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Rapid report

The *Terminal acidic SANT 1* (*Tacs1*) gene of maize is expressed in tissues containing meristems and encodes an acidic SANT domain similar to some chromatin-remodeling complex proteins

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Abstract

While screening for plant homologs of telomeric-complex proteins, we isolated a cDNA for the *Terminal acidic SANT 1* (*Tacs1*) gene of maize, encoding a 45-kDa protein with a C-terminal Myb/SANT-like domain. Gene expression and protein modeling data indicate that the TACS1 protein may function in chromatin remodeling within shoot primordia or other meristem-containing tissues.

Keywords: Telomere; Myb-like DNA-binding domain; SANT domain; Primordium; Surface electrostatic potential; Plant

Bioinformatics has emerged as a powerful tool in functional genomics, providing critical clues for assignment of likely biological functions to DNA sequences [1]. Sequence-similarity searches, although valuable, can lead to mistaken annotations, especially when experimental evidence is replaced by computational gene models. Within plant-science research, a wealth of gene and genome sequence data is available for computer-assisted genetic analysis [2,3]. Gene annotation problems also exist in plant science, exemplified by several sequences annotated as encoding telomere-binding proteins. Many of these proteins contain a so-called "telobox," a protein sequence motif that was first described as a single Myb-like DNA-binding domain (DBD) common to animal and fungal telomeric-complex proteins [4]. This motif was shown to be present in several plant proteins, including maize initiator-binding protein 1 (IBP1) [5], parsley Box P-binding Factor-1 (BPF-1) [6], and several uncharacterized open reading frames (ORFs) from rice and arabidopsis [4]. Analyses of these and related genes from plants provide evidence for at least two different classes of plant genes whose products bind to telomere repeat DNA in vitro. The IBP/RTBP1-type genes (named after maize *IBP1* and rice *RTBP1*) encode proteins of ~70 kDa with a single Myb-like telomere repeat DBD followed by a glutamine-rich stretch of ~50 residues at the –COOH terminus [7–10]. The SMH-type genes (named after maize *Smh1*) encode basic proteins of ~32 kDa with an N-terminal Myb-like DBD, a central linker histone-related domain, and a C-terminal coiled-coil domain [11–13]. Whether IBP/RTPB1-type or SMH-type proteins have in vivo telomeric functions remains to be determined, yet numerous sequence database entries have been annotated as "telomere binding," despite a lack of direct biochemical evidence [7–13]. We have discovered a third and new class of plant telobox-related genes, the TACS-type genes, which encode ~45 kDa proteins with a C-terminal acidic SANT (SWI3, ADA2, N-COR, and TFIIIB B″) domain. The SANT motif was first described as a putative DNA-binding domain found initially in nuclear receptor corepressors and later in subunits of several chromatin-remodeling complexes [14]. The SANT domain (cd00167 from http://

Abbreviations: BAC, bacterial artificial chromosome; DBD, DNA-binding domain; SANT, SWI3, ADA2, N-COR, and TFIIIB″; EST, expressed sequence tag; ORF, open reading frame; UTR, untranslated region

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www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml) is characterized as a ~50 amino acid motif with a high degree of sequence similarity to some Myb-like DBDs, including those of human telomeric proteins TRF1 and TRF2 [15,16]. Here we show that *Tacs1* is expressed in meristem-enriched tissues and that the C-terminal domain of the predicted protein is acidic, a recently recognized characteristic of SANT domains [17], providing new insights into its possible function.

