Novel TGACG-Motif Binding Protein of Soybean

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The promoters of a variety of plant genes are characterized by the presence of TGACG motif-containing sequences. These genes often exhibit quite diverse expression characteristics and in many case the TGACG-motif has been demonstrated to be essential for expression. Here we report the isolation and characterization of a soybean cDNA that encodes a novel basic/leucine zipper (bZIP) protein, STF1, that specifically interacts with Hex (TGACGTGG) and CRE (TGACGTCA) sequences. This protein contains a bZIP motif at C-terminus and an acidic domain at N-terminus. DNA binding specificities, heterodimer formation, and expression characteristics of STF1 were compared with a soybean TGA1 protein, STGA1. The soybean STF1 interacts with TGACG-sequences containing an ACGT core, while STGA1 requires TGACG as a sufficient binding sequence. The flanking sequences to the TGACG motif affected DNA binding of STF1 siginificantly. The STF1 mRNA is found mainly in dark grown soybean seedling with higher expression in apical and elongating hypocotyl, while STGA1 mRNA is highly abundant in roots of light grown plants. Furthermore, we demonstrate that STF1 heterodimerizes with G-box binding factors (GBFs) which was not observed with TGA1. The fact that STF1 possesses both distinct DNA binding speficities and heterodimerization properties suggest that STF1 belongs to a new family of plant bZIP proteins which recognize the Hex/CRE motif.

DNA-binding proteins play a key role in regulation of transcription. Many of these transcription factors are characterized by the presence of a basic and leucine zipper (bZIP) domain, a sequence specific DNA-binding domain. This bipartite DNA binding structure consists of a region enriched in basic amino acid (basic region) adjacent to a leucine zipper that characterized by several leucine residues regularly spaced at seven-amino acid intervals (Vinson et al., 1989). Whereas the basic region directly contacts the DNA, the leucine zipper mediated homodimerization and heterodimerization of protein monomers through a parallel interaction of the hydrophobic dimerization interfaces of two a-helices, resulting in a coiled-coli structure (O'Shea et al., 1989; Rasmunssen et al., 1991).

To date, molecular cloning studies have identified bZIP protein in diverse eukaryotic species ranging from higher plant to mammals (Katagiri and Chua, 1992). Of the more than 40 putative transcription factors cloned from higher plants, the largest group of proteins belong to the bZIP classification. These proteins can be distinguished on the basis of their DNA sequence specificity. Izawa et al. (1993) introduced a nomenclature for dyad symmetrical DNA binding sites containing an ACGT core. Previously, sequences containing a guanine 3' of the ACGT core sequence (CACGTG) have been designated G-boxes. Following this terminology, sequences containing cytidine, thymine or adenine were designated C-boxes, T-boxes or A-boxes, respectively. G-box binding factors (GBFs) are bZIP factors that preferentially bind to G-boxes. Proteins which belong to the TGA1 family differ form GBF in that this optimal binding site is a C-box (Izawa et al., 1993). A third class consists of proteins that have a relaxed specificity and bind to both G- and C-boxes (Hartings et al., 1989).

Recently, several bZIP proteins binding to TGACGT/C, a C-box related sequence, have been isolated from a variety of plants (Katagiri and Chua, 1992). Most of them have been shown to

interact with either the histone 3 hexamer (Hex) elements or the two motif TGACGT and TGACGC (as-1 element) identified in the CaMV 35S promoter and the ocs elements of the octopine and nopaline synthase promoters. The hex motif was known to bind two major class of plant bZIP factor, GBF and TGA1-related factors.

To further explore the question whether plants encode distinct classes of bZIP proteins with overlapping binding specificity to the Hex motif, and capability of forming a heterodimer with another bZIP protein families, we isolated a cDNA encoding a member of a new class of bZIP proteins, STF1, that strongly interacts with Hex and CRE (TGACGTCA) sequences. STF1 is distinct from the TGA1 and GBF families in a number of ways. STF1 is unable to recognize the as-1 (TGACGTAAxxxxTGACGACA) and Aux28B2 (TGACGACA) motifs, TGACG-motifs recognized by the TGA1 family, while STF1 binds strongly to Hex (TGACGTGG) and CRE (TGACGTCA) as does TGA1. Surprisingly STF1 also binds to the Hex (TGACGTGG) element as a heterodimer with two different soybean GBF proteins. The heterodimer formation was not observed between the TGA1 and STF1 proteins. Study of binding specificity demonstrates that STF1 is a CRE/Hex binding protein that can compete strongly with TGA1 and GBFs with distinct binding specificity.

