Structural Analysis of Arabidopsis thaliana Chromosome 5. V. Sequence Features of the Regions of 1,381,565 bp Covered by twenty one Physically assigned P1 and TAC Clones

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Abstract

The nucleotide sequences of 21 Pl and TAC clones which have been precisely localized to the fine physical map of the Arabidopsis thaliana chromosome 5, were determined, and their sequence features were analyzed. The total length of the regions sequenced in this study were 1,381,565 bp, bringing the total length of the chromosome 5 sequences determined so far to 6,691,670 bp together with the regions of the 69 clones previously reported. By computer-aided analyses including similarity search against protein and EST databases and gene modeling with computer programs, a total of 337 potential protein-coding genes and/or gene segments were identified on the basis of similarity to the reported gene sequences. An average density of the genes and/or gene segments thus assigned was 1 gene / 4,100 bp. Introns were identified in 76.7% of the potential protein genes for which the entire gene structure were predicted, and the average number per gene and the average length of the introns were 3.9 and 176 bp, respectively. These sequence features are essentially identical to those in the previously reported sequences. The numbers of the Arabidopsis ESTs matched to each of the predicted genes have been counted to monitor the transcription level. The sequence data and gene information are available on the World Wide Web database KAOS (Kazusa Arabidopsis data Opening Site) at http://www.kazusa.or.jp/arabi/.

Key words: Arabidopsis thaliana chromosome 5; genomic sequence; P1 genomic library; TAC genomic library; gene prediction.

To reveal the whole genetic information in a dicot model plant, Arabidopsis thaliana, we initiated largescale structural analysis of the genome. Of five chromosomes which comprise the A. thaliana genome of approximately 130 Mb, we chose chromosome 5 as the initial target. For precise localization of the clones for DNA sequencing, we first constructed the fine physical map of the chromosome 5^1 using three genomic libraries of A. thaliana Columbia, CICYAC,² P1³ and TAC (Transformation-competent Artificial Chromosome, Mitsui Plant Biotechonolgy Research Institute, Japan). The template clones were selected from the P1 and TAC libraries based on the DNA markers on the fine physical map by means of polymerase chain reaction (PCR) using marker-specific primers. The isolated P1 and TAC clones were then subjected to shotgun-based sequence analysis. We previously reported the sequences of a total of 5.31 Mb which were obtained by analysis of 69 P1 and TAC clones.⁴⁻⁷ In this paper, we newly determined

the sequences of 21 additional P1 and TAC clones. We describe gene organization and structural and functional information of the genes assigned in the sequenced regions which were deduced by computer-aided analysis.

1. Isolation and Sequencing of P1 and TAC Clones

Two types of genomic clones of A. thaliana Columbia, P1 and TAC, which are respectively represented by adding "M" and "K" to the first letters of the clone names, were used for sequence analysis. The average insert length of the P1 and TAC clones was approximately 80 kb. The P1 and TAC clones, containing the DNA segments which cover 21 different regions of chromosome 5, were isolated by screening the Mitsui P1 and TAC libraries by PCR with the primers designed from the sequence information of DNA markers of the defined positions, as described previously.⁴⁻⁷ The DNA markers and the selected clones (in parentheses) are: MOP10_Left (K18I23), g3837 (MOJ9), ends of MAC12 and MSH12 (MXE10), PAT1 (MPI7),

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Figure 1. Relative locations of the P1 and TAC clones sequenced in this study and the associated markers on the physical map of chromosome 5. The positions of DNA markers used for P1 and TAC isolation and of other major DNA markers were localized on the map on the basis of the YAC tiling path and map information in *ref.* 1. The vertical open bar represents the entire length of chromosome 5. The names of P1 and TAC clones are given at the right, and those of markers at the left. The distance (Mbp) from the telomeric site of the top arm is given on the vertical scale.

