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Review

Plant NF-Y transcription factors: Key players in plant-microbe interactions, root development and adaptation to stress☆

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ABSTRACT

NF-Ys are heterotrimeric transcription factors composed by the NF-YA, NF-YB and NF-YC subunits. In plants, NF-Y subunits are encoded by multigene families whose members show structural and functional diversifications. An increasing number of NF-Y genes has been shown to play key roles during different stages of root nodule and arbuscular mycorrhizal symbiosis, as well as during the interaction of plants with pathogenic microorganisms. Individual members of the NF-YA and NF-YB families have also been implicated in the development of primary and lateral roots. In addition, different members of the NF-YA and NF-YB gene families from mono- and dicotyledonous plants have been involved in plant responses to water and nutrient scarcity. This review presents the most relevant and striking results concerning these NF-Y subunits. A phylogenetic analysis of the functionally characterized NF-Y genes revealed that, across plant species, NF-Y proteins functioning in the same biological process tend to belong to common phylogenetic groups. Finally, we discuss the forthcoming challenges of plant NF-Y research, including the detailed dissection of expression patterns, the elucidation of functional specificities as well as the characterization of the potential NF-Y-mediated epigenetic mechanisms by which they control the expression of their target genes.

Plant NF-Y transcription factors (TF) are, in contrast to their animal counterparts, encoded by multigene families of variable sizes (Table 1). Members of these families show diverse and organ- or tissue- specific expression patterns [45,70,74,79,86]. In addition to this important transcriptional regulation, plant NF-YA genes are also known to be post-transcriptionally regulated either by alternative splicing [16], natural-antisense small interference RNAs (nat-siRNAs) [24] and/or microRNAs (miRNAs) [15]. miRNAs are short, single-stranded RNA molecules of 21–22 nucleotides in length that, in plants, negatively regulate gene expression either by mRNA cleavage or inhibition of translation [48,71]. Plant NF-YA coding genes are specifically regulated by miRNAs of the miR169 family, one of the largest and more conserved miRNA families with 14 genes reported in the model plant *Arabidopsis thaliana* (Arabidopsis). In this review, we will summarize the involvement of plant NF-Y and miR169 genes in biotic interactions with beneficial and pathogenic microorganisms, as well as during root development and the adaption to water scarcity and nutrient starvation. We will also discuss future directions of NF-Y research in plants, including the assessment of tissue- or cell- type specific expression patterns of NF-Y members, the elucidation of the mechanisms underlying transcriptional, post-transcriptional and post-translational regulation of NF-Ys, the identification of NF-Y target genes and the investigation of the NF-Y-mediated epigenetic mechanisms that govern expression of their target genes in plants.

1. NF-Y and beneficial microorganisms: rhizobia

Under low nitrogen conditions, plants belonging to the legume family can engage in a symbiotic interaction with soil bacteria collectively referred to as rhizobia. Early signaling during this interaction involves production by the bacteria of a lipochito-oligosaccharide called Nod factor. This signal is then perceived by the plant root, activating a transduction pathway that triggers a series of physiological, morphological and molecular changes. Several transcription factors (TFs) participate in the Nod factor signal transduction pathway that finally leads to the formation of a new lateral root organ called "root nodule" inside which atmospheric nitrogen is fixed for the benefit of the host plant. Ten years ago, the first NF-YA encoding gene and its associated miR169a were reported in the model legume *Medicago truncatula* (Medicago) as regulatory molecules with important roles during plant-rhizobia interaction [15]. *MtNF-YA1* (formerly *MtHAP2a*) was initially identified by a transcriptome approach as specifically and strongly up-regulated during

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Table 1
Number of NF-Y family members in different plant species +.

Species	NF-YA	NF-YB	NF-YC	Reference
Arabidopsis thaliana	10	13	13	Siefers et al. [79]
Nicotiana tabacum	15	9	8	Jin et al. [39]
Solanum lycopersicum	10	27	17	Li et al. [53]
Populus trychocarpa	57	38	27	Jin et al. [39]
Setaria italica	10	15	14	Feng et al. [22]
Oriza sativa	10	11	7	Thirumurugan et al. [89]
Triticum aestivum	10	11	14	Stephenson et al. [86]
Brachipodium distachyon	7	17	12	Cao et al. [12]
Zea mays	36	28	25	Jin et al. [39]
Medicago truncatula	8	14	8	Laloum et al. [43]
Lotus japonicus	6	11	9	Jin et al. [39]
Glycine max	21	32	15	Quach et al. [70]
Phaseolus vulgaris	9	14	7	Ripodas et al. [74]

root nodule organogenesis [21]. Later on, reverse genetic studies, including a specific RNA interference (RNAi) approach, overexpression of the miR169a [15] and a loss of function mutant identified by a TILLING approach [45], showed that *MtNF-YA1* controls different steps of nodulation, including rhizobial infection in the epidermis and the persistence of nodule meristems. Indeed, *MtNF-YA1*, together with its close paralog *MtNF-YA2*, belong to a legume specific clade of *NF-YA* genes [43] and play partially redundant roles during the Nod factor-signaling cascade, acting downstream of *Nodule Inception* (*NIN*) and upstream of *ERF Required for Nodulation* 1 (*ERN1*), two TFs with key regulatory functions in Nod factor-signaling and rhizobial infection [44]. *MtNF-YA1* appears as a very early nodulation specific TF; its expression pattern, studied in detail using RT-qPCR and promoter:GUS reporters, correlates with rhizobial infection in the root epidermis and nodule organogenesis in the pericycle and cortex [45]. The *nf-ya1-1* mutant also displays abnormal bulbous infection threads with thinner cell walls likely causing their frequent early arrest [45], a phenotype that is more pronounced in plants harbouring a *MtNF-YA1&2* double RNAi construct [44]. More recently, a fate map study described early nodule development in Medicago as a two step process [94]. First a nodule primordium is formed by divisions in the inner cortical cells (4th and 5th cortical layer) and to a lesser extent, in the pericycle and endodermis, followed by the formation of the nodule meristem in the third cortical layer, whose activity will allow the indeterminate growth of the nodule. Interestingly, formation and functioning of the nodule meristem are blocked in the *nf-ya1-1* mutant, whereas nodule primordium and lateral root formation are not strongly affected, suggesting a specific role of *MtNF-YA1* in nodule meristems.

