bZIP transcription factors in *Arabidopsis*

The bZIP Research Group (Marc Jakoby *et al.*)

In plants, basic region/leucine zipper motif (bZIP) transcription factors regulate processes including pathogen defence, light and stress signalling, seed maturation and flower development. The *Arabidopsis* genome sequence contains 75 distinct members of the bZIP family, of which ~50 are not described in the literature. Using common domains, the AtbZIP family can be subdivided into ten groups. Here, we review the available data on bZIP functions in the context of subgroup membership and discuss the interacting proteins. This integration is essential for a complete functional characterization of bZIP transcription factors in plants, and to identify functional redundancies among AtbZIP factors.

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Transcription factors (TFs) play crucial roles in almost all biological processes. Structurally, TFs are usually classified by their DNA-binding domains: basic region/leucine zipper (bZIP) TFs have a basic region that binds DNA and a leucine zipper dimerization motif (Box 1). Proteins with bZIP domains are present in all eukaryotes analysed to date. Some, such as Jun/Fos or CREB, have been studied extensively in animals and serve as models for understanding TF–DNA interactions, ternary complex formation and TF post-translational modifications (Box 1).

Arabidopsis has about four times as many *bZIP* genes as yeast, worm and human [1]. Genetic and molecular studies of a few of these *Arabidopsis thaliana* bZIP (AtbZIP) factors show that they regulate diverse biological processes such as pathogen defence, light and stress signalling, seed maturation and flower development. The early recruitment of bZIP TFs in plant evolution might contribute to this diversity, which contrasts with the apparently more confined functions of the plant-specific R2R3-MYB and WRKY TFs [2,3].

As a basis for future functional analysis, we present an overview of the potential *AtbZIP* genes encoded in the *Arabidopsis* genome. Using optimized gene predictions based on known *bZIP* gene structure and cDNA sequences obtained in our laboratories via the REGIA (Regulatory Gene Initiative in *Arabidopsis*) European project, we identified 75 putative genes encoding proteins with the bZIP signature (Box 1). Genes that were annotated as 'bZIP' in the various databases (TAIR, MAtDB, EMBL/GenBank, TIGR) but that do not show the exact bZIP signature were excluded from our analysis. Because our total number differs from the 81 *bZIP* genes identified by Jose Luis Riechmann *et al.* [1], we cannot exclude the existence of a few additional *AtbZIP* genes.

We gave a generic name (*AtbZIP1–AtbZIP75*) to each *bZIP* gene (Fig. 1), including those that had been named (sometimes twice) before. Our numbering system does not follow a distinct rationale but provides a unique identifier for each *bZIP* gene, as proposed for R2R3-MYB and WRKY TFs [2,3] and should help communication in the scientific community. Our results and the structured nomenclature were incorporated into the MAtDB database at MIPS (Munich Information Center for Protein Sequences).

Complexity of the bZIP family in *Arabidopsis*

Putative AtbZIP proteins were clustered according to sequence similarities of their basic region. Subsequently, the MEME analysis tool (http://meme.sdsc.edu/meme/website/meme.html) was used to search for domains shared by the AtbZIP proteins. This allowed us to define ten groups of bZIPs with a similar basic region and additional conserved motifs (Fig. 1). Proteins from the same groups also have additional features in common, such as the size of the leucine zipper (Table 1). Three AtbZIP proteins that did not fit into any group were not classified. Our classification is not based purely on phylogeny and is, therefore, partly subjective. Because we put some emphasis on conserved motifs, we hope that it reflects functional similarities and should aid in determining specific functions for each bZIP.

Structural features and functional characterization

For each of the ten bZIP groups, we review the structural features and functional information available from *Arabidopsis* and other plant species. The bZIPs from other plants were aligned with AtbZIPs to determine which group they matched with. Because members of a given group share a similar DNA-binding basic region, many of them probably recognize similar *cis* elements. However, the limited number of binding site selection experiments performed to date does not allow us to confirm this hypothesis (Table 1).