We screened cDNA libraries with DNA sequences corresponding to the Myb/SANT-like domain of the maize EST AI622625. From these screens we isolated, cloned, and sequenced several different TACS-type genes. A cDNA from a juvenile leaf and shoot mRNA library (gift of S. P. Moose, Univ. Illinois) was chosen for further analysis and represents a gene hereafter called *Terminal acidic SANT 1* (*Tacs1*). The *Tacs1* cDNA (GenBank accession AY738116) is 1820 bp in length and contains an ORF coding for a 422-amino-acid 45-kDa protein with an overall isoelectric point of 6.04. The ORF is preceded by a 52 bp 5′ UTR and followed by a 499 bp 3′ UTR (Fig. 1A). *Tacs1*-homologous genes were found in several plant species, including maize (GenBank Acc. AI622625), arabidopsis (GenBank Acc. At1g15720), rice (GenBank Acc. AY429017, AK071940), and sorghum (GenBank Acc. BG410798). One of these *Tacs1*-homologous genes was identified by transposon tagging as the *ANTHER INDEHISCENCE1* (*AID1*) gene of rice [18]. The recessive mutation of *aid1* results in partial to complete sterility of the spikelet, a reproductive structure defined as a small or secondary part of the inflorescence of grasses. Pair-wise protein sequence alignments revealed that AID1 has 65% identity (71% similarity) with TACS1 and that the homology extends beyond the SANT domain to the entire protein (GAP alignment, default parameters, Wisconsin Package Version 10.3, Accelrys Inc., San Diego, CA).

Zhu et al. [18] mapped the AID1 gene to chromosome 6 of rice near a *waxy* gene and suggested that the maize ortholog of *AID1* corresponds to the *male sterile2* (*ms2*) locus on maize chromosome 9 near the *waxy* locus. To test this hypothesis, we mapped *Tacs1*, as described by Marian et al. [12], using the IBM Recombinant Inbred Lines (RILs) DNA mapping kit via CIMDE as described by Sanchez-Villeda et al. [19]. Two primers, 954F and 1106R (Fig. 1A), were used to generate polymorphic PCR products from genomic DNAs of the two parental genotypes, B73 and Mo17. Cosegregation analysis of these products in the RIL population (n=94) allowed us to map the *Tacs1* PCR products to the genetic bin 2.08 (chromosome 2, bin 8) between the genetic markers umc1604 and mmc0381. This region of the maize chromosome 2 is not known to be syntenic with rice chromosome 6, nor is it known to be duplicate with the waxy region of maize chromosome 9.

To determine the genomic structure of the *Tacs1* gene, we used the map-position data to obtain linked BACs (from CHORI, http://www.bacpac.chori.org) and screened them by PCR for the presence of *Tacs1* sequences. We used DNA from a single PCR positive BAC (CH-201 123O8=ZMMBBc123O08) as a template to obtain PCR products, which we sequenced to locate the introns of *Tacs1*. We found four introns in *Tacs1* (at cDNA positions 680/681, 1030/1031, 1212/1213, and 1279/1280) using the program Spidey (http://www.ncbi.nlm.nih.gov/IEB/Research/Ostell/Spidey). The *Tacs1* genomic structure is nearly identical to that of the *AID1* gene of rice (Fig. 1B). Therefore two lines of evidence, sequence homology and gene structure, indicate that maize *Tacs1* and rice *AID1*