Depending on the legume species, there are two major categories of rhizobia-induced nodules. Temperate legumes, such as Medicago or *Pisum sativum* (Pea), form indeterminate nodules that posses a persistent meristem and elongate indeterminately, forming cylindrical shaped organs. Tropical legumes, as *Phaseolus vulgaris* (common bean), *Glycine* max (soybean) or *Lotus japonicus* (Lotus), form determinate nodules. These nodules originate from the outer cortex, do not have a persistent meristem and thus become globular and stop growing rapidly. Interestingly down-regulation of the Lotus ortholog of *MtNF-YA1*, *LjNF-YA1*, also strongly affects nodule organogenesis [85], despite the absence of a persistent nodule meristem. Hence, it will be of high interest to characterize the pathways controlled by NF-YA TFs in order to understand common and divergent mechanisms involved in the organogenesis of determinate and indeterminate nodules.

NF-YB and NF-YC subunits have also been implicated in legume-rhizobium interactions. In common bean, it has been shown that *PvNF-YC1* controls rhizobial infection and nodule development possibly by regulating cell cycle genes. In addition, overexpression of *PvNF-YC1* affected rhizobial partner selection [63,98]. In Lotus, *LjNF-YB1* was identified as a direct target of NIN and when co-expressed increased the effect of *LjNF-YA1* over-expression on cell divisions and lateral root organogenesis [85]. Interestingly, the orthologs of *LjNF-YB1* and *PvNF-YC1* in Medicago were independently identified by yeast two hybrid (Y2H) screens as direct interactors of MtNF-YA1. These B and C subunits form a NF-Y trimer with MtNF-YA1/2 subunits, both in vitro and *in planta*, playing a key role in nodulation [5]. The fact that an orthologous trimer is formed also in common bean [5] and the importance of the Lotus orthologs in nodule development suggest that these three subunits play an evolutionary-conserved role in leguminous plants during nodule development. In common bean, an additional PvNF-YC1-interacting TF, PvSIN1 (Scarecrow like 13 Involved in Nodulation), was identified by Y2H screening illustrating that the symbiotic NF-Y trimers also act within multiprotein complexes. This TF belongs to the GRAS family and was shown to play a role in both lateral root and nodule development [4]. Further evidence for the role of NF-Y subunits within multiprotein complexes during the legume-rhizobium symbiosis came from a recent report showing that Medicago DELLA1, 2 and 3 proteins interact with MtNF-YA1 and the Nodulation Signaling Pathway 2 (NSP2) TFs to regulate Nod factor signaling and rhizobial infection [23].

In addition to miR169-based regulation, plant NF-YA genes are also regulated by alternative splicing, a regulatory system frequently observed in animal NF-Ys [13]. In Medicago, as nodule development proceeds, an increasing proportion (up to 50%) of *MtNF-YA1* transcripts are alternatively spliced at their first intron, situated in the 5´ leader sequence. An upstream open reading frame (uORF) called uORF1, found within this first intron leads to the production of uORF1p, a small 62-amino acid peptide that negatively modulates *MtNF-YA1* expression using a mechanism complementary to miR169 [16]. All *NF-YA* genes of Medicago (except *MtNF-YA7)* and common bean [74] have an intron in the 5´ leader sequence, suggesting a putative conserved regulatory mechanism among most plant NF-YA-encoding genes. However, no uORF showing significant sequence homology to uORF1 has been identified outside *MtNF-YA1*.

In addition to the above-mentioned subunits, several additional NF-Y encoding genes have been found to be up-regulated during the legume-rhizobium symbiosis using transcriptome approaches. Among these, *MtNF-YB7* shows an intriguing expression pattern during early phases of the legume-rhizobium symbiosis being up-regulated only transiently in root hairs. Indeed, *MtNF-YB7* was up-regulated at 6 h (h), but not at 24 h after Nod factor-treatment. In isolated root hairs, *MtNF-YB7* levels increased only 24 h after rhizobial inoculation but not after 48 h. In addition, *MtNF-YB7* expression was almost undetectable in nodules, especially when compared to the other symbiotic NF-YB subunit-encoding genes *MtNF-YB16 and MtNF-YB18* ([75]a; [9]; Jardinaud 2016). Plants carrying insertions that create mutant alleles of *MtNF-YB7* are affected in rhizobial infection, but not in nodule development (Donna Cousins PhD thesis Norwich). In addition, the *MtNF-YB7* ortholog in common bean, *PvNF-YB4*, also presented its highest expression peak at 24 h post inoculation with rhizobia [74]. These results point to a role for this member of the NF-YB family during Nod Factor-signaling and early rhizobial infection. Interestingly, *MtNF-YB7* was also up-regulated during early stages of the mycorhizal symbiosis [34,35] (see below).

2. NF-Ys and beneficial microorganisms: mycorrhizal fungi

Fungi belonging to the phylum Glomeromycota interact with roots of the majority of land plants in a symbiotic association called the arbuscular mycorhizal (AM) symbiosis. This association leads to improved phosphate and nitrogen acquisition. During AM, hyphae emerge from germinating spores, penetrate the rhizodermis via hyphopodia, and proliferate in the inner cortex. Then, they form highly branched intracellular structures called arbuscules, which allow the nutrient exchange between the plant and the fungi [17,78]. As for nodulation, several transcriptome analyses have revealed NF-Y subunit-encoding genes that are up-regulated during mycorrhization in different plant species [18,26,28]. A transcriptome analysis of soybean roots during autoregulation of mycorrhization identified *GmNF-YA1a and b,* two

orthologs of *MtNF-YA2*- as positive regulators of AM symbiosis, which act downstream of the *clavata 1-like* receptor kinase called *NARK*. Indeed, RNAi constructs producing reduced transcript levels of *GmNF-YA1a/b* led to a 50% reduction in mycorrhization [77]. AM symbiosis does not involve organogenesis as root nodule symbiosis, but common NF-Y targets could exist during signaling and infection. A large scale transcriptome approach identified *MtNF-YC6* and *MtNF-YC11* as up-regulated specifically upon AM inoculation [35]. Promoter.GUS based expression analysis suggested a potential role for these subunits during the infection of cortical cells, although the highest expression correlated with mature mycorhizal stages, i.e. cortical cells already containing hyphae or functional arbuscules [34,35]. Future genetic approaches will provide more insights into the role of these particular NF-YC subunits during AM symbiosis.

