Regulatory mechanism of plant gene transcription by GT-elements and GT-factors

Dao-Xiu Zhou

GT-elements are regulatory DNA sequences usually found in tandem repeats in the promoter region of many different plant genes. Depending on promoter structure, GT-elements can have a positive or a negative transcription function. The cognate GT-element binding factors contain one or two trihelix DNA binding motifs, which have so far been identified in plant transcription factors only. GT-factors are ubiquitously expressed; in Arabidopsis they belong to a small family of transcription factors. The functioning of plant GT-elements and GT-factors shows complex regulatory features of plant gene transcription.

Transcriptional regulation of gene expression plays a fundamental role in plant development and in the response to environmental stimuli[1,2]. The analysis of regulatory elements of plant gene transcription revealed the existence of several classes of *cis*-acting DNA elements and cognate DNA-binding factors[2,3]. The specificity of gene expression depends on *cis*-elements present in the promoter and enhancer regions and their interaction with specific transcription factors. The activity of transcription factors themselves is regulated in a variety of ways in plants[1]. This review intends to update research information on the regulatory mechanism of plant GT-elements and GT-factors.

A highly degenerated cis-element

GT-elements were first identified in the pea ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) small subunit gene (*RBCS*-3A) promoter as Box II (5′GTGTGGTTAATATG)[4]. The cognate DNA-binding activity, named GT-1, also binds to several other related but divergent sequences found in this promoter[5] (Fig. 1). The deduced consensus core sequence is 5′-G-Pu-(T/A)-A-A-(T/A). GT-elements have been found in the promoter region of many other genes encoding diverse functions[5–23] (Table 1). Many of these genes are not regulated by light, indicating that the GT-element is not just a light-specific regulatory module. Most of these GT-elements were shown to be related to the GT-1 binding site (Box II of pea *RBCS*-3A) using *in vitro* competition DNA-protein binding assays[5,6,8,9,11–18]. A difference in GT-1 binding affinity exists generally between Box II and other GT-elements. This is because of a large variation between the Box II core sequence and other GT-elements[5,13]. One characteristic, common to all GT-elements, is a core sequence with four to five nucleotides, T or A, preceded by one or two G nucleotides at the 5′ end. This high degeneracy of GT-elements makes it difficult to identify them using a simple sequence search in the promoter region. The degenerated GT-elements are either bound by different GT-factors or have a different binding affinity for an individual GT-factor, resulting in differential regulatory function (see below).

GT-elements are usually present in tandem repeats within a relatively large promoter region (Fig. 1). This can be explained by the fact that GT-factors either bind to DNA as a dimer or bind two GT-elements at the same time. The spacing between two GT-elements is critical for activity. An increase in spacing between two sites by as little as two bp dramatically reduces the *RBCS*-3A transcript levels *in vivo*[5]. However, deletions of five to seven bp between them does not affect the *RBCS*-3A transcript level. None of the spacing changes affects the binding of GT-1 *in vitro*[5]. This might imply that the appropriate binding conformation of GT-factors is needed for activity.

