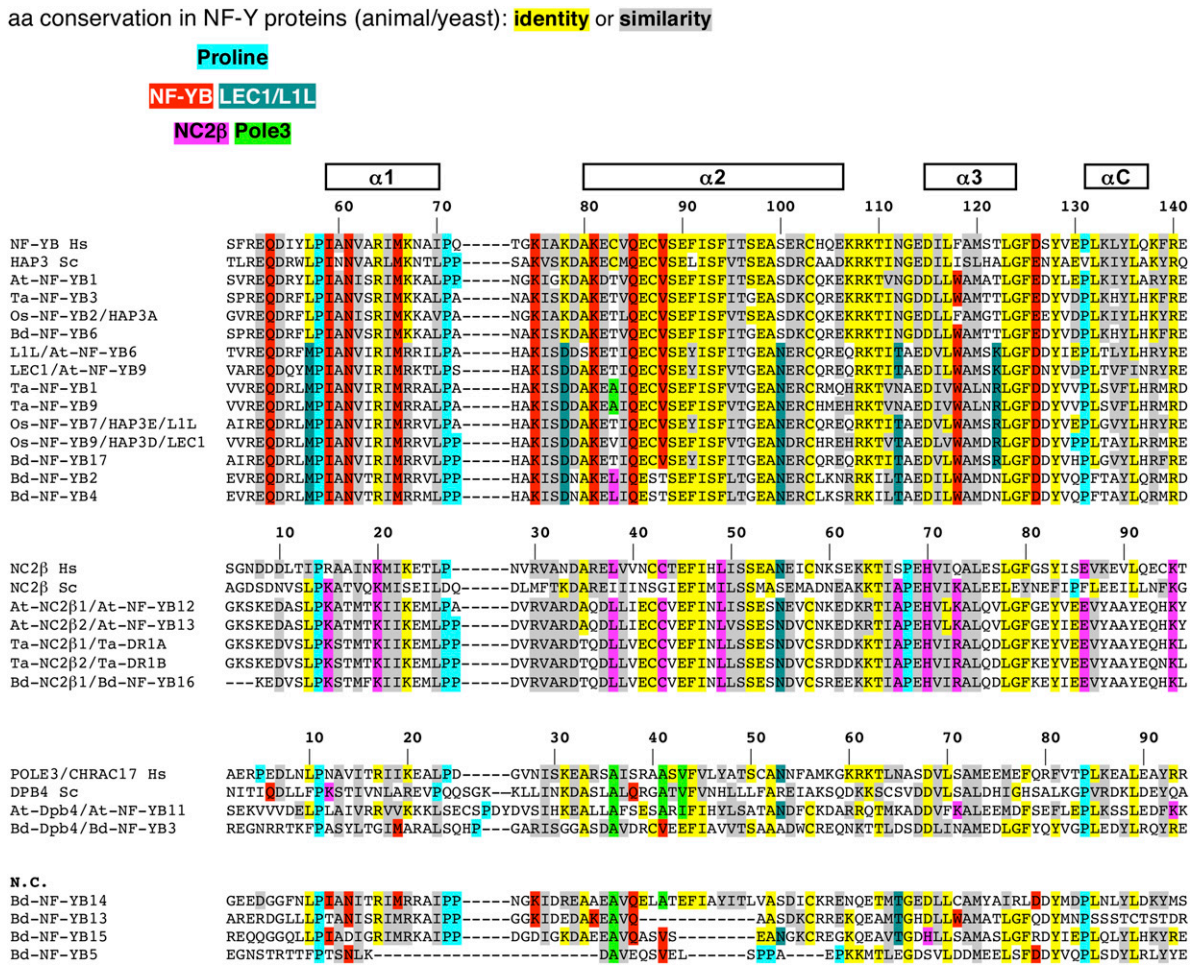

Figure 4. Protein Sequence Alignments of Conserved Domains of NF-YB, NC2β, and Dpb4.

Protein sequence alignments of NF-YB and putative NF-YB, NC2β, and Dpb4 conserved domains. Alignments were performed using the ClustalW program (Thompson et al., 2002). Amino acid residues conserved among listed proteins are shaded and gaps (dashes) were introduced for maximum matching. Hs, *Homo sapiens*; Sc, *Saccharomyces cerevisiae*; At, *Arabidopsis*; Bd, *B. distachyon*; Ta, *T. aestivum*; Os, *O. sativa*.

