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New Aspects of Functional Plant Nuclear Architecture

Nuclear lamina CRWN proteins regulate chromatin organization, gene expression, and nuclear body formation in plants

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Abstract
The metazoan cell nucleus is physically supported by nuclear lamina structures, which are mainly composed of filamentous protein lamins. CROWDED NUCLEI (CRWNs)/nuclear matrix constituent proteins are considered potential candidates of lamin analogs in plants. CRWNs specifically localize to the nuclear periphery, maintain nuclear morphology, and interact with several inner nuclear membrane proteins. CRWNs also regulate several nuclear events. In this review, I summarize the functions of CRWNs in regulating chromatin organization, gene expression, and nuclear body formation, and provide insights into novel plant nuclear lamina functions and structures.

Keywords Chromatin organization · CRWN · Gene expression · NMCP · Nuclear body · Nuclear lamina

Introduction

All eukaryotes have a nucleus to protect their genome from cytoplasmic enzymes and mechanical damage and to optimize replication, transcription, silencing, and repair. The nucleus is mechanically supported by a mesh-like structure known as the nuclear lamina. Lamin proteins (LMNs), which self-polymerize and form intermediate filaments in vivo and in vitro, are the major components of the metazoan nuclear lamina (Gruenbaum and Foisner 2015). LMNs are involved in not only the maintenance of the nuclear shape but also the regulation of chromatin organization, gene expression, cell differentiation, and metabolism. Some mutations in LMNs cause severe diseases, including laminopathies, such as Hutchinson–Gilford progeria syndrome and Emery–Dreifuss muscular dystrophy (Bonne et al. 1999; Eriksson et al. 2003; Raffaele di Barletta et al. 2000). Although LMNs are critical for metazoans, they were not identified in non-metazoans for a long time. However, some recent studies revealed that the orthologs of LMNs are widely conserved in eukaryotic groups including Opisthokonta; Amoebozoa; and Stramenopile, Alveolata, and Rhizaria (SAR) but not Plantae (Batsios et al. 2012; Koreny and Field 2016; Krüger et al. 2012). Although LMN orthologs are not found in plants, they have a similar mesh-like structure at their nuclear periphery, indicating the existence of functional analogs of LMNs (Fiserova et al. 2009; Hao et al. 1992). In this review, I focus on the functions of CROWDED NUCLEI (CRWN) proteins, lamin analogs in *Arabidopsis thaliana* (L.) Heynh., in nuclear events such as chromatin organization, gene expression, and nuclear body formation.

Identification of NMCP

The plant lamina analogs have been evaluated by immunoblotting and immunostaining using anti-intermediate filament antibodies, but their amino acid sequences have not been determined (Beven et al. 1991; Frederick et al. 1992; Galcheva-Gargova et al. 1988; Li and Roux 1992; McNulty and Saunders 1992; Mínguez and Moreno Díaz de la Espina 1993). Masuda et al. (1993, 1997, 1999) made the first attempt to determine the sequence of plant nuclear lamina protein using the nuclear matrix fraction from *Daucus carota* (Dc) calli. The nuclear matrix fraction, insoluble after several treatments (including DNase, RNase, and high salt conditions), was thought to contain the nuclear lamina and other

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nuclear scaffold proteins. They produced monoclonal antibodies against chromatographically purified proteins from the fraction, and one of the antibodies specifically recognized a peripheral protein in the nucleus (Masuda et al. 1993). The antigen was nuclear matrix constituent protein 1 (NMCP1) (Masuda et al. 1997). *Daucus carota* NMCP1 (DcNMCP1) similar to other NMCP proteins and lamins has a tripartite structure consisting of a central coiled-coil domain flanked by a globular head and tail domain, the later containing a nuclear localization signal. NMCPs have been identified in a wide range of plants, from Charophyta to terrestrial plants, but not in Chlorophyta or animals (Ciska and Moreno Díaz de la Espina 2013; Ciska et al. 2013, 2019). Importantly, the number of NMCP paralogs and subtypes increases depending on whole-genome duplication. For example, Charophyta, Marchantiophyta, Bryophyta, Lycopodiopsida, and Acrogymnospermae have just one type of ancestral NMCP. Whereas, monocotyledons have one member of both types 1 and 2 NMCP (except for a few species) and almost all dicotyledons have several members of both types 1 and 2 NMCPs. Three members of the NMCP1 type, namely, CRWN1, CRWN2, and CRWN3, and one member of the NMCP2 type, namely, CRWN4, are conserved in Arabidopsis (Dittmer et al. 2007; Meier 2006). As all functional analyses of NMCPs have been conducted in Arabidopsis, which has redundant members of NMCP1, I focused on the function of CRWNs.

