International Journal of Applied and Advanced Scientific Research (IJAASR)
Impact Factor: 5.255, ISSN (Online): 2456 - 3080
(www.dvpublication.com) Volume I, Issue I, 2016

PROMOTER DIVERSITY IN PLANTS – A REVIEW

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Cite This Article: M. Saranya & M. Kanchana, "Promoter Diversity in Plants – A Review", International Journal of Applied and Advanced Scientific Research, Volume 1, Issue 1, Page Number 209-217, 2016

Abstract:

The promoter sequence is the key regulatory region of a gene that controls and regulates gene expression. It has a major importance in the regulation of transcription, i.e. the transfer of the information contained in a DNA coding region into an mRNA transcript. Promoters play an important role in the regulation of gene expression at different locations and times during the life cycle of an organism or in response to internal and external stimuli. Investigating and unravelling the precise function of promoter components and the additional factors associated with their performance revealed new possibilities of genetic engineering. Thus, promoters have a huge influence in follow-on research and development in biotechnology, and a more detailed understanding will certainly further influence the development of GMOs. This review represents a summary of different types of promoters that have identified and characterized for gene transformation in plants.

Key Words: Gene Expression, Constitutive Promoter, Tissue-Specific Promoter & Inducible Promoter

Introduction:

Transgenic plant technology provides an indispensable and powerful tool for analysis of gene functions and stably expression of foreign genes (Daniell *et al*., 2001).Genetic engineering has been commonly used for introducing specific genes into plants for specific trait improvement because of the desirability in the global marketing. Many traits are included in biotechnology programs such as novel colour, grain size, quality and yield by the modulation of particular gene(s), without losing the useful agronomic qualities of the cultivar (Kasetsart *et al.,* 2006).A high level of gene expression is usually needed for the production of important genes for agronomical or commercial purposes in transgenic plants. To achieve this goal, we need to understand and exploit the mechanisms, plant developed to regulate the expression levels of their various genes during evolution (Lewin, 2000).

Gene expression in eukaryotes is a multi-stage process controlled at transcriptional, post-transcriptional, translational and post- translational levels (Qu and Sivamani, 2006). Transcription, the initial step of gene expression and one of the most important intracellular steps influencing gene expression, is regulated by several cis-elements and trans-factors. The eukaryotic promoter, a key sequence or center of transcription regulation, determines the direction and efficiency of transcription and type of RNA polymerase, which binds to the promoter sequence and initiates the transcription (Zhu and Li, 1997). Promoter is a DNA sequence normally located upstream of the transcribed region. It contains TATA box and serves to determine the start site of transcription (Dynan and Tjian, 1985).

Promoter can be divided into two regions: a proximal region, commonly known as the core and a distal region. The proximal region or the core is thought to be responsible for the RNA polymerase II attachment and for directing a basal level of transcription (Rombauts *et al*., 2003). Core promoter elements such as the TATA box, BRE (TFIIB recognition element), Inr (Initiator), MTE (motif ten element), DPE (downstream core promoter element), and DCE (downstream core element) were typically found in focused core promoters (Juven-Gershon *et al*., 2008). The distal region of the promoter is believed to contain regulatory elements for spatiotemporal expression (Fessele *et al*., 2002).The challenge of multiple coordinated transgene expression can be addressed using a promoter diversity approach, where different promoters are used to drive different transgenes increases due to the lack of available promoters with suitable expression profiles (Peremarti *et al.,* 2010).

Plant promoter can be classified as constitutive, inducible and organ or tissue-specific. A constitutive promoter directs the expression of a gene in all the tissues of a plant during various stages of development. A tissue-specific promoter directs the expression of a gene only in certain tissues and may or may not be activated during all the stages of development. An inducible promoter initiates gene expression in response to chemical, physical or biotic or abiotic stresses (Carneiro and Carneiro, 2011).

Constitutive Promoter:

Constitutive promoters are the most common promoters used to drive the expression of various genes in development of transgenics. A constitutive promoter may contain an element which responds to activators present in all tissues, all the time. Alternatively, there could be a transcription factor present in all the tissues, all the time, interacting with an element of a constitutive promoter (Virupakshi, 2008).