Group A

Seven members of group A have been studied (*AtbZIP39/ABI5*, *AtbZIP36/ABF2/AREB1*, *AtbZIP38/ABF4/AREB2*, *AtbZIP66/AREB3*, *AtbZIP40/GBF4*, *AtbZIP35/ABF1* and *AtbZIP37/ABF3*) and most of the functional information available suggests roles in abscisic acid (ABA) or stress signalling [4–7]. In vegetative tissues, ABA and abiotic stresses such as cold, drought or high salinity induce gene expression through *cis* elements that include the ABA response element (ABRE). ABRE binding factor (ABF) and ABA-responsive element binding protein (AREB) proteins can bind to different ABRE-containing promoters *in vitro* or in yeast [4,7]. The available data indicate that ABA or abiotic stresses induce *ABF/AREB* expression and that ABA triggers

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Box 1. What is a bZIP protein?

The bZIP domain consists of two structural features located on a contiguous α-helix (Fig. I) [a]: first, a basic region of ~16 amino acid residues containing a nuclear localization signal followed by an invariant N-x_7-R/K motif that contacts the DNA; and, second, a heptad repeat of leucines or other bulky hydrophobic amino acids positioned exactly nine amino acids towards the C-terminus, creating an amphipathic helix. To bind DNA, two subunits adhere via interactions between the hydrophobic sides of their helices, which creates a superimposing coiled-coil structure (the so-called zipper; Fig. II). The ability to form homo- and heterodimers is influenced by the electrostatic attraction and repulsion of polar residues flanking the hydrophobic interaction surface of the helices [a]. Examples of known heterodimerizations in plants are listed in Table 1 in the main text.

Plant bZIP proteins preferentially bind to DNA sequences with an ACGT core. Binding specificity is regulated by flanking nucleotides. Plant bZIPs preferentially bind to the A-box (TACGTA), C-box (GACGTC) and G-box (CACGTG) [b], but there are also examples of nonpalindromic binding sites [c,d].

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a Hurst, H.C. (1995) Transcription factors 1: bZIP proteins. *Protein Profile* 2, 101–168

b Izawa, T. *et al.* (1993) Plant bZIP protein DNA binding specificity. *J. Mol. Biol.* 230, 1131–1144

c Choi, H. *et al.* (2000) ABFs, a family of ABA-responsive element binding factors. *J. Biol. Chem.* 275, 1723–1730

d Fukazawa, J. *et al.* (2000) REPRESSION OF SHOOT GROWTH, a bZIP transcriptional activator, regulates cell elongation by controlling the level of gibberellins. *Plant Cell* 12, 901–915

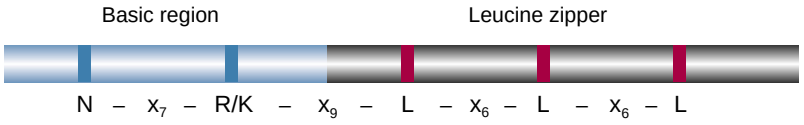


Fig. I. Primary structure of the bZIP domain. The basic region is shaded in blue and the highly conserved residues are highlighted with blue and red boxes. A consensus sequence is given below. The leucines are sometimes replaced by isoleucine, valine, phenylalanine or methionine.

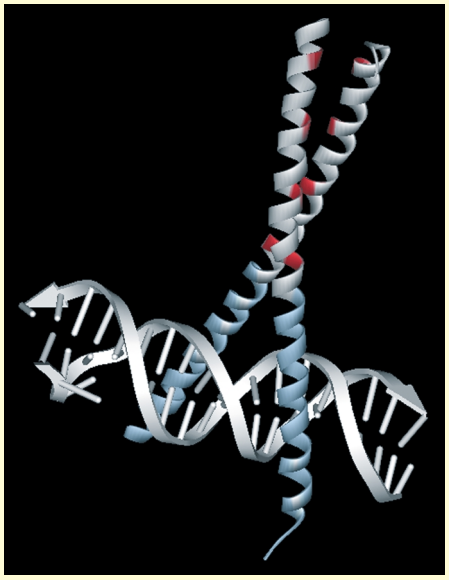


Fig. II. Three-dimensional structure of the GCN4 bZIP domain bound to DNA. The leucine residues are positioned on one side of each helix and form coiled coils via van der Waals interactions.

