

In Silico Identification of Potentially Functional Conserved Motifs in Two Components of the 5' to 3' mRNA Decay Pathway of Plants

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Abstract

Pathways of mRNA degradation influence the remodeling of the transcriptomes. The 5' to 3' mRNA decay pathway consist on three subsequently acting mechanisms: deadenylation, decapping and 5' to 3' exonucleolytic decay. Specific physical interactions between the components of this pathway are essential to generate functional complexes that properly destroy unnecessary transcripts in eukaryotes. Most of the information about the structure of the components of this pathway comes from studies in yeast and animals, but little is known about the conservation of protein-protein interaction domains and motifs in the homolog decay factors of plants. The decapping subunit DCP1 and the 5' to 3' exoribonuclease XRN4 are critical components of this pathway. To get an overview of the structure and conservation of these proteins in plants, the sequences of the corresponding homologs of angiosperms, bryophytes and the gymnosperm *Picea abies* were retrieved, aligned and subjected to search of conserved sequences. Comparisons revealed conserved domains and structural motifs in plants and metazoans, which implies shared physical interactions that might arise during the early evolution of eukaryotes, for example, the trimerization of DCP1 and the recognition of proline-rich sequences (PRS) by β -sheets of the Dcp1/EVH1-like domain. However, the *in silico* analysis revealed that plant decay factors contain specific motifs, such as the PRS in DCP1 itself, that could have emerged to confer specialized functions in plants. Furthermore, this analysis revealed that XRN4 homologs of angiosperms acquired a sequence reminiscent to the homolog 5' to 3' exoribonuclease of fruit fly that allow the interaction with DCP1.

Keywords: mRNA decay; Decapping; 5'-Exoribonuclease; Protein-protein interactions; Motif

Introduction

Transcript abundance is the result of the balance between the transcriptional activity mediated by transcription factors that recognize *cis*-regulatory elements in the promoters, and the rate and pathways of mRNA decay. Such balance is necessary to confer appropriate gene expression in different tissues or under specific environmental conditions such as stress or the incidence of another living being. Several mRNA decay pathways have been described, each pathway is mechanistically distinct and specialized in regulating de decay of specific transcripts [1,2]. The 5' to 3' mRNA degradation is a major decay pathway that starts with the removal of the poly(A)-tail mediated by deadenylases. Poly(A)-binding proteins (PABP) are necessary to promote translation initiation, thus, inhibition of translation caused by deadenylase activity is a pre-requisite step of mRNA degradation [3].

Decapping inhibits translational initiation and expose to mRNA to 5' to 3' exonucleolytic decay. In eukaryotic organisms, the decapping reaction is catalyzed by the regulatory subunit DCP2 [4]. DCP2 is a flexible enzyme that transits between open-to-closed conformation, being the closed conformation the active one [5]. In the fission yeast *Schizosaccharomyces pombe*, the binding of the regulatory subunit Dcp1p stabilizes the closed conformation of Dcp2p and increases the affinity to the substrates [6]. In spite of performed experiments, direct interaction between DCP1 and DCP2 in the model plant *Arabidopsis thaliana* has not been detectable, another proteins might bridge the physical proximity *in vivo* [7]. The closed/active conformation of DCP2 is stabilized *in vivo* and *in vitro* by enhancers of decapping, which are structurally diverse and can bind to DCP1, DCP2 or both. The proteins Edc1p, Edc2p, Edc3p, Scd6p, Dhh1p, Pat1p and the Lsm1-7 complex are well-known enhancers of decapping in the baker's yeast *Saccharomyces cerevisiae* that also can function as inhibitors of translation, which strengthen the observation that inhibition of translation and 5' to 3' decay are interconnected processes [8].

In spite of the wide distributions of these components, there are lineage-specific enhancers of decapping, for example EDC4/Ge-1/VCS, a scaffolding protein that promotes DCP1-DCP2 interaction, is conserved in metazoans and *Arabidopsis*, but lacking in baker's yeast [9], on the other hand, the enhancer of decapping PNRC2 is specific of humans and interacts with DCP1 [10]. After decapping, the accessible 5' phosphate makes the mRNAs prone to be degraded in the 5' to 3' direction, which is catalyzed by the 5' to 3' exoribonucleases (XRN). In mammals, this enzyme is known as XRN1 [11], PACMAN (PCM) or XRN1 in the fruit fly *Drosophila melanogaster* [12] and XRN4 in *Arabidopsis* (AtXRN4) [13].