3. NF-Y and plant pathogens

Much less evidence has been obtained concerning the role of NF-Y during defense against pathogen attacks. Overexpression of a rice NF-YA gene (*OsHAP2E*) conferred resistance to *Magnaporthe oryzae* and *Xanthomonas oryzae pv. oryzae*. However, these transgenic lines also showed increased tolerance to salinity and drought, suggesting that *OsHAP2E* is implicated in a more general mechanism of stress tolerance [1]. More recently, it was shown that a miR169 dependent pathway is involved in pathogenicity of bacterial wilt caused by *Ralstonia solanacearum* in Arabidopsis. Indeed, *Clavata 1* and *2 receptor kinase* mutants exhibited enhanced resistance to *R. solanaceorum* [31]. A transcriptome analysis showed that five out of nine genes up-regulated in non-inoculated plants as compared with wild type controls, encoded NF-YA proteins and that this was probably due to the drastic reduction in miR169 accumulation observed in *clavata 1* and *2* mutants [31]. As expected, overexpression of miR169 abolished the resistance phenotype of *clavata 1* and *2* mutants. Another study revealed that miR169 was negatively regulated during virus infection in grapevine [82]. Recently, a new role for *MtNF-YA1* in compatibility to *Aphanomyces euteiches,* a root pathogenic oomycete, was described [72]. The *Mtnf-ya1-1* mutant plants showed better survival rate, reduced symptoms and increased development of its root apparatus as compared to their wild type background. Reduction of *MtNF-YA1* transcript levels in the susceptible line F83005.5 either by overexpression of the *miR169q* gene or by RNAi approaches, leads to a strong enhancement of the resistance. Comparative transcriptome analysis of wild type and *Mtnf-ya1-1* mutant roots led to the identification of 1965 differentially expressed genes. Interestingly, changes in expression of these 1965 probes in uninoculated *Mtnf-ya1-1* mimicked the gene regulation observed in WT at one and six days following inoculation. This finding implies that part of the transcriptomic responses to *A. euteiches* is already constitutively expressed in *Mtnf-ya1-1* in non-challenged conditions. Hence, *MtNF-YA1* appears as a repressor of responses triggered in WT roots by *A. euteiches* invasion. Based on these results, one of the roles of MtNF-YA1 in the legume-rhizobium symbiosis might be to facilitate symbiotic rhizobial infection by local suppression of defense responses. This unexpected dual role for a symbiotic TF as a key player in the mechanisms of susceptibility against pathogen illustrates the thin line existing between pathogenic and symbiotic plant-microbe interactions [32,72]. Signaling pathways involving NF-YA genes can thus regulate both beneficial and pathogenic plant-microbe interactions and suggest the existence of common mechanisms between both types of biotic interactions.

4. NF-Ys and root architecture

In addition to providing support to the aerial part, plant roots play essential functions in water and nutrient acquisition. Thus, plant growth depends on the capacity of the root to adapt its growth and development in response to changes in environmental conditions. Root architecture is tightly regulated from embryogenesis to cell patterning, differentiation and the production of lateral roots. Three different zones are identified along the primary roots: the meristematic, the elongation and the differentiation zones. The primary root apical meristem is established during embryogenesis and consists of a group of undifferentiated cells that divide and then, subsequently, elongate, differentiate and acquire specialized functions [6,68]. Lateral roots develop from a group of mitotically activated cells in the pericycle of the differentiation zone, which then further expand causing lateral root emergence. After emergence, the lateral root meristem is activated and lateral root growth begins [19,83].

Individual NF-Y subunits have been implicated in root development at distinct developmental stages. First evidences of the involvement of NF-Ys in root development came from genetic studies in Arabidopsis of the central regulator of embryogenesis *LEAFY COTYLEDON1 (LEC1)* and the closely related *LEC1 LIKE (L1L)*, which encode the AtNF-YB9 and AtNF-YB6 subunits, respectively [42,46,58]. In addition to their roles during embryogenesis and seed maturation (for more detail see the review of Arabidopsis NF-Ys by Ben Holt and co-workers in this issue), both regulators also play non-embryonic functions during post-germinative etiolation. Ectopic or dexamethasone-induced expression of *LEC1* during or shortly after germination resulted in seedlings that have either suppressed their primary root growth or developed swollen primary roots, reminiscent of the triple response observed in etiolated seedlings [40,58]. The root tip diameter of swollen roots was thicker than that of wild type roots, but the symmetry or the number of epidermal, cortical and endodermal cells was not affected by ectopic expression of *LEC1/AtNF-YB9*. Induction of *LEC1* expression by dexamethasone treatment during the vegetative phase resulted in the development of embryonic structures in the root; however, the development of such structures was dependent on the exogenous application of abscisic acid (ABA) [40]. It is unclear whether these embryonic structures are derived from remaining undifferentiated stem cells or a consequence of a de-differentiation process.

At post-germination stages, two NF-YA subunits, *AtNF-YA2* and *AtNF-YA10,* have been implicated in primary root growth and LR initiation in Arabidopsis. Expression of a target mimicry of miR169defg (MIM169defg), which prevents miR169 from fully cleaving *AtNF-YA2* and *AtNF-YA10* mRNAs, negatively affected primary root growth and thickness of the root meristem by reducing the number of endodermal cells and the dimension of epidermal, cortical and endodermal cells [84]. This phenotype contrasts with that observed in roots that overexpress *LEC1* [40,58], suggesting that *AtNF-YA2* and *LEC1* might play opposite functions in regulating root meristem size. In addition, seedlings expressing the MIM169defg or a miR169 resistant version of *AtNF-YA2* exhibited enhanced density of emerged lateral roots and an increased number of lateral root primordia, suggesting that miR169-mediated regulation of *AtNF-YA2* is required for proper lateral root initiation. Thus, *AtNF-YA2/AtNF-YA10* and miR169defg form a regulatory unit that controls growth and development of both primary and lateral roots. Interestingly, promoter-GUS expression studies revealed that both *AtNF-YA2* and *AtNF-YA10* are highly expressed in the pericycle and to a lesser extent in the vasculature of the elongation/differentiation zone of the Arabidopsis root [79], where lateral roots are formed. The promoter of *AtNF-YA2* is active in lateral root primordia and in the tip of emerged lateral roots, whereas *AtNF-YA10* is expressed only in the vascular tissue of emerged lateral roots. *AtNF-YA2*, but not *AtNF-YA10*, is also expressed in the collumela of the root apical meristem. However, the composition of the trimeric complexes that are active in specific cell types of the root apical meristem or in lateral root primordia remains an open question.