Regulating chromatin organization

NMCPs play a central role in chromatin organization in plants. The first mechanistic link between NMCPs and chromatin organization was demonstrated in the Arabidopsis *crwn1crwn2* double mutants, in which both nuclear size and chromocenter number were significantly reduced when compared with the wild-type (WT) plants, without considerable effects on the total DNA content (Dittmer et al. 2007; Wang et al. 2013). This result suggests that the nuclear DNA density of the mutant plants was higher than that of the WT plants. These studies also demonstrated that the nuclear DNA content in the *crwn1* to *crwn4* single mutants, and *crwn2crwn3* and *crwn1crwn4* double mutants was comparable with that in the WT plants. Whereas the nuclear size of the *crwn1*, *crwn4*, *crwn1crwn4* mutants was smaller than that of the WT plants (Sakamoto and Takagi 2013). To clarify whether this disparity in nuclear DNA density has an effect on *crwn1* and *crwn4* chromatin architecture, two independent research groups employed a high-throughput chromosome conformation capture (Hi-C) approach (Grob et al. 2014; Hu et al. 2019). They revealed the three-dimensional chromatin architecture in the nuclei by detecting the frequency of specific interactions between chromatin regions throughout the genome. In the *crwn1* and *crwn4* mutants, inter-arm and inter-chromosomal interactions were enhanced whereas intra-arm interactions were comparatively reduced, probably reflecting a higher DNA compaction in these mutants. Furthermore, the analysis of local chromatin organization patterns such as loose structural (generally referred to as compartment A) and compacted structural domains (generally referred to as compartment B) demonstrated that the WT plants, and *crwn1* and *crwn4* mutants exhibited similar structural domain patterns, although intra-structural domain interaction was reduced and inter-structural domain interaction was enhanced in the mutants. Overall, these results indicate that the CRWN1 and CRWN4 mutations make each chromosome more compact but do not affect chromosome structural domain patterns. Importantly, although Grob et al. (2014) and Hu et al. (2019) used different inputs in the Hi-C analysis (all nuclei versus 2C nuclei isolated from whole seedlings, respectively), the results were consistent, highlighting the robustness of the interactions detected by Hi-C.

In addition to maintaining chromatin architecture, CRWNs can tether the specific genome region to the nuclear periphery. To gain further insights into this process, CRWN1-binding sites were determined by chromatin immunoprecipitation sequencing (ChIP-seq) using CRWN1::2HA-expressing Arabidopsis (Hu et al. 2019). The CRWN1-binding sites largely overlapped with the nucleoporin (NUP1/136)-binding sites, and they were mainly associated with repressive chromatin marks and low-expression genes that are not readily detectable by transposase-accessible chromatin (ATAC) sequencing (Bi et al. 2017). CRWN1 did not seem to recognize a specific epigenetic mark because the CRWN1-binding sites did not completely overlap with H3K9me1, H3K27me3, H2A.W, and DNA methylation, suggesting some degree of promiscuity (Hu et al. 2019). CRWN1 tethers heterochromatin in the nuclear periphery, and it may contribute to reduced trans-chromatin interactions (Grob et al. 2014; Hu et al. 2019).

Regulating gene expression

The effects of CRWNs on transcriptional regulation have been extensively investigated. RNA-Seq and qRT-PCR analyses showed that the transcriptional levels of the pathogenesis-related protein 1 (*PR1*) gene was exclusively enhanced in the *crwn1crwn2* double mutants without bacterial inoculation (Guo et al. 2017). *PR1* is an important gene for plant defense and immunity, and it is usually upregulated in response to bacterial infections and salicylic acid (SA) (Ali et al. 2018). Upon infection, the PR1 proteins are secreted to the extracellular spaces, and they exhibit antimicrobial properties (Ali et al. 2018). PR1 expression in the *crwn1crwn2* double mutants was increased before and after inoculation of *Pseudomonas syringae* pv. *maculicola* (Psm) ES4326 compared with the WT, and