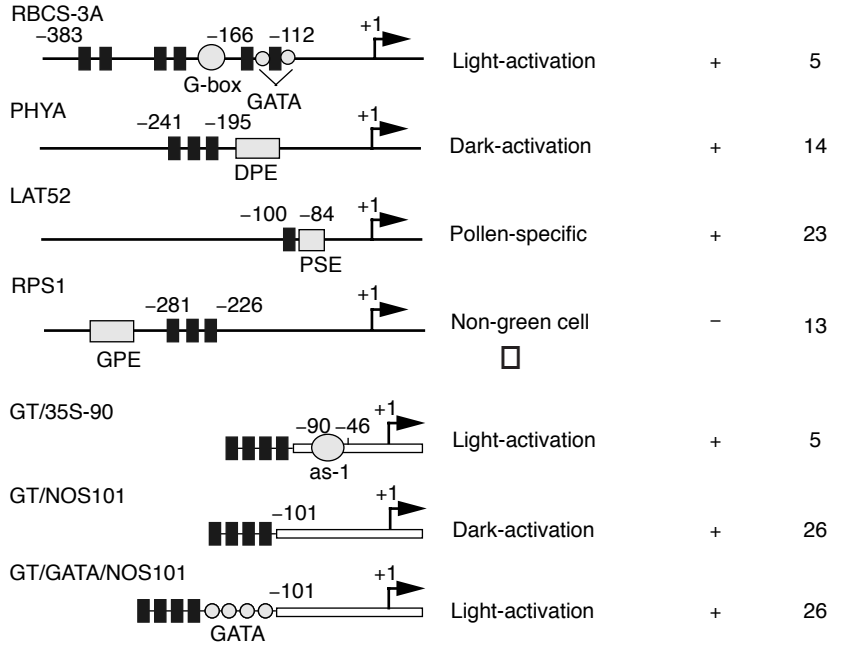

Fig. 1. Arrangement and function of GT elements in representative promoters. Both native (black line) and synthetic (white block) promoters are shown. GT-elements are represented by black boxes. Other well characterized *cis*-elements (as-1, G-box and GATA-motifs) are shown as light-gray circles. The *cis*-elements that are not well characterized are indicated by light-gray rectangles. Abbreviations: DPE, dark positive element; PSE, pollen-specific element; GPE, green cell-specific element; +, positive function; −, negative function. Relative positions to the transcriptional start site (arrow) of GT-elements are indicated by numbers.

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Differential regulatory function

A necessary but not sufficient element for light-activation

Deletion or point mutation of GT-elements in a few light-responsive genes does not affect light-induced transcription from these promoters[5]. This lack of effect might be at least partially caused by the presence of redundant GT-elements in these promoters. Gain-of-function experiments in transgenic tobacco showed that a tetramer of the GT-1 site (Box II) can confer light responsiveness to an otherwise light-irresponsive CaMV 35S-90 promoter (cauliflower mosaic virus 35S promoter region from nucleotide −90 to +8 relative to the transcription start site; Fig. 1), but not to the smaller version CaMV 35S-46 (−46 to +8) (Ref. 5). These results suggest that a *cis*-element, between −90 and −46 of the CaMV 35S promoter, possibly the *as*-1 element[5], is needed to build a light-responsive module with the GT-1 binding site (Fig. 1). It was later shown that a combination of GT- and GATA-elements is needed for light-induced expression of a −166 deletion of the pea *RBCS*-3A promoter[24]. When linked to a synthetic light-responsive promoter GATA/NOS101 (in which a tetramer of the GATA motif is linked to the 5′ of NOS101, the promoter region from −101 to +4 of the nopaline synthase gene), a tetramer of the GT-1 binding site could make the promoter more responsive to an even wider light spectrum. This confirms the cooperative interaction between GT- and GATA-elements[25,26] (Figs 1 and 2). These data together indicate that the GT-1 binding site is necessary, but not sufficient, to confer light-responsiveness.

Table 1. Genes shown to contain GT-elements in their promoter region

Genes	Species	Ref.
Chloroplast function		
Rubisco SSU, *RBCS*	Many	5
Chlorophyll *a* binding protein, *CAB*	Many	5
Rubisco activase, *RCA*	Spinach	6
Rubisco LSU N-methyltransferase	Tobacco	7
Plastocyanin, *Pc*	Spinach	8
Plastocyanin, *Pc*	*Arabidopsis*	9
Glutamyl-tRNA reductase	*Arabidopsis*	10
GAPDH B subnuit	*Arabidopsis*	11
ATP synthase, *atp*C1, *atp*C2	*Arabidopsis*	12
Ribosomal proteins, *rps1*	Spinach	13
Non-chloroplast function		
Phytochrome A, *PHYA*	Rice	14
Chalcone synthase, *CHS15*	Soybean	16
Chalcone synthase, *CHS*	Alfalfa	17
Pathogene-related, *PR-1a*	Tobacco	18
Alcohol dehydrogenase, *Adh1*	Maize	19
Related to dehydration, *rd22*	*Arabidopsis*	20
Phosphoenolpyruvate carboxylase	*Flaveria*	21
Cytochrome P450 reductase, *Cpr*	*Catharanthus roseus*	22
Pollen-specific, *LAT*52	Maize	23

