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RNA-binding Domain of the Key Structural Protein P7 for the *Rice dwarf virus* Particle Assembly

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Abstract The *Rice dwarf virus* (RDV) P7 structural protein is the key protein in the RDV particle assembly. The P7 protein was digested partially or completely by *Staphylococcus aureus* V8 protease and/or *Pseudomonas fragi* Asp-N protease. The molecular mass and the N-terminal amino acid sequence of the polypeptide fragments of the P7 protein were determined by SDS-PAGE and the Edman degradation method, respectively. Then the polypeptides were located in the deduced amino acid sequence of the RDV P7 protein based on the nucleotide sequence information, with the knowledge of the specific cleavage sites of the *Staphylococcus aureus* V8 and *Pseudomonas fragi* Asp-N protease, and the two RNA-binding domains in the P7 protein were identified. Domain 1 was located in the residue 128–249 containing 122 amino acids and domain 2 was located in the residue 325–355 containing 31 amino acids. Thus, these two domains may play an important role in the virus particle assembly by contributing to the packaging of viral dsRNAs inside the particles. The two domains may be novel RNA-binding domains, because no amino acid sequences highly similar to the conservative sequences of known dsRNA-binding domains reported so far. The similarity between the motif of domain 1 and the motif of the DNA-binding protein suggests that the DNA-binding activity of the RDV P7 protein may be due to this sequence. The similarity between the motif of domain 1 and the motif of the RNA polymerase domain suggests that the P7 protein may also play a role in RNA synthesis, besides its function in the assembly and subsequent packaging of viral dsRNA into core particles.

Key words RDV; RNA-binding protein; protein functional domain; virion assembly; RNA polymerase

Rice dwarf virus (RDV), a member of the genus *Phytoreovirus* in the family *Reoviridae* [1,2], has an icosahedral virion 693 Å [3] in diameter that consists of two layers of protein shells which enclose a genome of 12 double-strand (ds) RNA segments. The two shell capsids consist of 7 constructional proteins, and the outer one is composed of the 127 kD P2 protein [4,5], which is involved in the ability of the virus to infect insect vector cells, the 46 kD P8 outer capsid protein [6,7] and the recently discovered 30 kD P9 protein [8]. The inner shell is composed of the 114 kD P3 protein, which encloses the dsRNAs [9–11]; a 164 kD protein P1 that is the putative RNA polymerase [12]; a 91 kD protein P5 that is the putative guanylyltransferase with NTP-binding activity [13,14]; and a 55 kD protein P7 with nucleic acid-binding activity [15–17].

The P7 protein is able to bind all the 12 dsRNAs of the RDV genome and the mRNA with high affinity and is able to form a protein complex with P1 and P5. So it was assumed that at first the P7 protein forms a complex with the genomic dsRNA to assort and subsequently package dsRNA, then the P7 protein, either alone or with the P1 protein, combines with P3, the inner capsid protein. After that, the P8 outer capsid proteins bind the P3 protein, covering the virion outer layer. In the final stage, the P2 and P9 proteins, possibly together with the P8, bind some part of the particle surface and complete the virion assembly procedure. Therefore, the P7 protein is the key protein of the virion assembly, and the process in which the P7 binds with the nucleic acid is the key step in the whole RDV particle assembly [16] procedure.

This paper focuses on the analysis of the nucleic acid-

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binding domain of the P7 protein.

Materials and Methods

Virus preparation

The intact RDV particles were purified from rice leaves 60 days after inoculation with the O strain of RDV, according to the method reported earlier [16,18], but with some modifications. Carbon tetrachloride (CCl_4) was not used in order to obtain intact virions. The 10%–40% and the 40%–60% linear sucrose gradient solutions were made in 100 mM histidine containing 10 mM $MgCl_2$, pH 6.2 (His-Mg). After consecutive centrifugations in the sucrose gradients described above, the layer containing virions was taken from the tube, and centrifuged for 1 h at 96,000 *g*. The purified viral particles were obtained by resuspending the pellet in the His-Mg buffer and were kept at –70 °C. The viral particles were negatively stained with 2% aqueous uranyl acetate (UA) on carbon-coated collodion grids and examined using a Hitachi H-7000 electron microscope (Hitachi, Japan).

