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RESEARCH PAPER

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Plant ribosomes as a score to fathom the melody of 2'-O-methylation across evolution

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ABSTRACT

2'-O-ribose methylation (2'-O-Me) is one of the most common RNA modifications detected in ribosomal RNAs (rRNA) from bacteria to eukaryotic cells. 2'-O-Me favours a specific RNA conformation and protects RNA from hydrolysis. Moreover, rRNA 2'-O-Me might stabilize its interactions with messenger RNA (mRNA), transfer RNA (tRNA) or proteins. The extent of rRNA 2'-O-Me fluctuates between species from 3–4 sites in bacteria to tens of sites in archaea, yeast, algae, plants and human. Depending on the organism as well as the rRNA targeting site and position, the 2'-O-Me reaction can be carried out by several site-specific RNA methyltransferases (RMTase) or by a single RMTase associated to specific RNA guides. Here, we review current progresses in rRNA 2'-O-Me (sites/Nm and RMTases) in plants and compare the results with molecular clues from unicellular (bacteria, archaea, algae and yeast) as well as multicellular (human and plants) organisms.

2'-O-ribose methylation and its biochemical consequences

In all domains of life 2'-O-Me has emerged as an abundant and ubiquitous RNA modification. Activity of RMTase results in 2'-O-Me by catalysis of a methyl group transfer from S-adenosylmethionine (SAM) to the 2' hydroxyl group of a ribose residue, resulting in а methoxy group and S-adenosylhomocysteine (SAH) (Figure 1A). This modification is present in diverse RNAs, including rRNA, tRNA, mRNA and other small regulatory RNA such as: small interference RNA (siRNA) and microRNA (miRNA) (reviewed in[1]). Each of the four nucleotides can be 2'-O-methylated (N to Nm, where N is G, A, U or C) resulting in structural changes of the modified RNA. On the one hand, 2'-O-Me favours the A'-form RNA helix conformation, instead of the Z-form RNA, a left-handed conformation for the RNA double helix, favoured by a sequence composed of purine/pyrimidine repeats and especially CG-repeats [2]. Furthermore, we 2'-O-Me stabilizes alternative secondary structures in which the Nm-modified nucleotides are paired [3]. On the other hand, 2'-O-Me might stabilize rRNA-mRNA, rRNA-tRNA or rRNA-protein interactions [2,4]. Moreover, resistance of 2'-Omethylated RNA nucleotides to alkaline and enzymatic hydrolysis has allowed its detection and localization on various RNAs via high-throughput methods (reviewed in [5]).

Molecular mechanisms of C/D box snoRNP methylation

In yeast, archaea, plants and humans 2'-O-Me of rRNA, some snRNA and snoRNA, are guided by small nucleolar RNAs[84]

(snoRNAs), called C/D-box snoRNAs (C/D snoRNAs) (Figure 1B). The C box (5'RUGAUGA3') and D box (5'CUGA3') of C/D snoRNAs are short consensus sequences that localize a few nucleotides away from the 5'- and 3'-ends, respectively. In the central part, the C/D snoRNA might contain also less conserved C' and D' motifs. One or two sequences localize upstream of the D or D' box. They are about 10–21 nucleotides long and complementary to the rRNA sequence overlapping the site of 2'-O-Me. The rRNA nucleotide to be methylated is located precisely at the fifth position upstream from the D or D' box (Figure 1B) [6,7].

To guide methylation, the C/D snoRNAs interact with proteins to form small nucleolar ribonucleoprotein (snoRNP) complexes, including the SAM-binding domain containing methyltransferase Nop1/Nop1p/fibrillarin (in archaea/yeast/in mammals), Nop5/Nop56p/NOP56, Nop58p/ NOP58 and L7Ae/Snu13/L7Ae ([1,7–9] and Figure 1B).

In contrast, the genome of *Arabidopsis thaliana* encodes two fibrillarin proteins named FIB1 and FIB2, two NOP56 and NOP58 and four potential L7Ae genes [10–12]. The methyltransferase fibrillarin consists of an N-terminal GAR domain involved in nuclear signalling, a spacer region and a methyltransferase domain. The latter contains an RNA binding domain for guide RNA binding and methylation, while the C-terminal α -helix region interacts with NOP56/58. In Arabidopsis, the two fibrillarin proteins have similar structures in the methyltransferase domain [13]. The overlay of the structures indicates that the main structural difference results from an angle changed for the exposure of the GAR domain. Interestingly, Arabidopsis FIB1 and/or FIB2 can interact not

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Figure 1. rRNA 2'-O-methylation and phylogenetic conservation of RMTase. a) Methyl transfer reaction by RMTase from S-adenosylmethionine (SAM/AdoMet) to nucleophiles results in 2'-O-methylated RNA nucleotides and S-adenosylhomocysteine (SAH). b) Schematic representation of the mammalian C/D snoRNP complex with fibrillarin (FIB, green ellipse), NOP56 (red ellipse), NOP58 (Orange ellipse), L7Ae (blue ellipse) and C/D snoRNA (black line, conserved C/D and less conserved C'/D' boxes in black rectangles) interacting with the to be methylated site (yellow star) on the rRNA (red line). c) Top, Phylogenetic tree as a representation of the distribution of RMTases as stand-alone enzymes (blue) or forming C/D snoRNP complexes (red) in various species indicated by their latin names and a schematic representation. Only RMTases involved in 2'-O-Me are indicated. Bottom, representation of an evolutionary shift in the dominance of stand-alone to snoRNP complexes from bacteria to plants. d) Arrow chart shows the number of Nm conserved in Arabidopsis [14,21], tomato [59] and tobacco [54] plants and the number of Nm equivalent in other species: human [1,79], yeast [80], algae [34], archaea [81] and bacteria [29]

only with hundreds of C/D snoRNAs [14] but also with other small and long non-coding RNA (ncRNA), including viral, small nuclear and small interfering RNA [15,16]. In addition to its RNA 2'-O-Me activity, Arabidopsis FIB2 can also perform methylation of histone H2A [17], similar to human fibrillarin [18]

Spotlights on RMTases: from stand-alone enzyme to RNA guided methylation

In *E. coli*, 2'-O-Me of 16S and 23S rRNA are catalysed by sitespecific methyltransferases. Thus, the single methyltransferases RlmB, RlmM and RlmE (RlmJ) modify the ribose of G2251, C2498 and U2552 in the 23S rRNA, respectively

(Figure 1C and Table 1), whereas two separate methyltransferases, RsmI and RsmH, are responsible for 2'-O-Me of 16S-C1402. Interestingly, a homolog of E. coli RlmE (RlmJ) was also found in the archaea Haloarcula volcanii and likely catalyses 2'-O-Me of U2587 in Haloarcula marismortui. Ribose methylation of its equivalent site in the mitochondrial 21S-Um2791 of S. cerevisiae is also performed by a site-specific RMTase Mrm2 [19]. Its counterpart in the cytoplasmic 28S-Um2921 is implemented by the site-specific RMTase Spb1 and/or by a snoRNP associated with the guide RNA SnR52 (Lapevre and Purushothaman 2004). Spb1 is also responsible for the methylation of the neighbouring 28S-Gm2922 site. The methylation of the equivalent E. coli 23S-U2552 in human is performed by FTSJ3 [1,20]. The Arabidopsis 2'-O-Me sites 18S-Cm1645 and 25S-Gm2620, are the equivalents of E. coli 16S-Cm1402 and 23S-Gm2251, respectively, and 2'-O-Me reactions at these positions are guided and performed by C/D snoRNP complexes (Figures 1C and 2 as well as Table 1). Unlike those sites, no snoRNA guide has been reported for the Arabidopsis 25S-Um2922 (the equivalent of E. coli Um2552) [14,21].

Like in yeast and human cells, most of the 118 rRNA Nm sites detected in Arabidopsis have corresponding C/D snoRNAs [14]. As a result of extensive gene duplications the Arabidopsis genome encodes 230 C/D snoRNAs with up to four of them targeting the same rRNA Nm [22–24].

Despite this plethora of C/D snoRNAs nearly 10% of the identified 2'-O-Me sites in Arabidopsis seem to lack a corresponding C/D snoRNA guide. Among them, five 2'-O-Me sites (Am812, Am1188 and Um1554 in the 18S and Um378 and Am2561 in the 25S) have been reported specifically in 21-day-old plants [14]. In contrast, the 25S-Um2922 (Um2552 in *E. coli*) and -Gm2923 are mapped in both 9- and 21-day-old plants, whereas the 25S 2'-O-Me sites Um676 is mapped only in 9-day-old plants [14,21]. Their lack of corresponding C/D snoRNAs hints towards an alternative guide mechanism or a stand-alone enzyme for these rRNA sites.

The Arabidopsis genome encodes three proteins without yet proven 2'-O-Me activity, but which are phylogenetically related to yeast Trm7p, Spb1p and Mrm2p. Noteworthy, the yeast Trm7p can 2'-O-methylate tRNA [19,25]. The determination of methylation at Nm sites without corresponding C/D snoRNA in Arabidopsis (Table 1) requires further investigation.