AREB1/2 phosphorylation. This phosphorylation is necessary for AREB1/2 to induce downstream genes and could occur on the casein kinase II (CKII) phosphorylation sites present in the conserved domains (Fig. 1). ABA and stress therefore probably induce both transcriptional and post-translational regulation of several group-A bZIPs.

During late seed development, ABA induces the expression of the late embryogenesis abundant (LEA) genes, which are thought to participate in the acquisition of desiccation tolerance. Later, ABA also blocks seed germination and early seedling development. Analysis of the *abi5* mutant phenotype shows that *AtbZIP39/ABI5* regulates all these processes [5,6]. In addition, ABA induces *ABI5* expression, stabilizes the ABI5 protein and also modifies its phosphorylation status [5,6]. Like its rice counterpart, TRAB1 [8], ABI5 probably acts by recruiting the potent ABI3 transcriptional activator (named OsVP1 in rice) to the LEA promoter [9]. Group-A bZIPs therefore appear to function as important players in ABA signal transduction both in seeds and vegetative tissues.

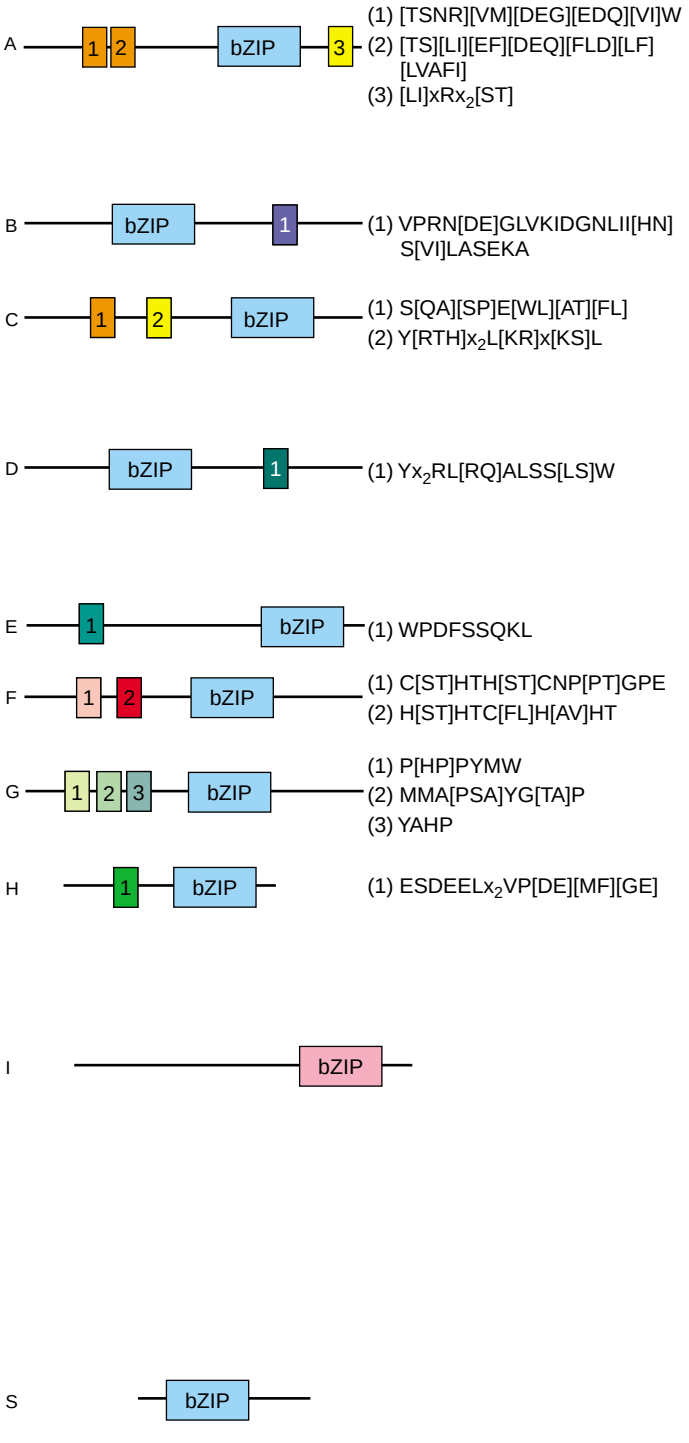
Group C

Members of this group share structural features with a well characterized family of plant bZIPs that includes maize *Opaque2* and parsley (*Petroselinum crispum*) *CPFR2* (Table 1). Most remarkable in this group, is an extended leucine zipper with up to nine heptad repeats. In addition, potential target sites for protein modification such as phosphorylation sites that regulate nuclear translocation and DNA-binding properties are also conserved [10]. The information available on *Opaque2* and closely related monocot genes indicates that they regulate seed storage protein production by interacting with the PBF protein [11–14], whereas CPFR2 and G/HBF-1 might be involved in responses to environmental or pathogen challenge [15,16]. It will be interesting to test whether the closest *Opaque2* homologues (*AtbZIP10* and *AtbZIP25*) regulate storage protein expression in the *Arabidopsis* embryo.

Group D

Group D genes participate in two different processes: defence against pathogens and development. Their involvement in defence mechanisms comes from work on the TGA factors in tobacco and *Arabidopsis* [17,18]. In response to pathogen attack, salicylic acid induces the expression of pathogenesis-related (PR) genes throughout the plant. TGA factors are believed to regulate this systemic induction because they bind to the *as-1 cis* element present in the promoters of PR genes, and because different TGA factors interact with the NPR protein, which is necessary for PR gene