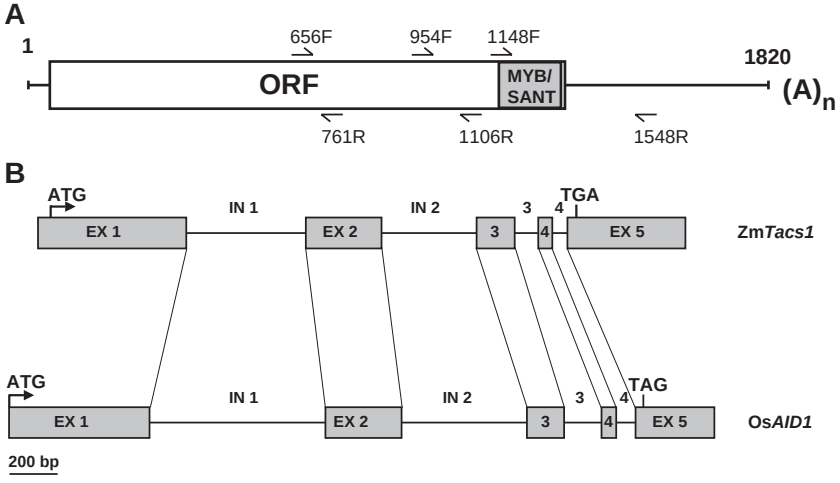

Fig. 1. cDNA and genomic structure of the *Tacs1* gene. (A) Structure of *Tacs1* full-length cDNA. The position of the Myb/SANT-like domain within the open reading frame (ORF) is indicated. The position and orientation of the primers are indicated and named according to the 5′ nucleotide (656F:17nt, 761R:20nt, 954F:21nt, 1106R:21nt, 1148F:21nt, 1548R:19nt). The position of the poly-A tail $(A)_n$ is indicated. (B) Comparison of the genomic structures of *Tacs1* rice *AID1* genes. The locations of the start (ATG) and stop (TGA or TAG) codons and the intron and exon numbers are indicated along with a scale bar (200 bp). Sequences for the full-length *Tacs1* cDNA (accession AY738116) and the intron-containing sequences (AY818403, AY818404, AY818405) are available from GenBank.

Table 1
Relative abundance of *Tacs1* mRNA in different tissues

Tissues[a]	cDNA library number[b]	Total EST number[c]	Number of hits[d]	PPM[e]
Ear primordia (2 mm)	3529	19,258	5	260
Tassel primordia (1–3 mm)	946	21,232	5	235
Immature ears (0.5–2 cm)	1091	9277	2	216
Endosperm[f]	Endosperm_4	10,267	2	195
Root	614	10,612	1	94
Juvenile leaf and shoot	949	10,708	1	93
Mixed tissues	ISUM5-RM	20,250	0	0
Mixed tissues	ISUM4-TN	9087	0	0
Mixed tissues	3530	8283	0	0
Two-week shoots	947	8878	0	0

[a] Tissues from which the libraries were derived; http://www.maizegdb.org/est.php.
[b] The cDNA library numbers are from http://www.maizegdb.org/est.php.
[c] Total number of ESTs in the library as of July 2004.
[d] Number of *Tacs1* hits better than e^{-50} as of July 2004.
[e] Abundance of the transcript expressed as parts per million (PPM) of ESTs in the given library.
[f] The Endosperm_4 library appears to include some ESTs from embryo-specific genes.

may be homologous, are possibly orthologous, but are apparently not in syntenic regions of the two genomes.

To learn more about the possible function of the *Tacs1* gene, we examined its expression using maize EST databases. BLASTn searches with the full-length *Tacs1* cDNA as a query allowed for a measure of *Tacs1* mRNA abundance in different tissues and organs of the plant. For this analysis we used only EST libraries that have been sequenced deeply (>8000 ESTs), using a threshold of e^{-50} as a cutoff for a match. Only 10 maize libraries matched the first criterion, and of these, only six had hits for *Tacs1* cDNA lower than e^{-50}. Table 1 summarizes the relative abundance of *Tacs1* ESTs as parts per million (PPM). We found that the *Tacs1* gene is expressed at relatively low levels in a specific subset of these libraries, consistent with the need for a sensitive procedure (RT-PCR) to detect rice AID1 transcripts [18]. In addition, RNA gel blot analysis with total RNA or poly(A) mRNA isolated from a variety of maize tissues repeatedly resulted in a lack of signal (data not shown). Although EST analysis is primarily an in silico survey of gene expression, these results are based on a survey of a relatively large body of sequence data. In this survey, we repeatedly found *Tacs1* cDNAs, but only in libraries from very young reproductive organs (Table 1), such as micro-dissected primordia of ear and tassel shoots. These observations are further consistent with our isolation of the *Tacs1* cDNA from a juvenile leaf and shoot library. The *Tacs1* mRNA is not merely present at a low level in all tissues, as evidenced by the absence of Tacs1 mRNAs from the 46,000 ESTs sequenced from the four libraries of mixed adult tissues (Table 1). The expression pattern of the *Tacs1* gene encoding a Myb/SANT-like domain raises the intriguing question of whether *Tacs1* plays a role in global nuclear processes associated with early developmental events such as organ initiation. Indeed, animal and fungal proteins that contain SANT domains are often associated with histone-modifying enzymes and ATP-dependent chromatin-remodeling enzymes [17].