Evolution of rRNA 2'-O-Me from bacteria to plants

Ribosomal RNA is the keystone of ribosome assembly and activity (reviewed in [26–30]). Among others, its biophysical properties are impacted by 2'-O-Me, which seems to be highly conserved in all kingdoms of life. In *E. coli*, 2'-O-Me can be found in four highly conserved nucleotides: in the 16S rRNA at position C1402 as well as in the 23S rRNA at positions G2251, C2498 and U2552 (Table 1). The 16S-Cm1402 participates in P-site (for peptidyl-tRNA) formation and seems to improve the precision of start codon selection, whereas the three Nm in the 23S are located in the Peptidyl Transfer Centre (PTC). Within the PTC, Gm2251 stays in close contact with the CCA-end of the P-site bound tRNA. U2552 is one of

Table 1. Rmtas	e and/or C/D snoRNP invo	olved in methylat	ion of conserve	ed rRNA sites in	bacteria (E. coli), Archaea	ı (H. marismortul), yeast (S.	<i>cerevisiae</i>), mam	mals (H. sapiens) and plants (A. thaliana.).
Bacteria (E. col	()	Archaea (H. n	narismortui)	Yeast	(S. cerevisiae)	Mammals (H.	sapiens)		Arabidopsis thaliana
2'-O-Me	RMTase	2'-O-Me	RMTase	2'-O-Me	RMTase	2'-O-Me	RMTase	2'-O-Me	RMT ase/snoRNA
16S-Cm1402	Rsml (YraL) and RsmH			18S-Cm1639		18S-Cm1703		18S-Cm1645	FIB1 or FIB2/At1gCDbox192 (AtU43)
23S-Gm2251	RImB (YfjH)	23S-Gm1950	aFIB+ sRNA	28S-Gm2619		28S-Gm4196		25S-Gm2620	FIB1 or FIB2/At1gCDbox25.2; At1gCDbox25.2 (AtU3/AtsnoR35)
23S-Cm2498	RImM (YgfE)								
23S-Um2552	RImE (RImJ or FtsJ)	23S-Um2587	RImE	28S-Um2921	Spb1, SnR52-snoRNP	28S-Um4498	FTSJ3	25S-Um2922	At3g19130 and At4g19610/nd
		23S-Gm2588	RImE?	28S-Gm2922	Spb1	28S-Gm4499	FTSJ3	25S-Gm2923	At3g19130 and At4g19610/nd
nd = not detec	ted snoRNA. See text for I	references.							

the conserved nucleotides in the A-site (for aminoacyl-tRNA) and interacts with incoming aminoacyl-tRNA (reviewed in [29]). In the archaea *H. marismortui*, all three detected rRNA Nm sites are located in the 23S rRNA (Table 1): at position G1950 (23S-Gm2251 in *E. coli*) as well as at the two neighbouring positions U2587 (23S-Um2552 in *E. coli*) and G2588 [31]. In archaea, the increased number of C/D snoRNAs was proposed to correlate with the increased growth temperature, which would necessitate 2'-O-methylation for the stabilization of rRNA folding [32].

There is clear evidence supporting the archaeal origin of eukaryotes. Archaea share 26 nucleotides signatures in ribosomal DNA with all living eukaryotes, no matter if protist, plant, fungus or animal [33]. However, 2'-O-Me profiles have evolved and display both conserved and kingdom-specific rRNA sites. In yeast, a total of 55 Nm is detected: 18 Nm in the 18S rRNA and 37 Nm in the 25S rRNA (sites conserved in plants are shown in Table 2 and Figure 2), but none in the 5S and 5.8S rRNA. In contrast, the 5.8S rRNAs of the unicellular marine alga and smallest photosynthetic eukaryote *Ostreococcus tauri* seems to contain two of the 101 Nm (sites conserved in plants are shown in Table 2). This prediction was based on genome annotated sequences of the C/D snoRNAs and locates the other rRNA Nm in the 18S (18 Nm) and 25S (29 Nm) rRNA [34].

Interestingly, higher eukaryotic cells have more Nm than single-cell organisms. For instance, in human and mouse rRNAs, up to 110 Nm sites (41 in 18S rRNA, 67 in the 28S rRNA and 2 in the 5.8S rRNA) have been detected so far ([35,36] and reviewed in [1,37] and Table 2).

In plants, the prediction of hundreds of potential rRNA 2'-O-Me sites relied majorly on bioinformatic analyses screening C/D snoRNAs encoding genes for short complementary rRNA sequences. However, only few of them have been experimentally verified in Arabidopsis and rice [12,37,and reviewed in 38,39]. Currently, the development of sequencing-based profiling methods allows the mapping of rRNA 2'-O-Me sites with and without annotated C/D snoRNAs [5,40,41]. Using RiboMethSeq, two independent studies mapped a total of 118 Nm sites in 9- and 21-day-old Arabidopsis plants [14,21]. Compared with RiboMethSeq from human and yeast, 51 rRNA 2'-O-Me sites seem to be Arabidopsis-specific, while a subset of 36 Nm is conserved in both yeast and human; only 5 Nm sites were conserved only in yeast and 28 Nm only in human (Figure 2 and Table 2).

Altogether the number of rRNA sites mapped in Arabidopsis by RiboMethSeq (up to 38 Nm in the 18S, 2 Nm in the 5.8S and up to 77 Nm in the 25S) is much lower compared to the 212 (78 Nm in the 18S, 3 Nm in the 5.8S and 131 Nm in the 25S) sites annotated as methylated or potentially methylated [39]. Whether or not these sites are 2'-O-methylated under specific plant growth conditions, development stages or in response to environmental stress remains to be investigated.

Regulating rRNA Nm during plant growth and development

Expression and assembly of the C/D snoRNP components have been associated with plant development in Arabidopsis.

Knockout of C/D snoRNAs HIDDEN TREASURE 2 (HID2) or SnoR28.1, triggers strong developmental and growth defects, which are even more pronounced for the double mutant [42,43].

Mutant plants for HID2 and SnoR28.1 exhibited pleiotropic developmental defects, including delayed seed germination, retarded root growth, and narrow, pointed leaves at the adult stage, and delayed transition to the reproductive phase was also observed in SnoR28.1 mutant plants. At the molecular level, knockout of SnoR28.1 appears to affect both methylation of the rRNA predicted target site and, to a less extent, pre-rRNA processing, whereas knockout of HID2 only affects pre-rRNA processing [42,43]. Furthermore, gene disruption of NUFIP, a C/D snoRNP assembly factor, inhibits 2'-O-Me at specific rRNA sites and leads to severe developmental phenotypes [44]. For instance nufip plants showed significant growth delay as compared with wild type plants or had premature growth arrest and did not reach the adult state. The *nufip* seedlings had pointed leaf phenotype, phyllotaxy defect, floral defects, reduced fertility or simply no seeds and sterility [44].

Despite that, no major profile changes were observed when comparing 9- or 21-day-old Arabidopsis plants [14,21]. Only a few Nm detected in specific growth or developmental conditions. For instance, the 25S-Am1871 and 25S-Um2954 sites were reported only in 21-day-old plants. All these sites have assigned C/D snoRNAs and, therefore, the methylation dissimilarities could be due to differential C/D snoRNP expression (of C/D snoRNAs or core proteins) or assembly. Similarly, 18S-Um1554 was detected in 21-day-old [14], but not in 9-day-old plants [21], while the 25S-Um676 was detected in 9-day-old plants but not in 21-day-old plants [21]. However, these sites do not have assigned C/D snoRNAs [14] and the methylation dissimilarities could be due to differential expression of a potential stand-alone RMTase. Besides differential expression of C/D snoRNAs and core proteins or stand-alone RMTases; modifications and turnover of proteins and C/D snoRNAs may also control 2'-O-Me activity. In particular, in human N6-methylation of adenine, was shown to disrupt K-turn formation and thus binding of the C/D snoRNP core protein15.5 kD [45]. In addition, snoRNP-associated factors may also affect 2'-O-Me activity (reviewed in [46]).

Ribosome 2'-O-Me

In yeast and animal cells, 2'-O-Me of rRNAs occurs during transcription of 45S rRNA, the precursor of the 18S, 5.8S and 25S rRNAs. The transcribed 45S pre-RNA is then subjected to a number of co-transcriptional or post-transcriptional cleavages and assembly reactions with ribosomal proteins to form 40S and 60S ribosomal particles (reviewed in [10,27,47]). Formation of ribosomes and translation is initiated, when the initiator tRNA carrying methionine (tRNA^{me}) attaches to the 40S ribosomal subunit. The 40S-tRNA^{met} complex interacts with the 5'-end of the mRNA, by recognizing the 5' GTP cap, scans to find the start codon (AUG) and allows binding tRNA^{me}::AUG. Then the 40S-tRNA^{met}::AUG is joined by the 60S ribosome subunit to complete the ribosomal

Table 2. List of 2'-O-methylation sites experimentally mapped in *A. thaliana* [14,21], tomato [59], tobacco [54] plants and human [1,60], yeast [5], algae [34], archaea [62,63] and bacteria [29]. Arabidopsis sites marked with an asterisk indicate Nm sites for which no C/D snoRNA has been identified. np = non-mapped sites in *A. thaliana*, tomato, tobacco. For human, yeast, algae and archaea only Nm sites conserved in plants are listed.