RESULTS

Isolation of a cDNA Encoding a New TGACG-Motif Binding Protein

A soybean expression cDNA library was screened using a concatemer of Hex as a probe as previously described to isolated soybean cDNA encoding proteins that interact with TGACG-motifs (Hong et al., 1995). Five different phage clones were isolated from a primary library consisting of 5×10^5 recombinants. The phage clones were further screened

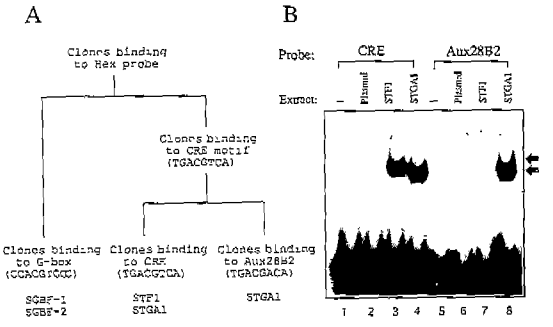

Figure 1. A) Schematic representation of the isolation of three different classes of bZIP factors from soybean. A G-box (B1 element: TCCACGTGTCA) and a TGACG-motif (B2 element: GCTGACGACAAG) are identified on the *GmAux28* gene (Nagao et al., 1993). The SGBF-1 and SGBF-2 clones bind to the G-box element and STGA1 clone binds to Aux28B2 probe and CRE probe. STF1 binds only to CRE probe. B) DNA binding assay of cloned soybean STF1 and STGA1. CRE and Aux28B2 probe was incubated with 3 μg of *E.coli* extracts containing STF1 and STGA1 proteins overexpressed in *E. coli* using pRSET vector (Invitrogen). Lane 1, 5 and 2, 6 contain no extract or extract from plasmid (pRSET) only, respectively. Lane 3, 4, 7 and 8 represent the individual protein-DNA complexes as indicated above.

with CRE (TGACGTCA), a palindromic TGACG-motif, and a G-box (GCCACGTGGC) sequence to differentiate protein (s) binding to CRE and G-box. Two clones, λSF25 and λSF32, which bound only to CRE, were further selected and tested for binding to the Aux28 B2 sequence (TGACGACA), a sequence lacking the ACGT core motif (Nagao et al., 1993). These two clones did not bind to the Aux28 B2 sequence. Partial sequencing of cDNA inserts revealed that two phage clones encoded proteins of a new class, distinguishable from the TGA1-related proteins. Further screening of the cDNA library with the Aux28 B2 probe resulted in isolation of two lambda clones, lJC-1, and lJC-2, which encoded a TGA1 binding activity of soybean, named STGA1: this gene was reported previously (Cheong et al., 1994). The protein encoded by one clone, lSF32, was designated STF1 and further characterized. A schematic view of the difference in binding properties of STF1 to the Hex, G-box, CRE, and Aux28 B2 motifs is shown in Figure 1A. The differential

