

ROLE OF PLANT PROMOTERS AND THEIR *CIS* REGULATORY ELEMENTS IN GENE EXPRESSION REGULATION

Rubab Zahra Naqvi^{*1}, Hira Mubeen^{1,2} and Shahid Raza²

¹National Institute for Biotechnology and Genetic Engineering, Faisalabad, Pakistan.

²University of South Asia, Lahore Pakistan

***Correspondence for Author: Rubab Zahra Naqvi**

National Institute for Biotechnology and Genetic Engineering, Faisalabad, Pakistan.

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ABSTRACT

Promoters are the important regulatory element that control gene expression. Promoter sequences that allow expression of foreign genes in plants are useful tools for producing genetically engineered crop plants with superior crop yields, higher crop quality, shorter growth periods and greater insect resistance. Plant gene promoters are categorized into constitutive, inducible, tissue-specific and synthetic/ hybrid promoters. Any of the mentioned promoters can be selected to develop transgenic plant depending upon the type of gene and the destination tissue. Identification and characterization of specialized promoters and their *cis*-regulatory elements is an important step in achieving controlled gene expression in biotechnological applications. The present review gives a comprehensive overview of promoter, its types and its *cis*-regulatory elements involved in regulation of gene expression.

KEYWORDS: Promoter, *cis*-regulatory, gene expression.

INTRODUCTION

Genetic engineering is a useful method for introducing desirable traits into crop plants. Successful application of gene transfer technologies for improving crops requires appropriate promoters. The choice of promoters depends on the desired expression e.g. tissue-specific expression. A number of constitutive, tissue-specific and inducible promoters have been isolated from a wide variety of organisms. Several well-characterized promoters are now used for genetic engineering of plants. Promoter is the non coding DNA region that occurs upstream of the coding region of a gene and is required for transcription of that specific gene. The promoter plays an important role in the process of plant gene expression and regulation (Dare et al, 2008). The promoter can roughly be divided in two parts. The first part represents **Core/proximal promoter**, which is the region within 100-250 bp around the transcription start site. The proximal part is believed to be responsible for correctly assembling the RNA polymerase II complex at the specific position and for a basal level of transcription (Nikolov et al., 1996; Nikolov and Burley, 1997; Berk, 1999). It is mediated by elements, such as TATA and initiator boxes through the binding of the TATA box binding protein, and other general transcription factors (TFs) specific for the RNA polymerase II (Featherstone, 2002). The second part comprises of a **distal part of the promoter**, which contains the elements that regulate the spatio-temporal expression (Tjian and Maniatis, 1994; Fessele et al., 2002). This region comprises of single to multiple *cis*-regulatory elements that can accelerate or decelerate the transcription by a given promoter. The

promoter region of any gene as described above presents a linear view of the promoter, while in reality; a complex structure is formed after bringing the transcription factors (TFs) together on a promoter, by adopting a three dimensional configuration, which activates the basal transcription machinery (Fig. 1.1 ; Buratowski, 1997; Berk, 1999; Struhl, 2001).

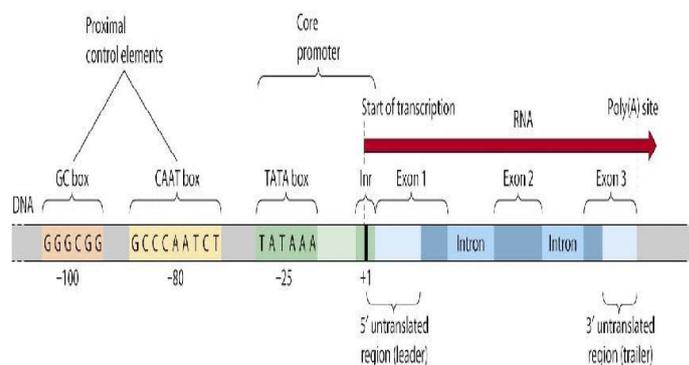


Fig. 1: The promoter of a eukaryotic gene- upstream region of a gene consists of two parts. 1; core promoter: the region 100-250 bp around the transcription start site characterized by initiator sequence and TATA box, and 2; Distal promoter: the region containing the *cis*-regulatory elements necessary for the regulation of gene expression (<http://www.mun.ca/biology/desmid/brian/BIOL2060/BIOL2060-23/2321.jpg>).

Types of the Plant Promoters

Plant promoters can be classified according to the type of control for gene expression. Generally the types of promoter expression can be constitutive, inducible and tissue specific (Zhang *et al.*, 2004). In addition, to these types the synthetic and hybrid promoters have also been reported.