Components of 5' to 3' decay, proteins related to posttranscriptional mechanisms and the translationally repressed mRNA substrates are aggregated into microscopically detectable cytoplasmic particles referred to as RNA Processing bodies (P bodies, PB) [14,15]. The protein composition of PB is highly conserved among organisms, and their assembly depends on multiple interactions between the decay factors, accessory proteins and the mRNAs loaded within. The mRNAs interacting with the 5' to 3' mRNA decay or bounded into PB cannot be translated, but eventually can be re-incorporated in ribosomes to undergo translation, or a molecular switch might promote the degradation. A set of protein-protein interactions

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between decapping subunits and 5' to 3' Exoribonucleases might be critical to mediate the proper degradation of transcripts that are no longer required. Several experimental evidences illustrate how these interactions occur in yeast and metazoans [8,14]. The Arabidopsis mutants *dcp1* and *dcp2* are seedling lethal, which evidences the indispensable role of decapping to plant development [16]. However, little is known about the molecular process that links the decapping to the 5' to 3' exonucleolytic degradation in plants, which might require physical interaction between decapping components and homologs of XRN4. The availability of fully sequenced genomes allows us to identify components of the 5' to 3' mRNA decay in angiosperms and bryophytes. Here, an *in silico* analysis of homologs of DCP1 and XRN4 suggests a number of domains and motifs potentially involved in protein-protein interactions are conserved in plants and metazoans, but also unique features characteristic of plants that might have a specific biological role.

Materials and Methods

Protein sequence retrieval

In order to avoid bias, one representative specie from twenty-seven different families of angiosperm were selected, as well as the early diverging angiosperm *Amborella trichopoda* three bryophytes from different families (*Pyscomitrella patens*, *Marchantia polymorpha* and *Selaginella moellendorffii*) and the gymnosperm *Picea abies*. Experimentally confirmed components of 5' to 3' mRNA decay of human, fruit fly, baker's yeast and *Arabidopsis thaliana* were used as query to obtain the corresponding homologs of the plants enlisted above by performing BLASTP at Uniprot [17], Phytozome v12 [18] and GreenPhylDB v4 [19] and NCBI. The closest related to the query was picked to further analysis. The list of entry numbers of the proteins is included in the Supplementary information.

Identification and analysis of conserved domains and motifs

Identification of domains protein sequences were confirmed by using the online tool InterProScan, available at the Interpro. Conserved motifs were detected after MUSCLE sequence alignment performed in MEGA6 [20] and confirmed by searches performed in MEME (Multiple Em for motif elicitation) [21]. Alignments and consensus sequences were created in BioEdit 7.2.5 and Weblogo [22], respectively.

Generation of 3D models

Ab initio modeling of the putative trimerization domains of *Arabidopsis thaliana* and *Marchantia polymorpha* were performed in QUARK [23]. Both predicted models and the human TD (2WX3) were visualized, refined and merged in PyMOL v1.7.4.

Results and Discussion

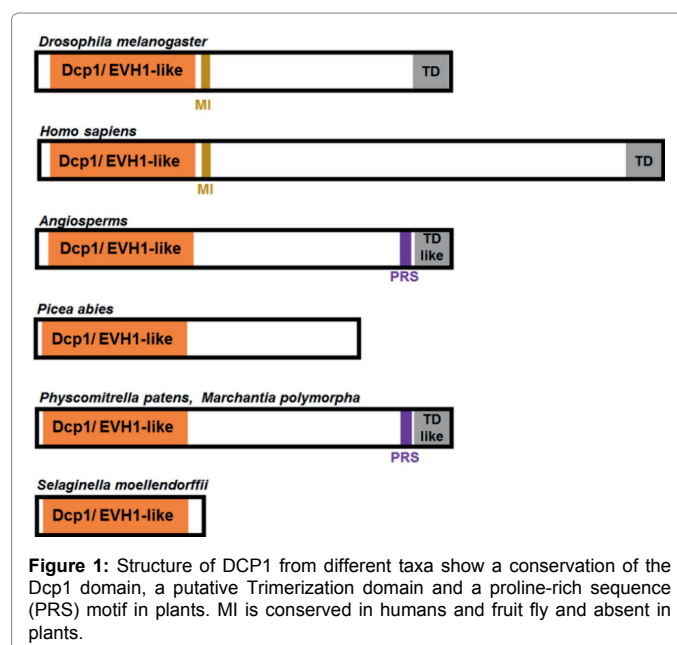
Structure of plant DCP1 proteins reveals potential interaction partners