A promoter target of the photoreceptor signaling pathway

Higher plants have at least three photoreceptor systems to sense light signals: phytochromes (Phy, for red and far red light), cryptochromes (Cry, for blue light) and UV light-receptors[27]. *Arabidopsis* contains several genes for phytochrome and crytochrome apoproteins (*PHYA, B, C, D, E*; *CRY1, 2*)[27–29]. PhyA is responsible for perceiving far-red light, whereas PhyB plays a primary role in perceiving red light[27,28]. By cooperating with the GATA motif, the GT-1 binding site could make the NOS101 promoter responsive to red, far-red and blue light[26]. These specific light responses require the presence of the corresponding photoreceptors[26]. Consistent with these results, it was shown that the GT-1 binding site in the *Arabidopsis CAB*2 promoter mediates PhyA and PhyB induction of *CAB*2 expression[30]. It has been shown that PhyA uses three photo-transduction pathways to signal nuclear gene expression[31]. One of the pathways, which is Ca^{2+}- or calmodulin-dependent, is required for regulating transcription of *RBCS*, *CAB* and photosystem II-related genes[31]. Experiments with co-microinjection into tomato *aurea* mutant cells that lack active phytochromes demonstrated that the promoter target of the PhyA Ca^{2+}-dependent signaling pathway was the GT-1 binding site[32] (Fig. 2a). A promoter construct, in which multiple copies of Box II were linked to the CaMV 35S-90, can be activated when co- injected with oat PhyA or Ca^{2+}, but not with other signaling molecules. CaMV 35S-90 alone is not responsive to PhyA or to Ca^{2+} (Ref. 32).

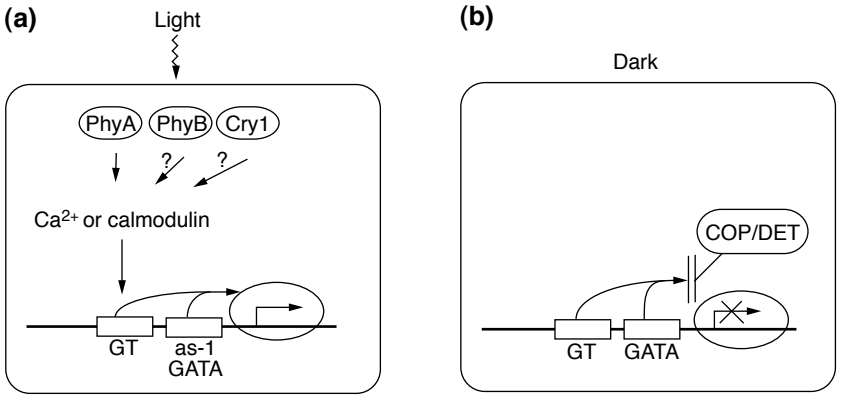

Fig. 2. GT-element light-responsive function. (a) Promoter target of the photoreceptor pathway. In the light, PhyA, possibly PhyB and Cry1, activate Ca^{2+} or calmodulin molecules to signal gene expression, with the GT-1 site as a promoter target. Cooperation between the GT-1 site and the as-1 or the GATA motif is needed to respond to the Ca^{2+} or calmodulin signal. (b) Promoter target for COP1 and DET1-mediated dark-repression. COP1 and DET1 are general photomorphogenic repressors of light-inducible genes in the dark. The repression requires the presence of the GT-1 binding site and its cooperation with the GATA motif in the promoter.