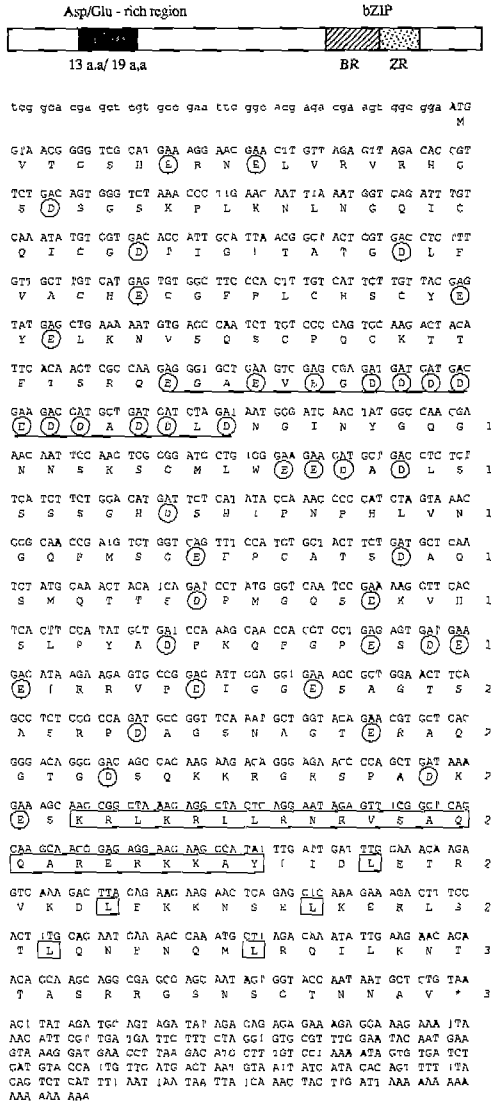

Figure 2. DNA sequence of STF1 cDNA and the deduced amino acid sequence of the protein. Top: Schematic presentation of STF1, indicating the location of the acidic region (Asp/Glu), the basic region (BR) and the leucine zipper domain (ZR). Bottom: The bZIP domain is represented by the basic region (boxed) and the leucine zipper (boxed letter). A region rich in acidic amino acids is underlined. Numbers on the left and right correspond to the base pair and amino acid positions, respectively.

binding activity of STF1 to CRE and Aux28 B2 sequences was confirmed by electrophoretic mobility shift assays (EMSAs) with IPTG-induced extracts of bacterial cells expressing the cloned gene (Figure 1B). While STGA1 interacted with both CRE and

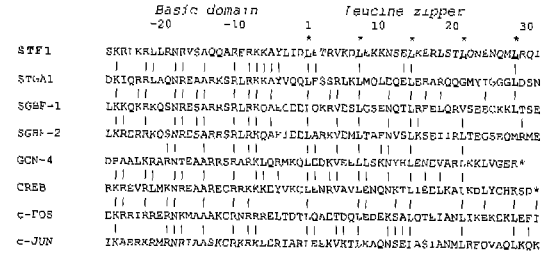

Figure 3. Sequence alignment of the bZIP regions of the STF1 protein with those of soybean GBFs, STGA1, GCN-4, CREB, c-FOS and c-JUN. The two subdomains of the basic region and leucine zipper are indicated. Within the bZIP region, the amino acids identical to STF1 are indicated by vertical bars. The leucine residues within the leucine zipper are underlined. STF1 (this study), STGA1 (Cheong et al., 1994), SGBF-1, -2 (Hong et al., 1995), GCN-4 , CREB, c-FOS, c-JUN. Positions of amino acid is numbered by taking the first leucine of the heptad repeat as position 1 (nomenclature according to Suckow et al., 1993).

Aux28 B2 probes, STF1 bound only to the CRE probe.

The complete nucleotide sequence of clone STF1 was determined (Figure 2). The total length of the cDNA clone was 1257 bp: the open reading frame encoded a putative protein of 320 amino acids with a molecular mass of 35 kDa and a pI of 5.26 which is quite acidic compared to STGA1 (pI 6.29) (Cheong et al., 1994) and SGBFs (pI 8.5-8.8) (Hong et al., 1995). This protein contains a basic region and a leucine zipper in the carboxy terminus, domains that define the bZIP family of proteins. In addition to the bZIP motif, STF1 contains a region rich in acidic amino acids in the N-terminus. STGA1, like other TGA1-related proteins, contained a glutamine-rich region in the carboxy terminus of the protein.