AtbZIP no.	Gene code	Published name	GenBank Acc.
AtbZIP12	At2g41070	DPBF4	AF334209
AtbZIP13	At5g44080		BN000023
AtbZIP14	At4g35900		BN000021
AtbZIP15	At5g42910		AJ419599
AtbZIP27	At2g17770		BN000022
AtbZIP35	At1g49720	ABF1	AF093544
AtbZIP36	At1g?	ABF2/ AREB1	AF093545
AtbZIP37	At4g34000	ABF3	AF093546
AtbZIP38	At3g19290	ABF4/AREB2	AF093547
AtbZIP39	At2g36270	ABI5	AF334206
AtbZIP40	At1g03970	GBF4	U01823
AtbZIP66	At3g56850	AREB3	AB017162
AtbZIP67	At3g44460	DPBF2	AJ419600
AtbZIP17	At2g40950		AV551374*
AtbZIP28	At3g10800		AJ419850
AtbZIP49	At3g56660		AJ419851
AtbZIP9	At5g24800	BZO2H2	AF310223
AtbZIP10	At4g02640	BZO2H1	AF310222
AtbZIP25	At3g54620		AJ010860
AtbZIP63	At5g28770	BZO2H3	AF310224
AtbZIP20	At5g06950	AHBP-1b/TGA2	D10042
AtbZIP21	At1g08320		AJ314757
AtbZIP22	At1g22070	TGA3	L10209
AtbZIP26	At5g06960	OBF5/TGA5	X69900
AtbZIP45	At3g12250	TGA6	AJ320540
AtbZIP46	At1g68640	PAN	AF111711
AtbZIP47	At5g65210	TGA1	X68053
AtbZIP50	At1g77920		AJ315736
AtbZIP57	At5g10030	OBF4/TGA4	X69899
AtbZIP65	At5g06839		AJ314787
AtbZIP34	At2g42380		AF401299
AtbZIP61	At3g58120		AF401300
AtbZIP19	At4g35040		N65677*
AtbZIP23	At2g16770		AV544638*
AtbZIP24	At3g51960		AI994442*
AtbZIP16	At2g35530		AV559248*
AtbZIP41	At4g36730	GBF1	X63894
AtbZIP54	At4g01120	GBF2	AF053228
AtbZIP55	At2g46270	GBF3	U51850
AtbZIP68	At1g32150		-
AtbZIP56	At5g11260	HY5	AB005295
AtbZIP64	At3g17609	HYH	AF453477
AtbZIP18	At2g40620		AY0744269
AtbZIP29	At4g38900		AF401297
AtbZIP30	At2g21230		AF401298
AtbZIP31	At2g13150		AF401301
AtbZIP32	At2g12980		AV566578*
AtbZIP33	At2g12900		-
AtbZIP51	At1g43700	VIP1	AF225983
AtbZIP52	At1g06850		AJ419852/53
AtbZIP59	At2g31370	PosF21	X61031
AtbZIP69	At1g06070		AJ419854
AtbZIP71	At2g24340		-
AtbZIP73	At2g13130		-
AtbZIP74	At2g21235		-
AtbZIP1	At5g49450		AF400618
AtbZIP2	At2g18160	GBF5	AF053939
AtbZIP3	At5g15830		AV549429*
AtbZIP4	At1g59530		AF400619
AtbZIP5	At3g49760		-
AtbZIP6	At2g22850		-
AtbZIP7	At4g37730		AI992458
AtbZIP8	At1g68880		AF400621
AtbZIP11	At4g34590	ATB2	X99747
AtbZIP42	At3g30530		-
AtbZIP43	At5g38800		-
AtbZIP44	At1g75390		AV566155*
AtbZIP48	At2g04038		-
AtbZIP53	At3g62420		AF400620
AtbZIP58	At1g13600		AF332430
AtbZIP70	At5g60830		-
AtbZIP75	At5g08141		-
AtbZIP60	At1g42990		AY045964
AtbZIP62	At1g19490		-
AtbZIP72	At5g07160		-



