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Transcriptional regulation of grass secondary cell wall biosynthesis: playing catch-up with *Arabidopsis thaliana*

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Secondary cell wall synthesis occurs in specialized cell types following completion of cell enlargement. By virtue of mechanical strength provided by a wall thickened with cellulose, hemicelluloses, and lignin, these cells can function as water-conducting vessels and provide structural support. Several transcription factor families regulate genes encoding wall synthesis enzymes. Certain NAC and MYB proteins directly bind to the SNBE and AC elements upstream of structural genes and other transcription factors. The most detailed model of this regulatory network is established predominantly for a eudicot, *Arabidopsis thaliana*. In grasses, both the patterning and the composition of secondary cell walls are distinct from that of eudicots. These differences suggest transcriptional regulation is similarly distinct. Putative rice and maize orthologs of several eudicot cell wall regulators genetically complement mutants of *A. thaliana* or result in wall defects when constitutively overexpressed; nevertheless, aside from a maize, ZmMYB31, and a switchgrass protein, PvMYB4, function has not been tested in a grass. Similar to the seminal work conducted in *A. thaliana*, gene expression profiling in maize, rice, and other grasses implicates additional genes as regulators. Characterization of these genes will continue to elucidate the relationship between the transcription regulatory networks of eudicots and grasses.

Keywords: transcription factors, secondary cell wall

INTRODUCTION

Plant cell walls are diverse in their polymer composition, which vary among plant species as well as cell types within a species. The primary cell wall, consisting mostly of cellulose, hemicelluloses, pectin, and proteins demarcates each plant cell. Secondary cell walls, composed mostly of cellulose, hemicelluloses, and lignin, are deposited between the plasma membrane and primary wall in specialized cell types following cessation of cell enlargement. Even though all plant cell walls contain a cell wall matrix made up of cellulose microfibrils, hemicelluloses, and other cell wall polymers, there are significant differences in polymer types and their relative abundance between dictos and monocots (Vogel, 2008). For instance, relatively high amounts of xyloglucan, pectins, and structural proteins are typically present in the primary walls of eudicots, non-commelinoid monocots, and gymnosperms. The commelinoid monocots like grasses contain glucuronoarabinoxylans, small quantities of pectin and structural proteins and high levels of hydroxycinnamates (Vogel, 2008). Apart from wall composition, eudicots such as *Arabidopsis thaliana* and monocots such as rice (*Oryza sativa* L.) exhibit distinct morphological characteristics in addition to their namesake two and single cotyledons. Pinnate or palmate venation is characteristic of eudicots while monocots posses parallel venation. Other morphological and anatomical distinctions exist in their vasculature, tissues highly enriched in secondary cell walls. Stem radial thickening in eudicots is derived from a specialized cell layer called the cambium that differentiates into the phloem and xylem. On the other hand, monocots lack a specialized cambium layer and therefore do not undergo secondary growth (**Figure 1**). The vascular bundles of grasses are often well defined by a single layer of bundle sheath cells surrounding the xylem and phloem and the organization of the bundles is distinct from eudicots. In *A. thaliana*, the vascular bundles are arranged as a ring along the periphery of the stem in a pattern known as eustelic, whereas monocot bundles posses an atactostele arrangement characterized by several circles around the periphery of a stem, as in rice and *Brachypodium distachyon* (**Figure 1**), or scattered throughout the stem as in maize (*Zea mays* L.; Kiesselbach, 1949).

With distinctions and similarities abound, it is decidedly unclear how the transcriptional regulation of secondary cell wall biosynthesis in eudicots and grasses relate. Plant cell wall biosynthesis is regulated at different molecular and cellular levels. Current evidence supports a complex regulatory network consisting of a handful of proteins from only a small portion of over 65 different transcription factor families (**Figure 2A**). Phylogenetic analysis has identified close homologs of *A. thaliana* regulators from both vascular and non-vascular plants and some of those regulators were capable of complementing *A. thaliana* cell wall mutants (Zhong et al., 2011). These findings suggest the evolutionary conservation of the transcriptional regulators in secondary cell wall biosynthesis. On the other hand, due to the pronounced differences between eudicot and monocot secondary wall composition and anatomy, there are likely unique aspects of the regulatory network yet to be resolved.