rRNA	A. thaliana	Tomato (S. lycopersicum)	Tobacco (N. tabacum)	Human (H. sapiens)	Yeast (S. cerevisiae)	Algae (O. tauri)	Archaea (P. abyssi)	Bacteria <i>(E. coli)</i>
18S	Am28	Am28	Am28	Am27	Am28	Am28		
185	Cm38	Cm38	Cm38	Um 121		Cm38		
185	Uff123	0m123 Cm140	0m123 Cm140	Umizi				
185	Am162	Am162	Am162	Am166			Gm157	
185	Um213	np	np	/////00			dinisi	
185	Gm246	Gm246	Gm246					
18S	np	np	Um373					
18S	Gm392	Gm392	Gm392	Gm436		Gm373		
18S	Cm418	Cm418	Cm418	Cm462	Cm414	Cm399		
18S	np	np	Am424	Am468	Am420	Am405		
18S	Am440	Am440	Am440	Am484	Am436		Am361	
185	Am468	Am468	Am468	Am512				
185	Cm473	Cm4/3	Cm4/3	Cm517	Am E 41	AmE26		
185	LIm582	Am581	LIm581	LIm627	LIm578	AIII520		
185	Gm599	Gm598	Gm598	Gm644	011370			
185	Um604	Um603	Ψm603				Gm512	
18S	Um615	Um614	Um614					
18S	Am623	Am622	Am622	Am668	Am619	Am604		
18S	Am780	np	np					
18S	Am796	np	np					
18S	Am801	Am800	Am800		Am796	Am770		
185	Am812*	np	np	A 1021	A 07 4	1046		
185	AM978	AM9/7	AM9//	Am 103 I	Am9/4	AM946		
185	Am1188*	nn	0111012 nn					
185	Cm1219	(m1218	Cm1218	Cm1272				
185	Um1235	Um1234	Um1234	Um1288		Um1202		
18S	Um1264	Um1263	np			Um1231		
18S	Um1266	Um1265	np					
18S	Um1273	Um1272	Um1272	Ψm1326	Um1269	Um1240		
18S	Gm1275	Gm1274	Gm1274	Gm1328	Gm1271			
18S	Am1330	Am1329	Am1329	Am1383		Am1297	Gm1064	
185	Um1384	Um 1383	Um1383	Um1442	Cm1429	Um 1348	Um1115	
105	Gm1434	Gm1433	Gm 1433	Gm1490	Gm1428	Um1412		
185	Um1554*	01111447 nn	0111447 nn			0111412		
185	Am1579	Am1579	Am1579					
18S	Cm1645	Cm1645	Cm1645	Cm1703	Cm1639	Cm1609	Cm1369	Cm1402
18S	Am1758	Am1758	Am1758			Am1720		
5.8S	Am47	Am48	Am46			Am42		
5.8S	Gm79	Gm80	Gm78	Gm75				
255	np	np	Cm40					
255	Um44	Um44	Um44			Line AC		
255	Um146	UIII40	UIII40			Um40		
255	nn	Am369	Am369			011142		
255	Um378*	np	Um378					
255	Gm399	Gm399	Gm399					
25S	Am661	Am660	Am660	Am1326	Am649	Am557		
25S	Cm675	Cm674	Cm674	Cm1340	Cm663			
25S	Um676	Um675	Um675					
255	np	np	Um/87					
255	0m803 Cm814	UM804 Cm915	UM804 Cm815	Cm1522	Cm905		Cm900	
233 255	Am816	Δm817	Am817	Am1524	Am807	Am604	ROULD	
255	Am876	Am877	Am827	Am1534	Am817	Am704		
25S	Am885	Am886	Am886	74111551	Am876	7411701	Am881	
25S	Gm917	Gm918	Gm918	Gm1625	Gm908			
25S	Am945	Am946	Am946				Am941	
25S	Um1067	Um1068	Um1068					
25S	Am1143	Am1144	Am1144	Am1871	Am1133	Am1015		
25S	np	Am1252	np			A 1125		
255	AM1263	Am 1264	np			AM1135	(m1222	
200 250	UIII12/8 Am1277	UIII 12/9 Am1270	np Am1379			Am1250	CIII 1233	
255 255	(m1447	(m1448	(m1448	(m2351	(m1437	(m1319		
255	Am1459	Am1460	Am1460	Am2363	Am1449	Am1331		
255	Gm1460*	Gm1461	Cm1461	Gm2364	Gm1450			
25S	Cm1479	Cm1480	Cm1480					
25S	Cm1518	np	np	Cm2422				
25S	np	Um1537	Um1537					
25S	Cm1847	Cm1849	Cm1849					
255	Cm1850	Cm1852	Cm1852					

Table 2. (Continued).