CaMV 35s promoter is valuable because it provides high expression in all regions of the transformed plant and is generally available in the cassette vector used for transformation which facilitates the sub-cloning of the transgene of interest (Potenza *et al*., 2004).Although widely used, the CaMV 35s promoter as a certain limitations such as its poor performance in monocots, its suppression by feeding nematodes (Goddijn *et al*., 1997; Urwin *et al.*, 1997). For this reason, alternative virus promoter with similar or improved properties has been sort. Examples include promoters from *Figwort mosaic caulimovirus* (FMV; Bhattacharyya *et al*. 2002), *Cassava vein mosaic virus* (CsVMV; Verdaguer *et al.*, 2002). *Cestrum yellow leaf curling virus* (CmYLCV; Stavolone *et al*. 2003), *Mirabilis mosaic virus* (MiMV; Dey and Maiti 1999) and *Peanut chlorotic streak virus* (Maiti and Shepherd 1998; Bhattacharyya *et al*., 2003).

The *Commelina yellow mottle virus* (CoYMV) promoter is active in tobacco (Medberry*et al*., 1992). The *Sugarcane bacilliform virus* (ScBV) promoter is active in monocots (banana, corn, millet and sorghum) and dicots (tobacco, sunflower, canola and *Nicotiana benthamiana*) and has shown to drive high level *gus*A expression in transgenic banana and tobacco plants (Schenk *et al.*, 2001).

Another commonly used high-level, constitutive promoter is rice *actin 1* gene (McElroy *et al*., 1990), ubiquitin promoter (Ubi) from maize and *Arabidopsis* (Cornejo *et al*., 1993). The ubiquitin extension protein (*uep*) gene, has been isolated from yeast and several plants, including tomato, barley and potato (Masura *et al*., 2010). Other constitutive promoter are also available such as CaMV 19S (Balazs *et al.*, 1985) and the tobacco promoter eIF4A-10 (Tian *et al.*, 2005) (Kalai *et al.*, 2008).

Tissue-Specific Promoters:

In recent years, a large number of tissue/organ or stage specific promoters sequences have been cloned and characterized (Zheng *et al*., 2007). Spatially and developmentally controlled gene expression can be achieved using different tissue-specific promoters. A wide range of promoters have been identified in promoter trap programs and following the characterization of gene expression patterns. They allow specific gene expression in virtually any desired cell type, tissue or organs (Deveaux *et al*., 2003).

(a) Seed Specific Promoters: Seeds are the storage organs which provide the optimal biochemical environment for the accumulation of large amounts of protein. In biofarming, recombinant protein production in seeds offers great benefits in terms of scalability and protein stability. The majority of available seed-specific promoters originate from seed-storage proteins (SSPs), such as rice glutelin and globulin, soya lectin and β-phaseolin. Seed storage promoters, arcelin 5-1 (*arc*5-1) and β-*phaseolin* from the common bean (*Phaseolus vulgaris*) have also been used to successfully express the murine single-chain variable fragment (scFv) G4 in transgenic *Arabidopsis* plants (Ezcurra *et al*., 2000). There is only one report of characterization of SAD genes from rapeseed (*Brassica napus* L.)(Jain *et al.*, 1999).

(b) Root-Specific Promoters: Root specific promoters have been of particular use in engineering resistance to nematodes and improving plant tolerance to environmentally stressful conditions such as water, salt and heavy metals. A number of plant gene promoters that confer root-specific expression have been isolated including the PR10 promoter from western white pine (Liu & Ekramoddoullah, 2003), the IDS2 promoter from barley (Kobayashi *et al*., 2003), the isoflavone synthase gene promoters (IFS1 and IFS2) from soybean (Subramanian *et al.*, 2004), the MsPRP2 promoter from alfalfa (Winicov *et al*., 2004). Root specific promoter such as the PHT1 gene of *Arabidopsis* (Koyama *et al*., 2005)(Kalai*et al*., 2008).