TRENDS in Plant Science

Fig. 1. Classification of *Arabidopsis* bZIP proteins. Ten groups of bZIP proteins were defined based on sequence similarity of the basic region and the presence of additional conserved motifs identified using the MEME tools (http://meme.sdsc.edu/meme/website/meme.html). The groups were named with letters referring to some of their prominent members (A for ABF/AREB/ABI5, C for CPRF2-like, G for GBF, H for HY5), to protein size (B for big and S for small), or alphabetically. Genes that did not fit in any group were left unclassified at the bottom of the figure. The bZIP domains are shown in blue except for the unusual bZIP domain in group I, which is shown in pink. In most cases, the function of a given motif is not known. Orange boxes indicate potential casein kinase II phosphorylation sites (S/TxxD/E, where x represents any amino acid), domains 1, 2 and 3 in group G are part of a proline-rich activation domain. Domain 1 in group H is part of the COP1 interaction domain. The last column of the table indicates the cDNA Accession number; the Accession numbers of expressed sequence tags are indicated by an asterisk.

induction but does not bind to DNA by itself [19]. In addition, AtbZIP57/OBF4/TGA4 interacts with AtEBP, which binds the ethylene response element present in many PR gene promoters [20]. Group D proteins might thus be involved in integrating different systemic signals (salicylic acid and ethylene) at the PR promoter level in response to pathogen infection.

Two other group D genes are involved in developmental processes: *AtbZIP46/Perianthia* controls floral organ number in *Arabidopsis* [21] and *Liguleless2* establishes the blade-sheath boundary during maize leaf development [22].

Group E

No functional data are available for members of group E. They are highly similar to members of *group I* in their zipper motif but they do not carry a lysine at position –10 and therefore have been put into a separate group.

Group G

The group G *GBF* genes from *Arabidopsis* and their parsley homologues *CPRF1*, *CPRF3*, *CPRF4a* and *CPRF5* have been mainly linked to ultraviolet and blue light signal transduction and to the regulation of light-responsive promoters [16,23,24]. Extensive *in vitro* analysis has shown that the GBF and CPRF proteins bind as homo- and heterodimers to symmetric and asymmetric G-boxes (Box 1) present in light-responsive promoters [23,25]. In addition, *GBF3*, *CPRF1* and *CPRF4a* show light-regulated expression, GBF2 and CPRF4a are translocated into the nucleus upon light treatment, and CPRF4a DNA-binding activity is modulated by light in a phosphorylation-dependent manner [16,23,24,26,27]. The three conserved proline-rich domains present in the N-terminus of group G proteins have also been shown to have transcriptional activation potential.