Comparison of the amino acid sequence of the bZIP regions of several plant bZIP proteins is shown in Figure 3. The STF1 did not show significant homology with known bZIP proteins even in the basic region, the most highly conserved region among plant bZIP proteins. The basic region of STF1 contains the three amino acids that are absolutely

conserved within all known bZIP proteins, asparagine, alanine and arginine at position -18, -14 and -10, respectively, (taking the first leucine of the heptad repeat as position 1(nomencluture according to Suckow et al., 1993). Two additional residues, glutamic acid at position -16 and serine at position -11, are common to all plant bZIP factors which recognize CRE and G-box sequences. However, the STF1 contains valine and alanine instead of glutamic acid and serine at positions -16 and -11, respectively, residues which are present in all plant bZIP factors.

DNA Binding Studies Differentiate STF1 from a TGA1-like Protein in Recognizing TGACG-Containing Sequences

To determine the binding properties of STF1, different TGACG- and G-box-related sequences were analyzed and compared with STGA1, a soybean TGA1 homologue. These binding sites were basically the same as those which were used for analyzing G-box factor (s) binding (Hong et al., 1995), except that the Aux28B2 sequence was included as an additional basis for differentiating binding activity (Figure 4A).

STGA1, like other TGA1-related proteins, bound to sequences containing TGACG (CRE, Hex, Hexm2, and Aux28B2) with varying degrees of affinity depending on the sequences flanking the TGACG motif (Figure 4C). STGA1 bound all tested sequences which contained the TGACG sequence, but STF1 did not bind to Aux28B2, which contained a TGACG sequence (Figure 4B). The Aux28B2 (TGACGACA) differs in only one base, T, thus lacking the ACGT core motif of the palindromic CRE sequence (TGACGTCA). Although Hexm2 (TGACGTCT) contained an ACGT core sequence, STF1 weakly bound to Hexm2. Further analysis showed that STF1 did not bind the CaMV 35S promoter, which contains *as*-1 sequences (TGACGTAAxxxxTGACGACA), while STGA1 bound this sequence (data not shown). Furthermore, the STF1 protein interacted with G-box-related sequences, Hexm1 (ATCACGTGGC) and palindromic (PA) G-box (GCCACGTGGC). The Hex and CRE motifs represented high affinity binding sites for both STGA1 and STF1.

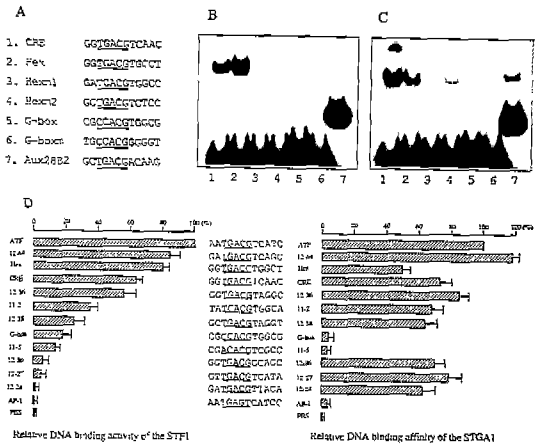

Figure 4. Relative differences in DNA binding specificities between STF1 and STGA1 proteins. A) DNA sequence of the oligonucleotides employed in DNA binding studies. The sequences underlined represent the TGACG-motifs.
B, C) Gel retardation pattern of STF1 (B) and STGA1 (C) proteins to selected binding sequences. Seven oligonucleotide sequences containing potential sites for both STF1 and STGA1 were used as probe for DNA binding analysis (lane 1 to lane 7).
D) Comparison of relative DNA binding activity of the STF1 and STGA1. Several DNA sequences selected by random oligonucleotide selection method were used as binding probes to compare relative binding affinity between STF1 and STGA1. The radioactivity of free and bound probe on EMSA gel were counted and the average of three binding experiments were compared with ATF-CRE as a relative control. Fragments containing multicloning sites of pBluscript (PBS) used as a non-specific binding site.

To further analyze the relative binding affinity to other TGACG-containing sequences, EMSAs were performed using several DNA sequences which were selectively bound by the STF1 fusion protein using the random-oligonucleotide selection method. Most of the selected sequences contained a TGACG-motif (Figure 4D). The ATF-CRE sequence (AA**TGACGTCA**TC), a mammalian derived sequence, showed strong binding activity and was used as a high affinity binding site for comparison.