the double mutants exhibited enhanced resistance against Psm. Moreover, the enhanced expression and resistance observed in the *crwn1crwn2* double mutants were suppressed by CRWN1 overexpression. These results suggest that CRWN1 negatively regulates plant immunity via the suppression of PR1 expression. CRWN1 can interact with the C-terminal region of NAC transcription factor-like 9 (NTL9) and suppressor of NPR1 inducible 1 (SNI1), and thus, play a synergistic role in the repression of PR1 transcription of the PR1 promoter (Kim et al. 2012). Furthermore, CRWN1 inhibited the activity of nonexpresser of PR genes 1 (*NPR1*), an activator of PR1. Overall, CRWN1 forms a protein complex with NTL9 and SNI1, suppressing the NPR1 activity on the PR1 promoter and repressing PR1 expression before infection. CRWN1 is degraded by a proteasome-dependent pathway and PR1 expression occurs upon viral infection. Choi et al. (2019) also reported a similar phenotype of the *crwn1crwn2* and *crwn1crwn4* double mutants. These mutants showed a significant increase in *PR1*, *PR2*, and *PR5* expression and pathogen resistance after infection with *P. syringae* (DC3000). Additionally, they also found that the amount of total SA in the mutants was significantly higher than that in the WT because SA induction-deficient (SID2), a key enzyme for SA biosynthesis, is highly expressed in these mutants. They reported that CRWNs repress SID2 to maintain a low total SA level under normal conditions, and this can inhibit PR expression. Further research should be conducted to elucidate how CRWN1 represses the NPR1 activity and SID2 transcription.

Recently, it was reported that CRWN1 can interact with PROLINE-TRYPTOPHANE-TRYPTOPHANEPROLINE INTERACTOR OF POLYCOMBS1 (PWO1), a plant-specific protein associated with histones and polycomb repressive complex 2 (PRC2) (Mikulski et al. 2019). PRC2 binds to chromatin and deposits the repressive histone mark H3K27me3 (Mozgova et al. 2015). As PWO1 forms nuclear speckles with a methyltransferase CURLY LEAF (CLF) in the nuclear periphery (Hohenstatt et al. 2018), the authors questioned the physical interaction between nuclear peripheral proteins and PWO1. Immunoprecipitation coupled with mass spectrometry, fluorescence resonance energy transfer, and yeast two-hybrid (Y2H) analyses revealed that CRWN1 binds to the C-terminal domain of PWO1 (Mikulski et al. 2019). A transcriptional analysis showed that similar gene sets were altered in the *pwo1* and *crwn1crwn2* double mutants, and concomitantly, upregulated genes in the *crwn1crwn2* mutants, and H3K27me3 target genes partially but significantly overlapped, suggesting that CRWN1 mediates the suppression of the *PRC2* target genes.

DcNMCP1-interacting partners were explored by far-western and Y2H screening (Mochizuki et al. 2017). The C-terminal region (975–1053 amino acids fragment) of DcNMCP1 was selected as bait, because this region is required for nuclear peripheral localization, and Arabidopsis cDNA library was used as a prey. The MYB3 and BIM1 transcription factors, and the putative E3 ubiquitin ligase SINAT1, were detected by Y2H, suggesting that DcNMCP1 can interact with transcription factors. However, whether this interaction affects the function of the transcription factors remains unexplored.

Degradation body formation

Zhao et al. (2016) found that the seeds of the *crwn1crwn3* double mutants display lower germination rates than WT plants with or without abscisic acid (ABA), a compound that enhances seed dormancy and inhibits germination. The authors investigated the genetic interaction between CRWNs and ABA INSENSITIVE 5 (ABI5), which is a member of the bZIP transcription factor family. ABI5 is a positive regulator in the ABA signaling pathway, as the protein levels of ABI5 directly affect ABA-dependent seed dormancy (Finkelstein and Lynch 2000; Lopez-Molina and Chua 2000; Lopez-Molina et al. 2001). Germination analysis of the *crwn1crwn3abi5* triple mutants revealed that the ABI5 mutation rescues low germination rates in the *crwn1crwn3* double mutants, suggesting that ABI5 functions as a downstream repressor of CRWN1 and CRWN3. The ABI5 protein is degraded after seed germination in the WT plants, but it is highly stable in the *crwn1crwn3* double mutants even after germination. Similarly, it was reported that the ABI5 protein is degraded in a 26S proteasome-dependent manner (Liu and Stone 2010; Lopez-Molina et al. 2001; Stone et al. 2006) and could form nuclear bodies important for protein degradation (Lopez-Molina 2003). CRWN3-YFP and ABI5-mCherry co-expression induces the formation of ABI5 nuclear bodies with the CRWN3 signals (Zhao et al. 2016). Although the authors did not provide any evidence, they mentioned that the direct interaction of CRWN3 and ABI5 could not be detected by the Y2H and co-immunoprecipitation assays. These results suggest that CRWN3 plays a role in regulating the ABI5 protein level via the formation of the degradation body in the nucleus.