RNA A. thailana (S. tyrapersizum) (N. tabacum) (P. abyss) (E. coll) 255 Gm1857 Gm1857 Gm1857 Gm1731 255 Gm1860 Cm1862 Cm2804 Cm1735 255 Mm1891 mp mp Am2815 Um1892 Um1893 Um1893 255 Mm1871 Gm12171 Gm12171 Gm1905 Gm1905 Gm1905 255 m2127 Am1239 Am2129 Am3716 Cm200			Tomato	Tobacco	Human	Yeast	Algae	Archaea	Bacteria
255 Gm1857 Gm1251 Gm1252 Gm1252 Gm1252 Gm1252 Gm1252 Gm1252 Gm1905 Gm1905 Sm1905	rRNA	A. thaliana	(S. lycopersicum)	(N. tabacum)	(H. sapiens)	(S. cerevisiae)	(O. tauri)	(P. abyssi)	(E. coli)
255 Cm1860 Cm1862 Cm1862 Cm1236 255 Mm1891 um 1994 Um12837 Um1898 255 Um1891 Um1894 Um12837 Um1955 255 Mm1714 Um1216 mp Gm1260 Gm1276 255 mp1 Gm1270 Gm1270 Gm1270 Gm1270 255 Gm1271 Am2200 Cm3701 Cm2197 Gm2060 255 Gm1282 Am2223 Am3724 Am2263 Gm2079 255 Am2271 Am2230 Am3760 Am2264 Am2063 255 Am2281 Am2284 Am3760 Am2280 Gm2079 255 Am2287 Am2289 Am3760 Am2280 Gm2079 255 Am2287 Am2284 Am3780 Gm2130 Gm2080 Gm2130 255 Gm2288 Gm2289 Gm2130 Gm2130 Gm2130 Gm2130 255 Gm2286 Gm2280 Gm2130 Gm2130 Gm2130 Gm2130 255 Gm2286 Gm2280 Gm2130 Gm2130 <td>25S</td> <td>Gm1855</td> <td>Gm1857</td> <td>Gm1857</td> <td></td> <td></td> <td>Gm1731</td> <td></td> <td></td>	25S	Gm1855	Gm1857	Gm1857			Gm1731		
255 Mn1871 np np An2215 254 Um1892 Um1892 Um1894 Um2807 Um1885 255 Um2114 Um2116 np Gn1965 Gn1905 255 Mn2127 Gn2126 Gm2127 Gm1965 Gm1905 255 An2127 An2200 Cm2200 Cm2707 Gm2079 255 An2217 An2239 Gm2239 An2206 An2079 255 Gm2237 Gm2239 Gm2339 Gm2136 Gm2131 255 Gm2237 Gm2239 Gm2339 Gm2139 Gm2130 255 An2252 Am2254 Am2254 Gm2380 Gm2130 255 An2327 Am2254 Am2324 Am2325 Gm2380 Gm2109 255 Am2327 Am226 Am239 Am382 Gm2160 Cm2109 255 Am2362 np np np Am367 Gm2109 Gm2109 255 Cm2388 Cm248 mp Gm2404 Gm2412 Gm252 255 Lm241 <	25S	Cm1860	Cm1862	Cm1862	Cm2804		Cm1736		
255 Um1892 Um1894 Um2837 Um1888 255 Um1214 Um1216 Gm12126 Gm1218 Gm1205 Gm1905 255 Gm1217 Gm1217 Gm1200 Gm3701 Gm2197 Am1988 255 Gm1217 Gm2200 Gm3701 Gm2079 Gm2079 Gm2079 255 Am2237 Am2238 Am2229 Am3760 Am2298 Gm2079 255 Am2287 Am2284 Am2289 Am3760 Am2298 Gm2079 255 Am2287 Am2284 Am2284 Am3780 Am2299 Gm2079 255 Am2282 Am2284 Am2284 Am3780 Am2299 Gm2079 255 Gm2289 Gm2281 Gm2079 Gm2131 Gm2131 Gm2131 255 Gm2288 Gm2284 Cm2386 Cm2080 Gm2190 Gm2190 Gm2190 255 Gm2394 Gm2398 Gm3999 Gm2191 Gm2192 Gm2191 Gm2192 255 Gm2394 Gm2412 Gm2412 Gm2251 Gm2251 Gm2251	25S	Am1871	np	np	Am2815				
255 um2114 Um2116 np Gm1965 Gm1905 255 Gm2125 Gm1917 Gm12127 Am1968 255 Am2127 Am2123 Am2123 Am2123 255 Cm2139 Cm200 Cm270 Cm2197 255 Gm2237 Gm2239 Gm2239 Am2266 Am2200 255 Gm2237 Gm2239 Gm2239 Am3760 Am2256 Am209 255 Gm2237 Gm2239 Gm2291 Gm3792 Gm2266 Am2063 255 Gm2238 Am2244 Am3785 Am2266 Am2063 Gm2109 255 Gm2289 Gm2291 Gm3907 Gm2109 Gm2109 255 Am2322 Am2329 Am3230 Cm2337 Cm2100 Cm2100 255 Am2327 Am2329 Am3230 Cm2337 Cm2100 Cm2100 255 Am2326 mg Cm2340 Cm3240	25S	Um1892	Um1894	Um1894	Um2837	Um1888			
255 np Gm1926 Gm1927 Gm1905 255 Gm1217 Gm1217 Gm1927 Am1968 255 Am2127 Am2129 Am2129 Am2197 255 Am2131 np np np Am3718 255 Am2237 Am2299 Am2299 Am2290 Gm2290 255 Am2237 Am2299 Am2290 Gm2291 Gm2291 255 Am2232 Am2344 Am3878 Am2281 255 Gm2289 Gm2291 Gm3792 Gm2289 Gm2190 255 Am2327 Am3324 Am3825 Gm2109 Cm2100 255 Am2327 Am3320 Gm2109 Cm2100 Cm2120 255 Am2327 Am3340 Cm2340 Cm3471 Cm2100 Cm2120 255 Am2362 np np Am3667 Cm208 Cm2100 Cm2120 255 Gm2394 Gm2394 Gm2394 Gm2291 Gm251 Gm2521 255 Gm2461 Gm2469 Cm2208 Cm210 Gm2521	25S	Um2114	Um2116	np			Um1955	_	
255 Gm2125 Gm2127 Gm2127 Gm2127 Gm2127 Gm2127 Gm2128 Gm2199 255 Gm2138 Cm2109 Cm2200 Cm2200 Gm2197 Gm203 255 Gm2231 Mm2223 Am2223 Am3724 Am2220 Gm2039 255 Gm2237 Gm2233 Gm2234 Am3785 Am2281 Gm2039 255 Gm2294 Gm2296 Gm2296 Gm2196 Gm2197 255 Gm2294 Cm2296 Gm2296 Gm2197 Gm2109 255 Gm2294 Cm2296 Gm2297 Gm2109 Cm2109 255 Am2327 Am2329 Am3830 Gm2109 Cm2109 255 Am2327 Am2329 Am3870 Cm2180 Cm2101 255 Gm2386 Cm2368 Cm2368 Cm2108 Cm2109 255 Am2327 Am3830 Gm2109 Cm2100 Cm2100 255 Mm241 Um2347 Cm2108 Cm2109 Cm2120 255 Mm2450 Um2450 Cm2208 Cm210 Cm2	25S	np	Gm2126	Gm2126			Gm1965	Gm1905	
255 Am 212 Am 129 Am 129 Am 129 Am 129 Am 129 255 Am 2217 m pp m p Am 3718 Am 2203 Am 2210 Am 2063 255 Am 2217 Am 2223 Am 2239 Am 2230 Am 2260 Am 2063 255 Am 2217 Am 2239 Am 2239 Am 2240 Am 2099 255 Am 2241 Am 2244 Am 3786 Am 2261 Am 2099 255 Am 2224 Am 2244 Am 3786 Am 2261 Cm 2146 Am 2016 255 Am 2327 Am 2324 Am 2329 Am 380 Cm 2140 Cm 2140 <td>25S</td> <td>Gm2125</td> <td>Gm2127</td> <td>Gm2127</td> <td></td> <td></td> <td></td> <td></td> <td></td>	25S	Gm2125	Gm2127	Gm2127					
255 Cm.2193 Cm.2200 Cm.2101 Cm.2197 255 Am.2215 Am.2223 Am.2233 Am.2234 Am.2264 Am.2267 256 Am.2257 Am.2293 Am.2293 Am.2266 Am.2267 Am.2293 255 Am.2257 Am.2294 Am.2294 Am.2785 Am.2281 Am.2099 255 Am.2294 Am.2294 Am.2785 Am.2281 Cm.2136 255 Am.2327 Am.2296 Cm.2066 Cm.2196 Cm.2196 255 Am.327 Am.2294 Am.3297 Am.3297 Cm.2180 Cm.2106 255 Am.3327 Am.2329 Am.3290 Am.3290 Cm.2106 Cm.2108 Cm.2208 Cm.2208 Cm.2208 Cm.220	255	Am2127	Am2129	Am2129	6 9794	C 0407	Am1968		
Abs Ams211 np np np Ams218 Ams2220 Ams2063 255 Gm2237 Gm2239 Gm2239 Ams226 Ams2063 Gm2079 255 Ams2281 Ams2281 Ams2281 Ams2063 Gm2079 255 Ams2281 Ams2284 Ams2281 Gm2131 Gm2137 255 Ams2284 Ams2284 Ams285 Ams285 Gm2131 Gm2131 255 Ams227 Ams284 Ams284 Ams285 Gm2109 Gm2109 255 Ams297 Ams280 Ams284 Ams287 Gm2100 Gm2100 255 Ams297 Ams290 Cm2368 Gm2109 Gm2100 Gm2100 255 Ams297 Gm2394 Gm2398 Gm2398 Gm2208 Gm2208 255 Gm2302 Gm2404 Um2424 Um3925 Um2421 Um2264 255 Mm2411 Um2424 Um3925 Um2421 Um2264 Gm2252 255 Mm2468 Np Gm2453 Gm2451 Gm2252 255 Mm24	255	Cm2198	Cm2200	Cm2200	Cm3/01	Cm2197			
225 An1221 An1223 An1223 An1224 An12263 255 An1237 An12239 An12263 An12263 An12263 255 An1237 An12299 An12264 An1275 An12267 255 An12327 An12299 An12765 An12261 An12267 255 An12322 An12324 An12324 An12325 An12267 255 An12327 An12324 An12329 An13830 Gm2109 255 An12327 An12329 An13830 Gm2109 Cm2180 Cm2180 255 An12327 An12329 An13823 Gm2189 Cm2180 Cm1280 255 An12362 np np An1243 Gm2189 Cm2180 Cm1280 255 An1242 Um2434 Um3245 Gm2289 Gm3289 Gm2252 Gm2289 Gm2252 Gm2252 Gm2252 Gm2252 Gm2252 Gm2252 Gm2252 Gm2252 Gm2251 Gm225	255	Am2215	np	np	Am3/18	4	A		
225 Gm2237 Gm2239 Am2239 Am3760 Am2256 Am2099 255 Am2282 Am2284 Am3785 Am2286 Am2099 255 Am2282 Am2296 Gm2291 Gm3792 Gm2288 Gm2110 255 Am3237 Am3330 Am3340 Am3237 Cm2180 Cm2109 255 Am3237 Am3330 Cm3240 Cm3841 Cm2337 Cm2180 Cm2120 255 Am3237 Am3330 Cm3240 Cm3841 Cm2337 Cm2180 Cm2120 255 m3366 Cm3298 Gm3299 Gm2288 Cm3869 Cm2208 255 Gm3396 Gm3298 Gm2289 Gm2252 Gm2410* Gm2252 255 Mp3411 Um2413 Gm2252 Gm2410* Gm2251 Gm2412 Gm2251 255 Mp3466 Mp Mp Gm2251 Gm2411 Um2264 Gm2251 255 Mp3461 Mp 263 Gm4042 Gm2412 Gm2251 Gm2451 Gm2251 255 Mp Gm3486 Mp Gm	255	Am2221	Am2223	Am2223	Am3724	Am2220	Am2063		
235 Am.237 Am.239 Am.2429 Am.3780 Am.2281 235 Am.2284 Am.3785 Am.2281 235 Gm.2289 Gm.2191 Gm.3792 Gm.2288 Gm.2131 235 Gm.2289 Gm.2314 Am.3225 Gm.216 Gm.2169 235 Am.322 Am.3237 Am.3234 Am.3229 Am.3830 Gm.2109 235 Am.327 Am.3234 Am.3250 Gm.2368 Cm.2384 Cm.2208 235 Am.3262 mp mp np Am.3669 Cm.2208 235 Gm.2364 Cm.2368 Cm.2368 Cm.2208 Gm.2208 235 Gm.2364 Cm.2368 Cm.2368 Cm.2208 Gm.2252 236 Gm.2410* Gm.2412 Gm.2412 Gm.2412 Gm.2251 235 Gm.2410* Gm.2424 Um.3925 Um.2421 Um.2264 Gm.2251 255 Um.424 Um.2424 Um.3925 Um.2421 Um.2264 Gm.2251 255 Mp Gm.2429 Gm.2429 Gm.2429 Gm.2429	255	Gm2237	Gm2239	Gm2239	Am 2760	Am 2250	Gm2079		