Constitutive promoters

Constitutive promoters express the genes constitutively and are being used to drive alien gene expression in most transgenic engineering experiments requiring ubiquitous expression of a gene in all tissue types. Cauliflower mosaic virus (CaMV) 35S gene promoter and nos (nopaline synthase) promoter (Yutao *et al.*, 2003) are some of the widely used constitutive viral origin promoters (Odell *et al.*, 1985). 35S promoter and its derivatives have shown high transgene expression in dicotyledonous plants (Battraw and Hall, 1990; Benfey *et al.*, 1990), while the expression by these promoters in monocotyledonous plants is very low (Christensen *et al.*, 1992; Gupta *et al.*, 2001; Weeks *et al.*, 1993). Other strong constitutive promoters include, maize and tobacco ubiquitin promoters (Christensen and Quail, 1996; Genschik *et al.*, 1994; Plesse *et al.*, 2001), and the rice actin1 promoter (McElroy *et al.*, 1990). However, the expression of monocot derived promoters is higher in monocots than in dicots (Cornejo *et al.*, 1993). The exploration of more monocot and dicot promoters is very essential with respect to gene and tissue specific expression (Park *et al.*, 2010).

Inducible promoters

Inducible promoters are another important type of promoters which are expressed only when exposed to any biotic or abiotic stresses e.g. chemicals like alcohol, steroids, or physical factors e.g. light or temperature (Zhu *et al.*, 2010). Examples of inducible promoters are *wun1* gene promoter (Siebertz *et al.*, 1989), and proteinase inhibitor II (*pin2*) gene promoter, both of them show wound inducible expression.

Tissue-specific promoters

Tissue-specific promoter can drive gene expression in particular tissues or controls developmental stage-specific expression. The isolation, identification and application of such promoters, e.g. seed and fruit specific promoters, have become an important aspect in transgenic plant development (Yutao *et al.*, 2003). Examples of tissue specific promoters are tuber-specific patatin promoter identified from potato (Jefferson *et al.*, 1990), fruit-specific E8 promoter from tomato (Deikman *et al.*, 1992), tuber-specific sporamine promoter from sweet potato (Maeo *et al.*, 2001), and seed specific alpha globulin promoter from cotton (Sunilkumar *et al.*, 2002).

Hybrid/Synthetic promoters

A functional promoter containing DNA sequence elements from two or more well characterized promoters is called hybrid promoter. Construction of a synthetic

promoter is done by the modular arrangement of cis-acting elements. These have the ability to function independently from their natural promoter (Potenza *et al.*, 2003). An example of hybrid promoter is the Mac promoter. It is engineered by combining some region of mannopine synthase promoter and the enhancer region of cauliflower mosaic virus 35S promoter (Dai *et al.*, 2000; Ziegelhoffer *et al.*, 1999). Another example is the E8/E4 hybrid promoter that is a composite of polynucleotide segments of E8 and E4 gene promoters from tomato. This hybrid promoter gives a high level fruit specific expression in tomato (United States Patent 6118049; Bestwick *et al.*, 2000).

Cis-regulatory elements

Plants receive multiple stimuli such as light, temperature and water availability from its external environment by means of different signaling mechanisms, and consequently respond to the environmental factors. Such communication of plant and its environment is named as cell signaling. Cell signaling harmonizes basic cellular activities and interactions of a cell with its environment for growth, development and eventually to ensure survival of the plant. Plants respond to the environmental factors at cellular and molecular levels, as well as at physiological levels. One of the primary ways to respond to a stimulus is by controlling the gene expression. The expression levels of many plant genes change in response to environmental signals. Plant cell signaling pathways are partly dependent on transcriptional regulatory networks containing circuits of transcription factors (TFs) and regulatory DNA elements that control the expression of target genes. One aspect of plant cell signaling is represented by the transcriptional regulatory networks that constrain organ-specific and cell-specific patterns of gene expression and mediate communications with the environment (Priest *et al.*, 2009).

The transcriptional regulation in plants is mediated by the binding of these TFs to the DNA on specific cis-acting regulatory elements (CAREs) and devises the initiation of transcription. CAREs are short conserved DNA motifs of five up to 20 nucleotides generally found in the promoter region of a gene for the specific binding of RNA polymerase and for the efficient transcription in specific tissues at specific times. TFs interact with these specific DNA elements, other TFs, and the basal transcriptional machinery to regulate the highly specific patterns of gene expression (Rombauts *et al.*, 2003).

Carbohydrate metabolite signal responsive element (CMSRE)

Another, DNA sequence element (TGGACGG) named as CMSRE (carbohydrate metabolite signal responsive element) is present in several sugar inducible genes. It plays an important role in the sucrose inducible expression of a group of plant genes (Morikami *et al.*, 2005).