CIC12F2L (MLE8), MWP19_Left (MXH1), ends of MXA21 and MXI10 (MSI17), CIC4E7R (MKD10), CIC4A3R (K3K3), MPO12_Left (MSN9), CIC4A3L (MHK7), MLN1_Right (K9L2), CIC4E12R (K21C13), T14190 (MPL12), CIC7B9L (MDK4), MWA11_Left (MDA7), m558a (MUA2), MUP24_Right (MUF9), pC-ITd110 (MNA5), CIC4B2R (K2A18), and MSN2_Right (MUD21). Relative positions of the markers and the sequenced clones on chromosome 5 are shown in Fig. 1. The orientation of each clone on the fine physical map of chromosome 5¹ has been confirmed by anchoring both ends of the clone to those at the corresponding positions of the map.

The nucleotide sequence of each P1 or TAC insert was determined according to the bridging shotgun method described previously.⁴⁻⁷ The length of the nucleotide sequence of each P1 or TAC insert finally confirmed is given in parentheses after the clone name at the top of Fig. 2. The total of the DNA regions sequenced in this study

was 1,381,565 bp, bringing the total length of the regions of chromosome 5 sequenced so far to 6,691,670 bp.

2. Assignment of Potential Coding Regions

Potential protein coding regions were assigned by similarity search, and gene modeling was performed using prediction programs, as described in the previous papers.⁴⁻⁷ In brief, similarity search against the nonredundant protein sequence database, owl (release 29), was carried out using the BLASTP⁸ program, and information obtained were integrated into the gene models constructed with the aid of the following computer programs: Grail,⁹ FEXA in GeneFinder,¹⁰ ER (Murakami, K., personal communication), ASPL in GeneFinder,¹⁰ GENSCAN¹¹ and NetPlantGene programs.¹² The transcribed regions were assigned based on a comparison of the nucleotide sequences with Arabidopsis ESTs^{13,14} in the non-redudant library of GenBank (release 104) and EMBL (release 52) databases using the BLASTN program.⁸

The potential protein-coding regions assigned were divided into three categories. A single exon or a region containing consecutive multiple exons showing similarity to a single reported gene throughout the alignment was designated as a potential protein gene; they were denoted by numbers with the clone names followed by sequential numbers from one end to another of the insert. A region which matched only to portions of a reported gene and only to Arabidopsis ESTs were assigned as a potential exon(s) and a transcribed region, respectively. These regions were denoted by adding "p" and "t" between the clone names and the sequential numbers in the identifiers, respectively. All the genes and gene segments assigned in each P1 and TAC clone according to the above procedure were schematically represented in Fig. 2, and the assignment data were listed in the table below each figure. In total, 257 potential protein genes, 23 potential exons, and 57 transcribed regions were assigned in the 1,381,565 bp regions. The number of genes and gene segments assigned so far in the total of 6,691,670 bp (including the previously reported sequences) is 1,573, and an average density of the genes in the three categories is estimated to be 1 gene per 4,254 bp. However, the possibility remains that additional genes may be discovered in the future among the genes and gene segments assigned so far, because our prediction is principally based on similarity to the registered sequences.

In addition to the protein coding regions, RNA coding regions were assigned on the basis of sequence similarity to the reported structural RNAs, and of prediction by the tRNAscan-SE program¹⁵ in the case of tRNA genes. As indicated in Fig. 2, 4 tRNA genes corresponding to 4 amino acid species were identified in the 1,381,565 bp regions. These genes were denoted with the clone names followed by "r" and sequential numbers.

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Features	257genes ^{a)}	1,001 genes ^{b)}
Gene length (bp) including introns	194-10,730 (2,056)	164-11,377 (2,037)
Product length (amino acids)	41-2,756 (458)	41-2,756 (442)
Genes with introns	197	777
Number of introns/genes	0-25(3.9)	0-42 (3.9)
Exon length (bp)	3-4,287 (283)	2-4,287 (270)
Intron length (bp)	24 - 2,110(176)	20-5,405 (181)
GC content of exon	44%	44%
GC content of introns	32%	32%

Structural features of the 257 potential protein genes assigned in this study^{a)} and the 1,001 genes assigned so far^{b)} are listed. Average values are shown in parentheses.