Sequence analysis of polypeptide fragments from P7 protein

The RDV virions were incubated at room temperature for 10 min in the sample buffer solution of 2% SDS and 2% 2-mercaptoethanol, then heated at 100 °C for 3 min. The proteins in the sample were separated by SDS-PAGE (10% polyacrylamide; acrylamide:bisacrylamide=30:0.8) [19] and stained with Coomassie brilliant blue (CBB R-250). The P7 protein band was cut out and the protein was electroeluted from the gel pieces using a protein extraction unit (Nihon-eido, Tokyo, Japan). The purified protein was digested partially or completely with the *Staphylococcus aureus* V8 protease (Pierce, Rockford, USA) (0.1 mg/ml) in the 0.1% SDS solution by changing the reaction time. Fragments were separated by 18% SDS-PAGE, and transferred onto a PVDF membrane. Meanwhile, the gel pieces containing partially digested peptide fragments whose molecular mass was about 30 kD were cut out and electro-eluted. This 30 kD polypeptide was digested thoroughly with *Pseudomonas fragi* Asp-N protease (Boehringer Mannheim, Germany) (0.1 mg/ml) in 50 mM phosphate buffer, pH 8.0. The digested polypeptide fragments were separated by 18% SDS-PAGE and transferred onto the PVDF membrane. The PVDF membranes were stained with CBB G-250 and each of the stained bands was cut out and subjected to Edman degradation using an automated protein sequencer (Applied Biosystems 492, Applied Biosystems, USA) [20].

Preparation of labeled polynucleotide probes

dsRNAs were extracted from the purified RDV according to the method described elsewhere [16,21]. They were then dephosphorylated with orthophosphoric-monoester phosphohydrolase (Boehringer Mannheim, Germany) and the 5′ end was labeled *in vitro* by phosphate transfer from [γ-^{32}P]ATP (>3000 Ci/nmol; Amersham International, USA) with T4 polynucleotide kinase (TaKaRa, Japan).

Northwestern blotting analysis

Northwestern blotting analysis to detect nucleic acid-binding polypeptide fragments of the P7 protein of RDV was performed according to the method described elsewhere [16,22]. The protease-digested fragments of P7 protein were separated by SDS-PAGE and transferred onto PVDF membranes (Millipore, USA). The membranes were blocked for 30 min at room temperature in standard binding buffer (SBB) containing 10 mM Tris-HCl, pH 7.0, 1 mM EDTA, 0.02% BSA, 0.02% polyvinylpyrrolidone, 0. 02% Ficoll and 50 mM NaCl, and were washed three times for 10 min each in the same buffer at room temperature. The PVDF membranes were then incubated overnight with ^{32}P-labeled RDV dsRNA probes (3×10^4 cpm/ml) in SBB. Unbound ^{32}P were removed by three cycles of washing with SBB containing 0.05% Tween-20 for 10 min at room temperature. The PVDF membranes containing fragments of P7 protein that bind the dsRNA of RDV were air dried and autoradiographed at –70 °C with intensifying screens.

Database search analysis

The websites for the homology search were:
http://www.ncbi.nlm.nih.gov
http://www.ebi.ac.uk
http://www.ddbj.nig.ac.jp

The websites for the domain and motif search were:
http://www.ebi.ac.uk/interpro
http://www.toulouse.inra.fr/prodom.html
http://smart.embl-heidelberg.de

Results

Pattern analysis of the RDV P7 protein fragments digested by proteases

Nine polypeptide bands were detected after the separation by SDS-PAGE following the digestion of the RDV P7

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protein for 30 min by the *Staphylococcus aureus* V8 protease [**Fig. 1(A)**, lane 1]. Seven bands were detected after 1 h of digestion [**Fig. 1(A)**, lane 2]. The SDS-PAGE gel pattern after 8 h of digestion was similar to that after 1 h of digestion [**Fig. 1(A)**, lane 3]. Then, Northwestern blotting was carried out to see the bands that react to the polypeptide bands observed above. Seven of the 9 bands (bands 1, 2, 4, 5, 6, 7 and 8) were detected by the 30 min digestion of the P7 protein, and 4 of the 7 bands (bands 10, 12, 13 and 14) were detected by the 1 h and 8 h digestions, which bound the dsRNA of RDV [**Fig. 1(B)**, lanes 1–3]. These results indicate that some polypeptides of the P7 protein react specifically to RDV dsRNA and suggest that there must be some RNA-binding domains in the P7 protein of RDV.