In Lotus, two NF-Y subunits, namely LjNF-YA1 and LjNF-YB1, have been also linked to lateral root development. Indeed *LjNF-YA1* overexpression produced lateral roots with malformed tips, and the co-expression of *LjNF-YB1* exaggerated such root tip abnormalities. In addition, the distance between lateral roots was reduced in roots that co-

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expressed *LjNF-YA1* and *LjNF-YB1*, and extra cell divisions were observed in the pericycle, which is the origin of the lateral root primordium [85]. This phenotype was accompanied by an increment of expression foci of the cell division marker *LjCyclinB1-1*. All together, the results obtained by Soyano and co-workers revealed that LjNF-YA1 and LjNF-YB1, the NF-Y subunits involved in root nodule symbiosis, also function stimulating cell divisions during lateral root formation. Additional indirect evidences of the influence of NF-Y subunits on lateral root development arose from the functional characterization of the above mentioned GRAS transcription factor PvSIN1 in common bean [4]. Knock-down of *PvSIN1* by RNAi revealed that the product of this gene plays a critical role in lateral root elongation. Interestingly, induction of the G2/M transition cell cycle genes *CyclinB1* and *cdc2* in response to rhizobia inoculation was altered in both *PvSIN1* and *PvNF-YC1* silenced roots [4,98]. The role of the *PvNF-YC1* gene in lateral root initiation or elongation has not yet been genetically investigated; however constitutive expression of *PvNF-YC1* correlated with higher transcript levels of the G2/M transition cell cycle genes in non-inoculated roots, suggesting that PvNF-YC1 might also function by stimulating cell division under non symbiotic conditions [98]. All together, these results point to an interesting connection between NF-Y TFs and the initiation and growth of lateral roots. The phytohormone auxin is a key player in lateral root formation and auxin-mediated lateral root initiation involves the activation of cell cycle progression in the pericycle through the control of cell cycle genes [33,90]. Further studies are necessary to elucidate whether there a link exists between the activation of cell cycle genes mediated by NF-Y TFs- and/or its interacting proteins- and the auxin mediated control of the cell cycle progression during lateral root formation. There are striking yet obvious similarities between the development of nodules and lateral roots and the roles that NF-Y TFs play in the regulation of these two lateral root organs. Unraveling the common and specific NF-Y regulated pathways leading to the formation of roots and nodules is a challenging yet exciting next step to be taken.

5. NF-Ys as key players in the adaptation of plants to water and nutrient limitation

Water availability is paramount for plant growth and development and a major environmental factor limiting crop productivity. A picture of the tortuous network of TFs regulating drought responses is starting to emerge and NF-Y TFs are part of it [81]. Over the past decade, different NF-Y subunits emerged as key regulators of drought tolerance in different plant species. In 2007, Nelson et al. [65] showed that the *AtNF-YB1* subunit confers drought tolerance in Arabidopsis. In the same report, the authors showed that constitutive expression of the *AtNF-YB1* ortholog in *Zea mays* (maize), *ZmNF-YB2,* enhances tolerance to drought in greenhouse and field experiments, based on a number of stress-related parameters (e.g. chlorophyll content, stomatal conductance, leaf temperature, reduced wilting and maintenance of photosynthesis). Moreover, overexpression of *ZmNF-YB2* improved corn yields of maize grown under water limited-conditions in field trials conducted in two consecutive years [65]. These results suggest a functional conservation of the drought tolerance pathway involving NF-YB subunits in mono- and di-cotyledonous plants. A later study conducted in Arabidopsis described that the *AtNF-YA5* transcript, a target of miR169a, was significantly up-regulated under drought conditions or in response to the exogenous application of ABA. By contrast, levels of miR169a were down-regulated under these conditions [50]. A genetic approach revealed that both an *nfya5* mutant and a miR169a overexpressing line displayed enhanced water loss and were more sensitive to drought stress than wild-type plants. Plants overexpressing *AtNF-YA5* were, on the contrary, more resistant to drought and exhibited enhanced expression of a number of drought stress–responsive genes as compared to the wild type plants [50]. Interestingly, it has been shown that *nfya5* mutants were hypersensitive to ABA [92], suggesting that AtNF-YA5 can mediate ABA-dependent responses during drought stress. In addition, the *cis*-natural antisense transcript of *AtNF-YA5*, *NF-YA5 Enhancing RING FINGER* (*NERF*, which encodes a RING E3 ligase), can produce siRNAs from their overlapping region that affect *AtNF-YA5* transcripts by functioning together with miR169, adding a new layer of post-transcriptional regulation of *AtNF-YA5*. Analysis of NERF knock-down plants and NERF overexpression lines showed that, like *AtNFYA5*, *NERF* is important for controlling stomatal aperture and drought resistance [24]. These results indicate that, during adaptation to water limiting conditions, *AtNF-YA5* is regulated at the transcriptional level by ABA-dependent mechanisms and at the post-transcriptional level by the action of miR169 and *AtNF-YA5*/*NERF* derived siRNAs. An unresolved question is whether these regulatory mechanisms occur in all or in specific cell types, as well as whether they operate simultaneously or sequentially during drought stress. Subsequent studies revealed other members of the NF-YA family with functions in drought tolerance. Arabidopsis plants overexpressing *AtNF-YA3*, *AtNF-YA7* and *AtNF-YA10* were more sensitive to ABA and showed less severe stress-induced damage by drought [49]. In addition, these TFs act as negative regulators of early stress response genes leading to the proposal that this genetic response may participate in the acclimation to water stress [49]. More recently, it was shown that overexpression of the *Triticum aestivum* (wheat) *TaNF0-YA10-1* in *Arabidopsis* confers drought tolerance as determined by root length and shoot growth [59]. However, plants overexpressing *TaNF-YA10* also exhibited increased sensitivity to salt stress [59,60], suggesting that this subunit functions independently in salinity and drought stress. In Rice *OsNF-YA7* expression was up-regulated by drought but not by ABA, whereas *OsNF-YA4* showed the reverse pattern. Overexpression of *OsNF-YA7,* but not *OsNF-YA4,* confers drought tolerance in rice, suggesting an important role for *OsNF-YA7* in an ABA-independent water acquisition signaling pathway [47]. In addition, overexpression of an *Amaranthus hypochondriacus* NF-YC gene also enhanced root elongation and increased survival during water stress in Arabidopsis [67].