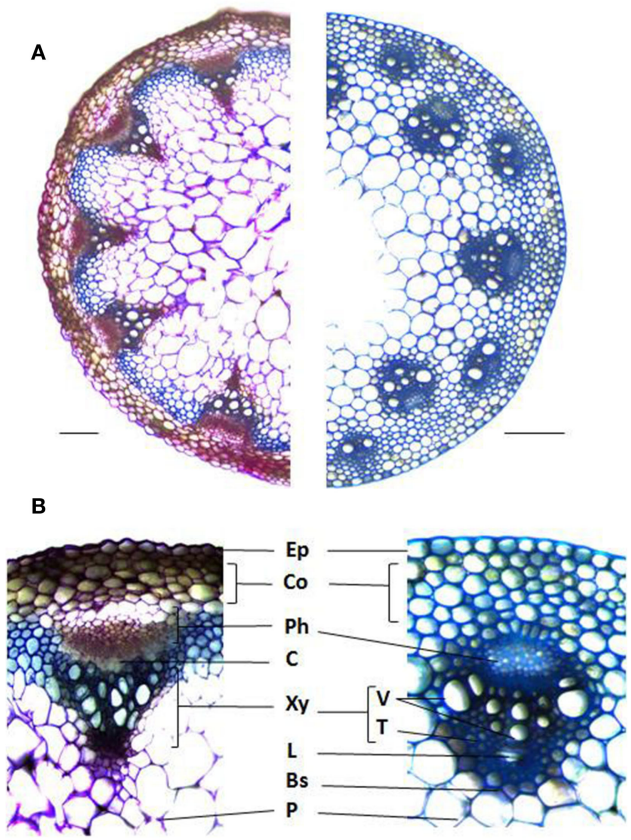

FIGURE 1 | Stem cross sections illustrating the different cell types and arrangements between dicots and monocots. (A) *Arabidopsis thaliana* (left) and *Brachypodium distachyon* (right) stained with Toluidine blue. **(B)** Vascular bundle anatomy of *A. thaliana* (left) and *B. distachyon* (right). Ep, Epidermis; Co, Cortex; Ph, Phloem; C, Cambium; Xy, Xylem; V, Vessels; T, Tracheads; L, Lacuna; Bs, Bundle Sheath; P, Pith. Bars = 0.1 mm.