Relative affinity was calculated as the percentage of radioactivity bound by a given sequence vs. radioactivity bound by the ATF-CRE sequence. STGA1 bound strongly to all sequences containing TGACG. STF1 bound well to sequences containing TGACGTC/G, of which CRE and Hex are representatives. However, in contrast to STGA1, STF1 bound weakly to sequence 12-27 (GTTGACGTCAT), containing a palindromic TGACGTCA sequence, which is very different from the strong STGA1 binding. This indicates that the flanking sequence to TGACGTCA, e.g. -5 or -6 positions when the central two nucleotides, C and G, flanking the axis of symmetry are designated -1 and +1, can affect binding significantly. In addition STF1 binds G-box- like sequences with somewhat higher affinity than STGA1.

Heterodimerization Analysis of the STF1, STGA1 and SGBF

Leucine zipper proteins have been shown to interact with their respective recognition sites as dimers (Vinson et al., 1989). This dimer formation is mediated by the leucine zipper domain and is required for DNA binding (Rasmunssen et al., 1991). GBFs of *Arabidopsis* and parsley have been shown to selectively heterodimerize (Shindler et al., 1992). However, heterodimer formation was restricted to members of the same bZIP protein family. To determine if STF1 heterodimerizes with STGA1 or with GBFs of soybean, members of different bZIP families, protein dimerization assays were performed. Different portions of four cDNAs-corresponding to full length or truncated versions of STGA1, STF1, SGBF-1 and SGBF-2 (Figure 5A) were transcribed and translated *in vitro*, and the translation products were employed in DNA binding studies. Since four soybean bZIP proteins (STF1, STGA1, SGBF-1 and SGBF-2) bound strongly to the Hex probe, the Hex probe was used for the heterodimerization assay. As shown in Figure 5B, STF1 bound strongly as homodimer to the Hex probe (lane 1 to 3).

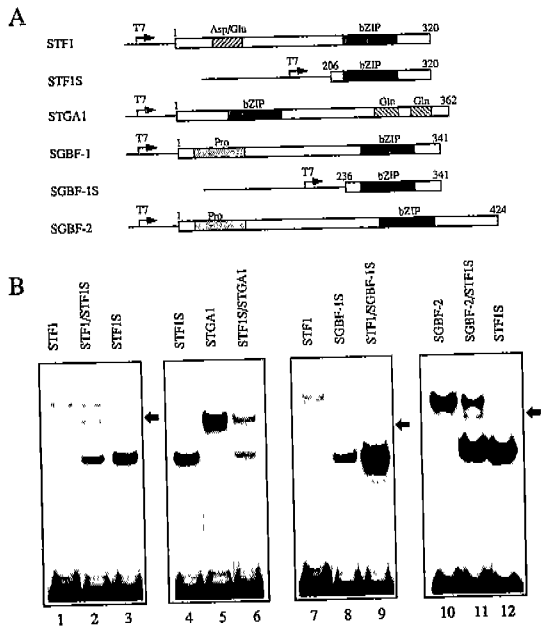

Figure 5. Heterodimerization analysis between STF1 and other soybean bZIP proteins. A) Schematic presentation of plasmid vectors used for generating full-length and truncated soybean bZIP proteins. The acidic (Asp/Glu), glutamate (Gln), proline (Pro)-rich regions and basic leucine zipper (bZIP) region are highlighted. Start and end point of each *in vitro* translation product are shown above each construct. The location of the T7 promoter is indicated (T7).

B) Heterodimer formation between STF1 and SGBFs. Lane 1, 3, 4, 5, 7, 8, 10 and 12 represent the individual protein-DNA complexes obtained with the full-length or truncated proteins as indicated above each lane. For lane 2, 6, 9 and 11, the indicated proteins were mixed and incubated for 15 min at 42°C prior to the addition of the binding site DNA. The heterodimeric protein-DNA complex of intermediate mobility is marked by an arrowhead

However, STF1 did not bind the probe as a heterodimeric complex with STGA1 (lane 4 to 6). Surprisingly, STF1 formed a heterodimeric complex with both GBF proteins (lane 7 to 12). By contrast STGA1 did not heterodimerize with either GBF protein (data not shown). These results indicate that no heterodimeric complexes are formed between TGA1 and GBFs or STF1 families, while STF1 heterodimerizes with the GBF family.