3. Structural Features of Potential Protein Genes

In this report, the complete structures of 257 potential protein-coding genes were predicted by a combination of similarity search and computer prediction. Structural features of these genes, as well as those of 1,001 genes including those previously deduced which correspond to approximately 5.0% of the total gene constituents (20,000 genes) assumed for A. thaliana, are listed in Table 1. The average gene length including introns was approximately 2 kb, and 78% of these genes contained introns at an average number of 3.9 per gene. The average lengths of exons and introns were 270 bp and 181 bp, respectively.

4. Expression Level of Potential Protein Genes and Gene Segments

The nucleotide sequence of each of the potential protein-coding genes was compared with those in the Arabidopsis EST database, and the number of matched Arabidopsis ESTs was counted. Of the 337 genes and gene segments that we assigned in chromosome 5 in this study, 166 carried matched ESTs, and 770 out of 1,573 genes and gene segments assigned so far matched ESTs suggesting that the current EST database represents 49% of the gene complement in A. thaliana. The putative products of the genes which hit 10 times or more to the EST files include those showing sequence similarity to chlorophyll a/b-binding protein in Pisum sativum (MDK4.7), methionine synthase in Mesembryanthemum crystallinum (MPI7.9), cysteine protease in P. sativum (MUF9.1), elongation factor 1-alpha in A. thaliana (MUF9.2), 14-3-3-like protein gf14 kappa in A. thaliana (MNA5.10), tubulin beta-4 chain in A. thaliana (K9L2.9), reticuline oxidase precursor in Eschscholtzia californica (K9L2.12), CLC-a chloride channel protein in A. thaliana (MHK7.8), ketoconazole resistance protein in A. thaliana (K2A18.6), alpha subunit of proteasome in A. thaliana (K2A18.13), and ferredoxin-NADP reductase precursor in Vicia faba (K2A18.15). These genes are suggested to be a class of highly expressed genes. The

sequence data as well as the gene information shown in this paper are available through the World Wide Web at http://www.kazusa.or.jp/arabi/.

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Figure 2. Gene organization in the 21 P1 and TAC clones. The orientation of each clone in this figure (left to right) corresponds to that in Fig. 1 (top to bottom). Positions of the assigned or predicted genes and gene segments in each insert of the P1 and TAC clones were schematically presented by color-coded boxes above (rightward) and below (leftward) the wide line in the middle which represents the entire sequenced region. The insert length is given in parentheses together with the clone name at the top. Arrowheads indicate the directions of the DNA strands (5' to 3'). Dark and faint blue boxes with numbers represent the positions of the assigned potential protein genes and potential exons, respectively, and red bars represent the positions of structural RNA genes. Gray boxes with numbers indicate the positions of the transcribed regions. The regions which showed similarity to the sequences in the protein database are shown by yellow, orange and red bars, corresponding to BLASTP scores of 70-100, 100-250, and 250 or more, respectively. The green bars indicate the positions of the potential exons predicted by the Grail program. The three different shades of green correspond to the region with Grail scores of less than 70, 70-90, and 90 or more, respectively. The potential protein genes, the gene segments and the potential RNA genes assigned as described in the text are listed below each of the figures. The accession numbers are as follows: AB011474 (K2A18), AB010694 (K3K3), AB011475 (K9L2), AB010692 (K18123), AB010693 (K21C13), AB011476 (MDA7), AB010695 (MDK4), AB011477 (MHK7), AB011478 (MKD10), AB010696 (MLE8), AB011479 (MNA5), AB010697 (MOJ9), AB011480 (MPI7), AB010698 (MPL12), AB011481 (MSI17), AB010699 (MSN9), AB011482 (MUA2), AB010700 (MUD21), AB011483 (MUF9), AB011484 (MXE10), and AB011485 (MXH1).