(c) Floral Tissue-Specific Promoters: In contrast to other plant organs, flowers are composite structures composed of several organs that form an ordered pattern. The typical flower consists of four organs arranged in whorls. The sepals consist of the outermost whorl followed by the petals in the next whorl and stamens (male reproductive organs) in the third whorl and carpels (female reproductive organs) in the innermost whorl (Theiszen and Saedler., 2001) Each of these whorls consist of unique genes targeted to the specific organ and several homeotic genes that affect the fate of organ primordial (Coen *et al*., 1990).Targeted genetic engineering, by utilizing promoters obtained from genes specifically expressed in a specific whorl is highly desirable for targeted gene expression and can be exploited by using specific promoters (Yang *et al*., 2011).Some of the traits that can be engineered in the floral tissues include increased vase life (Bovy *et al*., 1999; Chang *et al*., 2003; Serek *et al*., 2006),flower color modification (Tanaka *et al*., 2005; Savin *et al*., 1995; Aida *et al*., 2000), fragrance (Zuke *et al*., 2002; Verdonk *et al*., 2005; Aranovich *et al*., 2007) and male and female sterility (Goetz *et al*., 2001; Mariani *et al*., 1992; Mitsuda *et al*., 2006) among others. Chalcone synthase (*CHS*) is synthesized in the flower corolla, tube and anthers and is important for the biosynthesis of flavonoid antimicrobial phytoalexins and anthocyanin pigments in plants (Ferrer *et al*., 1999).Various CHS promoters has been studied extensively in many plants, especially in *Phaseolus vulgaris*, antirrhinum, petunia and parsley (Faktor *et al*., 1997; Koes *et al*., 1990).

(D) Fruit-Specific Promoters: A number of fruit-specific genes that are activated during ripening have been isolated from plant species with either climacteric or non-climacteric fruits. Although fruit-specific promoters have been isolated and analyzed for a number of species, tomato has long served as the primary model for the investigation of fruit and ripening specific promoters (Nicholas *et al*., 1995). It has also served as a heterologous

system to test the function of putative promoter sequences isolated from other fruit species, such as apple (Atkinson *et al*., 1998) and pepper (Kuntz *et al*., 1998).

Fruit-specific promoters such as tomato polygalacturonase (Nicholas *et al*., 1995) and E8 (Deikman *et al*., 1998) promoters have attracted much interest because of their practical use in the manipulating fruit metabolism and the production of valuable pharmaceutical proteins such as antibodies, and edible vaccines in genetically engineered fruits. However, the essential *cis*-elements have not been identified. Recently, a novel *cis*-acting element that determines fruit-specific, high-level expression of cucumisin was identified and functionally characterized in melon (Yamagata *et al*., 2002).

(e) Endosperm-Specific Promoters: Endosperm is a storage organ for starch and protein for cereal crops, which provide the major source of calories and proteins for humans. Improvement of the endosperm composition and quality via genetic modification is attractive, and there have been great achievements. Some endosperm specific expression promoters have been isolated and characterized from rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.) and barley (*Hordeum vulgare* L.)(Xu *et al*., 2010).

(f) Inducible Promoters: Inducible promoters are responsive to environmental stimuli and provide precise regulation of transgene expression through external control. Promoters that are induced under certain stress conditions, both biotic and abiotic are interesting biotechnological tools for use in plant breeding programs. In general, the stress-inducible promoters contain a cis-acting sequence which is recognized by specific transcription factors that induce the synthesis of proteins only under condition of stress (Jaglo *et al*., 2001).