DCP1 interacts with DCP2 through the Dcp1 domain (IPR010334), also known as Eva/Vasp homology 1-like (EVH1-like) domain at the N-terminus [24], it is necessary to maintain decapping activity, which is a member of the Pleckstrin Homology (PH) domain-like superfamily (IPR011993). The Dcp1/EVH1-like domain of DCP1 is composed by two α -helices flanking seven β -sheets. The first helix is required to interact with DCP2, and the NR-loop, located between the third and fourth β -sheets, increases decapping activity *in vitro*, but does not contribute in the physical interaction between DCP1 and DCP2 [25]. The peculiar array of the β -sheets of the PH variants allows the

recognition of distinct Proline-rich sequences (PRS) [26]. It is worth to mention that PRS are lacking in DCP2, therefore, Dcp1 domain recognizes PRS found in enhancers of decapping such as Edc1p in fission yeast [6] and PNRC2 in humans [10]. In fruit fly, DCP1 interacts with a PRS of the C-terminus of XRN1/PCM, this sequence is known as DCP1-binding motif (DBM) [27]. In order to elucidate the structure of DCP1 in plants, DCP1 homologs of representative plant families, mostly angiosperms, were retrieved from UNIPROT, Phytozome, GreenPhylDB and Genbank. Dicot plants present one single gene of DCP1, but monocots have two, three or four copies of genes with similar architecture that might be products duplication events. In the case of monocots, the gene that presented more similarity with the Arabidopsis DCP1 was selected.

The PH domain-like was *in silico* identified in the N-terminus of the homologs of DCP1 analyzed here, as well as other potentially functional sequences (Figure 1). The region encompassing the β -sheets of Dcp1 domain is highly conserved among plants and animals (Figure 2), including the amino acids required to the binding of PRS, suggesting that β -sheets might confer a functional structure that has been preserved during evolution as a way to recruit specific PRS-containing proteins to enhance the decapping reaction, or to connect decapping with the exonucleolytic decay. So far, PRS sequences that recognize plant DCP1 proteins are not reported, but the high conservation of the residues of β -sheets suggests PRS-binding activity.

Surprisingly, a highly conserved and PRS is located at the C-terminus of DCP1 proteins from angiosperms, the basal angiosperm *Amborella trichopoda*, and the bryophytes *Pyscomitrella patens* and *Marchantia polymorpha* (Figure 3). The β -sheets of (PH) domain-like superfamily proteins form a cleft that recognizes PRS of four residues [26]. The PRS identified in plant homologs of DCP1 is longer compared to the PRS harbored in decay factors of yeast and animals, but it might be relevant to demonstrate whether a portion of this novel PRS is able to interact *in cis* or *trans* with the β -sheets of DCP1. The conservation of this sequence in angiosperms and bryophytes suggests that DCP1 of plants might have specific partners. In Arabidopsis, movement of PB through actin cytoskeleton depends on the interaction of AtDCP1