ABA is a hormone that accumulates during drought stress tolerance and plays a critical role mediating many of the responses that help the plant to survive during these stresses. Interestingly, different Arabidopsis NF-Y subunits form alternative complexes with specific bZIP proteins, such as the At-NF-YC2/LEC1/bZIP67 complex involved in ABA-mediated activation of promoters containing ABA response elements (ABRE) [41,95]. Another bZIP member, AtbZIP28, forms a heterodimer that is assembled into a large transcriptional complex with the NF-Y trimer NF-YB3/NF-YC2/NF-YA4 on the promoter of genes that participate in the unfolded protein response caused by adverse environmental condition in plants [56]. Thus, NF-Y subunits can act in combination with bZIP TFs to regulate the expression of ABRE containing genes during the adaptation to environmental stress conditions.

Under well watered conditions, plant productivity depends on the availability of nutrients present in the soil, e.g. nitrogen and phosphorous. Nutrient availability also has a strong effect on root architecture by altering the length and diameter of the primary roots, as well as the number and length of lateral roots [57]. Nitrogen deficiency stimulates primary and lateral root elongation, but has no effect on the number of lateral roots. On the other hand, under limited phosphorous availability, primary root elongation is inhibited and the number of lateral roots increases [55,76]. NF-Y TFs also participate in the adaptive responses to nutrient deprivation. Seminal evidences of the involvement of NF-Ys in nitrogen starvation came from transcriptome studies showing that *AtNF-YA5* was highly induced in response to low concentrations of nitrate [91]. A later report showed that, in addition to *AtNF-YA5*, other members of this family (i.e. *AtNF-YA2, AtNF-YA3* and *AtNF-YA8*) were strongly induced, whereas miR169 was down-regulated, under nitrogen deficiency conditions [99]. Transgenic Arabidopsis constitutively expressing miR169a were more sensitive to nitrogen deficiency, exhibited reduced expression of the nitrate transporters genes *AtNRT1.1* and *AtNTR2.1* and accumulated less nitrogen in both roots and shoots. All

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these evidences indicate that post-transcriptional regulation of NF-YA members by miR169a contribute to the adaptative responses that help plants to cope with low nitrogen availability in the soil [99]. More recently, it has been shown that a C subunit of the NF-Y complex, NF-YC4, is linked to nitrogen and carbon allocation in mono- and dicotyledonous plants. NF-YC4 from Arabidopsis and its homologs from soybean, rice and maize physically interact with a Qua-Quine Starch (QQS) protein, the product of an orphan gene unique to Arabidopsis that regulates nitrogen and carbon partitioning among proteins and carbohydrates. Overexpression of NF-YC4 in Arabidopsis and rice recapitulates the QQS-overexpression phenotype, by decreasing leaf starch content and increasing protein content [52]. These results revealed that NF-Y TFs can also play a role in the regulation of primary metabolism in plants.

6. NF-Y subunits involved in the same biological process are phylogenetically related

The fact that NF-Y-encoded genes have largely expanded in plants together with the above mentioned results clearly indicate that individual plant NF-Y TFs play functions in beneficial and pathogenic interaction with microorganisms, at different stages of root development and in the response to water or nutrient deprivation. Table 2 summarizes the NF-Y subunits with an assigned function in different species. To get insight into the phylogenetic-function relationship of these subunits, we performed phylogenetic trees of the NF-YA, NF-YB and NF-YC genes that were discussed in this review. Fig. 1 shows that NF-Y subunits involved in the same processes tend to cluster together across species. In particular, NF-YA subunits involved in the root nodule symbiosis from three distant legume species, as well as NF-YB and NF-YC subunits from Lotus and Medicago and from common bean and Medicago, respectively, are closer to each other than to other NF-Y members, further arguing in favor of a group of conserved legume specific orthologous genes specialized in this beneficial interaction [5]. Interestingly, the NF-YA genes playing a role in the AM symbiosis are embedded in the specific clade shown to be important for root nodule symbiosis. This proximity makes sense, knowing that molecular mechanisms of root nodule symbiosis probably evolved from the more ancient AM symbiosis and that both interactions share common signaling pathways [27]. The next group of NF-YAs, which is closest to the symbiotic clade of NF-YAs, plays a role in root development. This was not unexpected since as a dual role in root and nodule development was described for *LjNF-YA1*. This clustering analysis further illustrates the diversification of plant NF-Y proteins and represents a starting point to unravel the specific and common pathways involved in both beneficial symbiosis or in the organogenesis of nodules and lateral roots. In the future, it will be exciting to dissect and compare these pathways by identifying the target genes controlled by these specialized NF-Y subunits. On the other hand, the NF-YA and NF-YB subunits involved in nutrient and water supply belong to a phylogenetically distinct group of NF-Y proteins but also cluster together across species suggesting that the NF-Y-controlled regulatory pathways involved are conserved between mono- and di-cotyledonous plants. Furthermore, the reports of drought resistance triggered by overexpression of these specific NF-Y subunits in different plant species open up perspectives of biotechnological application to produce drought resistant crops, which are particularly important in a context of global warming.

7. Future perspectives

A major challenge for future research on plant NF-Y will be to understand the differences and similarities that exist between animal and plant NF-Ys. One fundamental question remains: why, while animals have only one gene coding for each NF-Y subunit, do plants possess so many NF-Y transcription factors? Another long standing question is whether the theoretical combinatorial heterotrimer complexity is

Table 2
NF-Y members functionally characterized in distinct biological processes in plants.