The SANT domain shares not only sequence but also structural similarities with the DBD of Myb-related proteins; they both have a three-helix-bundle structural motif. Despite these similarities, the SANT domain is increasingly being recognized as chemically and functionally distinct from the DNA-binding Myb-like domain, as summarized by Boyer et al. [17]. Specifically, many SANT domains are characterized by an acidic isoelectric point and a negative electrostatic surface potential. We therefore examined the properties of the maize TACS1 Myb/SANT-like domain to determine whether it has the characteristic properties of a SANT domain. The Myb/SANT-like domain at the C-terminus of TACS1 has a predicted secondary structure with three alpha helices as illustrated in Fig. 2 (panel A). This triple helical bundle arrangement is a common feature of Myb, Myb-like, and SANT domains. Within this domain, TACS1 shares high similarity with several different plant proteins (Fig. 2B). These domains fall into one of two categories on the basis of their calculated isoelectric point, basic or acidic. Surprisingly, all of the TACS-type protein domains analyzed had an acidic p*I* (Fig. 2B). In contrast, the Myb-like domains of known DBDs such as IBP1, SMH1, and TRF1 all have basic isoelectric points (Fig. 2B). These results further strengthen the possibility that TACS1 contains a SANT domain.

To examine this possibility further, we performed protein homology modeling on several SANT, Myb, and Myb-like domains using SWISS-MODEL [20–23]. We used the solved structure of human TRF1 [24] as a template (PDB 1ityA). The Myb-like/SANT domain sequences (boldface in Fig. 2B) were threaded through the TRF1 structure to generate models shown as green ribbon diagrams in Fig. 3. All of the homology-modeled protein domains (TACS1, AID1, At1g15720, IBP1, and SMH1) fit very well with the template, adopting the triple-helix-bundle structure. We next calculated the surface electrostatic potential of these models using DeepView/Swiss-PdbViewer [22]. A SANT domain (ISWI, Fig. 3A) and Myb DBD (MYBR2, Fig. 3B) were included to illustrate the negative (red) and positive (blue) electrostatic

A

B

GENE	Alignment of MYB/SANT domains	TYPE	DB	pI
ZmTacs1	KNNNRRKARRWSLFEEETLRKGVEEYGVGNWRDILD--NNAEAFTGRTPVDLKDKWRNMLFR*	TACS	n.d.	4.7
SbBG41798	NKNRRRRARKWCLLEEETLRQGVEQYGSGNWKDILN--NNPDVFIGRTPVDLKDKWRNMINR*	TACS	n.d.	4.8
OsAID1	NKAKRRKARKWCALEEETLRKGVEQYGNGNWKDILT--NNPDVFIGRKAMDLKDKWRNMMR*	TACS	n.d.	6.4
ZmAI622625	PTCAYKIRKKWSKIEIETLLEGVGKYGIGNWKDIKL--AYPGVFEERSTVDLKDKFRNLGKRPHESF*	TACS	n.d.	6.4
OsAK071940	PTAAHKTRKKWSEEQEKTMLEGVEKYGKGNWKDIKM--AYPDVFEDRSTVDLKDKFRNLERHLCA*	TACS	n.d.	5.0
At1g15720	RPRPRRPMKFWTSEEVAALREGVKEYGKS-WKDIKN--SYPVVFADRSEVDLKDKWRNLLGRQ*	TACS	n.d.	6.4
ZmIBP1	EQGHRRIRRPFSVAEVEALVLAVEKLGTGRWRDVKLR-AFDN-AKHRTYVDLKDKWKTLVHTASI(n)	IBP	+	9.6
ZmSmh1	MGAPKQRWTPEEEAALKAGVAKHGPGKWRTILRDSDFSALLRLRSNVDLKDKWRNLSVTAGG(n)	SMH	+	9.8
HsTRF1	EKHRARKRQAWLWEEDKNLRSGVRKYGEGNWSKILL--HYK--FNNRTSVMLKDRWRTMKKLKLISSDSED*	TRF	+	10.1
HsTRF2	STTNITKKQKWTVEESEWVKAGVQKYGEGNWAAISK--NYP--FVNRTAVMIKDRWRTMKRLGMN*	TRF	+	9.3