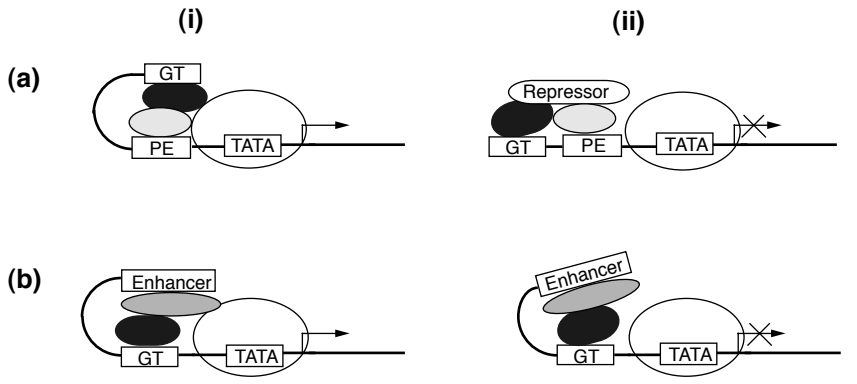

Fig. 3. Possible models of GT-element and GT-factor-mediated transcriptional regulation. (a) Modulating function: when located close to a positive *cis*-element (PE; such as GATA, as-1, dark-positive and pollen-specific elements) in promoters (such as GT-CaMV 35S-90, GT/GATA/NOS101, *PHYA* and *LAT52* promoters, see Fig. 1), GT-elements act cooperatively with these PEs by interacting with their cognate binding factors to activate transcription, which is induced by the corresponding signal (i). In the absence of the signal (ii), a modified or a different GT-factor will bind to the promoter so that it cannot undergo cooperative interaction with the PE-binding protein, or a repressor will bind to the promoter and repress transcription. (b) Silencing function: when a cell type-specific enhancer is involved in the activation of a promoter (*rps*1) (i), GT-elements in this type of promoter are not essential for the cell type-specific activation. However, in other cell types (ii), GT-elements will be bound by a modified or a different GT-factor that interferes with enhancer-binding factors and prevents the enhancer from functioning.

Dark-repression target of general photomorphogenic repressors

Genetic studies have suggested that the pleiotropic COP/DET/FUS genes act as repressors of photomorphogenic development and light-induced gene expression in the dark[33]. Mutations of these genes produce constitutive photomorphogenic phenotypes and light-induced gene expression[33]. The GT-GATA-NOS101 (but not GATA-NOS101) promoter, can be activated in the dark in *cop1* and *det1* mutants[26]. This suggests that the GT-element or its interaction with the GATA motif is required for COP1- or DET1-mediated dark repression of light-induced genes (Fig. 2b). These results are consistent with the observation that when introduced between the enhancer and the minimal region of the 35S promoter, GT-elements can silence this light-insensitive promoter in the dark, but have no effect in the light[5].

Dark-activation or light-repression function

GT-elements in the light-repressed rice *PHYA* gene play an essential role in the dark activation of this gene by modulating a dark-specific promoter element[14] (Figs 1 and 3a). The dark-activation function of GT-elements is also observed when they are linked to the NOS101 promoter. This synthetic promoter (GT-NOS101) is repressed by a wide light spectrum[25,26]. The repression requires the presence of specific photoreceptors[26]. Therefore, depending on the promoter context, GT-elements can modulate both light activation (or dark repression) and light repression (or dark activation) in response to specific photoreceptor-activated signal molecules.

Cell-type-specific transcription function

The 52/56 box in the pollen-specific gene *LAT52* is closely related to the GT-1 binding site (Box II), which differs only by four bp over a 16 bp segment[23]. The 52/56 box is needed to modulate the transcriptional activity of the downstream pollen-specific element (PSE) in the *LAT52* promoter[23] (Figs 1 and 3a). Conversion of the 52/56 box to the perfect GT-1 site (Box II) increases the pollen-specific transcription to ~1.5 fold. Other point mutations strongly reduce the promoter activity[23]. Nuclear genes encoding chloroplast ribosomal proteins are highly induced in green cells in a light-independent manner. Mutation or deletion of multiple GT-elements in these genes can increase transcription in transgenic roots or in transiently transfected protoplasts prepared from cultured cells, but have no effect in transgenic leaves[34,35] (Figs 1 and 3b). Similarly, deletion of the GT-1 site in the light-induced *RCA* gene promoter increases the expression of a reporter gene 100-fold in transgenic tobacco roots, but has no effect on the expression in leaves[6]. These data indicate that GT-elements in these promoters play a transcription repression role in non-green cells. This GT-element-mediated repression might be achieved by binding to a different or a modified GT-factor that prevents the green cell-specific enhancer from functioning (Fig. 3b). Therefore, GT-elements can have both a positive and a negative function in modulating cell-type-specific transcription.