Role in plant biology	NF-Y Subunit	Plant species	Gene ID	Reference
Legume-rhizobia symbiosis	MtNF-YA1	*Medicago truncatula*	Medtr1g056530	Combier et al. [15]
	MtNF-YA2	*Medicago truncatula*	Medtr7g106450	Laloum et al. [44]
	PvNF-YA1	*Phaseolus vulgaris*	Phvul.001G196800	Ripodas et al. [74]
	PvNF-YA9	*Phaseolus vulgaris*	Phvul.007G267100	Ripodas et al. [74]
	LjNF-YA1	*Lotus japonicus*	chr5.CM0571.340.r2.m	Soyano et al. [85]
	MtNF-YB7	*Medicago truncatula*	Medtr8g091720	Hogekamp et al. [35], 2013)
	MtNF-YB16	*Medicago truncatula*	Medtr4g119500	Baudin et al. [5]
	MtNF-YC1	*Medicago truncatula*	Medtr1g082660	Baudin et al. [5]
	MtNF-YC2	*Medicago truncatula*	Medtr7g113680	Baudin et al. [5]
	PvNF-YC1	*Phaseolus vulgaris*	Phvul.006G093200	Zanetti et al. [98]
Arbuscular mycorrhizal symbiosis	GmNF-YA1a	*Glycine* max	Glyma03g36140	Schaarschmidt et al. [77]
	GmNF-YA1b	*Glycine* max	Glyma19g38800	Schaarschmidt et al. [77]
	MtNF-YC6	*Medicago truncatula*	Medtr2g081600	[35], 2013)
	MtNF-YC11	*Medicago truncatula*	Medtr2g081630	[35], 2013)
Plant-pathogen interaction	OsNF-YA2	*Oryza sativa*	Os03g29760	Alam et al. [1]
Root development	AtNF-YA2	*Arabidopsis thaliana*	AT3G05690	Sorin et al. [84]
	AtNF-YA10	*Arabidopsis thaliana*	AT5G06510	Sorin et al. [84]
	LjNF-YA1	*Lotus japonicus*	chr5.CM0571.340.r2.m	Soyano et al. [85]
	LjNF-YB1	*Lotus japonicus*	LjSGA_022269.1	Soyano et al. [85]
	AtNF-YB6 (L1 L)	*Arabidopsis thaliana*	AT5G47670	Kwong et al. [42]
	AtNF-YB9 (Lec1)	*Arabidopsis thaliana*	AT1G21970	Lotan et al. [58]
Drought tolerance	AtNF-YA3	*Arabidopsis thaliana*	AT1G72830	Leyva-Gonzalez et al. [49]
	AtNF-YA5	*Arabidopsis thaliana*	AT1G54160	Li et al. [50]
	AtNF-YA7	*Arabidopsis thaliana*	AT1G30500	Leyva-Gonzalez et al. [49]
	OsNF-YA7	*Oryza sativa*	Os08g09690	Lee et al. [47]
	AtNF-YA10	*Arabidopsis thaliana*	AT5G06510	Leyva-Gonzalez et al. [49]
	TaNF-YA10	*Triticum aestivum*	KM983028	Ma et al. [59,60]
	AtNF-YB1	*Arabidopsis thaliana*	AT2G38880	Nelson et al. [65]
	ZmNF-YB2	*Zea mays*	DQ333304	Nelson et al. [65]
N starvation	AtNF-YA2	*Arabidopsis thaliana*	AT3G05690	Zhao et al. [99]
	AtNF-YA3	*Arabidopsis thaliana*	AT1G72830	Zhao et al. [99]
	AtNF-YA5	*Arabidopsis thaliana*	AT1G54160	Wang et al. [91]
	AtNF-YA8	*Arabidopsis thaliana*	AT1G17590	Zhao et al. [99]

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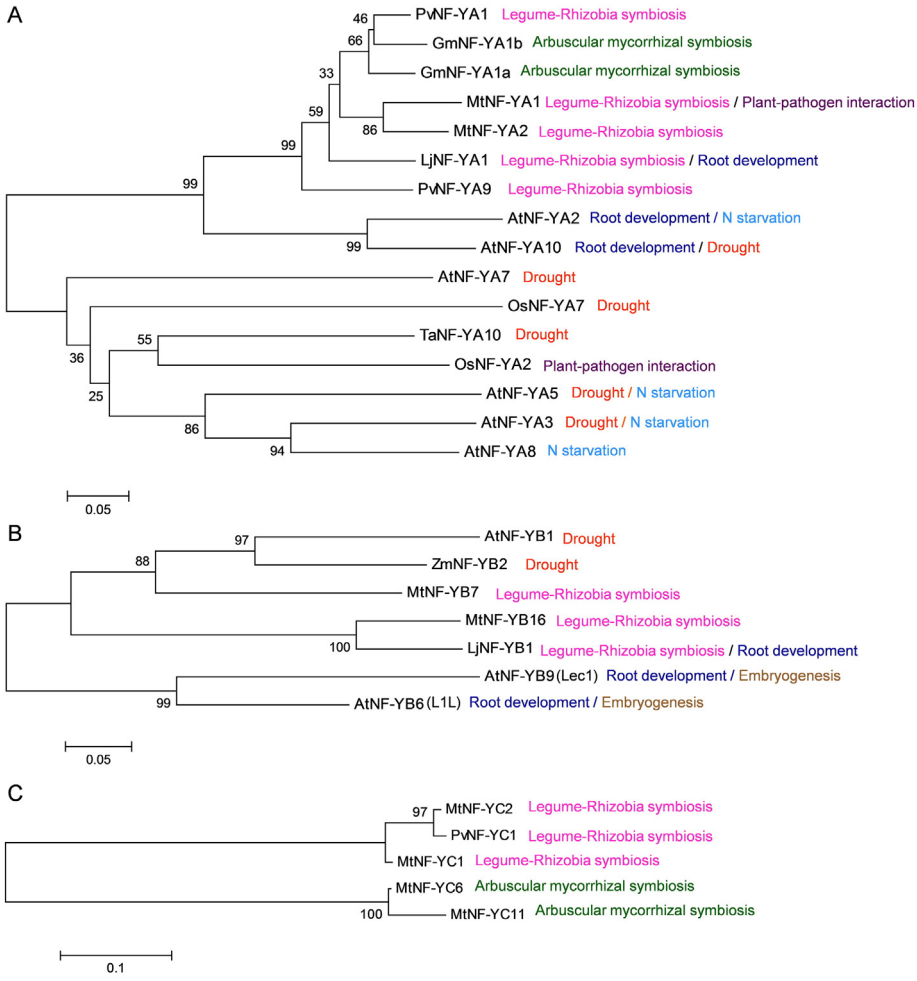