Fig. 2. Characterization of the SANT domain of TACS1 and related proteins. (A) Amino-acid sequence and predicted secondary structure of the Myb/SANT-like domain of TACS1. The positions of the alpha helices were determined as previously described [12] and are shown as cylinders above the sequences. (B) Multiple sequence alignments of selected SANT and single Myb-like domains of TACS1-related proteins (from ClustalW, http://www2.ebi.ac.uk/clustalw, [25]). The bold sequences (bracketed at bottom) indicate the region for isoelectric point (p*I*) calculations with Compute pI/MW (http://www.us.expasy.org/tools/pi_tool.html; [26–28]). The known DNA-binding activity is indicated (DB; + for known DNA-binding, n.d. for not determined) along with the type of protein (TYPE). The sequences used in this figure are listed under GENE and indicate species (Zm, *Zea mays*; Sb, *Sorghum bicolor*; Os, *Oryza sativa*; At, *Arabidopsis thaliana*; Hs, *Homo sapiens*) followed by the gene name or accession number.

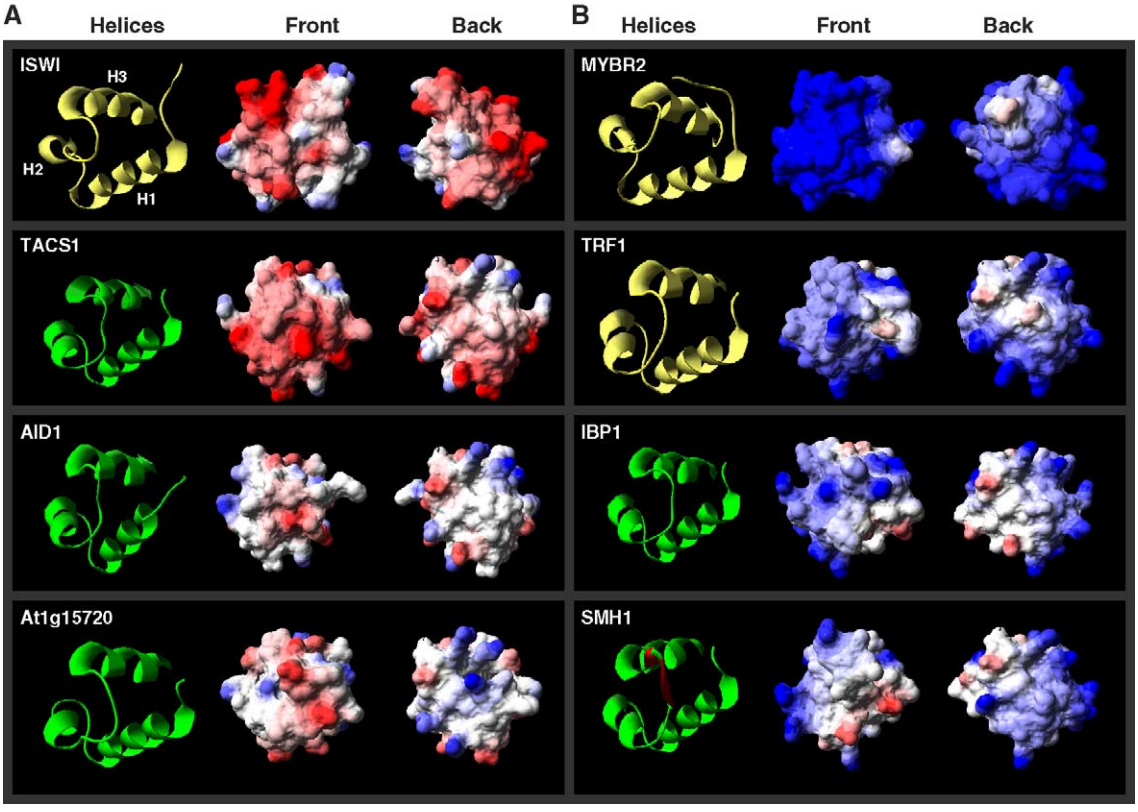

Fig. 3. Homology modeling, tertiary structure, and electrostatic surface potential of the Myb/SANT domains of TACS1 and related proteins. Ribbon models (Helices, yellow for solved structures, green for homology models) show the three helices (H1, H2, and H3) in the upper left panel for the SANT domain of ISWI [29]. Space-filling models showing the electrostatic surface potential are presented from two viewpoints for each model (front, matching the ribbon model; back, 180° rotation around the *Y* axis). Residue charges are coded as red for acidic, blue for basic, and white for neutral by the Compute Surface Potential tool in the program DeepView/Swiss-PdbViewer. Sequences used for threading are described in the legend of Fig. 2. A true SANT domain from ISWI (PDB 1OFC) and a true Myb domain (MYBR2, PDB 1GV5) are included for comparison. (A) SANT or SANT-like acidic domains. (B) Myb or Myb-like basic domains.