TRANSCRIPTIONAL REGULATION IN *A. THALIANA*

Transcriptional regulation is one of the most important processes controlling plant cell wall biosynthesis, mediated by the interaction and interplay of *cis*-regulatory DNA elements and the *trans*-acting transcription factor proteins. Recent evidence suggests the involvement of an AP2 family protein *SHINE/WAX INDUCER 1* (*SHN*) as a global level regulator of cell wall biosynthesis (Ambavaram et al., 2011). Constitutive overexpression of *A. thaliana SHN* in rice results in the activation of cellulose and other cell wall-associated genes and the repression of lignin pathway genes. This protein is also capable of activating key *NAC* and *MYB* regulators and electrophoretic mobility shift assays (EMSA) demonstrate the direct binding of SHN protein to promoters of rice cell wall-associated transcription factors (Ambavaram et al., 2011). A WRKY family transcription factor, WRKY12, acts as a global repressor of secondary wall biosynthesis (Wang et al., 2010). Transcripts of this gene are abundant in the cortex and pith cells of *A. thaliana* that lack secondary walls. Loss-of-function *wrky12* mutants exhibit increased expression of transcription factors associated with secondary wall biosynthesis as well as ectopic depositions of lignin, cellulose, and xylan and consequently, and overall increase in plant biomass (Wang et al., 2010). In the presence of WRKY12 protein, pith stem cells are maintained parenchymatous and the deposition of secondary cell walls is repressed. MYB32 similarly acts as a repressor of secondary wall biosynthesis, but in cells where this pathway has been activated; thus, it may provide negative feedback (Preston et al., 2004). Transgenic overexpression of *MYB32* resulted in the repression of *SECONDARY WALL-ASSOCIATED NAC-DOMAIN PROTEIN 1* (*SND1*), a higher order activator of secondary wall biosynthesis (Wang et al., 2011). Interestingly, the SND1 protein directly binds the *MYB32* promoter to activate gene expression (Wang et al., 2011). A group of NAC-domain transcription factors, *NAC SECONDARY WALL THICKENING FACTOR 1* (*NST1*), *NST2, SND1* (also known as *NST3*), *VASCULAR-RELATED NAC-DOMAIN 6* (*VND6*), and *VND7*, collectively known as the secondary wall NACs (SWNs) are implicated as positively acting master regulators in a variety of tissues (Demura and Fukuda, 2007; Zhong and Ye, 2007). Among the NACs, *SND1* functions as a key switch governing the regulation of all secondary wall polymers (Zhong et al., 2006; Mitsuda et al., 2007). Overexpression of *SND1* leads to ectopic deposition and activation of cellulose, hemicellulose, and lignin biosynthesis genes. Conversely, dominant repression of *SND1* results in the absence of secondary wall development in vascular and interfascicular fibers (Zhong et al., 2006; Mitsuda et al., 2007). It also directly activates itself and is repressed by MYB transcription factors under the direct influence of *MYB46* (Wang et al., 2011). The SND1 protein directly binds the *cis*-regulatory regions of *MYB46*, *MYB83*, and *C3H14* genes to activate their expression (Zhong et al., 2008; Ko et al., 2009; McCarthy et al., 2009). It also acts as a direct regulator of *F5H*, a gene encoding a key enzyme involved in lignin biosynthesis (Zhao et al., 2010). Another direct target of *SND1* is the KNOX type Homeodomain transcription factor, *KNAT7*, which interacts with OVATE FAMILY PROTEIN 4 to repress secondary wall biosynthesis (Li et al., 2011). Loss-of-function mutants of *knat7* display an increase in cell wall gene expression, wall thickening in interfascicular fiber cells, and an increase in lignin content (Li et al., 2011). Interestingly, a weak activator of cell wall gene expression, MYB75, was found to physically interact with KNAT7 protein to repress cell wall biosynthesis (Bhargava et al., 2010). These results imply that wall regulators can play multiple roles by interacting with different *trans*-acting factors in different cell types to provide more flexibility and complexity to the regulatory network.

The *SND1* homologs *NST1* and *NST2* play a crucial role in the *A. thaliana* anther endothecium (Mitsuda et al., 2005). In this tissue, these proteins are activated by *MYB26* which is essential for anther dehiscence and proper pollen release (Yang et al., 2007). Other SWNs, in particular *VND6* and *VND7*, regulate metaxylem and protoxylem development and are repressed by the *VND-INTERACTING2 NAC* protein (Kubo et al., 2005; Yamaguchi et al., 2010). The VND proteins VND6 and VND7 driven by *SND1* promoter were capable of complementing the *snd1/nst1* mutant phenotype implying their conserved functionality (Zhong et al., 2007a). They are positively regulated by *ASYMMETRIC*