Regulation of promoters by WRKY genes

WRKY genes are involved in defense responses in different plant species. WRKY genes encode the proteins that bind to the cis-acting element called as W box. W box is a hexamer of TTGAC(C/T), which is found in the promoter regions of many pathogenesis related genes. Based on the core sequence (TTGAC) of a W box, there are variants of W boxes, which include TTTGACA, TTTGAC(C/T), TTGACTT, TTGAC(A/C), TTGAC(A/C)A, and TTGAC(A/C) (C/G/T), and a W box like element, TGAC(C/T) (Maleck *et al.*, 2000; Navarro *et al.*, 2004).

A conserved DNA element the I box GATAAG, is found in most RBCS genes, is also commonly found 5' proximal to the 'TATA' box of most chlorophyll a/b binding protein (CAB) genes (Giuliano *et al.*, 1988; Castresana *et al.*, 1987; Gidoni *et al.*, 1989). It has been reported that PAL1 promoter of phenylalanine ammonia lyase (PAL) gene in parsley contains the motifs CTCCAACAACCCCTTC and ATTCTCACCTACCA, involved in the responses to both UV irradiation (Rodrigo *et al.*, 1989). Stress inducible gene expression has been shown by a 9bp conserved sequence, TACCGACAT, known as the dehydration responsive element (DRE). It is an essential cis-acting element for ABA independent response to dehydration and cold (Yamaguchi and Shinozaki, 1994). A 9bp sequence, ACTCATCCT, in the Pro dehydrogenase (ProDH) promoter is necessary for the efficient expression of ProDH in response to Proline (Pro) and hypoosmolarity. Several Pro-inducible genes have the ACTCAT that is a core cis acting element PRE (Pro or hypoosmolarity responsive element) sequences in their promoter regions and play an important role in Pro-responsive and hypoosmolarity responsive expression of ProDH (Satoh *et al.*, 2002). Hormone-inducible promoters have some conserved elements such as ABRE (Simpson *et al.*, 2003), P box (TGTAAG) (Kim *et al.*, 1992), and the TCA element (Pastuglia *et al.*, 1997; Liu *et al.*, 2009). The cis-regulatory elements ACGTGG/TC known as ABA responsive element (ABRE; Zhu, 2002), CE1 (TGCCACCGG), and CE3 (ACGCGTGCTC) are involved in ABA responsive gene expression in different plants (Shen *et al.*, 1996). The cis-acting elements, GGCCGACAT named C repeat (CRT) and GGCCGACGT known as low-temperature-responsive element (LTRE), both containing an A/GCCGAC motif have been reported to regulate cold inducible promoters (Thomashow, 1999; Jiang *et al.*, 1996; Yamaguchi and Shinozaki, 2005).

DISCUSSION

Promoters are regions of the DNA upstream of a gene's coding region that contain specific sequences recognized by proteins involved in the initiation, acceleration or suppression of transcription. (Buchanan *et al.* 2000). They are important in controlling overall expression profile of a gene and can drive or prevent transcription at specific developmental stages. There are different cis-

regulatory elements located on promoter region required for altering the behavior or fate of the gene product under different conditions e.g. stress or at different developmental stages of an organism (Picot *et al.* 2010). A few examples of such elements are TATA box (Featherstone, 2002), G box (CACGTG) (Siberil *et al.*, 2001), A box (TACGTA) and C box (GACGTC) (Foster *et al.*, 1994; Song *et al.*, 2008). The TATA box is the first eukaryotic core promoter motif to be identified (Goldberg, 1979; Breathnach and Chambon, 1981). In the beginning it was known that TATA box has resemblance to the -10 region (Pribnow box) of prokaryotic promoters, but it appears that the eukaryotic and prokaryotic TATA box regions are not homologous. TATA box is present close to TSS and is involved in the formation of a transcription initiation complex (Pribnow, 1975a, b).

G box (CACGTG) has been reported in several plant promoters. It regulates expression in response to different factors, such as light, hormones, and environmental conditions. It is also involved in tissue specific expression (Giuliano *et al.*, 1988; Schulze-Lefert *et al.*, 1989; Donald and Cashmore, 1990; Kim *et al.*, 1992; Menkens *et al.*, 1995; Ishige *et al.*, 1999; Hudson and Quail, 2003). G boxes are usually recognized by a group of bZIP proteins termed GBF (G box binding factors; Schindler *et al.*, 1992; Menkens *et al.*, 1995; Siberil *et al.*, 2001).

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