surfaces of previously characterized proteins. The ISWI SANT model and the TACS-type models all produced a negative electrostatic surface potential (red in the surface models of Fig. 2B). In contrast, the DBDs of MYBR2, TRF1, IBP1, and SMH1 all produced models with positive electrostatic surface potentials (blue in surface models of Fig. 2B). These results are in agreement with the p*I*-based classification (Fig. 2A) of the domains into two distinct groups. The acidic patches observed on the surfaces of the plant TACS-type proteins are not compatible with direct DNA binding and may reflect areas for the binding of basic moieties, such as histone tails or basic regions of other proteins. Consistent with this idea, the TACS-type proteins shown in Fig. 3 are not known to bind DNA, despite repeated efforts with in vitro DNA-binding assays (C. O. Marian and H. W. Bass, unpublished results, for TACS1; Karamysheva et al. [30] for the Myb/SANT domain of At1g15720). The combined approach of sequence alignments with 3-D protein modeling may be a method of differentiating between two closely related domains, reducing the possibility of misclassification. For example, the *Arabidopsis thaliana* protein At1g15720 was identified in databases as a "myb family transcription factor," but by the approach we used, At1g15720 can be identified as a SANT domain. In addition, our data suggest that the rice Myb-like DBD of *AID1* is also a SANT domain. This prediction has important implications for the interpretation of the pleiotropic nature of the *aid1* mutant phenotype. Investigation of the role of TACS-type proteins in protein–protein interactions or their role in chromatin-remodeling complexes may therefore be important.

In summary, we have isolated and characterized a cDNA for the *Tacs1* gene of maize. In silico expression analysis revealed that *Tacs1* is expressed in meristem-enriched tissues and shares extensive cDNA sequence and gene structure similarity with the rice *AID1* gene. Computer-assisted protein-structure analysis allowed us to identify the Myb-like/SANT domain of TACS1 as a SANT domain. This overall approach appears to provide a valuable means of distinguishing Myb-like DBDs from SANT domains and may provide insight into the functional role of the *Tacs1* gene.

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References

[1] D.A. Benson, I. Karsch-Mizrachi, D.J. Lipman, J. Ostell, D.L. Wheeler, GenBank: update, Nucleic Acids Res. 32 (2004) D23–D26 (Database issue).