A large number of polypeptide bands with molecular masses about 35 kD and 30 kD were detected in the gel after SDS-PAGE of the P7 protein that had been digested for 10 min with the *Staphylococcus aureus* V8 protease. These polypeptides reacted with dsRNAs, as shown by the Northwestern blotting, suggesting that the 30 kD polypeptide contains an RNA-binding domain (data not shown). Therefore, the 30 kD polypeptide was further digested using the *Pseudomonas fragi* Asp-N protease for 1 h and separated by SDS-PAGE, and 7 polypeptide bands were obtained in the gel stained with CBB. Among the 7 polypeptide bands, there was a very small quantity of band 23 [**Fig. 1(A)**, lane 4]. After 8 h of digestion followed by an SDS-PAGE separation, 6 peptide bands were detected, of which band 22 was very faint [**Fig. 1(A)**, lane 5]. The Northwestern blotting analysis showed that five of these polypeptide bands reacted with RDV dsRNA [**Fig. 1(B)**, lanes 4 and 5].

We discovered that triosephosphate isomerase (26625D), myoglobin (16950D) and aprotinin (6512D), which are some of the standard protein molecular mass samples produced by the Bio-Rad Company (USA), can bind with the RDV dsRNA [**Fig. 1(B)**, lane M2]. This discovery played a very important role in the processing of the experimental data.

Analysis of the dsRNA-binding domain of RDV P7

About 10 N-terminal residues of all the polypeptide fragments of the P7 protein were sequenced, and we compared the amino acid sequence of these peptides with the RDV O strain P7 sequence to confirm each peptide band's initial site in the P7 protein. Then, we located the ending site of the different peptide bands in the P7 protein (**Table 1**) according to the P7 protein amino acid sequence, the molecular mass of the peptide bands, the specific clea vage site of the *Staphylococcus aureus* V8 protease, which is the C-ending of the Glu, and the specific cleavage site of the *Pseudomonas fragi* Asp-N protease, which is the N-ending of the Asp and Cys.

There were some peptide fragments detected in the same

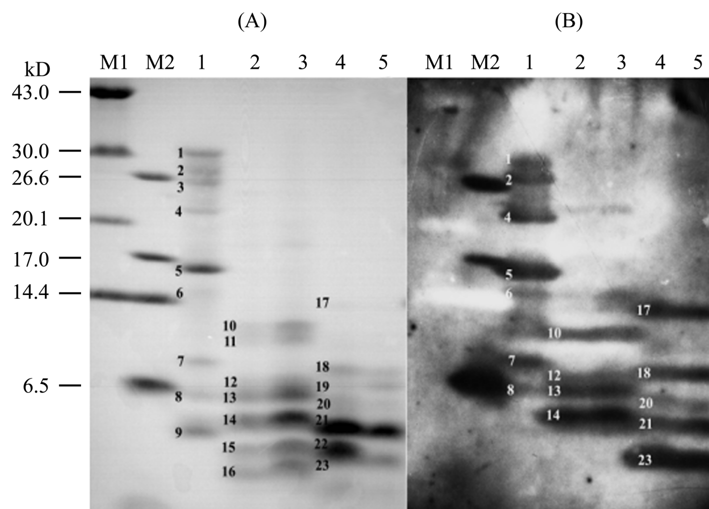

Fig. 1 The pattern of the protease-digested P7 protein and the result of the Northwestern blotting

The protease-digested RDV P7 protein was separated by SDS-PAGE, and stained with CBB G-250. M1 is the standard protein molecular mass marker produced by Pharmacia Biotech Company (USA), and M2 is the standard protein molecular mass sample produced by BIO-RAD Company (USA). The molecular masses of the markers are indicated on the left. (A) 1, 2 and 3, polypeptide fragments digested with the *Staphylococcus aureus* V8 protease for 30 min, 1 h and 8 h, respectively; 4 and 5, polypeptide fragments obtained by the digestion of the 30 kD peptide fragment (after digestion of the P7 protein by the *Staphylococcus aureus* V8 protease for 10 min) for 1 h and 8 h with *Pseudomonas fragi* Asp-N protease. (B) Northwestern blotting of the polypeptide fragments.