225 Am.224 Am.224 Am.224 Am.224 Am.224 255 Gm.2294 Gm.2291 Gm.2291 Gm.2291 Gm.2291 255 Am.2327 Am.2324 Am.2324 Am.3223 Am.3830 Gm.2109 255 Am.2327 Am.2329 Am.3840 Cm.2344 Cm.2347 Cm.2109 255 Am.237 Am.2329 Am.3800 Cm.2387 Cm.2109 Cm.2109 255 Am.2362 np um.2340 Cm.3841 Cm.2377 Cm.2108 Cm.2109 255 Cm.2366 Cm.2388 Cm.2368 Cm.2369 Cm.2208 Cm.200 255 Gm.2397 Gm.2398 Gm.3299 Gm.2251 Gm.2252 Gm.2251 Gm.2251 Gm.2252 Gm.2251 Gm.2252 Gm.2251 Gm.2251	200	Am2257	Am2259	Am 2204	Am 2705	Am2200	Am2099		
223 0m/229 0m/229 0m/229 0m/228 0m/248 0m/248 <td>200</td> <td>Am2282</td> <td>Am2284 Cm2201</td> <td>AII12284</td> <td>AII13/85</td> <td>AM2281</td> <td>Cm2121</td> <td></td> <td></td>	200	Am2282	Am2284 Cm2201	AII12284	AII13/85	AM2281	Cm2121		
223 Clif2294 Clif239 Clif239 223 Am2327 Am2329 Am2324 Am3825 Gm2109 235 Am2327 Am2329 Am3380 Gm2109 255 Am2327 Am2329 Am3380 Gm2109 255 np Um2350 Um2340 Cm2340 Cm2180 255 Am2527 Am2384 Gm2384 Cm2386 Cm2208 255 Gm2396* Gm2398 Gm2398 Gm2292 Cm2464 255 Gm2410* Gm212 Gm2412 Gm2412 Gm2412 255 Um2411 Um2413 Um2413 Um2421 Um2421 Um2421 255 Um2425 Um2428 np Gm255 Gm2407 Gm2497 np 255 Um2444 Pp np np Cm2497 Gm2491 Gm251 Gm251 255 Um2456 Um2488 np Gm2491 Gm2451 Gm251 Gm251 255 m2614 Am2644 Am2643 Am2640 Am2647 Gm2492 Gm251 Gm251 <td>200</td> <td>Gm2289 Cm2204*</td> <td>GM2291</td> <td>Gm2291</td> <td>GI13792</td> <td>GI12288</td> <td>Gm2131</td> <td></td> <td></td>	200	Gm2289 Cm2204*	GM2291	Gm2291	GI13792	GI12288	Gm2131		
225 Am.222 Am.222 Am.222 Am.2327 Am.2329 Am.2329 Am.2329 Am.2329 Cm.2180 Cm.2109 255 Cm.2338 Cm.2140 Cm.2330 Cm.2137 Cm.2180 Cm.2120 255 Pp Um.2350 Um.2350 Um.2347 Cm.2108 Cm.2108 255 Gm.2392 Gm.2394 Gm.2368 Cm.3869 Cm.2208 Cm.2108 255 Gm.2392 Gm.2394 Gm.2398 Gm.2398 Gm.2397 Cm.2020 255 Gm.2410 Lm.2424 Um.2424 Um.3925 Um.2421 Um.2264 255 Um.2422 Um.2424 Um.2424 Um.3925 Um.2421 Um.2264 255 Um.2456 Lm.2488 np Gm.4042 Gm.201 Gm.201 255 Um.2464 Pp np Cm.4054 Am.2613 Gm.211 Gm.2251 255 Mm.2521 Um.2644 Am.2643 Cm.2619 Gm.2451 Gm.2421 255 Gm.2620 Gm.2623 Gm.2619 Gm.2483 Cm.2429 Cm.2429 Cm.2429 </td <td>200</td> <td>Am2222</td> <td>CIII2290</td> <td>CIII2290</td> <td>Am2025</td> <td></td> <td>CIIIZISO</td> <td></td> <td></td>	200	Am2222	CIII2290	CIII2290	Am2025		CIIIZISO		
223 Anil2227 Anil2229 Anil2229 Anil2230 Imp 200 225 Anil2220 Um2350 Um2370 Um2370 Imp 200 225 Anil222 Dimp Anil226 Cm2388 Cm2368 Cm2308 Cm2208 255 Cm2366 Cm2394 Gm2394 Gm2394 Gm2394 Cm2208 255 Gm2396* Gm2398 Gm2398 Gm2398 Gm2392 Cm2208 255 Gm2410* Gm2412 Gm2412 Gm2410* Gm2410* 255 Um2411 Um2413 Um2414 Um2424 Um2421 Um2264 255 Um2456 Um2458 Np Gm4042 Gm255 Gm2251 Gm2252 Gm2251 Gm2251 Gm2251 Gm2251 Gm2251 Gm2251 Gm2251 Gm2252 Gm2252 Gm2251 Gm2252 Gm2251 Gm2252 Gm2252	200	AIII2522	AIII2524	AIII2524	AIII5025			Cm2100	
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225 hp np np Am3867 235 Am2362 np np Am3867 235 Gm2396 Gm2394 Gm2394 Gm2394 255 Gm2396* Gm2398 Gm2398 Gm2392 255 Gm2410* Gm2412 Gm2412 Gm2412 255 Um2411 Um2413 Um2424 Um3925 Um2421 Um2264 255 Um2456 Um2486 np Gm4042 Um2264 Um2264 255 np Gm2497 np Gm2497 Gm2497 Gm2497 255 np Gm2497 np Gm2417 Gm2251 255 np Gm2497 np Gm2411 Gm2251 255 np Gm2497 np Gm2411 Gm2451 Gm2251 255 np260 Gm2623 Gm2643 Gm2483 Gm2483 Gm2412 Gm2429 Gm242	255	CIIIZSSO	LIn2350	LIm2350	CIII5641	LIm2347	CI112 160	CIIIZIZU	
225 An12302 inp inp inp An13007 255 Gm2394 Gm2394 Gm2394 Gm2394 255 Gm2392 Gm2394 Gm2398 Gm2398 255 Gm2410* Gm2412 Gm2412 Gm255 255 Um2411 Um2413 Um2413 Um2413 255 Um2422 Um2444 Um2424 Um3255 Um2421 Um264 255 Um2456 Um2448 np m Gm255 Gm2486 np Gm255 255 Um2494 np np np Gm2610 Gm2451 Gm2251 255 Mm2601 Mm2633 Um4227 Gm2483 Gm2451 Gm2492 255 Gm2654 Gm2283 Gm279 Gm2483 Gm2492 Gm2493 255 Gm2654 Gm2284 Gm279 Gm2483 Gm2493 Gm2493 255 Gm2796 Gm2794 Gm2791 Gm2623 Gm2791 Gm2647 Gm2493 255 Gm2792 Gm2797 Gm2794 Gm2793 Gm2647	255	11p Am2362	0112550	0112550	Am3867	0112347			
225 Gm2302 Gm2304 Gm2304 Gm2304 Gm2304 255 Gm2302 Gm2304 Gm2308 Gm2308 Gm2302 255 Gm2410* Gm2410* Gm2410* Gm2410* Gm2252 255 Um2411 Um2413 Um2424 Um395 Um2421 Um2264 255 Um2456 Um2458 np Gm4042 Gm255 Gm2306 Gm251* Gm255 255 um2494 np np Gm2633 Gm2622 Gm4196 Gm2619 Gm2451 Gm2251 255 Gm2620 Gm2633 Gm2622 Gm4196 Gm2483 Gm2483 255 Gm2650 Gm2654 Um4228 Gm2483 Gm2492 Gm2492 255 Gm2632* Gm2636* Gm2483 Cm2429 Gm2492 Gm2494 Gm2493 Gm2493 Gm2422 255 Gm2630* Gm2635 Gm2644 Am2643 Am2641 Am2644 Am2643 Gm2493 Gm2429 Gm2429 Gm2429 Gm2429 Gm2429 Gm2449 Gm2493 Gm2449 Gm2493	255	Cm2366	(m2368	Cm2368	Cm3860		Cm2208		
255 Gm2392 Gm2398 Gm2398 Gm3899 255 Gm2410* Gm2412 Gm2412 Gm2522 255 Um2411 Um2413 Um241 Um2264 255 Um2456 Um2458 mp Gm2592 255 Um2456 Um2456 mp Gm4042 255 np Gm2486 np Gm2604 255 np Gm2620 Gm2623 Gm2622 Gm4196 Gm2619 Gm2451 Gm2251 255 Am2641 Am2644 Am2643 Am2640 Am2472 Gm2429 Gm2429 255 Gm2652* Gm2654 Gm4128 Gm2483 Gm2492 Gm2492 255 np um2732 Um4306 Um2729 Cm2429 Gm2493 Gm2493 Gm2494 Gm2493 Gm2493 Gm2493 Gm2493 Gm2494 Gm2493 Gm243 Gm2493	255	Gm2302	Gm2304	Gm2304	CIIISOOS		CIIIZZOO		
225 Gm2410* Gm2412 Gm2412 Gm2412 255 Um2411 Um2413 Um2421 Um2264 255 Um2456 Um2424 Um3925 Um2421 Um2264 255 Um2456 Um24744 Um3925 Um2421 Um2264 255 np Gm240* np Gm2410* Gm2252 255 np Gm2479* np Gm4042 Gm2410* Um2484 255 np Gm2621* np np Gm251* Gm252* 255 Gm2600 Gm2633 Gm2622 Gm4196 Gm2619 Gm2431 Gm2251 255 Gm2651 Um2664 Vm2653 Um4227 Gm2644 Am2640 Am2440 Am2443 255 Gm2652 Gm2655 Gm2644 Gm2790 Gm2792 Gm2791 Gm2429 Gm2429 Gm2429 Gm2429 Gm2451 Gm2429 Gm2429 Gm24483 Gm24483 Gm24483 Gm24483 Gm24483 Gm2444 Gm2499 Gm2444 Gm2499 Gm2494 Gm2791 Gm2663 Gm2449 <td< td=""><td>255</td><td>Gm2396*</td><td>Gm2398</td><td>Gm2398</td><td>Gm3899</td><td></td><td></td><td></td><td></td></td<>	255	Gm2396*	Gm2398	Gm2398	Gm3899				
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255 Um2422 Um2424 Um3925 Um2421 Um264 255 Um2456 Um2458 np Gm4042 255 np Gm2497 np Gm4042 255 np Gm2497 np Gm2497 255 Um2494 np np np 255 Um2494 np np np 255 Um2604 Am2611 Am2641 Am2644 255 Gm2651 Um2654 Ym2653 Um4227 255 Gm2651 Um2654 Ym273 Gm2483 255 np np np nm272 255 Gm2652* Gm2666 Cm2483 Cm2429 255 np np Um2721 Um270 255 np np Um2733 Um4306 Um2729 255 Gm2794 Gm2797 Gm2797 Gm2633 255 Gm2794 Gm2797 Gm2797 Gm2643 255 Gm2816 Gm2818 Gm2491 Cm2668 255 Cm2884	255	Um2411	Um2413	Um2413			0112252		
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255 np Gm2486 np Gm4042 255 np Cm2497 np Cm4054 255 lm2494 np np np 255 dm2601 Gm2623 Gm2622 Gm4196 Gm2619 Gm2451 Gm2251 255 Gm2620 Gm2623 Gm2623 Um4264 Am2640 Am2472 255 Gm2655 Gm2655 Gm2654 Gm2283 Gm2483 255 JUn2654 Vm2653 Um4227 Gm2483 Cm2429 255 np up Um2720 Cm2429 Gm255 Gm2794 Gm2799 Um2732 255 Gm2794 Gm2797 Gm2796 Gm4370 Gm2793 Gm2647 255 Gm2794 Gm2819 Gm2818 Gm2647 Cm2668 Cm2711 255 Gm2819 Gm2819 Gm2924 Um498 Um269 Um2552 255 Gm2918 Gm2921 Gm2647 Cm2668 Cm2711 Cm2668	255	Um2456	Um2458	np	01110720	0	0		
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Arabidopsis sites marked with an asterisk indicate Nm sites for which no C/D snoRNA has been identified. np = non-mapped sites in A. thaliana, tomato, tobacco. For human, yeast, algae and archaea only Nm sites conserved in plants are listed.