Repair body formation

The *crwn1-4* single mutants and *crwn1crwn3*, *crwn2crwn3*, and *crwn2crwn4* double mutants show hypersensitivity to the genotoxic agent methyl methanesulfonate (MMS) (Wang et al. 2019). Excess reactive oxygen species and severe genomic DNA damage were detected in the *crwn* mutants after MMS treatment, by 3,3′-Diaminobenzidine staining and the random amplified polymorphism DNA method, respectively. The expression levels of DNA damage-responsive genes such as *BRCA1*, *PARP2*, *CYCB1;1*, *TSO2*, and

Table 1 Clarified functions and binding proteins of NMCPs

Name	Organism	Functions	Possible binding proteins
CRWN1	*Arabidopsis thaliana*	Nuclear morphology Chromatin organization Gene expression DNA repair body formation	PWO1 (Mikulski et al. 2019) NTL9 and SNI1 (Guo et al. 2017) SUN1/2 (Graumann 2014) KAKU4 (Goto et al. 2014)
CRWN2	*A. thaliana*	Nuclear morphology Chromatin organization Gene expression DNA repair	–
CRWN3	*A. thaliana*	Nuclear morphology Chromatin organization Gene expression Protein degradation body formation DNA repair	–
CRWN4	*A. thaliana*	Nuclear morphology Chromatin organization Gene expression DNA repair body formation	PWO1 (Mikulski et al. 2019) KAKU4 (Goto et al. 2014)
DcNMCP1	*Daucus carota*	–	MYB3, BIM1, SINAT1, ARP7 (Mochizuki et al. 2017)

RAD51 were upregulated in the *crwn* mutants after the MMS treatment compared with those in the WT plants. These results suggest that the CRWN proteins are related to DNA damage response and/or repair. Hirakawa and Matsunaga 2019) elucidated the mechanisms of CRWN-mediated DNA damage response using imaging techniques. They visualized DNA-repair events with RAD54-EYFP, which accumulates in DNA damage sites forming a fluorescent focus and repairing the damage via the homologous recombination pathway. They found that the RAD54-EYFP foci attached to the nuclear periphery after gamma ray irradiation in the WT plants, whereas the foci were detached from nuclear periphery in the *crwn1crwn4* double mutants. Additionally, they also evaluated a high MMS sensitivity of the *crwn1crwn4* double mutants compared with the WT plants. Overall, the CRWN proteins may tether the DNA damage sites to the nuclear periphery and form a repair body, which may contribute to the effective repair of DNA damage.

Conclusions

In this review, I highlighted nuclear events related to CRWNs (see Table 1). CRWNs function as scaffold proteins in the nuclear periphery, regulating nuclear morphology, chromatin distribution and structure, and affecting transcriptional regulation. Specifically, in Arabidopsis, CRWNs bind to heterochromatin and silenced genes, and physically interact with PRC2, suggesting that the inactive regions of the genome are specifically tethered to the nuclear periphery, as observed in animal cells (Hu et al. 2019; Mikulski et al. 2019). Therefore, NMCPs most likely contribute to the maintenance of an inactive chromatin. However, because some studies reported that the nuclear periphery enhances gene expression in plant cells (Feng et al. 2014; Smith et al. 2015), the nuclear periphery may be a chimeric region containing both active and inactive chromatins. Although it has been revealed that NMCPs are multi-functional proteins in the plant nucleus, several questions main; for instance, how NMCPs regulate nuclear morphology, what proteins connect NMCPs with chromatin, how NMCPs recognize DNA damage sites, and how these sites move to the periphery.

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