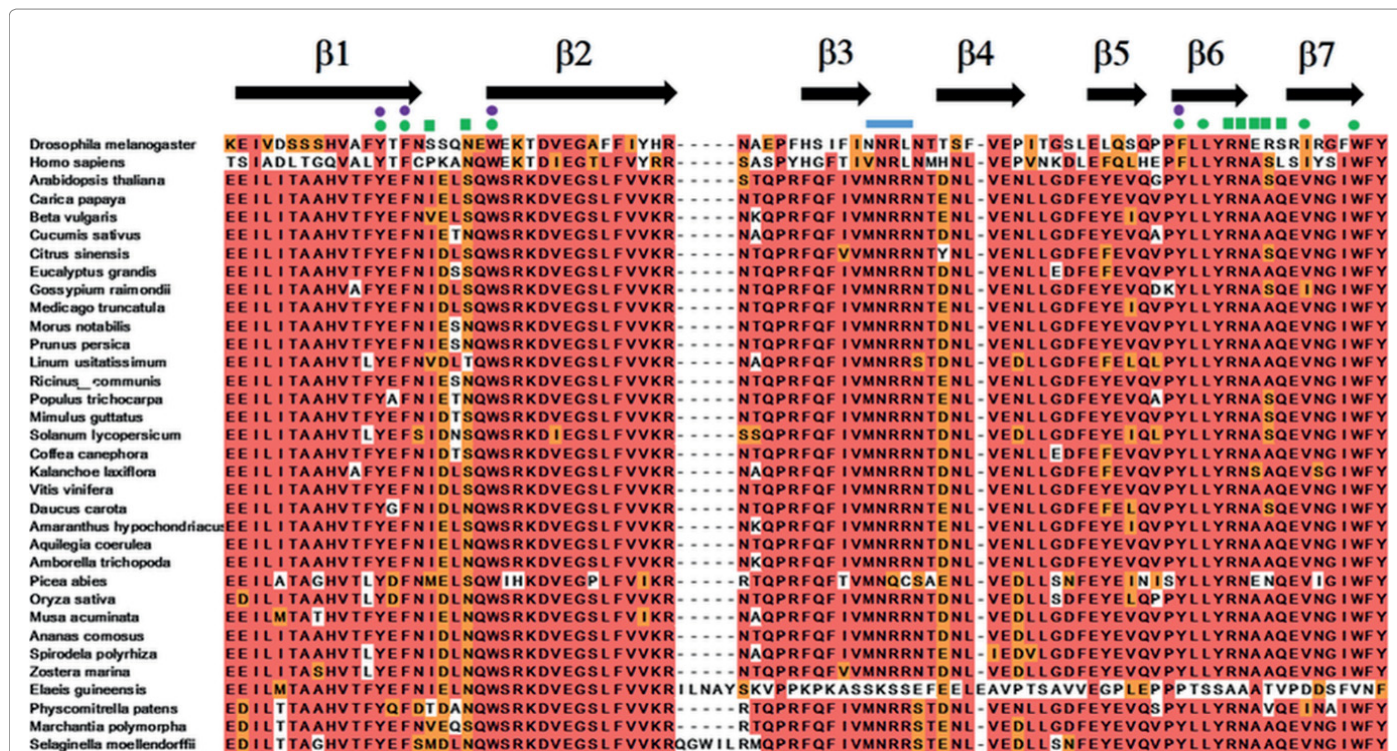


Figure 2: Alignment of the Dcp1/EVH1-like domain fragment that encompass β -sheets of selected DCP1 proteins. Hydrophobic and hydrophilic residues of dmdcp1 involved in binding of DBM of PCM/XRN1 are marked as green circles and green squares, respectively. Residues of hsdcp1 involved in binding of the PRS of PNRC2 are marked with purple circles. Residues below blue line encompass the NR-loop. Positions of each β -sheet are represented by the arrow.