However, there are no genetic data showing that these genes function in light-regulated signal transduction, and the evidence that the *Phaseolus vulgaris* GBF-like proteins ROM1 and ROM2 [28] might regulate storage protein gene expression suggests that group G proteins might also play a role during seed maturation.

Group H

Group H has only two members (*AtbZIP56/HY5* and *AtbZIP64*). HY5's role in promoting photomorphogenesis is most obvious in light-grown *hy5* mutant seedlings: they resemble wild-type seedlings grown in the dark, which have elongated hypocotyls, poorly developed cotyledons and reduced expression of several light-inducible genes [29]. HY5 directly regulates the expression of some of these genes by binding to G-boxes present in their promoters. The control of HY5 activity by light is also well documented [30]: in dark-grown *Arabidopsis*, HY5 is targeted for degradation via interactions with the WD40 protein COP1; a small portion of HY5 escapes degradation because it is phosphorylated on a CKII site, but it has a low activation potential. When seedlings are illuminated, COP1 is exported from the nucleus and HY5 protein accumulates. Additionally, CKII activity is reduced, and the newly synthesized, unphosphorylated HY5 has a high activation potential. This leads to rapid induction of light-induced HY5 target genes. AtbZIP64 and HY5 both have a CKII phosphorylation site and a WD40 interaction domain [31], suggesting that these factors could have overlapping functions. This hypothesis is consistent with the finding that, in *hy5* null alleles, photomorphogenesis is not completely impaired [29].

Group I

Members of group I share a characteristic lysine residue in the basic domain that replaces the highly conserved arginine (N-x_7-R to N-x_7-K, where x represents an amino acid) (Fig. 1; see Fig. I in Box 1). This amino acid exchange might determine the specific binding site requirements for these bZIPs because it correlates with a higher affinity to non-palindromic binding sites [32]. Studies of group I genes from several species indicate that they might play a role in vascular development. The *RSG* gene from tobacco is specifically expressed in the phloem and activates the *GA3* gene of the gibberellin biosynthesis pathway. Production of a dominant-negative form of RSG blocks activation of the *GA3* promoter [32], resulting in decreased gibberellin synthesis and dwarfed transgenic plants. *RF2a* was isolated from rice as an activator of phloem-specific gene expression. Like tobacco plants producing the dominant-negative RSG, rice *RF2a* antisense suppression lines show a dwarfed phenotype and might therefore also be affected in gibberellin biosynthesis. In addition, these plants display aberrant vascular tissue development [33]. Tomato *VSF-1* is expressed in vascular tissues and activates a gene encoding a structural protein from the cell wall [34]. There are thus converging lines of evidence that some group I bZIPs might regulate vascular development.

Table 1. Characteristic features of the ten *bZIP* groups in *Arabidopsis*

Group	Exon number	Size (in aa)	Basic domain position	Number of Leu-repeats	Known interactions with other proteins[a]	Known binding sites[b]	Additional features
A	1–4	234–454	C-terminal	3–4	ABI5 with ABI3 [5]. In rice, TRAB1 with OsVP1 [8]	C**ACGT**GG/tC, CG**CGT**G for ABF1* and TRAB1 [4,8]	Conserved motifs containing phosphorylation sites
B	2, 4	523–675	Central to N-terminal	5	Not known	Not known	Putative transmembrane domain in C-terminus of AtbZIP17 and AtbZIP28. Proline-rich domain C-terminal of bZIP domain
C	6, 7	294–411	Central to C-terminal	7–9	Opaque2 with PBF [14]	GTG**AGT**CAT for barley BLZ1 and BLZ2 [11,41]. CC**ACGT**GG and TGACGTCA for CPRF2 [25]	N-terminal hydrophobic or acidic signature (activation domain), Ser/Thr cluster + acidic aa stretch. Putative phosphorylation sites.
D	7, 8, 10–13	325–481	N-terminal	3 plus G at position 4	TGA3, 2 and 5 with NPR1 [19], TGA4 with AtEBP [20]	TG**ACGt**/g for TGA1–6 [42]	None
E	4		C-terminal	6–7	Not known	Not known	N-terminal stretches of basic aa
F	1, 2	157–260	Central	8, Q at position 4	Not known	Not known	None
G			C-terminal	5	GBF1, 2 and 3 heterodimerize pair-wise [23]	CC**ACGT**GG for GBF1*, GBF2 and 3 [23]	Proline-rich N-terminal activation domain
H	3, 4	148, 169	C-terminal	5	HY5 with the N-terminus of COP1 [29]	AC**ACGT**GG for HY5 [43]	COP1 interaction domain
I	1–5	157–553	Central to C-terminal	7	NtRSG with 14-3-3 proteins [44]	TCC**AGCT**TGA, TCCAACTTGGA for tobacco RSG [32]. GCTCCGTTG for tomato VSF-1 [34]	Conserved lysine in position –10 of the basic region
S	1	145–186 (–305)	Central	8–9	Snapdragon bZIP910 and 911 heterodimerize [36]. Tobacco BZI-2,3 and 4 heterodimerize with BZI-1 (group C) [38]	TG**ACGT**G for snapdragon. bZIP910*/bZIP911* [36]	Short N- and C-terminal extensions