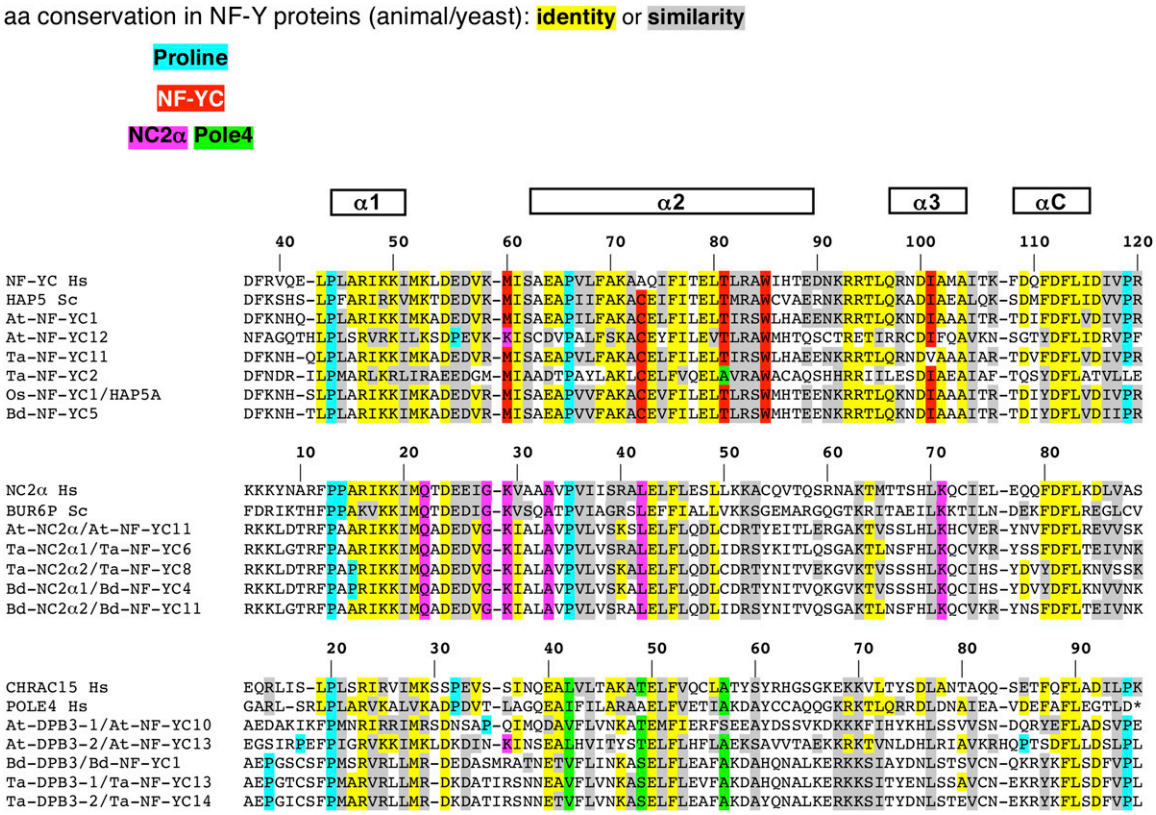

Figure 5. Protein Sequence Alignments of Conserved Domains of NF-YC, NC2α, and Dpb3.

Protein sequence alignments of the conserved domains as in Figure 4.

amino acids addition in the α3 helix, which extends it for an additional turn, thus displacing the loop (LC) and αC helix. Note that these proteins interact with At-NF-YA6 in vitro (Calvenzani et al., 2012).

A second level of variability is represented by formation of the trimer. The NF-YA side of the trimerization surface is in the A1 helix. Many At-NF-YAs are able to interact with HFD subunits (Liu and Howell, 2010; Hackenberg et al., 2011; Calvenzani et al., 2012). At-NF-YA4 showed no interaction with the At-L1L/ NF-YC2 dimer in both ABA-mediated recruitment assays and electrophoretic mobility shift assays (EMSAs; Yamamoto et al., 2009; Calvenzani et al., 2012), but a positive interaction was reported from EMSA with At-NF-YB3/At-NF-YC2 (Liu and Howell, 2010). Further biochemical work on At-NF-YA4 is required to verify its trimerization and DNA binding specificity. Overall, the lack of impediment to subunit association, valid for the HFD dimers, should also apply for trimerization. In summary, highly selective NF-Y complexes are very likely the exception rather than the rule.