structure, creating the decoding centre and peptidyl-transferase activity (PTC) containing ribosome binding sites A, P and the exit (E) site.

The current view is that rRNA 2'-O-Me maintain stable ribosome structure [36,48,49]. In Arabidopsis, ribosome turnover is relatively low, replacing the population every 3–4 days [50] compared to a few hours in yeast [51]. Interestingly, the majority of 2'-O-Me modifications occur in conserved rRNA regions. Clustering of 2'-O-Me in the central, major and minor domains of the 18S rRNA locate them in the decoding centre. Other clusters were identified in domain IV and V of the 25S rRNA, which are involved in PTC activity and tRNA binding. All in all, these data support the role of ribose methylation in translation [52].

Interestingly, nearly half of the rRNA Nm sites detected in Arabidopsis have not been reported in yeast or animal cells ([14,21] and Figure 2 and Table 2). These Arabidopsis-specific rRNA Nm are in the central, 5' major and 3' minor domains of the 18S, in the 5.8S and in all domains of the 25S rRNA (Figure 2). Notably, Arabidopsis (plant) specific Nm are



Figure 2. rRNA 2'-O-methylation sites (Nm) in a) 18S and b) 5.85/25S cytoplasmic rRNA in plants (magenta), bacteria (yellow), archaea (turquoise) and human (orange) as well as specifically in Arabidopsis (green), tomato (blue) and tobacco (black) plants. Nm conserved in several or all species are labelled in brown, the species-specific are labelled as indicated before. The main function region of the rRNA are marked with red lines: DC (decoding centre; [82] in the 18S rRNA and PTC (peptidyl transferase centre); the intersubunit bridge [52] and GAC (GTPase associated centre; [83] in the 25S rRNA.

mapped in the hairpin structures H24 (Um1013), H31 (Am1188), H34 (Gm1448) and H44 (Am1758) forming the decoding centre. The loss of rRNA modifications of the decoding centre impairs pre-rRNA processing and ribosome translation in yeast [4]. Similarly, the Arabidopsis-specific rRNA Nm are mapped in functional domains of the 25S. In

domain I, the H24 (Um378) interacts with SRPs and in turn with specific sequences in nascent translating polypeptides [53]. In the domain II, the H38 (Um1067) is involved in the formation of the intersubunit bridge between the 60S and 40S and it is contacting the A-site bound tRNA [54,55]. Meanwhile, H43 (Am1260) and H44 (Um1278) form the



Figure 2. (continued).

conserved GTPase centre [56]. In the domain III, the H47 (Cm1479) is required for processing of pre-27SB and 27SA into 25S [57]. And in the domain IV, the H68 (Gm2237), is involved in the formation of the inter-subunit bridge between the 40S and 60S [55,58] and it contains two E-sites [33]. In contrast, 2'-O-Me is not detected in the ES27, which is essential for translational fidelity, regulating amino acid incorporation and preventing frameshift errors. ES27 is also a scaffold for the conserved methionine amino peptidase (MetAP) that removes, co-translationally the first methionine from the nascent polypeptide chain. Similarly, the conserved sarcin/ricin loop (S/R-loop), which enables proper binding of elongation factors, does not seem to be 2'-O-methylated either. An attack of the S/R-loop by the ribonuclease α -sarcin and the RNA N-glycosidase ricin inhibits translation [26,54,59].

2'-O-Me profiling in tobacco and tomato ribosomes

To the best of our knowledge, 2'-O-Me profiling using RiboMethSeq or any other sequencing-based profiling methods have not been reported for any plant species other than *A. thaliana*. However, Cryo-EM structure (2.2 Å resolution) studies of 80S ribosomes located rRNAs Nm from tomato [59] and tobacco [54]. In tomato, a total of 110 rRNA Nm were detected in the 18S (32 Nm), in the 25S (76 Nm) and in the 5.8S (2 Nm). In tobacco, a total of 107 rRNA Nm were detected in in the 18S (32 Nm), in the 5.8S (2 Nm) and in the 25S (73 Nm) (Table 2 and Figure 2).

Remarkably, the tobacco 18S-Cm1645 and 25S-Gm2622 (the equivalents of 16S-Cm1402 and 23S-Gm2351 in *E. coli*) locate at the P-site next to the mRNA and P/E tRNA in the small ribosomal subunit and at the P-site in the large ribosomal subunit next to the CCA tail of the A/P tRNA, respectively (Figure 2). A structural role of 25S-Gm2796 in the P/E tRNA and 25S-Am2259/25S-Gm2818 in the A/P tRNA site was also observed [54]. Furthermore, Cryo-EM density map allowed to propose that Gm1857 and Cm1849 together with Am827 might shape the N-terminal region of the ribosomal protein eL37 and is involved in constructing the peptide exit tunnel. Similarly, Am886 and Cm2920 interacts with methylated ribosomal protein uL3, which is crucial for proper rRNA processing [59].

These structural studies show that most of the rRNA Nm identified in Arabidopsis are detected in tomato and tobacco (Table 2). Regarding the predicted sites in Arabidopsis, 15 Nm were only mapped in tobacco and/or tomato, while 16 Nm were detected only in Arabidopsis but not in tobacco or tomato. Noticeably, the tobacco/tomato specific Nm in the 18S rRNA are located only in the 5' domain, while the 25S specific Nm are in all five domains (I–V). In contrast, the Arabidopsis specific Nm in the 18S are distributed in the 5', central and 3' major domains and the 25S specific Nm are located only in the domain V; and more specifically the Am2935 in the A loop. Whether or not this indicates some kind of plant specific 2'-O-Me of the 40S and 60S ribosome remains to be investigated.

Altogether, Arabidopsis, tobacco and tomato plants have a total of 97 conserved Nm sites. While other species share a similar number of Nm sites, their level of conservation is very variable compared to plants. The most intriguing example is Archaea, which share only 13 of their 93 Nm sites with plants. Even *Ostreococcus*, phylogenetically quite close to plants, shares only half of its Nm sites with them. Algae therefore show a similar number of conserved Nm sites as human cells but their positions are not always identical. Then, it would seem that eukaryotic ribosomes need a similar number of Nm for their general function but their location meets speciesspecific needs (Figure 1D and Table 2).

While bacteria and yeast share 75% of their Nm sites with them, only half of the Nm sites in human and algae are among these conserved sites. From these sites 56, 41, 45 13 are also found in Nm in bacteria and yeast are conserved in plants

Ribosome 2'-O-Me: major players

Evidence of ribosome heterogeneity at the rRNA level has been reported in mammals [36,48]. Differential expression of C/D snoRNAs has been reported in blood serum and plasma [60], changes of rRNA ribose methylation have been observed in developing tissues in mice [36] and alterations of 2'-O-Me have been associated to diseases, mainly cancer and autoimmune syndromes, and linked to tumour suppressor p53 [61,62].

Under normal cell conditions, p53 binds the fibrillarin gene promoter sequence and diminishes its expression level. In cancer cells, loss of function of tumour suppressor p53 provokes high fibrillarin activity resulting in the production of ribosomes with modified 2'-O-Me profile. These modified ribosomes translate mRNA with a lower fidelity and increase internal ribosome entry site (IRES)-dependent translation initiation of key cancer genes [62]. In contrast, inhibition of fibrillarin gene expression induces a global decrease in 2'-O-Me of the pre-rRNA in HeLa cells [48,62–64]. Likewise, p53 interacts with and re-localizes nucleolin in response to stress conditions [65]. Nucleolin is a multifunctional nucleolar protein required for rDNA expression, processing of rRNA and assembly of ribosomes. Nucleolin is also involved in DNA repair, remodelling and organization (reviewed in [66–68])

The homologue of p53 in plants is ANAC02 [69]. Disruption of ANAC082 in plant mutants for ribosomal biogenesis factors restores plant growth and developmental phenotypes but not the rRNA processing defects. The impact of ANAC082 on fibrillarin or nucleolin gene expression remains unknown.

Fibrillarin interacts also with the nucleolin protein in a large nucleolin-U3 snoRNP complex, which is involved in the processing of the largest rRNA precursors in yeast, mammals and plants [70–72]. Nucleolin protein could also affect C/D snoRNP assembly and/or methylation activity. Interestingly, inactivation of the homolog of the yeast nucleo-lin (Nrs1) depletes snoRNPs from the Dense Fibrillar Component (DFC) in the nucleolus, provoking their accumulation in a nucleolar body [73]. Nucleolin directly binds pre-rRNAs and snoRNPs, and could, thus, facilitate interactions of snoRNPs with pre-rRNAs (reviewed in [7]). Finally, nucleolin might also stimulate IRES-dependent translation [74].