[2] Q. Dong, S.D. Schlueter, V. Brendel, PlantGDB, plant genome database and analysis tools, Nucleic Acids Res. 32 (2004) D354–D359 (Database issue).

[3] R. Alba, Z. Fei, P. Payton, Y. Liu, S.L. Moore, P. Debbie, J. Cohn, M. D'Ascenzo, J.S. Gordon, J.K. Rose, G. Martin, S.D. Tanksley, M. Bouzayen, M.M. Jahn, J. Giovannoni, ESTs, cDNA microarrays, and gene expression profiling: tools for dissecting plant physiology and development, Plant J. 39 (2004) 697–714.

[4] T. Bilaud, C.E. Koering, E. Binet-Brasselet, K. Ancelin, A. Pollice, S.M. Gasser, E. Gilson, The telobox, a Myb-related telomeric DNA binding motif found in proteins from yeast, plants and human, Nucleic Acids Res. 24 (1996) 1294–1303.

[5] T. Lugert, W. Werr, A novel DNA-binding domain in the Shrunken initiator-binding protein (IBP1), Plant Mol. Biol. 25 (1994) 493–506.

[6] O. da Costa e Silva, L. Klein, E. Schmelzer, G.F. Trezzini, K. Hahlbrock, BPF-1, a pathogen-induced DNA-binding protein involved in the plant defense response, Plant J. 4 (1993) 125–135.

[7] E.Y. Yu, S.E. Kim, J.H. Kim, J.H. Ko, M.H. Cho, I.K. Chung, Sequence-specific DNA recognition by the myb-like domain of plant telomeric protein, RTBP1, J. Biol. Chem. 275 (2000) 24208–24214.

[8] C.M. Chen, C.T. Wang, C.H. Ho, A plant gene encoding a Myb-like protein that binds telomeric GGTTAG repeats in vitro, J. Biol. Chem. 276 (2001) 16511–16519.

[9] M.G. Hwang, I.K. Chung, B.G. Kang, M.H. Cho, Sequence-specific binding property of *Arabidopsis thaliana* telomeric DNA binding protein 1 (AtTBP1), FEBS Lett. 503 (2001) 35–40.

[10] S.W. Yang, D.H. Kim, J.J. Lee, Y.J. Chun, J.H. Lee, Y.J. Kim, I.K. Chung, W.T. Kim, Expression of the telomeric repeat binding factor gene NgTRF1 is closely coordinated with the cell division program in tobacco BY-2 suspension culture cells, J. Biol. Chem. 278 (2003) 21395–21407.

[11] M. Feldbrugge, M. Sprenger, K. Hahlbrock, B. Weisshaar, PcMYB1, a novel plant protein containing a DNA-binding domain with one MYB repeat, interacts in vivo with a light-regulatory promoter unit, Plant J. 11 (1997) 1079–1093.

[12] C.O. Marian, S.J. Bordoli, M. Goltz, R.A. Santarella, L.P. Jackson, O. Danilevskaya, M. Beckstette, R. Meeley, H.W. Bass, The maize single myb histone 1 gene, Smh1, belongs to a novel gene family and encodes a protein that binds telomere DNA repeats in vitro, Plant Physiol. 133 (2003) 1336–1350.

[13] P. Schrumpfova, M. Kuchar, G. Mikova, L. Skrisovska, T. Kubicarova, J. Fajkus, Characterization of two *Arabidopsis thaliana* myb-like proteins showing affinity to telomeric DNA sequence, Genome 47 (2004) 316–324.

[14] R. Aasland, A.F. Stewart, T. Gibson, The SANT domain: a putative DNA-binding domain in the SWI-SNF and ADA complexes, the transcriptional co-repressor N-CoR and TFIIIB, Trends Biochem. Sci. 21 (1996) 87–88.

[15] L. Chong, B. van Steensel, D. Broccoli, H. Erdjument-Bromage, J. Hanish, P. Tempst, T. de Lange, A human telomeric protein, Science 270 (1995) 1663–1667.