DNA Binding

Another fundamental question is whether all NF-Y trimers bind DNA with the same specificity as their mammalian and yeast orthologs (Mantovani R., 1998). In general, many of these genes are so similar to mammalian NF-Y, it seems highly likely that they also exhibit DNA binding. The HFD dimer contributes to DNA binding through the α1 helices and the L1 and L2 loops (Romier et al., 2003, and references therein), with residues equivalent to those in H2A/H2B that contact the DNA phosphate backbone in the nucleosome (Luger et al., 1997). Specifically, all the "right" residues are found in the right place in all At-NF-YBs with two possible exceptions, LEC1/NF-YB9 and L1L/NF-YB6. Experiments with chimeric constructs demonstrated that the HFD domain is necessary and sufficient for LEC1 function in embryos, specifically pinpointing Asp-55 as a crucial residue (Lee et al., 2003; Figure 4 and Figure 6; Asp-55 corresponds to human Lys-78). L1L also has an Asp at this signature position for the subfamily. Asp-55 is located at the beginning of the α2 helix in a region that lies on the surface of the dimer; most other *Arabidopsis* and mammalian NF-YBs have a Lys (or Arg), as in H2B, predicted to be involved in protein–DNA interactions based on the nucleosome model (Luger et al., 1997; Romier et al., 2003). In theory, the change in charge might abolish DNA binding, but this is not the case, since LEC1/ NF-YC3 and L1L/ NF-YC3 bind to CCAAT with efficiencies that are marginally lower than the mammalian homolog (Calvenzani et al., 2012). As for At-NF-YCs, only two members were negative in CCAAT-based EMSAs, NF-YC7 and NF-YC8, possibly because of a lack of NF-YA

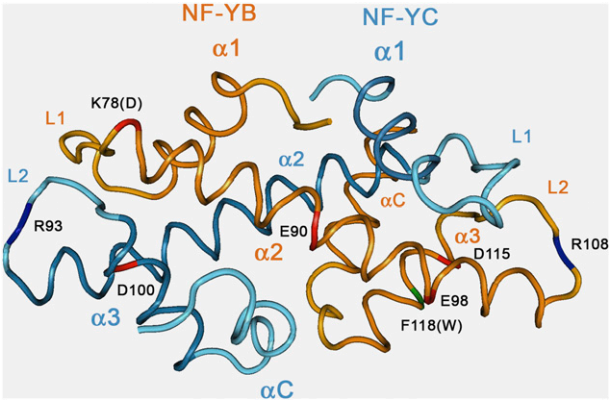

Figure 6. Structure of the Human NF-Y HFD Subunit Dimer.

Ribbon representation of human NF-YB/NF-YC dimer structure (Protein Data Bank code: 1N1J) and location of selected residues, determined by Romier et al. (2003). NF-YB and NF-YC main chains traces are represented in orange and cyan color, respectively. Secondary structure elements are labeled, and main chain location of selected relevant residues described in the text (human numbering) is highlighted in blue (positive) or red (negative) for side-chain charge. NF-YB Lys-78 (Asp in LEC1/L1L proteins) is colored in red. Human NF-YB Phe-118 (Trp in plants) is highlighted in green.

interactions (discussed above) or DNA binding peculiarities. Finally, EMSAs indicate that the majority of At-NF-YAs bind to CCAAT (Calvenzani et al., 2012), with the exception of NF-YA2 and NF-YA4 (discussed above). Slight variations in sequence specificities, or in the purification procedure/tags, might influence these in vitro results. With such complex interfamily interactions, combined genetic and biochemical approaches will be necessary to solve the many NF-Y puzzles.

Interactions with CCT Proteins

Tomato NF-YC proteins were shown to physically interact with a tomato CO-Like protein through the conserved CCT domain (Ben-Naim et al., 2006). This discovery was extended to *Arabidopsis*, where it was shown that CO can bind numerous HFD subunits in Y2H assays (At-NF-YB1/2/5/LEC1/L1L and At-NF-YC1/C2/C3/C5/C6/C7/C9; Wenkel et al., 2006). Although there remains a minor controversy over the existence of direct association of NF-YB and CO (Kumimoto et al., 2010; Cao et al., 2011a), these interactions are relevant as (1) higher order mutants in both NF-YB and NF-YC families phenocopied the late flowering of *co* mutants (Kumimoto et al., 2008, 2010), and (2) NF-YB and NF-YC were at least partially required for CO action in vivo (Kumimoto et al., 2010; Tiwari et al., 2010). More recently, work from Li et al. (2011) confirmed and extended these data in wheat by showing that the CCT domain–containing VRN2 proteins ZCCT1 and ZCCT2 interact with selected NF-YB and NF-YC family members. Furthermore, they can compete with CO for this behavior (Li et al., 2011).