(g) Promoters Induced by Abiotic Stress: Hormones play a key role in regulating plant growth and development. Auxin play an important role in root formation, apical dominance, tropism, senescence and differentiation inside the plant cell. The most extensively studied auxin-responsive plant gene promoters are those from the pea PS-IAA4/5 gene (Abel *et al*., 1996). The promoters of the rice OsNCED3 and Wsi18 genes implicated in the synthesis and signaling of ABA, were highly inducible after drought, ABA, and high-salinity treatments in transgenic rice (Bang *et al*., 2013; Yi *et al*., 2011). The *Arabidopsis* Rd29A promoter was successfully used to mediate drought-specific expression of DREB1A in transgenic wheat (Pellegrineschi *et al*., 2004). The common stress-responsive elements comprise the dehydration-responsive element DRE implicated in the regulation of cold and dehydration responses in *Arabidopsis*, and the ABA responsive element ABRE that regulates dehydration and salinity responses in *Arabidopsis* and rice (Yamaguchi- shinozaki and Shinosaki, 2006). The GLP promoter isolated from *Tamarix hispida* which was highly induced by drought, salt and low temperature, its expression occurring in leaves and roots (Li *et al*., 2010).

(h) Promoters Induced by Biotic Stress:

Chimeric promoters are becoming new powerful tool to direct gene expression in targeted locations or developmental stages of plants in response to specific biotic. Several chimeric promoters have been created for different purposes, such as enhancing activity of minimal promoters (Tornoe *et al*., 2002), achieving organ-specific gene expression (Martinelli and Simone 2005), exploring the signaling pathway of plant-pathogen interaction (Rushton *et al*., 2002). Biotic stress-induced promoters also deserve attention because they are induced by the pathogens that are quickly activated in response to stress and are effective in plant defense process (McDowell and Woffenden, 2003). A well induced stress promoter is Gst 1 promoter from potato which activates gene transcription in responsive to infection by bacterial and fungal pathogens in transgenic apple (Malnoy *et al*., 2006). In transgenic citrus plants, the same promoter promoted gene expression in response to injury or to the pathogen *Xanthomonas axonopodis* sp. (Barbosa-mendes *et al*., 2009). Another promoter that has an important role in the plant defense system is the promoter belongs to class 10 PR (pathogenesis related). Coutos-thevenot *et al*., (2001) related the combination of this pathogen-inducible promoter and a defense gene, the Vst1 gene which increase tolerance against fungi in grape vine.

(i) Status about Promoter: The identification and availability of the Cauliflower Mosaic Virus promoter (CaMV) was a big step from an industrial and molecular genetics point of view, since it was the first promoter showing a strong expression in almost all plant tissue and therefore it became almost universally applied. Until recently most of the antisense genes for different traits were cloned under the control of this promoter and introduced into various crops. However this 'Constitutive' and strong promoter has several drawbacks, the gene of interest is also expressed in tissues and at times when it is not necessary or even unwanted (Trindade, 2003). A second generation of promoters comprises of mainly maize poly ubiquitin1 (Ubi 1) promoter (Christensen *et al*., 1992), actin (Act 1) promoter (McElroy *et al*., 1991), ubiquitin (OsUbi1) promoter (Bhattacharyya *et al*., 2012), Cytochrome c1 (OsCc1) promoter (Jang *et al*., 2002), L- ascorbate peroxide (APX) and cystolic 6-phosphogluconate dehydrogenase (PGD1) promoter (Park *et al.*, 2010). These promoters were somewhat better adapted to particular requirement; however a fine regulation of expression was not possible even with these promoters (Liu *et al*., 2013).

Conclusion:

The most widely used promoter for directing strong constitutive expression of the target gene in transgenic dicotyledonous plants is CaMV 35S promoter, which is generally active at high levels even in the absence of stress. In contrast, most promoters of plant defensive genes are activated only after exposure to biotic

or abiotic stresses. The application of native plant promoters can also help to avoid transgene silencing, which is associated with the presence of promoters of non-plant origin in the plant genome. To overcome these limitations it is important to identify novel genes and their upstream regulatory regions. Also, the determination of gene expression pattern in response to stress and a better understanding of their functions in stress adaptation will provide the basis for an effective engineering strategy to improve stress tolerance in plants.