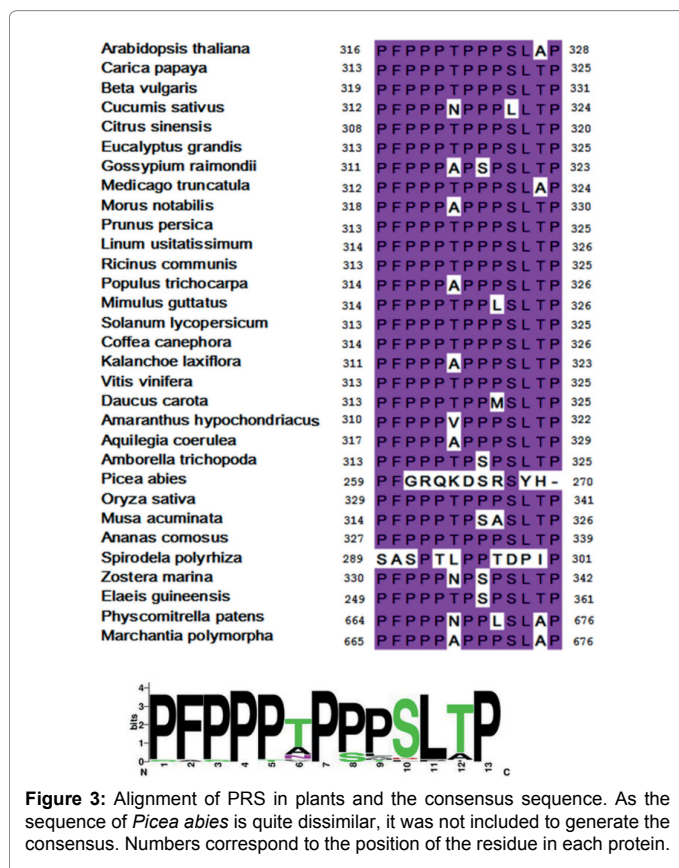


Figure 3: Alignment of PRS in plants and the consensus sequence. As the sequence of *Picea abies* is quite dissimilar, it was not included to generate the consensus. Numbers correspond to the position of the residue in each protein.

with plant-specific class XI myosins [28]. Furthermore, the association between PB and actin has been reported in tobacco [29]. In contrast to plants, the movement of PB in animals is dependent on the cap-binding protein eIF4E that interacts with the Myosin Va [30]. ODCP1 of plants could acquire features that diversify physical interactions and the underlying molecular functions, for example, the movement through actin cytoskeleton. AtDCP1 also interacts with SPIRRING (SPI), which is required to the assembly of the PB [31]. The residues of AtDCP1 required to interact with class XI myosins and SPI are unknown, but interestingly, SPI harbors a PH domain that might recognize the conserved PRS found in AtDCP1, but other domains of SPI such as WD40 might be also considered as necessary to set this interaction.

The Motif I (MI) or short helical leucine-rich motif (HLM) is adjacent to the PH domain-like of DCP1 of metazoans, it is absent in yeast, and was not identified in the vascular plants and bryophytes presented in this research. MI is required to recruit EDC3 and DDX6 to increase decapping activity [32]. The conservation of this lineage-specific motif might be favored by the selection pressure of the conserved interactors Edc3 and DDX6/Me31B, which are apparently absent in plants.

A conserved TD-like sequence suggests trimerization of plant DCP1 proteins

At one point, a single molecule of DCP1 undergoes a limited number of protein-protein interactions due to physical and spatial constraints. Interactors of DCP1 might be exchanged according to the requirements of the cell or the sort of mRNAs that have to be regulated. In metazoans, DCP1 forms trimers *in vivo* [32]. Trimerization increases the surface of recruitment of enhancers of decapping and increases the

size of PB. AtDCP1 immunoprecipitates with itself when is transiently expressed in *Nicotiana benthamiana* [7], but the number of AtDCP1 molecules that can simultaneously interact is unknown.

Trimerization of DCP1 is mediated by the Trimerization Domain (IPR031953, TD) located at the C-terminal of the protein. TD is an L-shaped domain composed by two hydrophobic α -helices separated by a kink of an aspartate residue [32]. MUSCLE alignments revealed that TD is conserved in the majority of the plant proteins analyzed. The exceptions are the DCP1 of *Spridodela polyrhiza* and *Picea abies* that present a very divergent C-terminus sequence, and the shorter polypeptide DCP1 of *Selaginella moellendorffii* (Figure 1). The structure-based alignment of TD from metazoans and the putative TD-like sequences detected in plants reveals conserved critical residues of the hydrophobic α -helices as well as charged residues to form hydrogen bonds (Figure 4A). The residue D558 of human DCP1 (HsDCP1) and D345 of the fruit fly DCP1 (DmDCP1) form a kink that separates the two α -helices of their respective TD. Such residues or residues with similar charge are detected in the same position of the TD-like sequences of plants. Mutations in hydrophobic residues in the α -helices of the human HsDCP1 decreases decapping activity *in vivo*. The wider surface of the trimer DCP1 conferred by the hydrophobic residues might facilitate the assembly of enhancers of decapping that ensure the closed/active state of DCP2.