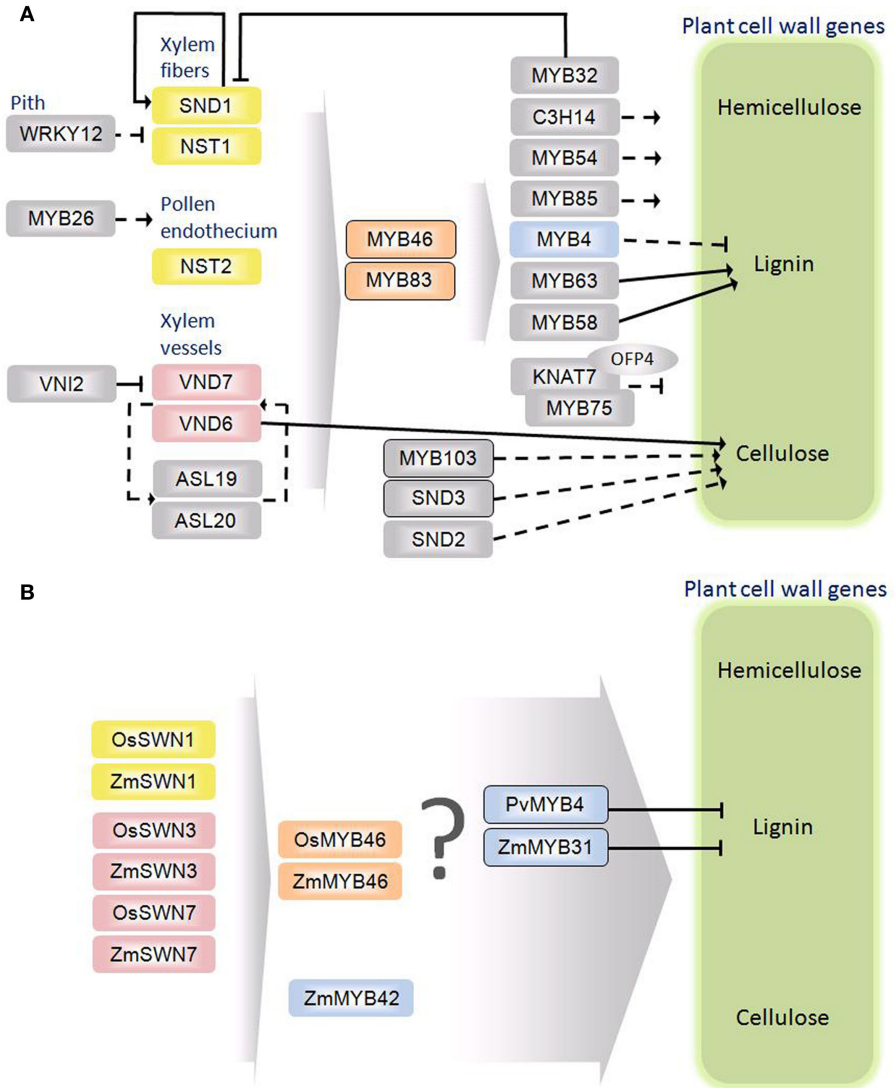

FIGURE 2 | Schematic diagrams of the secondary cell wall regulatory networks in *Arabidopsis thaliana* (A) and monocots (B). Rectangles represent transcription factors. The oval indicates an interacting protein. Solid arrows and bordered rectangles signify evidence for direct interactions. Dashed arrows indicate no evidence for direct interaction. Orthology between *A. thaliana* and grasses is denoted by color.

LEAVES2-LIKE19 (*ASL19*) and *ASL20* (Soyano et al., 2008). Transgenic overexpression of *ASL19* and *ASL20* induces trans-differentiation of non-vascular tissues into treachery elements and an increased cell wall thickening in mutant lines. They are also able to partially recover the dominant negative effect of the VND6 and VND7 repressor lines (Soyano et al., 2008). The SWNs, *SND1*, N*ST1*, *NST2*, *VND6*, and *VND7* activate a cascade of downstream transcription factors such as *SND2*, *SND3*, *MYB103*, *MYB85*, *MYB54*, *MYB46*, *MYB69*, *MYB63*, *MYB83*, and *KNAT7* (Zhong et al., 2008; Ko et al., 2009; McCarthy et al., 2009). Some of the downstream regulators, *SND2*, *SND3*, and *MYB103* exclusively activate cellulose biosynthesis where as the others such as *MYB63*, and *MYB58* regulate lignin biosynthesis (Zhong et al., 2008). Even though direct protein–DNA interactions have been shown for some of the cellulose and lignin specific regulators, further characterization of many downstream regulators is needed.

Discovery of the *trans*-acting transcription factors of cell wall biosynthesis facilitated the opportunity to identify common *cis*-elements shared among the master regulators. The tracheary-element-regulating *cis*-element (TERE) is one such 11-bp motif, CTT/(C)NAAA/(C)GCNA(T), involved in tissue specific cell wall biosynthesis and programmed cell death. First identified in the *Zinnia cysteine protease 4* promoter and is present in numerous cell death and xylem differentiation genes such as *Cysteine protease 1* (*XCP1*), *XCP2*, *Serine protease 1*, and several other genes associated with wall function that include xylanases and acetyltransferases (Pyo et al., 2007). More recent studies demonstrated the physical interaction between VND6 protein and the TERE (Ohashi-Ito et al., 2010). Other SWNs bind a 19-bp imperfect palindromic

sequence (T/A)NN(C/T)(T/C/G)TNNNNNNNA(A/C)GN(A/C/T)(A/T) referred to as the secondary wall NAC binding element (SNBE; Zhong et al., 2010). A synthetic promoter harboring six copies of the SNBE fused to a GUS reporter revealed specific expression in xylem and interfascicular fibers, phenocopying native *MYB46* promoter behavior (Zhong et al., 2007b). Other direct targets of SND1, including *MYB83*, *MYB103*, *SND3*, and *KNAT7* also posses the SNBE element (Zhong et al., 2010). A similar *cis*-element, TACNTTNNNNATGA, was identified recently in the *SND1* promoter and is the target of binding that serves as a target of positive feedback from SND1 itself (Wang et al., 2011).