Trihelix DNA-binding GT-factors

There is no differential GT-element (Box II) binding activity observed in nuclear extracts from green or etiolated leaves[5]. However, tobacco root cell extracts contain a different Box II binding activity with a distinct sequence specificity and form a DNA–protein complex of higher electrophoretic mobility[35]. Moreover, the GT-element (Box II) binding activity from *det* mutant leaf nuclear extracts has a higher electrophoretic mobility than the one from normal plant leaves[36], suggesting possible modification of the GT-element binding complex in the mutant in which light-induced genes are activated in the dark[33].

Nuclear proteins that bind to GT-elements were initially cloned from rice and tobacco by affinity screening of cDNA expression libraries using labeled GT-elements as probes. The GT-factor from rice, named GT-2, was cloned using the rice *PHYA* promoter sequences GT2-box (5′-GGTAATT) and GT3-box (5′-GGTAAAT)[14,15]. GT-2 contains two separate trihelix (helix–loop–helix–loop–helix) structures that are predicted to bind to DNA (Fig. 4)[15]. The amino proximal trihelix preferentially binds to the GT3-box, whereas the carboxyl proximal helix prefers the GT2-box of the *PHYA* promoter. Neither motif binds efficiently to Box II of the pea *RBCS*-3A promoter sequence. The GT-binding factor from tobacco, named GT-1a or B2F, was isolated similarly using a tetramer of Box II of the pea *RBCS*-3A promoter as a binding probe[37,38]. GT-1a has only one trihelix domain, which is responsible for the specific binding to the Box II core sequence (Fig. 4) and binds only weakly to other GT-elements. GT-1a appears to bind to DNA as dimer, and the carboxyl terminal part is critical for dimerization[39]. Tobacco GT-1a is homologous (with 40% identity) to the trihelix region of the rice GT-2, but not elsewhere[37,38]. The cDNA clones corresponding to the rice GT-2 and the tobacco GT-1a were isolated from *Arabidopsis* by DNA hybridization[37,38]. *Arabidopsis* homologs (AtGT-1, AtGT-2) appear to have the same DNA-binding preference as their counterparts from rice or tobacco[40,41]. Library screening by DNA hybridization found two additional *Arabidopsis* genomic clones named AtGTL1 and AtGTL2. Both AtGTL1 and AtGTL2 have