STF1 and STGA1 Genes Show Dramatically Different Patterns of Expression

TGA1a has been shown to be highly expressed in tobacco roots while its transcript level was about 10-fold lower in leaves (Katagiri et al., 1989). To see if the STF1 and STGA1 may be regulated differently, we examined the tissue specificity of the STF1 gene expression. Total RNA was isolated from various parts of 4-day-old etiolated soybean seedlings and of 1-month-old green plants. mRNAs encoding both STF1 (~1.4 kb) and STGA1 (~1.8 kb) were detected in all RNA preparations (Figure 6). The STGA1 is highly expressed in soybean roots of light grown plants. In hypocotyl of soybean seedlings, STGA1 is highly expressed in the mature hypocotyl and root tissues. In light-grown plants, STGA1 is abundant in roots, mature leaves, and petiole tissues, while little expression is observed in young immature leaf tissue. By contrast, STF1 is abundant in all seedling tissues including hypocotyl, plumule and root tissues. In hypocotyls of soybean seedlings, STF1 mRNA is present as a major form of TGACG-motif binding protein except in mature hypocotyl. The level of STF1 RNA was most abundant in apical hypocotyl and gradually decreased from apical to mature tissues. This pattern of STF1 gene expression in the hypocotyl is very different from that of STGA1 which is weakly expressed in the apical and elongating hypocotyl. In light-grown plants, STF1 is also expressed in all tissues but at a lower level than in etiolated seedling tissue. Overall, STF1 mRNA is the major form of message for TGACG motif-binding factors in the dark-grown seedlings and in young leaf tissues while STGA1 mRNA is the major form in roots, mature hypocotyl, mature leaves, and petioles.

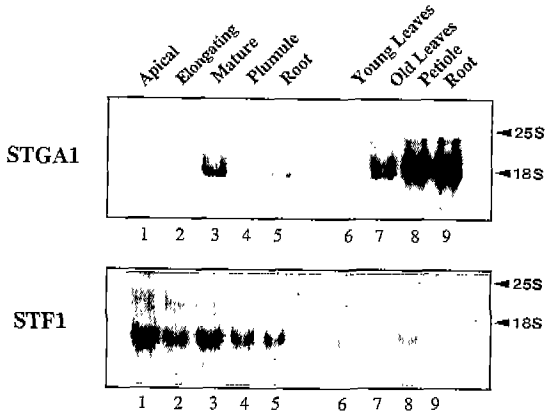

Figure 6. Expression pattern of the STGA1 and STF1 mRNAs. Total RNAs (20 μg per lane) isolated from apical, elongating, mature hypocotyl, plumule, and roots of 4-day old soybean etiolated seedlings and young leaves, old leaves, petiole, and roots of 1-month-old light grown plants were hybridized with ^{32}p-labeled STGA1 and STF1 cDNA probes. The positions of the 18S and 25S ribosomal RNA molecular weight markers are indicated.

DISCUSSION

In this study, we have shown that plants have a new class of bZIP proteins which is distinguishable from the TGA1 family and which is able to form heterodimers with G-box binding factors. To date no such TGACG-motif-binding protein has been identified which exhibits the capacity to heterodimerize with GBFs. In this study, the binding specificity and dimer formation were examined.