A series of MYB transcription factor family proteins are also implicated in the cell wall regulatory network, a majority of which act downstream of the SWNs. One such protein, MYB46, acts subsequent the SWNs (**Figure 2A**). Lignin biosynthesis is specifically regulated by MYB63 and MYB58 interacting with the AC/Pal-box promoter sequences. This motif was first identified in the promoter of parsley *PHENYLALANINE AMMONIA-LYASE 1* and subsequently identified as three AC rich elements AC-I (ACCTACC), AC-II (ACCAACC), AC-III (ACCTAAC) involved in lignin gene regulation (Lois et al., 1989; Hatton et al., 1995; Raes et al., 2003). Binding of MYB proteins to the AC elements *trans*-activates the respective promoters thus, activating the genes in a xylem specific manner repressing the expression of the same genes in phloem or the cortical cells (Hatton et al., 1995). The consensus sequence of the AC element was recently expanded to include four more forms interchanging a T with the C at the last position; thus, ACC(T/A)A(A/C)(C/T) (Zhong and Ye, 2012). This 7-bp sequence, the secondary wall MYB responsive element (SMRE), is bound by both *MYB46* and *MYB83* proteins and is sufficient for the activation of a suite of transcription factor and cell wall biosynthetic genes (Zhong and Ye, 2012). The MYB46-responsive *cis*-element (M46RE) is an 8-bp sequence (A/G)(G/T)T(A/T)GGT(A/G) found in the *C3H14* promoter, which is a direct target of MYB46 (Kim et al., 2012). *Trans*-activation assays coupled with EMSA reveled M46RE is required and sufficient for the activation of *C3H14*. The 8-bp core sequence was present in nearly 43% of the genes in the *A. thaliana* genome but was enriched in the downstream genes activated by MYB46 along with secondary cell wall related structural genes (Kim et al., 2012). Apart from the key SWNs and MYBs, a handfull of downstream MYBs, NACs, and transcription factors from other families are involved in this complex cell wall regulatory network. A closely related homolog of *MYB32, MYB4*, functions as a repressor of *CINNAMATE-4-HYDROXYLASE* (C4H; Jin et al., 2000). Loss-of-function mutants of *MYB4* exhibited elevated levels of sinapoyl malate, a component in the lignin pathway, and an increase in *C4H* expression. Collectively, these findings suggest a complex and hierarchical transcription regulatory network for eudicot cell wall biosynthesis (**Figure 2A**). While this review primarily discusses discoveries in *A. thaliana*, it should be noted that a number of regulators have been characterized in other eudicot species such as *Populus trichocarpa, Eucalyptus gunnii, Nicotiana tabacum, Antirrhinum majus, Pinus taeda, Vitis vinifera*, and *Medicago truncatula*.