CO and VRN2 belong to a large family of plant specific regulators containing the CCT domain (Putterill et al., 1995; Yan et al., 2004), a 43–amino acid stretch conserved across species, sharing homology with the conserved domain of NF-YA (Figure 7). The homology is striking in the DNA binding A2 helix. Indeed, known mutations that affect CO (*co-9*, *co-5*, *co-7*, and *ppd-H1*), VRN2, and TOC1 activity in vivo alter amino acids within the A2 homology region (Wenkel et al., 2006; Distelfeld et al., 2009). The N-terminal part of CCTs does not superimpose as well with the corresponding region of NF-YA, but both are predicted to form an α-helical structure (Wenkel et al., 2006). As with NF-YAs, it is rich in basic amino acids potentially responsible for association to a highly negatively charged domain of the HFD dimer (Romier et al., 2003). These similarities between NF-YA and CCT proteins led to the hypothesis that they may compete for interactions with HFD dimers (Wenkel et al., 2006; Distelfeld et al., 2009), which was then formally demonstrated as a possibility in yeast three-hybrid assays (Li et al., 2011). Two key issues to address are (1) whether CO and other CCT proteins need to form complexes with additional proteins (e.g., NF-Ys) to bind DNA (Blackman and Michaels, 2010; Tiwari et al., 2010) and (2) whether the HFDs/CO trimers bind DNA with variations of the CCAAT sequence. Now that the minimal *FT* promoter has been defined (Adrian et al., 2010), future experiments should focus on in vivo binding assays for both CO and NF-Y proteins in conjunction with directed promoter mutagenesis to address the nature of NF-Y/CO DNA binding during flowering.

Interactions between NF-Y and Unrelated Proteins

The above mentioned At-bZIP28/NF-YB3/NF-YC2/NF-YA4 complex that regulates ER stress (Liu and Howell, 2010) and At-NF-YC2/LEC1/bZIP67 activating an ABA-responsive element in the promoters of seed-specific genes (Yamamoto et al., 2009) suggest that a bZIP activator might be more widely targeted by NF-Y subunits. Intriguingly, overexpression of At-NF-YA4/5/7/9 in reporter assays interfered with gene activation by At-bZIP67/LEC1/NF-YC2, suggesting that activation is not CCAAT dependent and possibly due to a tethering phenomenon, through other DNA-bound transcription factors. At least one other study indicates that noncanonical NF-Y complexes can be formed in plants: The rice MADS box protein MADS18, alone or in combination with the natural partner MADS6, is able to interact with Os-NF-YB1 (Masiero et al., 2002).

Finally, two interacting proteins with no overt transcriptional role were described: (1) *Arabidopsis* Pirin1, an iron-containing member of the cupin superfamily involved in a pathway leading to an ABA-mediated delay in seed germination, binds to LEC1, potentially serving as coactivator of NF-YA5, LEC1 or L1L, and At-NF-YC1/4/9 (Warpeha et al., 2007); (2) *P. wilsonii* HAP5a, related to At-NF-YC3/9, interacts with FKBP12 (Yu et al., 2011), a member of a large family shown to have a multitude of cellular functions in both mammals and plants. The growing list of transcription factors and cofactors interacting with NF-Y subunits strongly suggests that a large part of the expansion might have occurred to accommodate such interactions, either at the levels of nearby DNA elements or promoter tethering mechanisms.