The *ab initio* modeling program QUARK was used to predict the tri-dimensional structure of the TD-like sequence of the DCP1 of the angiosperm Arabidopsis and the bryophyte *Marchantia polymorpha*. The predicted model is composed by two helices separated by an aspartate, similar to the experimentally elucidated TD structure of HsDCP1 and DmDCP1, especially the first α -helix (Figure 4B). However, the two residues that separate the aspartate of the kink and the conserved phenylalanine of the second α -helix (D558 and F561 of HsDCP1) are not conserved in plants, where only one residue is intercalated. The stretch of residues from D558 to F561 influence the orientation of the second α -helix of the TD of humans, which forms a right angle formed between the two α -helices. The slight difference in the corresponding stretch of the TD-like sequence of plant DCP1 analyzed here might compromise the formation of the right angle. The predicted models exhibit the aspartate that interferes the progression of the first α -helix, and an acute angle between the two α -helices. The points out to potential trimerization of DCP1 as a conserved attribute of the 5' to 3' mRNA decay pathway of animals and plants.

Plant homologs of atxrn4 share unique motifs

As decapping and 5' to 3' exonucleolytic mRNA decay are coupled processes, physical proximity between DCP1, DCP2, enhancers of decapping and the 5' to 3' exoribonucleases might be necessary to avoid accumulation of unlikely translatable decapped mRNAs and secure an effective mRNA degradation. Therefore, 5' to 3' exoribonucleases have

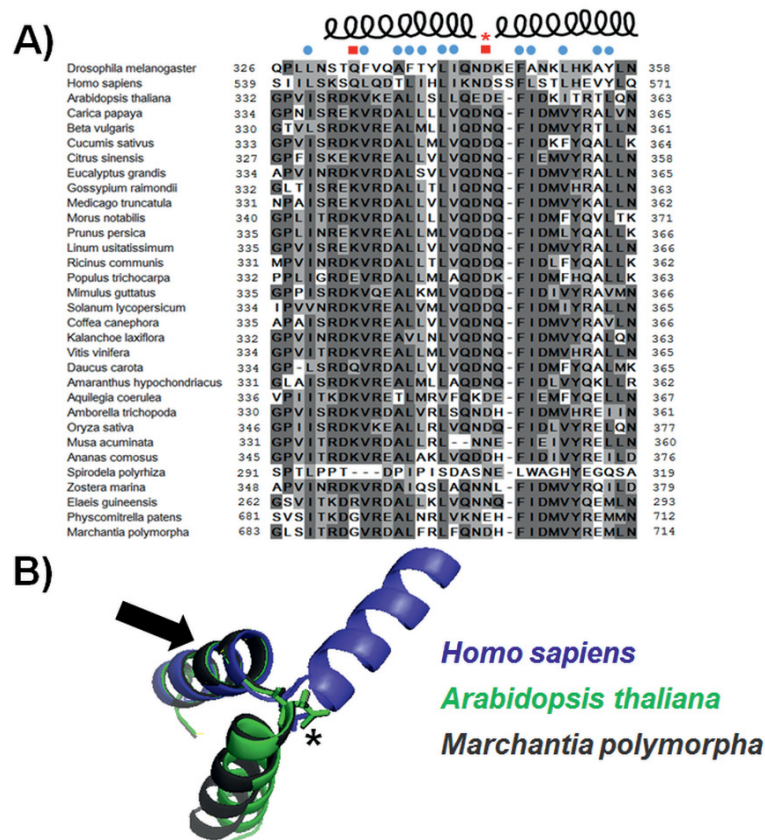


Figure 4: Structure-based alignment of the putative TD reveals that most of the plant DCP1 might form trimers. Positions of the residues inside the proteins are indicated by the numbers. **A)** Amino acids below blue circles form the hydrophobic core to promote trimerization in human DCP1. Amino acids below red squares mediate hydrogen bonds both in human DCP1. Asterisk denotes the aspartate of the kink. **B)** *Ab initio* modeling of TD from Arabidopsis and *Marchantia polymorpha* reveals a similar structure of the human TD although the second helices are distinctly oriented. The arrow points out the first helix and the asterisk indicates the aspartate of the kink.