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3K3.3 3K3.4	-		9676	14219 18060	2 2	U 2	1466	AC002062 U75192	1453 222	36.9	Sequence of BAC F20P5 from chromosome 1 germin-like protein	Arabidopsis thaliana Arabidopsis thaliana
363.5	+		30427	32550	6	1	303	S77427	327	24.8	hypothetical protein	Synechocystas sp
3K3 7	1		42876	46544	1	a	1223	X98130	916	41 2	81kb genomic sequence	Arabidopsis thaliana
3K3 8 3K3 9	-		50996 52756	51882 54664	23	0	246 320	L'30481 \$53082	229	54.6	expansin At-EXP2 hypothetical protein, pollen allergen homolog	Arabidopsis thaliana Thermus aquaticus
3K3 10	-	- 1	55230	56199	2	U	252	U64893	228	56.1	expansio	Pinus taeda
3K3 12			61944	62880	2 2	0	263	C64893	248	55.6	expansion	Pinus laeda
JK3 13	-	-	63797	64994	2	0	284	U30481	220	57.7	expansin At-EXP2	Arabidopsis thahana
tential	exona											
entifier	Dites	Petion	sition 5	3.	No of Exon	No. of EST hit	Length (aa)	Accession	Overlap (aa)	Identity (%, aa)	Definition	Species
3K3 P1	-		1	643	r	D.	214	¥12321	211	33.2	SLG-Sc and SLA-Sr genes and Melmoth retr	o- Brassica olerarea
K3 P2	+		67768	68889	1	5	374	U53418	374	91.4	UDP-glucose dehydrogenase	Glycine maz
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DK4	(78596	5 bp)	11			8 8 11	1	1	1	11 10	1	Grail exon Protein db hit EST db hit
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stantial autifier SK41 SK42 SK43 SK43 SK43 SK43 SK43 SK43 SK43 SK43	(78596	tion	sition 5 4970 9968 11374 4970 53562 24498 60027 65567 67555 60503 85567 67555 60503 85567 778096	3 9402 9502 9505 10521 17552 20607 32733 22733 22607 22607 22607 22607 20607 22607 20507 20507 2	No. of Exon 2 6 3 3 8 17 3 3 11 10 9 9 1 1 1 1 1 10 9 1 1 1 1 1 1 1	No. of EST ht 0 0 0 2 2 2 3 5 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	7 7 (aa) (aa) (aa) (aa) (aa) (aa) (aa) (Accession 207343 D43970 AC00232 S3270 33172 S3152 S515	Overlap (ia) 1508 2002 2002 2002 2002 2002 2002 2002 2	Identity (%, aa) 33.0 35.0 35.0 35.0 35.0 35.0 35.0 35.0	Definition chromosane 4. ESSA 1 contrg fragment No. 8 CPRDA protein CPRDA protein CaMB-channel protein protein Construction protein Construction protein Construction mysear heavy chain ATM22 mysear heavy chain ATM22	Grail exon Protein db hit EST db hit Gene EST db hit Protein db hit Grail exon Species Arabidopsis thatana Yugaa ungucaiata Arabidopsis thatana Mus masculus Pixim satusu Burno sapica Arabidopsis thatana Mus masculus Pixim satusu Arabidopsis thatana Burno sapica Arabidopsis thatana Arabidopsis thatana Burno sapica Arabidopsis thatana Arabidopsis thatana
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MLE8 (15871 bp)





potential exons												
		Position		No. of	No. of	Length	Accession	Overlap	Identity	Definition	Species	
identifier	Direction	5	3.	Exon	EST hit	(44)	- In the Market	(aa)	[哭. 65]		n and a reason was a second a reasonal	
MSN9 P1		29310	30227	3	0	144	Z97339	165	67.9	chromosome 4. ESSA I contig fragment No. 4	Arabidopus thaliana	
MSN9 P2	-	37865	60841	15	1	345	149127	455	31.1	intracellular protein	Unknown.	
transcribe	d regions											
		Position					Accession	Overlap	Identify	Definition		
identifier	Direction	2.	3.					(nt)	1% nt			
MSN9 T1	+	21815	22332		- 1877 - E	1.5	AA042237	518	91.2	CD4-13 cDNA clone E4G6T7		



potential	RNA genes										
designation	Direction	Pontion	-	No. of	No of EST ha	Length	Accession	Overlap	Identity	Definition	Species
K9L2 R1	Diferencia	13613	13684	1	0	72	L20948	57	89.0	(RNA-Lys/UUU)	Leishmania tarentolae
K9L2 R2		\$1708	51780	1		73	X17513	73	82.0	(RNA-Val(TAC)	Home sapiens