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Table 1 The sequence of the P7 protein fragments and their binding with RDV dsRNAs

Band No.	N-terminal amino acid sequence of the polypeptide fragment	Detected initial site	Presumed sequence range	Theoretical MW (Da)	Northwestern blotting analysis
1	MSAIVGLCLLSE	1	1–273	29693	++
2	VSKLYKLNRG	24	24–273	27247	++
3	MSAIVGLCLLSE	1	1–239	25953	–
4	LSELKRTDSDAY	300	300–497	21754	++
5	LSELKRTDSDAYEKLYSE	300	300–452	16869	++
6	TISKHVSDGSYG	318	318–452	14740	+
7	LKRTDSDAYEKL	303	303–379	8694	++
8	LKRTDSDAYEKL	303	303–370	7607	+
9	LFSMGSGKREPLALE	240	240–288	5408	–
	LTDAGILVESTGPDR	453	453–506	5870	
	STGPDRVRRSPKVLA	462	462–506	4958	
10	ISYLVMVIGP	128	12–249	13013	+
11	VSKLYKLNRG	24	24–127	11607	–
	ISYLVMVIGP	128	128–239	11919	
12	LKRTDSDAYEKL	303	303–370	7607	+
	ALSGNGLVTDSN	380	380–452	7863	
	NIVVCFKNGFPN	421	421–497	8427	
13	TISKHVSDGSYG	318	318–379	6894	++
14	TISKHVSDGSYG	318	318–370	5807	++
15	PLALEFRKDN	250	250–290	4531	–
	ALSGNGLVTD	380	380–420	4339	
	NIVVCFKNGF	421	421–461	4455	
	STGPDRVRRS	462	462–506	4958	
16	VSKLYKLNRG	24	24–69	5293	–
	PLALEFRKDN	250	250–288	4315	
	ALSGNGLVTD	380	380–420	4339	
	NIVVCFKNGF	421	421–452	3543	
17	DGSYGNRVII	325	325–450	13743	++
18	DGSYGNRVIISH	325	325–400	8322	++
19	ALSGNGLVTD	380	380–452	7863	–
20	DVYDRCMDLD	193	193–257	7232	+
	DAYEKLYSET	309	309–371	7070	
	DGSYGNRVII	325	325–388	6954	
21	DEVSKLYKLNRGNVKE	22	22–69	5538	++
	DIIGSPSNTAPQTAFQ	82	82–142	6527	
	DGSYGNRVIISHKMSR	325	325–371	5168	
	DAGILVESTGPDRVRR	455	455–506	5656	
22	DRCMDLDGILLSQAL	196	196–239	4691	–
	DFNTVKKNLSSRSGE	356	356–396	4480	
	DGNKKSENIVVCFKN	414	414–454	4516	
	STGPDRVRRSPKVLA	462	462–506	4958	
23	DGSYGNRVII	325	325–355	3391	++
	DGNKKSENIV	414	414–450	4058	

MW, molecular weight. "++" means the most intensive Northwestern blotting signal, "+" means the band can be detected, while "–" means no signal.

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band probably due to their similar molecular mass. Based on the sequence information of the P7 protein and the specificity of the protease cleavage site, we can easily find out the amino acid sequence of these peptides. The different capacity of these peptide fragments to bind with the RDV dsRNA seems to result in the discrepancy between the consistency of the CBB G-250 bands and the intensity of the Northwestern blotting.

The results of the Northwestern blotting of bands 1, 2 and 10 prove that the amino acid residue 128–249 has RNA-binding activity, while bands 3 and 11 show that those peptide fragments with the amino acid residue 128–239 have no RNA-binding activity. Band 9 also proves that the amino acid residue 240–288 does not have RNA-binding activity [**Fig. 1(B)**]. From these results, we can draw the conclusion that some portion of the 122 amino acid residues (128–249) whose sequence is ISYLVMVIGPPSGFMDTPNVSSAQSSVHTVSNADVDLNDIIAINSTMAKSTKLVSASTLQAMLVNDVYDRCMDLDGILLSQALPFFRNYVNVQSKGSLPPAVAACLNTPIKELFSMGSGKRE is the minimum required sequence for RNA-binding activity. We have named it the RDV P7 protein RNA-binding domain 1.