Knockout gene expression of Arabidopsis nucleolin or fibrillarin activities has been demonstrated to provoke

hypomethylation [14,21]. However, only *nuc1* plants show plant growth and developmental phenotypes [75–77]. A particular phenotype for *fib1* or *fib2* plant mutants has not been observed under normal or standard plant growing conditions, likely due to FIB1 FIB2 redundancy [21]. Interestingly, the amount of hypomethylated rRNA sites is similar in *nuc1* and *fib1* (80 Nm and 75 Nm, respectively) but higher compared to the number of sites in *fib2* (38 Nm). Among these sites 18 Nm are *nuc1* and 6 Nm *fib1/2* specific. Strikingly, disruption of the three genes never results in an increase of any 2'-O-Me at any rRNA position [14,21]. Finally, disruption of FIB2 provokes pathogen infection resistance [78]. A link with ribosome activity or methylation of stress/pathogen responsive genes has not yet been demonstrated.

Concluding remarks

Despite their sessile nature, plants are able to adapt dynamically to environmental stresses through proteome modulation, primarily via translation regulation. Ribosomal RNA modifications, particularly 2'-O-Me, are crucial for ribosome activity and/or stability across all kingdoms of life. The species-specific profiles indicate adaptation to translational demands. The quantity of Nm increases along the phylogenetic tree with a transition from site-specific methyltransferases to a single (or two in Arabidopsis) methyltransferase. It is of interest to consider that the latter system is more energy efficient and easier to coordinate with the growing number of Nm. The presence of redundancy in targeting C/D snoRNAs and distinct 2'-O-Me profiles in single mutant of fibrillarin methyltransferases suggest that these C/D snoRNP component have specific roles in stress response and development, emphasizing the dynamic nature of rRNA methylation. In this context, rRNA Nm were identified without a corresponding snoRNA, which warrants further investigation of their methylation mechanism. It would be of interest to determine whether this is merely redundancy, ensuring the methylation of essential Nm despite the presence of hundreds of C/D snoRNAs. Additionally, a single C/D snoRNA can contain two antisense sequences, which raises the question how two different sequences evolve in the same C/D snoRNA. Here, emerging connections between ribosome 2'-O-Me, major players such as fibrillarin and nucleolin are also highlighted. However, further exploration of their role in C/D snoRNP assembly, rRNA methylation and its impact on translation efficiency is needed.

Disclosure statement

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Data availability statement

There is no unpublished data mentioned in this review.

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References

- Ayadi L, Galvanin A, Pichot F, et al. RNA ribose methylation (2'-O-methylation): occurrence, biosynthesis and biological functions. Biochim Biophys Acta Gene Regul Mech. 2019;1862:253–269.
- [2] Blanchard SC, Puglisi JD. Solution structure of the A loop of 23S ribosomal RNA. Proc Natl Acad Sci USA. 2001;98:3720–3725.
- [3] Abou Assi H, Rangadurai AK, Shi H, et al. 2'- O-Methylation can increase the abundance and lifetime of alternative RNA conformational states. Nucleic Acids Res. 2020;48:12365–12379.
- [4] Liang XH, Liu Q, Fournier MJ. Loss of rRNA modifications in the decoding center of the ribosome impairs translation and strongly delays pre-rRNA processing. RNA. 2009;15:1716–1728.
- [5] Marchand V, Blanloeil-Oillo F, Helm M, et al. Illumina-based RiboMethSeq approach for mapping of 2'-O-Me residues in RNA. Nucleic Acids Res. 2016;44:e135.
- [6] Brown JW, Echeverria M, Qu LH. Plant snoRNAs: functional evolution and new modes of gene expression. Trends Plant Sci. 2003;8:42–49.
- [7] Massenet S, Bertrand E, Verheggen C. Assembly and trafficking of box C/D and H/ACA snoRNPs. RNA Biol. 2017;14:680–692.
- [8] Watkins NJ, Bohnsack MT. The box C/D and H/ACA snoRNPs: key players in the modification, processing and the dynamic folding of ribosomal RNA. Wiley Interdiscip Rev RNA. 2012;3:397–414.
- [9] Yu G, Zhao Y, Li H. The multistructural forms of box C/D ribonucleoprotein particles. RNA. 2018;24:1625–1633.
- [10] Sáez-Vásquez J, Delseny M. Ribosome biogenesis in plants: from functional 45S ribosomal DNA organization to ribosome assembly factors. Plant Cell. 2019;31:1945–1967.
- [11] Pih KT, Yi MJ, Liang YS, et al. Molecular cloning and targeting of a fibrillarin homolog from Arabidopsis. Plant Physiol. 2000;123:51-58.
- [12] Barneche F, Steinmetz F, Echeverria M. Fibrillarin genes encode both a conserved nucleolar protein and a novel small nucleolar RNA involved in ribosomal RNA methylation in Arabidopsis thaliana. J Biol Chem. 2000;275:27212–27220.
- [13] Rodriguez-Corona U, Pereira-Santana A, Sobol M, et al. Novel ribonuclease activity differs between fibrillarins from arabidopsis thaliana. Front Plant Sci. 2017;8:1878.
- [14] Azevedo-Favory J, Gaspin C, Ayadi L, et al. Mapping rRNA 2'-Omethylations and identification of C/D snoRNAs in Arabidopsis thaliana plants. RNA Biol. 2021;18:1760–1777.
- [15] Rakitina DV, Taliansky M, Brown JW, et al. Two RNA-binding sites in plant fibrillarin provide interactions with various RNA substrates. Nucleic Acids Res. 2011;39:8869–8880.
- [16] Seo JS, Diloknawarit P, Park BS, et al. ELF18-INDUCED LONG NONCODING RNA 1 evicts fibrillarin from mediator subunit to enhance PATHOGENESIS-RELATED GENE 1 (PR1) expression. New Phytol. 2018;221:2067–2079.
- [17] Loza-Muller L, Rodríguez-Corona U, Sobol M, et al. Fibrillarin methylates H2A in RNA polymerase I trans-active promoters in Brassica oleracea. Front Plant Sci. 2015;6:976.

- [18] Tessarz P, Santos-Rosa H, Robson SC, et al. Glutamine methylation in histone H2A is an RNA-polymerase-I-dedicated modification. Nature. 2014;505:564–568.
- [19] Pintard L, Bujnicki JM, Lapeyre B, et al. MRM2 encodes a novel yeast mitochondrial 21S rRNA methyltransferase. EMBO J. 2002;21:1139–1147.
- [20] Ringeard M, Marchand V, Decroly E, et al. FTSJ3 is an RNA 2'-Omethyltransferase recruited by HIV to avoid innate immune sensing. Nature. 2019;565:500–504.
- [21] Wu S, Wang Y, Wang J, et al. Profiling of RNA ribose methylation in Arabidopsis thaliana. Nucleic Acids Res. 2021;49:4104–4119.
- [22] Barneche F, Gaspin C, Guyot R, et al. Identification of 66 box C/D snoRNAs in Arabidopsis thaliana: extensive gene duplications generated multiple isoforms predicting new ribosomal RNA 2'-O-methylation sites. J Mol Biol. 2001;311:57–73.
- [23] Brown JW, Clark GP, Leader DJ, et al. Multiple snoRNA gene clusters from Arabidopsis. RNA. 2001;7:1817–1832.
- [24] Qu LH, Meng Q, Zhou H, et al. Identification of 10 novel snoRNA gene clusters from Arabidopsis thaliana. Nucleic Acids Res. 2001;29:1623–1630.
- [25] Pintard L, Lecointe F, Bujnicki JM, et al. Trm7p catalyses the formation of two 2'-O-methylriboses in yeast tRNA anticodon loop. EMBO J. 2002;21:1811–1820.
- [26] Wilson DN, Doudna Cate JH. The structure and function of the eukaryotic ribosome. Cold Spring Harb Perspect Biol. 2012;4: a011536-a011536.
- [27] Bassler J, Hurt E. Eukaryotic ribosome assembly. Annu Rev Biochem. 2018;88:281–306.
- [28] Saez-Vasquez J, Raynal M, Delseny M. A rapeseed cold-inducible transcript encodes a phosphoenolpyruvate carboxykinase. Plant Physiol. 1995;109:611–618.
- [29] Sergeeva OV, Bogdanov AA, Sergiev PV. What do we know about ribosomal RNA methylation in *Escherichia coli*? Biochimie. 2015;117:110–118.
- [30] Londei P, Ferreira-Cerca S. Ribosome biogenesis in Archaea. Front Microbiol. 2021;12:686977.
- [31] Grosjean H, Gaspin C, Marck C, et al. RNomics and modomics in the halophilic archaea *Haloferax volcanii*: identification of RNA modification genes. BMC Genom. 2008;9:470.
- [32] Omer AD, Ziesche S, Decatur WA, et al. RNA-modifying machines in archaea. Mol Microbiol. 2003;48:617–629.
- [33] Xie Q, Wang Y, Lin J, et al. Potential key bases of ribosomal RNA to kingdom-specific spectra of antibiotic susceptibility and the possible archaeal origin of eukaryotes. PLOS ONE. 2012;7:e29468.
- [34] Bousquet L, Hemon C, Malburet P, et al. The medium-size noncoding RNA transcriptome of Ostreococcus tauri, the smallest living eukaryote, reveals a large family of small nucleolar RNAs displaying multiple genomic expression strategies. NAR Genom Bioinform. 2020;2:lqaa080.
- [35] Krogh N, Jansson MD, Häfner SJ, et al. Profiling of 2'- O -Me in human rRNA reveals a subset of fractionally modified positions and provides evidence for ribosome heterogeneity. Nucleic Acids Res. 2016;44:7884–7895.
- [36] Hebras J, Krogh N, Marty V, et al. Developmental changes of rRNA ribose methylations in the mouse. RNA Biol. 2020;17:150–164.
- [37] Chen CL, Liang D, Zhou H, et al. The high diversity of snoRNAs in plants: identification and comparative study of 120 snoRNA genes from Oryza sativa. Nucleic Acids Res. 2003;31:2601-2613.
- [38] Streit D, Shanmugam T, Garbelyanski A, et al. The existence and localization of nuclear snoRNAs in Arabidopsis thaliana revisited. Plants (Basel). 2020;9. DOI:10.3390/plants9081016
- [39] Streit D, Schleiff E. The Arabidopsis 2'-O-Ribose-Methylation and Pseudouridylation Landscape of rRNA in Comparison to Human and Yeast. Front Plant Sci. 2021;12:684626.
- [40] Jaafar M, Paraqindes H, Gabut M, et al. 2'O-ribose methylation of ribosomal RNAs: natural diversity in living organisms, biological processes, and diseases. Cells. 2021;10:1948.