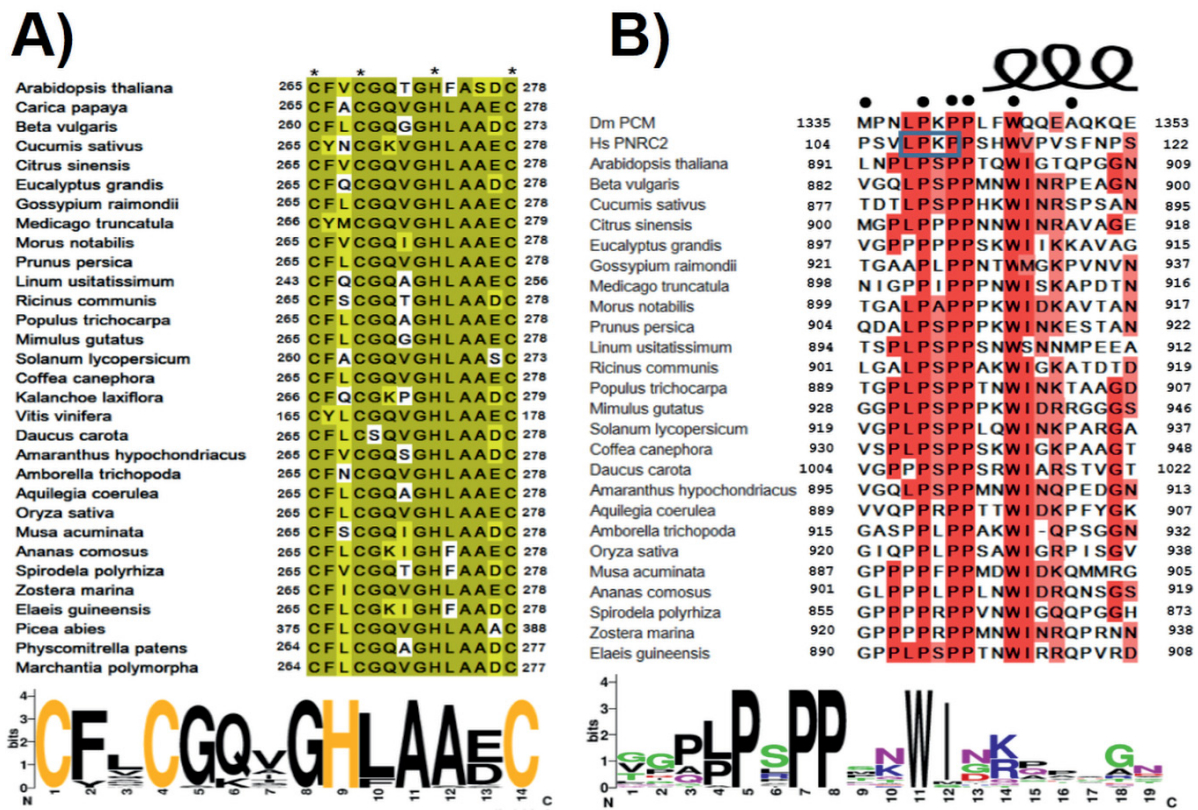


Figure 6: Motifs and their consensus in XRN4 homologs. Numbers indicate the position of the residues in the protein. (A) A zinc knuckle (ZnK) is highly conserved. Hydrophobic residues prevail into this motif. (B) A DBM-like sequences is specific of angiosperms, black circles indicate the residues of PCM/XRN1 that recognize the β -sheets of Dcp1/EVH1-like domain [27], which are conserved in angiosperms. A motif of PNRC2 was included in the alignment because of its binding activity [10]. The sequence LPKP that directly contacts Dcp1/EVH1-like is marked inside the blue square.