The result of band 22 proves that the peptide containing the amino acid residue 414–454 has no RNA-binding activity. This shows that the RNA-binding activity of band 23 was due to the amino acid residue 325–355. Bands 4, 5, 6, 7, 8, 12, 13, 14, 17, 18, 20 and 21 all show RNA-binding activity [**Fig. 1(B)**], and all contain the amino acid residue 325–355 (**Table 1**). These results suggest that the amino acid residue 325–355 might be the minimum entity of the RNA-binding domain. The results of the Northwestern blotting of bands 9, 15, 16, 19 and 22 show that the amino acid residue 250–290 or behind 355 has no RNA-binding activity. This result shows that the 31 amino acids composed of DGSYGNRVIISHKMSRLSNGGVKIIGRFKIS residue 325–355 might be the minimum entity of the RNA-binding domain. We have named it the RDV P7 protein RNA-binding domain 2.

Comparative analysis of the RDV-P7 protein RNA-binding domain

Through the homology comparison, we found that the RDV P7 protein does not contain amino acid sequences highly similar to the conservative sequences of known dsRNA-binding domains that have been reported so far [23]. The results of the domain and motif search show that the peptide fragments 155–187 and 172–221 of the RDV P7 protein RNA-binding domain 1 (amino acid residue 128–249) are similar to the motif of the poxvirus nucleic acid-binding protein VP8/L4R and the DM DNA-binding protein from the DM protein family, respectively (**Table 2**). The amino acid residue 133–183 is similar to the motif of the RNA polymerase Rpb 2, domain 7. The RDV P7 protein RNA-binding domain 2 shows no similarity with any known domain.

Discussion

The RNA-binding domains of the P7 proteins of RDV

Table 2 The domain comparison analysis of RDV P7 protein RNA-binding domain 1

Functional protein	Blocks database accession No.	Residue	Matching sequence (capital)	Score
Poxvirus nucleic acid-binding protein VP8/L4R	IPB007586D		-T-S--DV-LND-IA------KS--L-S--T--	1013
RDV P7 protein RNA-binding domain 1		155–187	HTVSNADVDLNDIIAINSTMAKSTKLVSASTLQ	
DM DNA-binding protein from DM protein family	IPB001275		-T-AK------ASTL-A------Y--CM-LD-ILLSQ----RN-VN---	1001
RDV P7 protein RNA-binding domain 1		172–221	STMAKSTKLVSASTLQAMLVNDVYDRCMDLDGILLSQALPFFRNYVNVQS	
RNA polymerase Rpb 2, domain 7	IPB007641J		-VIGP-S----P--S-AQS--H-V----V----------T-A----L-S-	1051
RDV P7 protein RNA-binding domain 1		133–183	MVIGPPSGFMDTPNVSSAQSSVHTVSNADVDLNDIIAINSTMAKSTKLVSA	

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were narrowed down by amino acid sequence analysis and molecular mass analysis of the partially or completely digested peptide fragments of the RDV P7 protein, and referring to the predicted amino acid sequence of the P7 protein which is deduced from the nucleotide sequence information. The results shown in this study suggest that the combination of digestion by different proteases and the various digestion times can be used to detect protein domains with specific functions.

This research proves that there are two RDV P7 protein RNA-binding sites that contain regions which do not have conservative sequences identical to those of known dsRNA-binding domains [23], suggesting that the two regions are novel in their dsRNA-binding property. The RDV P7 protein has DNA-binding activity [16], and part (residue 155–221) of domain 1 is similar to the DNA-binding protein motif. This result suggests that the DNA-binding activity of the RDV P7 protein may be due to the property of this fragment. We have found that the amino acid residue 128–239 has no RNA-binding activity, but achieves this activity only when the polypeptide is extended to the amino acid residue 249, suggesting that the C-terminal 10 amino acids of the fragment would have a specific binding activity. This indicates that the RDV P7 protein RNA-binding domain may be larger than the DNA-binding domain.

During the replication and construction procedure of the RDV particle, the P7 protein is considered to play an important role in the assembly and subsequent packaging of viral dsRNA into core particles. We discovered that part (residue 133–183) of the RDV-P7 protein RNA-binding domain 1 is similar to the motif of the RNA polymerase Rpb 2, domain 7. Therefore, it would be interesting to study whether the P7 protein has the RNA synthesis activity besides the functions of assembly and packaging of viral dsRNA into virus particles.

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