[16] D. Broccoli, A. Smogorzewska, L. Chong, T. de Lange, Human telomeres contain two distinct Myb-related proteins, TRF1 and TRF2, Nat. Genet. 17 (1997) 231–235.

[17] L.A. Boyer, R.R. Latek, C.L. Peterson, The SANT domain: a unique histone-tail-binding module? Nat. Rev., Mol. Cell Biol. 5 (2004) 158–163.

[18] Q.H. Zhu, K. Ramm, R. Shivakkumar, E.S. Dennis, N.M. Upadhyaya, The ANTHER INDEHISCENCE1 gene encoding a single MYB domain protein is involved in anther development in rice, Plant Physiol. 135 (2004) 1514–1525.

[19] H. Sanchez-Villeda, S. Schroeder, M. Polacco, M. McMullen, S. Havermann, G. Davis, I. Vroh-Bi, K. Cone, N. Sharopova, Y. Yim, L. Schultz, N. Duru, T. Musket, K. Houchins, Z. Fang, J. Gardiner, E. Coe, Development of an integrated laboratory information management system for the maize mapping project, Bioinformatics 19 (2003) 2022–2030.

[20] J. Kopp, T. Schwede, The SWISS-MODEL repository of annotated three-dimensional protein structure homology models, Nucleic Acids Res. 32 (2004) D230–D234 (Database issue).
[21] T. Schwede, J. Kopp, N. Guex, M.C. Peitsch, SWISS-MODEL: an automated protein homology-modeling server, Nucleic Acids Res. 31 (2003) 3381–3385.
[22] N. Guex, M.C. Peitsch, SWISS-MODEL and the Swiss-PdbViewer: an environment for comparative protein modeling, Electrophoresis 18 (1997) 2714–2723.
[23] M. Pietsch, Protein modeling by e-mail, Bio/Technology 13 (1995) 658–660.
[24] T. Nishikawa, H. Okamura, A. Nagadoi, P. Konig, D. Rhodes, Y. Nishimura, Solution structure of a telomeric DNA complex of human TRF1, Structure (Cambridge) 9 (2001) 1237–1251.
[25] J.D. Thompson, D.G. Higgins, T.J. Gibson, CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice, Nucleic Acids Res. 22 (1994) 4673–4680.
[26] B. Bjellqvist, G.J. Hughes, C. Pasquali, N. Paquet, F. Ravier, J.C. Sanchez, S. Frutiger, D. Hochstrasser, The focusing positions of polypeptides in immobilized pH gradients can be predicted from their amino acid sequences, Electrophoresis 14 (1993) 1023–1031.
[27] B. Bjellqvist, B. Basse, E. Olsen, J.E. Celis, Reference points for comparisons of two-dimensional maps of proteins from different human cell types defined in a pH scale where isoelectric points correlate with polypeptide compositions, Electrophoresis 15 (1994) 529–539.
[28] M.R. Wilkins, E. Gasteiger, A. Bairoch, J.C. Sanchez, K.L. Williams, R.D. Appel, D.F. Hochstrasser, Protein identification and analysis tools in the ExPASy server, in: A.J. Link (Ed.), 2-D Proteome Analysis Protocols, Humana Press, Totowa, NJ, 1998.
[29] T. Grune, J. Brzeski, A. Eberharter, C.R. Clapier, D.F. Corona, P.B. Becker, C.W. Muller, Crystal structure and functional analysis of a nucleosome recognition module of the remodeling factor ISWI, Mol. Cell 12 (2003) 449–460.
[30] Z.N. Karamysheva, Y.V. Surovtseva, L. Vespa, E.V. Shakirov, D.E. Shippen, A C-terminal Myb-extension domain defines a novel family of double-strand telomeric DNA binding proteins in *Arabidopsis*, J. Biol. Chem. 279 (2005) 47799–47807.