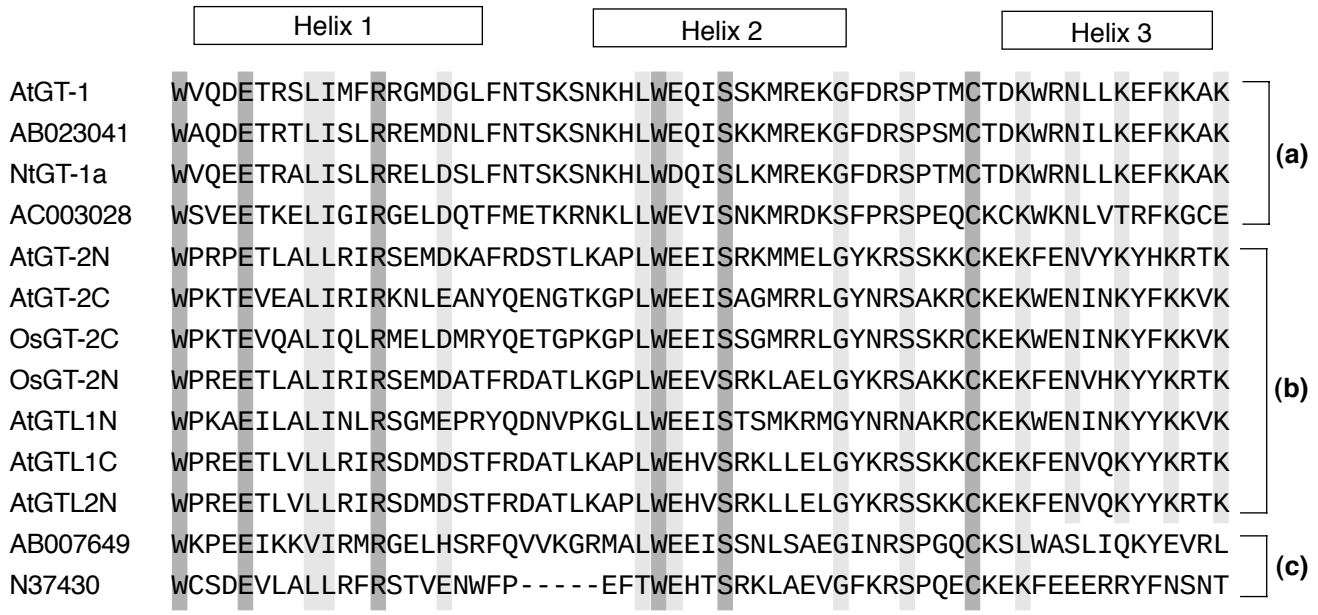

Fig. 4. The trihelix-binding domains from identified GT-factors from *Arabidopsis* (At), tobacco (Nt) and rice (Os), and EST (N37430) and genomic (AB023041; AC003028; AB007649) sequences from *Arabidopsis*. Dark-gray indicates that amino acid residues are conserved in all sequences, light-gray indicates that amino acid residues are conserved in most sequences. (a) Single-trihelix domain proteins; (b) twin-trihelix proteins; (c) sequences with only two conserved helices.

two predicted trihelix motifs, with the carboxyl one truncated in AtGTL2 (Fig. 4)[42]. The DNA-binding activity of AtGTL1 and AtGTL2 has not been determined. To date, the trihelix DNA-binding proteins have been found only in plants.

The expression of all of the cloned GT factors appears to be ubiquitous and independent of light, except that AtGTL1 mRNA is more abundant in siliques[14,37,38,40–42]. GT-factor-mediated light activation or light repression should be achieved by post-translational modifications and/or by differential interactions with other light-responsive transcription factors. The possibility that a light-regulated GT-factor might exist has not been excluded but has yet to be identified. AtGT-1 and AtGT-2 are targeted to the nucleus[41,43], two independent nuclear localization signals have been identified in the rice GT-2, with one in each trihelix motif of the protein[43]. Functional analysis showed that rice GT-2 and AtGT-1 can activate transcription *in vivo*[44,45]. The *trans*-activation activity of AtGT-1 appears to reside in the C-terminal part of the protein, in which an acidic domain has been observed[41]. *In vitro* experiments have shown that AtGT-1 can interact with the TFIIA–TBP–TATA complex, suggesting that AtGT-1 might activate transcription through direct interaction with the minimal pre-initiation complex[45]. A mutation in genes encoding the trihelix DNA-binding protein has not been characterized in *Arabidopsis* so far.

The genes of AtGT-2 and AtGTL-1 are both located on chromosome I (Ref. 42). Databank searches have found a few new potential GT-factor genes scattered on *Arabidopsis* chromosomes II, III and V (Fig. 4). The total number of identified genes encoding GT-factors is much smaller than that of other classes of transcription factors, such as myb and b-zip found in *Arabidopsis*. GT-factors appear to belong to a small family of plant transcription factors.

A variety of specific regulations of many different genes by a small number of GT-factors appears to be reconciled by the high degeneracy of GT-elements, which might have been subjected to the principal evolutionary change. Competition between GT-factors for a given GT-element might produce distinct transcription activity. Modification and dimerization between GT-factors, as well as their interaction with other transcription factors, appear to play a major role in producing a distinct regulatory function. Therefore, identification of factors that interact with, or modify, GT-factors, will be crucial in deciphering their molecular mechanism of action. Cloning additional trihelix DNA-binding factors, determining expression profiles and defining the target DNA-binding sites of each of the GT-factors are essential to study this category of plant transcription factor. Functional analysis of GT-factors by creating dominant negative and over-expression lines will be extremely important in establishing the regulatory hierarchy of GT-factors by monitoring gene expression profile changes at the genomic scale.

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Dao-Xiu Zhou is at the Laboratoire de Génétique Moléculaire des Plantes, Université de Picardie Jules Verne, 33, rue Saint Leu, 80039 Amiens, France (tel +33 3 2282 7038; fax +33 3 2282 7976; e-mail dao-xiu.zhou@sc.u-picardie.fr).