To date, more than 30 bZIP proteins have been isolated from various plant species. When the sequences of plant bZIP proteins were compared, these proteins fell primarily into two well conserved classes, the TGA1-related bZIP proteins and the GBF-related proteins (Shindler et al., 1992). These two classes of proteins differ in organization of the bZIP domain, in their primary structure, and in the types of putative transactivation domains. Proteins of the TGA1 family contain a bZIP domain at the amino-terminus and a glutamine-rich domain at the carboxy terminus. The GBF proteins contain a bZIP domain at the carboxy terminus and a proline-rich domain at the amino terminus. STF1 does not belong to either of these two classes. The corresponding structure of STF1 contains a C-terminal bZIP domain and a N-terminal acidic

domain. There are some other bZIP proteins which also are not related to the two large families, namely, the parsley CPRF-2, maize O2, tobacco PosF21A, TGA1b, tomato VSF-1 and maize OCSBF1 (Katagiri et al., 1989). CPRF-2 differs from other GBF-related factors of parsley, CPRF-1 and CPRF-2, in that the protein binds both to G-box and to *as-1* motifs. The STF1 binds strongly to CRE and weakly to G-box, properties rather similar to those of CPRF-2. However, STF1 is clearly different from CPRF-2 in that it does not bind to *as-1* nor to *nos1*. The maize O2 protein binds to AP1 (TGACTCA), a half-spaced CRE: however, the STF1 protein does not bind to this sequence. Although binding studies with other non-GBF- and non-TGA1-related factors are not well documented, STF1 is unique in that it does not bind as-1/ocs-related sequences.

The Hex sequence is known to bind to many plant bZIP proteins. Data presented here showed that STF1 bound strongly to Hex. GBFs and TGA1 factors were known to bind the Hex sequence effectively. The Hex sequence is a type I element, a well-conserved regulatory element found in the proximal promoter region of a certain class of plant histone genes. The element plays an important role in S-phase-specific transcription of the histone genes. The strong binding of STF1 to Hex, compared to STGA1 and GBFs (data not shown) indicates that STF1 may play an important role in transcription regulation in the apical, active cell division zone, and the cell elongation regions of soybean seedling hypocotyl.

Many transcription factors bind to DNA as a dimer. Dimer formation is characteristic of bZIP proteins. This is mediated through hydrophobic amino acid residues located in the vicinity of the dimeric interface. Fos and Jun represent a well known example of heterodimer-forming bZIP proteins. Since the three bZIP protein families reported in this study bound to the Hex sequence, the Hex sequence was used as a binding site to study heterodimerization between members of the different bZIP families. SGBF-1 and SGBF-2, GBFs of different families in soybean were known to form both homo- and heterodimers (Hong et al., 1995). The TGA1 of *Arabidopsis* failed to form heterodimers with GBFs (Shindler et al., 1992). Analyses showed that heterodimerization occurred between STF1 and both GBFs (SGBF-1 and SGBF-2) (Figure 5). However, no protein association was observed between STF1 and STGA1. The presence of a bZIP domain at the carboxy terminus in both STF1 and GBF proteins is consistent with characteristics of dimer formation. Since STF1 formed heterodimers in combination with soybean GBFs, heterodimer formation among these bZIP proteins may generate an expanded repertoire of regulatory potential for gene expression in plants. That is, interaction of members of these two families of proteins increases the number of possible regulatory complexes available to participate in the regulation of transcription of specific cellular genes.

The demonstration that STF1 binds to DNA as a homodimer and can interact with GBF to form heterodimers has potentially interesting implications for gene regulation involving TGACG-motif and G-box regulatory elements of soybean gene. STF1 possesses an acidic amino-terminal domain and lacks the glutamine- or proline-rich domain found in TGA1- and GBF-related proteins, respectively. From these observations, it follows that the transcriptional activation properties of STF1, TGA1, and GBFs are different. Furthermore, the heterodimeric protein-DNA complex, STF1/GBF1 or STF1/GBF2, would be expected to differ from those of the corresponding STF1 and GBF homodimers. The binding of STF1 protein to G-box as well as to Hex/CRE sequence and protein heterodimerization with GBFs demonstrate a complex nature of transcription factor interaction at the sites containing Hex, CRE, and G-box. The molecular analyses presented in this study indicate that the STF1 is involved in the interplay in transcription regulation and 'cross-talk' between components of the two major signal transduction pathways involving GBFs and TGA1

bZIP factors. Further studies require a detailed understanding of both cellular expression characteristics of the respective DNA binding bZIP proteins and the transcription regulatory properties of the individual homo- and heterodimers.

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