- [41] Marchand V, Pichot F, Thüring K, et al. Next-generation sequencing-based RiboMethSeq protocol for analysis of tRNA 2'-Omethylation. Biomolecules. 2017;7:13.
- [42] Zhu P, Wang Y, Qin N, et al. Arabidopsis small nucleolar RNA monitors the efficient pre-rRNA processing during ribosome biogenesis. Proc Natl Acad Sci USA. 2016;113:11967–11972.
- [43] Cao Y, Wang J, Wu S, et al. The small nucleolar RNA SnoR28 regulates plant growth and development by directing rRNA maturation. Plant Cell. 2022;34:4173–4190.
- [44] Rodor J, Letelier I, Holuigue L, et al. Nucleolar RNPs: from genes to functional snoRNAs in plants. Biochem Soc Trans. 2010;38:672–676.
- [45] Huang L, Ashraf S, Wang J, et al. Control of box C/D snoRNP assembly by N(6)-methylation of adenine. EMBO Rep. 2017;18:1631–1645.
- [46] Webster SF, Ghalei H. Maturation of small nucleolar RNAs: from production to function. RNA Biol. 2023;20:715–736.
- [47] Klinge S, Woolford JL Jr. Ribosome assembly coming into focus. Nat Rev Mol Cell Biol. 2019;20:116–131.
- [48] Erales J, Marchand V, Panthu B, et al. Evidence for rRNA 2'-Omethylation plasticity: control of intrinsic translational capabilities of human ribosomes. Proc Natl Acad Sci USA. 2017;114:12934–12939.
- [49] Natchiar SK, Myasnikov AG, Hazemann I, et al. Visualizing the role of 2'-OH rRNA methylations in the human ribosome structure. Biomolecules. 2018;8:125.
- [50] Salih KJ, Duncan O, Li L, et al. The composition and turnover of the Arabidopsis thaliana 80S cytosolic ribosome. Biochem J. 2020;477:3019–3032.
- [51] Pestov DG, Shcherbik N. Rapid cytoplasmic turnover of yeast ribosomes in response to rapamycin inhibition of TOR. Mol Cell Biol. 2012;32:2135–2144.
- [52] Decatur WA, Fournier MJ. rRNA modifications and ribosome function. Trends Biochem Sci. 2002;27:344–351.
- [53] Beckmann R, Spahn CMT, Eswar N, et al. Architecture of the protein-conducting channel associated with the translating 80S ribosome. Cell. 2001;107:361–372.
- [54] Smirnova J, Loerke J, Kleinau G, et al. Structure of the actively translating plant 80S ribosome at 2.2 A resolution. Nat Plants. 2023;9:987–1000.
- [55] Spahn CM, Beckmann R, Eswar N, et al. Structure of the 80S ribosome from *Saccharomyces cerevisiae*-tRNA-ribosome and subunit-subunit interactions. Cell. 2001;107:373–386.
- [56] Ryan PC, Draper DE. Detection of a key tertiary interaction in the highly conserved GTPase center of large subunit ribosomal RNA. Proc Natl Acad Sci U S A. 1991;88:6308–6312.
- [57] Granneman S, Petfalski E, Tollervey D. A cluster of ribosome synthesis factors regulate pre-rRNA folding and 5.8S rRNA maturation by the Rat1 exonuclease. EMBO J. 2011;30:4006–4019.
- [58] Gigova A, Duggimpudi S, Pollex T, et al. A cluster of methylations in the domain IV of 25S rRNA is required for ribosome stability. RNA. 2014;20:1632–1644.
- [59] Cottilli P, Itoh Y, Nobe Y, et al. Cryo-EM structure and rRNA modification sites of a plant ribosome. Plant Commun. 2022;100342.
- [60] Stepanov GA, Filippova JA, Komissarov AB, et al. Regulatory role of small nucleolar RNAs in human diseases. Biomed Res Int. 2015;2015:206849.
- [61] Daniely Y, Dimitrova DD, Borowiec JA. Stress-dependent nucleolin mobilization mediated by p53-nucleolin complex formation. Mol Cell Biol. 2002;22:6014–6022.
- [62] Marcel V, Ghayad S, Belin S, et al. p53 acts as a safeguard of translational control by regulating fibrillarin and rRNA methylation in cancer. Cancer Cell. 2013;24:318–330.
- [63] Sloan KE, Warda AS, Sharma S, et al. Tuning the ribosome: the influence of rRNA modification on eukaryotic ribosome biogenesis and function. RNA Biol. 2017;14:1138–1152.
- [64] Monaco PL, Marcel V, Diaz JJ, et al. 2'-O-methylation of ribosomal RNA: towards an epitranscriptomic control of translation? Biomolecules. 2018;8:106.

- [65] Daniely Y, Dimitrova DD, Borowiec JA. Stress-dependent nucleolin mobilization mediated by p53-nucleolin complex formation. Mol Cell Biol. 2002;22:6014–6022.
- [66] Durut N, Saez-Vasquez JN. Dual roles in rDNA chromatin transcription. Gene. 2015;556:7–12.
- [67] Picart C, Pontvianne F. Plant nucleolar DNA: green light shed on the role of Nucleolin in genome organization. Nucleus. 2017;8:11–16.
- [68] Ugrinova I, Petrova M, Chalabi-Dchar M, et al. Multifaceted nucleolin protein and its molecular partners in oncogenesis. Adv Protein Chem Struct Biol. 2018;111:133–164.
- [69] Ohbayashi I, Lin C-Y, Shinohara N, et al. Evidence for a role of ANAC082 as a ribosomal stress response mediator leading to growth defects and developmental alterations in arabidopsis. Plant Cell. 2017;29:2644–2660.
- [70] Gallagher JE, Dunbar DA, Granneman S, et al. RNA polymerase I transcription and pre-rRNA processing are linked by specific SSU processome components. Genes Dev. 2004;18:2506–2517.
- [71] Saez-Vasquez J, Caparros-Ruiz D, Barneche F, et al. A plant snoRNP complex containing snoRNAs, fibrillarin, and nucleolin-like proteins is competent for both rRNA gene binding and pre-rRNA processing in vitro. Mol Cell Biol. 2004;24:7284–7297.
- [72] Turner AJ, Knox AA, Prieto JL, et al. A novel small-subunit processome assembly intermediate that contains the U3 snoRNP, nucleolin, RRP5, and DBP4. Mol Cell Biol. 2009;29:3007–3017.
- [73] Verheggen C, Mouaikel J, Thiry M, et al. Box C/D small nucleolar RNA trafficking involves small nucleolar RNP proteins, nucleolar factors and a novel nuclear domain. Embo J. 2001;20:5480–5490.
- [74] Izumi RE, Valdez B, Banerjee R, et al. Nucleolin stimulates viral internal ribosome entry site-mediated translation. Virus Res. 2001;76:17–29.

- [75] Kojima H, Suzuki T, Kato T, et al. Sugar-inducible expression of the nucleolin-1 gene of Arabidopsis thaliana and its role in ribosome synthesis, growth and development. Plant J. 2007;49:1053-1063.
- [76] Petricka JJ, Nelson TM. Arabidopsis nucleolin affects plant development and patterning. Plant Physiol. 2007;144:173–186.
- [77] Pontvianne F, Matía I, Douet J, et al. Characterization of AtNUC -L1 reveals a central role of nucleolin in nucleolus organization and silencing of AtNUC - L2 gene in arabidopsis. Mol Biol Cell. 2007;18:369–379.
- [78] Udomchalothorn T, Plaimas K, Sripinyowanich S, et al. OsNucleolin1-L expression in arabidopsis enhances photosynthesis via transcriptome modification under salt stress conditions. Plant Cell Physiol. 2017;58:717–734.
- [79] Bergeron D, Paraqindes H, Fafard-Couture É, et al. snoDB 2.0: an enhanced interactive database, specializing in human snoRNAs. Nucleic Acids Res. 2023;51:D291–D296.
- [80] Lestrade L, Weber MJ. snoRNA-LBME-db, a comprehensive database of human H/ACA and C/D box snoRNAs. Nucleic Acids Res. 2006;34:D158–162.
- [81] Gaspin C, Cavaille J, Erauso G, et al. Archaeal homologs of eukaryotic methylation guide small nucleolar RNAs: lessons from the Pyrococcus genomes. J Mol Biol. 2000;297:895–906.
- [82] Schluenzen F, Tocilj A, Zarivach R, et al. Structure of functionally activated small ribosomal subunit at 3.3 angstroms resolution. Cell. 2000;102:615-623.
- [83] Rakauskaite R, Dinman JD. An arc of unpaired "hinge bases" facilitates information exchange among functional centers of the ribosome. Mol Cell Biol. 2006;26:8992–9002.
- [84] Omer AD, Lowe TM, Russell AG, et al. Homologs of small nucleolar RNAs in Archaea. Science. 2000;288:517–522.