The structure of PCM/XRN1 includes additional domains: PAZ/tudor, KOW, Winged helix, and SH3-like, as well as a glutamine-and-proline rich tract (QP), all of them do not affect the catalysis, but might be required to stabilize the whole protein structure [12]. These domains are not conserved in XRN4 of plants. The assembly between components of decapping and 5' to 3' exoribonucleases might be critical to the progression of mRNA decay. 5' to 3' exoribonuclease must be placed in the nearby of decapping reactions in order to have accessible substrates. In baker's yeast, XRN1p interacts with the inhibitor of translation Pat1p and the Lsm1-7 complex, involved in tethering mRNAs to 5' to 3' decay and stimulation of decapping [8]. Although there is a biochemical link between XRN1p, Pat1p and the Lsm1-7 complex, motifs involved in the interaction are unknown. In humans, XRN1 stays close to the decapping complex due to the interaction with the scaffold protein EDC4, which also interacts with DCP1 and DCP2. The interaction between the human XRN1 and EDC4 depends on the EDC4-binding motif (EBM) (Figure 4A) located at the C terminus, that recognizes the α -helical domain of EDC4 [25]. EBM is specific of human XRN1 and it is not conserved in fruit fly, baker's yeast and plants.

In fruit fly, PCM/XRN1 interacts with DmDCP1 though the DCP1-binding motif (DBM), a PRS located at the C terminus [27]. Proline and a tryptophan residues of DBM are essential to bind the cleft formed by the β -sheets of the Dcp1/EVH1-like. Residues of the second half of DBM form a α -helix. The PRS of the human PNRC2 has a similar sequence and structure. The sequence LPKP in the middle of the PRS of PNRC2 makes multiple hydrophobic interactions and Van

der Waals contacts with Dcp1/EVH1-like, and a tryptophan residue is also important [10].

In spite of the divergence between the sequences of PCM/XRN1 and plant XRN4, a search of conserved sequences at the C terminus of plant XRN4 by MEME [21] found a consensus motif (DBM-like) reminiscent to the DBM and the PRS of PNRC2 (Figure 6B). The conservation of the prolines and the tryptophan is remarkable. DBM-like is characteristic of the angiosperms included in this research, except *Carica papaya* and *Vitis vinifera*, re-annotations and the release of further version of their genomes will be necessary to confirm or reject this finding. Due to DBM-like is not detected in AtXRN3 -involved in distinct pathways- and XRN4 homologs of bryophytes and *Picea abies*, this novel motif seems to be a specific feature of the XRN4 of angiosperms and an evidence of orthology. Furthermore, DBM-like was identified in the early divergent flowering plant *Amborella trichopoda*, suggesting the motif arose before diversification of angiosperms. As DBM-like is not detected in XRN3 and other nuclear 5' to 3' exoribonucleases (data not shown), its potential functionality might contribute to the specialization to this enzymes in the cytoplasmic 5' to 3' mRNA decay that requires a biochemical link with decapping. *In vivo* interaction between the Arabidopsis DCP1 and XRN4 was previously reported [38], but the residues involved in the interaction were not identified. Therefore, a potential association DCP1-XRN4 in angiosperms might occur through the β -sheets of the Dcp1 domain and the DBM-like, which is similar to the interaction between DmDCP1-PCM/XRN1 and HsDCP1-PNRC2.

Conclusions

The β -sheets of the Dcp1/EHV1 domain of DCP1 are highly conserved in plants and quite similar to the corresponding sequences of metazoans. Consequently, PRS have to be the ligands of this domain. DCP1 proteins of angiosperms and the bryophytes *Physcomitrella patens* and *Marchantia polymorpha* present an extended PRS that might recognize Dcp1/EHV1 domain or similar folds, it might contribute to unique functions. A TD-like sequence in angiosperms, possibly composed by two hydrophobic helices might mediate trimerization of DCP1 in angiosperms, *Physcomitrella patens* and *Marchantia polymorpha*, possibly to increase decapping activity in these plants. A ZnK is a common feature of plant 5' to 3' exoribonucleases that might influence enzymatic activity. A DBM-like motif is characteristic of XRN4 of angiosperms, and, as in the case of the fruit fly, it might confer interaction with DCP1, which might guarantee the synchrony and increase the efficiency of the 5' to 3' mRNA decay pathway.

Conflict of Interest

The author claims no conflict of interest. This research has not been submitted to any other journal.

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