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MP17 (40548 bp)

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							-				Gene
	1	3		S 174		é.					
		in in		3 14		5					EST db hit
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potential	protein genes		-								
American	Direction	Position	- 1	No of	No of	Length	Accession	Overlap	Identity (% aa)	Definition	Species
MPIT 1	-	3190	4899	1	0	570	AC000106	595	34.0	Sequence of BAC F7G19 from chromosome 1	Arabidopus thaliana
MP17.2	+	\$366	8683	1	3	105	P11892	106	52 8	50s ribosomal protem cl25, chloroplast precursor	Pisum saturum
MPI7 3	-	9598	13645	4	0	1133	AC002354	1138	38.5	genomic sequence of BAC F06P23 from chromo- some IV	Arabidopsis thaliana
MP17.4	+	17564	20763	-4	1	861	AC002354	769	46.0	genomic sequence of BAC F06P23 from chromo-	Arabidopsis thaliana
MPIT 5		20831	21895	1	0	355	L'53154	347	23.3	creamid C33G8	Casnorhabdutus elegans
MPI7.6	+	25693	26888	1	0	398	P55081	424	44.8	microfibrillar-associated protein 1	Homo sapiens
MPI7 7	+	28455	31427	1	0	991	U.52064	997	21.4	ORF73 homolog	Kaposi's sarcoma-associate herpes-like cirus
MPI7.8	+	31664	32838	1	2	385	151116	444	26.4	NF-180	Unknown.
MP17-9	+	36320	39741	ц	21	765	L'84889	765	89 7	methionine synthase	Mesembryanthemam crystallmum
potential	*XOD#										
	0.000	Position	-	No. of	No of	Length	Accession	Overlap	Identity	Definition	Species
identifier	Direction	5	3	Exon	EST hit	(44)	242 222 AL	(aa)	(%, aa)		and the second sec
MPI7 P1	+	3	1478	1	0	492	AC000105	527	35 7	Sequence of BAC F7G19 from chromosome 1	Arabidopsis thaliana
transcribe	d regions										
direction .	Discourse	Position					Accession	Overlap	Identity	Definition	
MOIT TI	Direction	18121	15905		-		702077	1011	(3), n()	AT NHC IN A close MARTE	1771
MPIT T2		22591	23152				R29784	562	69.2	Lambda-PRL2 cDNA clone 159D4T7	
the second se		23672	23901				F15223	191	91.0	clone GBGD299: 3 and	
MPIT T3							F15224	21.5	86.8	clone GBGD299, 5 end	
MPI7 T3	+						I LUAR I				
MP17 T3 MP17 T4	<u>+</u>	27128	27376				F14281	249	92.4	cione YAY871 3' end	

MSI17 (26624 bp)



potential protein genes												
identifier	Direction	Position 3	3.	No of Exon	No. of EST hit	Length (aA)	Accession	Overlap	Identity (X. aa)	Definition	Species	
MSH7.1	+	3359	5134	5	0	264	Z92539	218	31 7	cosmid SCY10G2	Mycobacterium tuberculosus	
porential e	XUUS	Position	-	No. of	So of	Length	Accession	Overlap	Identity	Definition	Species	
identifier	Direction	5	2.	Exon	EST hat	ias)		(00)	17. sai		- Print	
MSI17 P1	-	1	411	1	D	137	L47183	137	62.8	feverse transcriptase	Arabidopsis thaliana	
MS117 P2	+	20263	26344	7	0	1329	Z97342	1322	38.5	chromosome 4. ESSA I contig fragment No. 7	Arabidonsis thaliand	



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