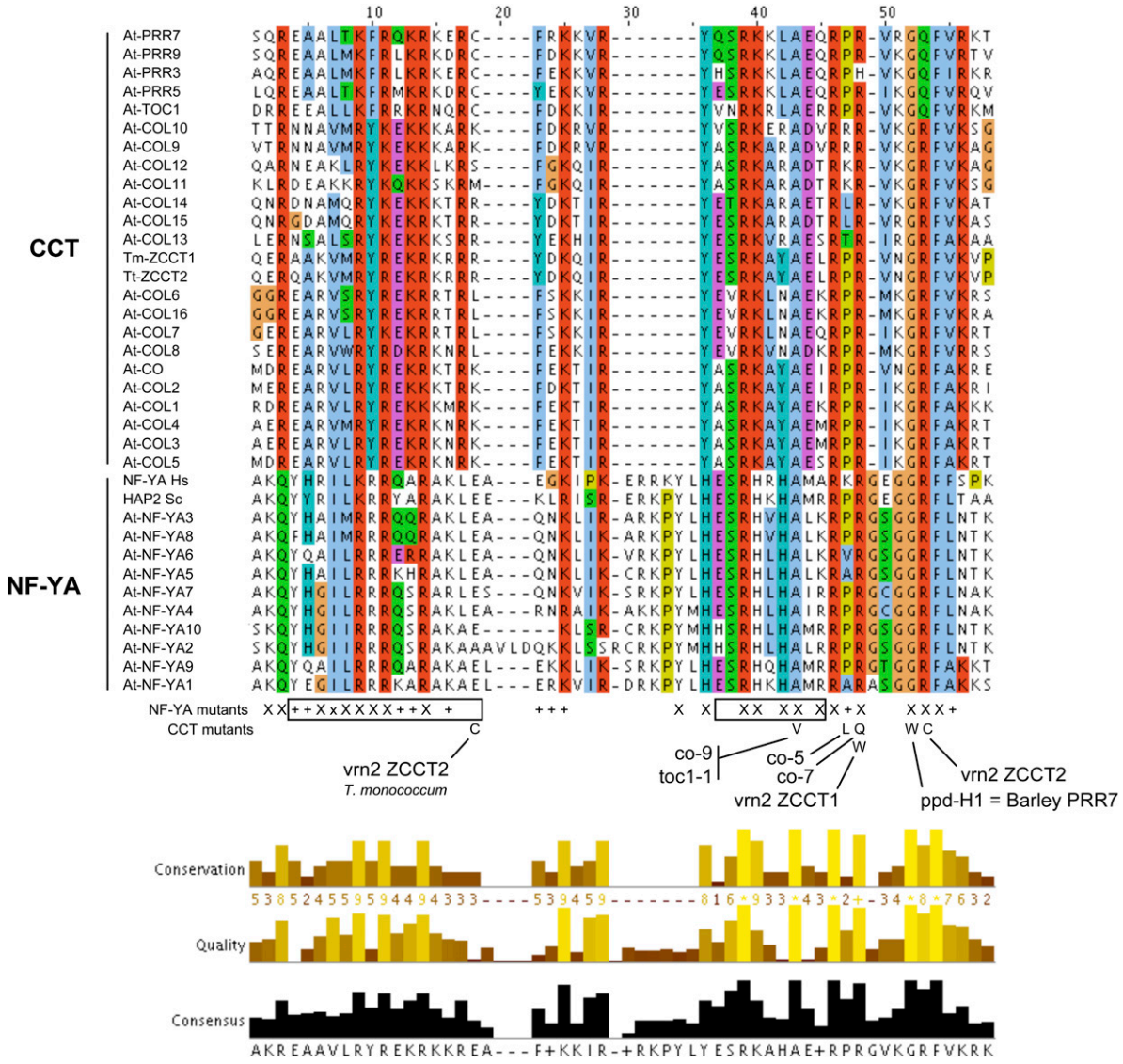

Figure 7. Amino Acid Alignments of the A2 Helix of NF-YA and CCT Proteins.

Alignments were performed using the ClustalW program (Thompson et al., 2002). Amino acid residues conserved among listed proteins are shaded and gaps (dashes) were introduced for maximum matching. Below the alignment, the location of mutations that affect CCT proteins CO, VRN2, TOC1, PPR7 (*co-9*, *co-5*, *co-7*, *ppd-H1*, *toc1-1*, and *vrn2*), or NF-YA/HAP2 activity in vivo (X symbols) are indicated.

CONCLUSIONS AND PERSPECTIVES

We anticipate that the plant NF-Y field will further expand in several directions: (1) further systematic genetic experiments on NF-Y subunits in different plant models, including higher order mutants, which might be required to observe phenotypes of related members of the families; (2) discovery of NF-Y posttranslational modifications, which are currently poorly understood even in the mammalian system; (3) determining the structure of NF-YA, and possibly CCT proteins, in complex with HFDs and the DNA, which will give us mechanistic details on the plant variants; (4) a thorough bioinformatic analysis of plant promoters for the presence of CCAAT and CCAAT-like sequences and genome-wide analysis of association of single-plant NF-Y subunits by chromatin immunoprecipitation sequencing.

Supplemental Data

The following materials are available in the online version of this article.

Supplemental Data Set 1. Alignment of NF-YA Amino Acid Sequences Used to Generate Figure 1.

Supplemental Data Set 2. Alignment of NF-YB Amino Acid Sequences Used to Generate Figure 2.

Supplemental Data Set 3. Alignment of NF-YC Amino Acid Sequences Used to Generate Figure 3.

AUTHOR CONTRIBUTIONS

K.P., R.W.K., N.G., V.C., and M.F. performed and edited alignments of the figures and Table 2. C.T., B.F.H., and R.M. contributed to writing the article.

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