[a]Interactions of bZIPs and other proteins in *Arabidopsis* and other plants, and heterodimerization between bZIP proteins.
[b]Binding sites that have been experimentally determined. An asterisk (*) after the protein name indicates that binding site selection experiments have been performed. The ACGT core (or part of it) is shown in bold when present.
Abbreviation: aa, amino acid.

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Group S

Group S is the largest bZIP group in *Arabidopsis* but only *ATBZIP11 / ATB2* has been analysed in detail. Transcription of this gene is upregulated by light, in carbohydrate-consuming (i.e. sink) tissue and in the vascular system [35]. The *ATB2* transcript has a long 5′ leader containing three upstream open-reading-frames (uORFs) that are involved in post-transcriptional repression by sucrose. Small uORFs are also present in the leader sequences of some other group S genes from *Arabidopsis* (*AtbZIP1*, *AtbZIP2*, *AtbZIP44* and *AtbZIP53*) and from snapdragon (*Antirrhinum majus*), where their importance has been shown [36]. As proposed for ATB2, several group S bZIP might thus be involved in balancing carbohydrate demand and supply [35].

Data derived from monocot and dicot species suggest that homologues of group S bZIPs are also transcriptionally activated after stress treatment (e.g. cold, drought, anaerobiosis, wounding) [37] or are specifically expressed in defined parts of the flower [36,38]. This suggests that group S members probably do not function only in sucrose signalling.

Defining the roles of bZIP factors in regulatory networks

As in other TF families, many bZIP proteins probably have overlapping functions that will complicate the analysis of mutant phenotypes. Our identification of all *bZIP* genes is thus a necessary prerequisite for the dissection of individual bZIP protein function. By studying the sequence of the 75 putative AtbZIPs, we have defined ten groups of related proteins in which functional overlaps are most probable.

To date, mutations have been described in only four *bZIP* genes (*HY5*, *PERIANTHIA*, *ABI5* and *AtbZIP18*). This small amount of genetic data does not allow us to predict with confidence that members of a given group will work in a common process or share functions. However, we do think that our classification is an important starting point for functional analysis. The next step in understanding bZIP relationships will be to compare *bZIP* expression patterns, especially within a given group, to detect potential overlapping functions. For example, in the MADS box TF family, the *SEPALLATA* genes have overlapping expression pattern and redundant

function [39]. By contrast, the WER and GL1 Myb TFs are functionally interchangeable but not functionally redundant, because they are expressed in different tissues [40].

Finally, it will be useful to exploit defined protein–protein interaction motifs (such as the COP1 interaction domain present in HY5 and AtbZIP64) and post-translational modification sites as starting points to identify factors that function with or regulate the AtbZIPs. The *Arabidopsis* genome sequence and the increasing ease of obtaining mutants promise new studies on *AtbZIP* gene function in the near future. We hope that this analysis will be stimulated by the work presented here.

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