Fig. 1. Phylogenic tree of N-YA (A), NF-YB (B) and NF-Y (C) subunits from different species with known function in legume rhizobia symbiosis, arbuscular mycorhizal symbiosis, root development, drought and N starvation. For each NF-Y family, the alignment of full length proteins was generated using the Clustal Omega [80] and used to construct phylogenetic trees by the neighbor joining method using the MEGA5 software [88]. Numbers represent bootstrap values obtained from 10,000 replicates.

constrained by the specificity of NF-Y expression patterns or protein-protein interactions. An additional, but closely related question is whether the different *NF-Y* genes have acquired new functions and/or novel regulatory mechanisms.

7.1. Addressing the tissue- or cell-specific expression pattern of NF-Ys and regulatory mechanisms

Defining which NF-YA, NF-YB, and NF-YC subunits are actually expressed and interact with each other in a given cell type during specific developmental stages or physiological conditions is one of the keys to understand the role of NF-Y diversity in plants and a major technical challenge for the future. First answers came from studies exploring tissue expression patterns for individual NF-Y subunits in shoot and root of Arabidopsis seedlings [79] or in different tissues of the Medicago nodules or roots using laser capture micro-dissection (LCM) [5,18,38,54,75]. However, the tissue-specific expression data available are far from comprehensive and do not include the analysis of many developmental stages or responses to environmental conditions. The application of technologies that enables cell- or tissue-specific gene expression analysis [3,87] such as fluorescent activated cell sorting (FACS) [7], isolation of nuclei tagged in specific cell types (INTACT) [20] and translating ribosome affinity purification (TRAP) [64,97] will reveal the specific accumulation of individual NF-Y transcripts in the multiple cell types involved in development, interaction with microorganisms or adaption to adverse environmental conditions. Given the promiscuity of the interaction between NF-Y subunits, particularly between NF-YB and NF-YC subunits [11,30], such a spatial expression map of NF-Ys would certainly help to delineate the NF-Y complexes that are present in each cell type and how these cell-specific responses are coordinated during such diverse biological processes.

As discussed earlier plant NF-Y genes are subjected to various levels of transcriptional and post-transcriptional regulation (Fig. 2). In Medicago, it has been shown that *MtNF-YA1* and *MtNF-YC2* can also be regulated at the level of recruitment of mRNA to the translational machinery in response to rhizobial infection [73]; however this layer of regulation has not been investigated in other species and/or other biological processes. Another question is whether plant NF-Ys, as their animal counterpart, are subjected to post-translational modifications such as phosphorylation [14,96], ubiquitylation and acetylation [61]. These modifications could affect the stability of NF-Y TFs and their DNA binding or transcriptional activity. With such multiple tiers of regulation, (illustrated in Fig. 2), an ultimate goal should be to unravel the cell- or tissue-specific expression of NF-Y proteins by combining INTACT and proteomic profiling using liquid chromatography coupled to tandem mass spectrometry (LC-MS/MS) [2].

7.2. NF-Y target genes and assembling of combinatorial TF complexes

In order to move forward in our understanding of the function of plant NF-Y genes it is important to unravel and compare both the network of target genes they control and other regulatory proteins