GRASS CELL WALL REGULATORS

From the time of eudicot and monocot divergence 140–150 million year ago, the transcription factor families have disproportionately expanded and the regulatory networks have likely diverged; thus, the existing eudicot network model for transcription regulation is not wholly generalizable to monocots (Chaw et al., 2004; Shiu et al., 2005). Conversely, recent functional characterization of grass transcription factors implies great commonality in how a similar network could regulate grass cell wall biosynthesis. While many cell wall genes have been characterized in grasses, almost nothing is known about the regulation of walls in monocots. The *A. thaliana* model, which is by far the best developed, is admittedly nascent. This stands in stark contrast to the model for grasses that consists of only a few genes (**Figure 2B**). Maize *CAFFEIC ACID-O-METHYL TRANSFERASE* (*COMT*) is a key lignin pathway gene with an AC-III element recognized by R2R3-MYB transcription factors (Vignols et al., 1995; Fornalé et al., 2010). Group four R2R3-MYB transcription factors are described as repressors and based on sequence homology to the know *A. thaliana* MYB repressors, five maize transcription factors, ZmMYB31, ZmMYB42, ZmMYB2, ZmMYB8, and ZmMYB39 were identified as candidates for direct repression of *ZmCOMT* (Fornalé et al., 2006). When overexpressed in *A. thaliana*, *ZmMYB31* and *ZmMYB42* resulted in down regulation of lignin associated genes and subsequently reduced lignin content (Fornalé et al., 2010). Overexpression of *ZmMYB42* caused a reduction in leaf size, an adaxial curvature indicative of less tertiary vein formation, reduction of the syringyl lignin monomers, and dwarfism in *A. thaliana* (Sonbol et al., 2009). The absence of results in a monocot is likely due to the relative recalcitrance of crop species to genetic study; thus, *A. thaliana* serves as an imperfect heterologous system to study grass gene function. The maize gene, *ZmMYB31* is the first wall specific regulator characterized in a grass (Fornalé et al., 2010). Chromatin immunoprecipitation demonstrated the direct interaction between ZmMYB31 and *ZmCOMT* promoter and an AC element similar to AC-II was identified as the binding motif. The switchgrass (*Panicum virgatum* L.) protein PvMYB4, an ortholog to *A. thaliana* MYB4, is another recently characterized repressor of lignin (Shen et al., 2012). Ectopic expression of *PvMYB4* in switchgrass resulted in a reduction in total lignin and altered lignin monomer ratio (Shen et al., 2012). The AC element is also implicated as the binding site of PvMYB4, which results in repression of lignin pathway genes (Shen et al., 2012). In addition, rice and maize orthologs of *A. thaliana* SWNs and MYB46 were shown to activate secondary wall biosynthesis when overexpressed in *A. thaliana* (Zhong and Ye, 2012). Moreover, OsSWNs and ZmSWNs were able to complement and partially rescue the pendant stem phenotype of the *A. thaliana snd1*/*nst*1 double mutant. Similarly, *OsMYB46* and *ZmMYB46* under the control of *AtMYB46* promoter were able to complement the loss of helical secondary wall thickening in vessels of *A. thaliana myb46/myb83* double mutant. In addition, SNBEs were identified in *OsMYB46* and *ZmMYB46* promoters and were bound and activated by the rice and maize SWNs in *A. thaliana* transient protoplast assays (Zhong and Ye, 2012). While studies in a heterologous system have proven informative, further functional characterization in a grass species is necessary. Contrary to expectations of distinct aspects of monocot

cell wall regulation, the existing model is populated exclusively by homologs of known *A. thaliana* genes.

Gene expression profiling was critical in identifying many of the candidates that formed the foundation of the existing *A. thaliana* cell wall regulatory network (Oh et al., 2003; Ehlting et al., 2005; Kubo et al., 2005; Zhao et al., 2005). Similar tools can be applied to grasses to identify candidates for functional characterization, especially those specific to monocots. Accordingly, a comparison of the transcriptome of maize elongating and non-elongating internodes revealed several transcription factors that are feasibly involved in cell wall regulation (Bosch et al., 2011). Likewise, the expression of three barley (*Hordeum vulgare* L.) NACs, *HvNAC033*, *HvNAC034*, and *HvNAC039*, were significantly greater in stem tissue where extensive secondary cell wall biosynthesis occurs. One of these proteins, HvNAC033, is the closest barley homolog to *A. thaliana* NST1, further supporting the possible role of this protein in grass cell wall regulation (Christiansen et al., 2011). Comparison of expression networks across species similarly reinforces the notion of shared features across eudicots and monocots and revealed potential distinctions. Genes with expression patterns similar to secondary wall *CELLULOSE SYNTHASE A* genes in rice included those most similar to *A. thaliana MYB63*, *MYB103*, *NST1*, *SND2*, and *KNAT7* (Ruprecht et al., 2011). Conversely, several rice transcription factors were co-expressed with structural genes that do not share sequence homology to co-expressed or characterized *A. thaliana* genes. These include MYB and NAC as well as bZip and AP2 family genes (Ruprecht et al., 2011). As with *ZmMYB42* and *PvMYB4*, candidates identified using sequence similarity and expression profiling require further characterization in the native systems in order to solidify both overlap and divergence between eudicot and grass cell wall regulatory networks.

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