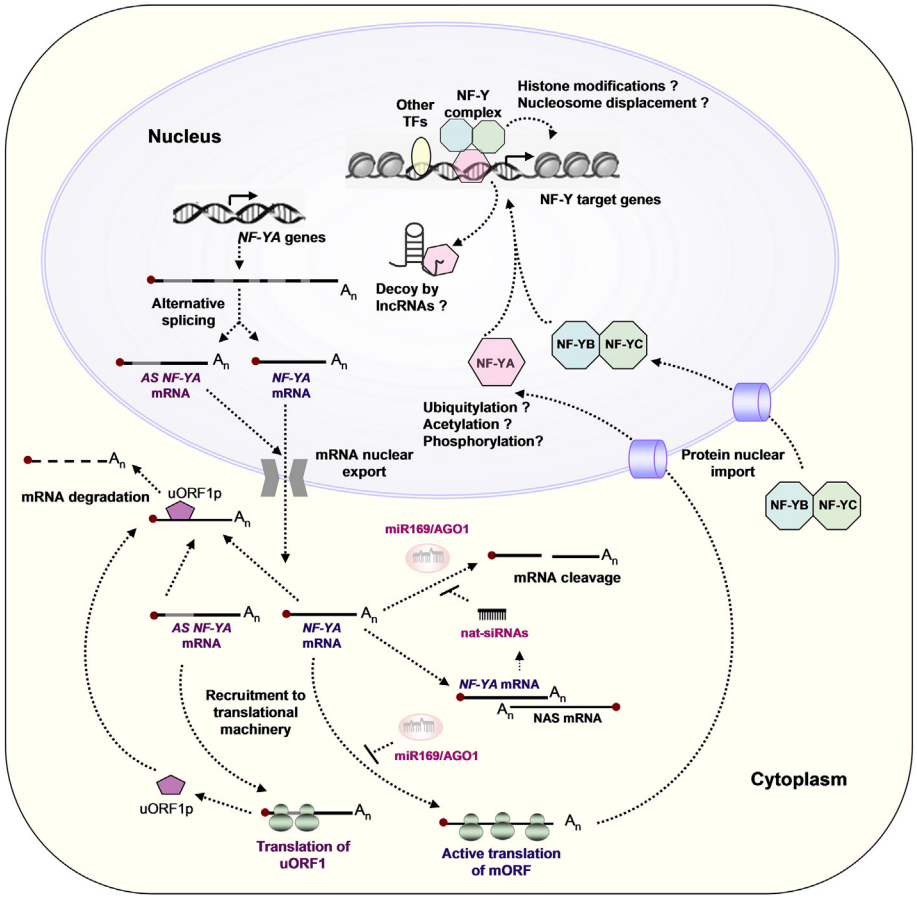

Fig. 2. Overview of the multiple levels of regulation of NF-Ys and their mechanisms of action. NF-YA subunits are regulated by alterantive splicing (*AS NF-YA* mRNA). Retention of the first intron in the 5′ leader sequence leads to translation of the upstream Open Reading Frame 1 (uORF1) and the production of a peptide (uORF1p) that binds to and destabilizes both *AS NF-YA* and *NF-YA* mRNAs. Recruitment of the fully spliced *NF-YA* mRNA to the translational machinery leads to the translation of the main ORF (mORF) and the synthesis of the NF-YA subunit, which is imported into the nucleus. NF-YB and NF-YC subunits heterodimerize in the cytoplams and, after nuclear import, bind to the NF-YA subunits to form the functional heterotrimer. Stability and/or translation of NF-YA mRNAs are post-transcriptionally controlled by the action of miR169/Argonatute 1 protein (AGO1) silencing complex. A natural antisense (NAS) mRNA that overlaps *NF-YA5* mRNA leads to the production of natural antisense small interference RNAs (nat-siRNAs), which decrease miR169 levels and enchace *NF-YA* mRNA levels by yet unkown mechanisms. Once in the nucleus, NF-YA subunit might, as its animal counterpart, be subjetced to post-translational modifications (phosphorylation, ubiquitylation and acetylation) that affect DNA binding or protein stability. As in animals NF-YA subunits could be sequestered/decoy by long-non coding RNAs (lncRNAs) that prevent DNA binding. NF-Y complexes can also interact with other transcription factors (TFs) prior to or after DNA binding. Binding of NF-Y complexes to DNA can also modulate the dynamics of histone modifications and promote nucleosome displacement in the promoters of NF-Y target genes.

they interact with in multimeric complexes. A few direct targets of NF-Y transcription factors have been identified by Chromatin immunoprecipitation (ChIP) followed by quantitative PCR or Electrophoretic Mobility Shift Assay (EMSA). For example, the *Cruciferin C* and *Sucrose synthase 2* genes have being identified as direct targets of the complex formed by LEC1/L1 L and NF-YC2 in Arabidopsis [95] and *MtERN1* is a target of MtNF-YA1/MtNF-YB16/MtNF-YC2 in Medicago[5,44]. However, the repertoire of genes containing *CCAAT* boxes in their promoter and being identified as direct targets of NF-Y complexes is far from complete. ChIP studies followed by high throughput DNA sequencing (ChIP-seq) are required to identify the set of genes that are direct targets of each NF-Y subunit in vivo in different physiological or developmental contexts. The information obtained for one subunit in a given biological process can be compared with the targets of its NF-Y partner subunits to get an insight into the heterotrimeric complexes that can be functional during these processes. The identification of solid lists of direct targets will also benefit from crossing ChIP results with transcriptome analyses in WT and NF-Y mutants plants in specific physiological or developmental conditions.

In addition to the acquisition of knowledge about direct targets, identifying and comparing proteins present in multimeric complexes together with different NF-Y proteins should shed some light on the function of different NF-Y genes. In plants, for example NF-YB and NF-YC proteins have been shown to interact with TFs like MADS18, bZIP28, bZIP67, CO, CO-like, VR2 and SIN1 ([4,51,56,62,93,95]. The yeast two hybrid system was used to identify most of the above mentioned NF-Y interactors. However, the Tandem Affinity Purification (TAP) method coupled to MS (TAP/MS) is one of the most powerful techniques for systematically identifying protein complexes and protein networks [8,69]. Its use in the NF-Y field could lead to significant advances in identifying the *in planta* composition of multimeric complexes containing NF-Y subunits.

7.3. Plant NF-Y transcription factors and epigenetic modifications

In mammals, NF-Ys are considered to be pioneer transcription factors, whose binding and transcriptional activity on their target genes, (e.g., cell cycle gene) has been linked to epigenetic modification and chromatin remodeling [29,66]. In humans, NF-Y has indeed been shown to regulate gene expression by histone acetylation [25] and by promoting both positive and negative histone methylation marks [13]. In plants, epigenetic control by NF-Ys has been described during floral transition in Arabidopsis, where a defined NF-Y complex modulates histone methylation dynamics and expression of its target genes [36]. Elucidation of the mechanisms by which NF-Y complexes promote transcriptional activation during other developmental processes or in

response to environmental stimuli, will require a systematic analysis of the correlation between NF-Y binding, nucleosome occupancy and the status of histone acetylation/methylation and DNA methylation in the promoter region of the target genes. The epigenetic landscape can be determined by the use of ChIP–Seq with different antibodies against histone modifications (for example anti-H3K9ac as a mark of active genes and anti-H3K27me3 as a mark of inactive genes). Nucleosome loss at promoters is a conserved hallmark of active regulatory chromatin. In addition to mapping histone modifications, the use of the ATAC-Seq (assay for transposase-accessible chromatin using sequencing) technique is a high-throughput procedure to isolate and map nucleosome depleted chromatin regions that should provide a genome-wide map of NF-Y-dependent-nucleosome occupancy [10].

Finally, the binding of the mammalian NF-Y complex to the promoter of pro-apoptotic genes is affected by the interaction of the NF-YA subunit with the long non-coding RNA (lncRNA) PANDA [37]. Knock-down of PANDA lncRNAs resulted in an enhanced expression of NF-YA target genes and increase of NF-YA occupancy at target promoters, suggesting that PANDA can sequester NF-YA and prevent its binding to the chromatin. Such a mechanism has not yet been reported in plants and its identification will require the specific co-immunopurification of NF-Y subunits and their associated RNAs followed by the sequencing of the co-purified RNAs.

In conclusion, NF-Ys are relevant players for developmental and environmental processes in plants. In order to exert their functions, they are subjected to multiple tiers of regulation that alter their DNA binding or transcriptional activity (see Fig. 2). We anticipate that research on plant NF-Ys will benefit from novel approaches that expose the epigenetic, post-transcriptional and post-translational levels of regulation combined with technologies that enable tissue-or cell- specific cell expression analysis. This will provide a better understanding of the functionality, specificity and mechanisms of action of NF-Ys in plants.

Conflict of interest

All authors hereby declare that they have no conflict of interest.

Transparency document

The Transparency document associated with this article can be found, in the online version.

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