Table 1: List of constitutive promoters

S.No	Promoter	Origin	Crop use	References
1	BSV	Banana streak badna virus	Banana,	Schenk *et al*., (2001)
2	CaMV 35S	Cauliflower mosaic virus	Apple, broccoli citrus chrysanthemum cocoa	Mesa *et al*., (2004); Jong *et al*., (1994); Dhandi *et al*.(2009); Gasic *et al*.,(2003).
3	CMPS	Cestrum Yellow Leaf curling virus	Grape	Vaccari *et al*., (2009)
4	Mannopin synthase	Gladiolus	Gladiolus	Kamo, 2003
5	RolD	*A. rhizogenes*	Gladiolus	Kamo, 2003
6	Uep1	Oil palm	Oil palm, tobacco	Masura *et al*., (2011)
7	Ubiquitin	Grape, gladiolus	Grape, gladiolus	Dadi *et al*., (2009)

Table 2: Examples of seed-specific promoter

S.No	Promoter	Origin	Crop use	References
1	2S	Grape	Grape, tobacco	Li *et al*.,(2005)
2	CuMFT1	Citrus	*Arabidopsis*	Nishikawa *et al*., (2008)
3	Dc3	Carrot	*Arabidopsis*	Kim *et al*., (1997)
4	HaG3-A	Sunflower	Tobacco	Bogue *et al*., (1990)
5	LeB4	*Vicia faba*	Tobacco	Baumlein *et al*., (1991)
6	LegA	Pea	*Helianthus*	Shirsat *et al*., (1989)
7	NapA	*Brassica napus*	Tobacco	Stalberg *et al*., (1996)
8	Phas	Bean	Tobacco	Sengupta *et al*., (1985)
9	Psl	Pea	Tobacco	Pater *et al*., (1996)
10	Str	*Catharanthus roseus*	Tobacco	Ouwerkerk and Memelink, (1999)
11	USP	*Vicia faba*	Tomato	Fiedler *et al*., (1993)

Table 3: Examples of root-specific promoter

S.No	Promoter	Origin	Crop use	References
1	B33	Potato	Potato	Farren *et al*., (2002)
2	FaRB7	Strawberry	Tobacco	Vaughan *et al*., (2006)
3	Glb3 5'	*Sesbania rostrata*	Lotus	Szabados *et al*., (1990)
4	MipB	*Mesembryanthemum crystallinum*	Tobacco	Yamada *et al*., (1997)
5	Npv30	Bean	Lotus	Carsolio *et al*., (1994)
6	PsENOD12A PsENOD12B	Pea	*Vicia hirsuta*	Vijn *et al* ., (1995)
7	RB7	Tobacco	Tomato	Vaughan *et al*., (2006)
8	SLREO	Tomato	Tomato	Jones *et al*., (2009)
9	VfLb29	*Vicia faba*	*Vicia faba*	Vieweg *et al*., (2004)
10	Sporamin	Sweet potato	Potato, tobacco	Wang *et al*., (2002); Hong *et al*., (2008)

Table 4: Examples of floral tissue-specific promoter

S.No	Promoter	Origin	Crop use	References
1	BAN215-6	*Brassica campestris*	Tobacco	Kim *et al*., (1997)
2	CHS	Bean	Petunia, tobacco	Koes *et al*., (1990) Schmid *et al*., (1990)
3	END1	Pea	Tobacco	Gómez *et al*., (2004)
4	GTCHS1	*Gentiana triflora*	Petunia	Kobayashi *et al*., (1998)
5	LAT52	Tomato	*Lilium longiflorum*	Miyoshi *et al*., (1995)
6	PsTL1	*Pyrus serotina*	Tobacco	Sassa *et al*., (1998)

7	SK2	Potato	Potato	Ficker *et al*., (1997)
8	TomA108	Tomato	Tobacco	Xu *et al*., (2006)

Table 5: Examples of Fruit-specific promoters

S.No	Promoter	Origin	Crop use	References
1	ACC-oxidase	Peach, apple, tomato, banana	Tomato, banana	Atkinson *et al*., (1998) Barry *et al*., (1996)
2	ADP-glucose pyrophosphorylase	Watermelon	Tomato	Yin *et al*., (2009)
3	Expansin	Cherry, cucumber	Tomato, cucumber	Karaaslan *et al*., (2010) Unni *et al*., (2012)
4	Cucumisin	Melon	Melon	Yamagata *et al*., (2002)

Table 6: Examples of promoters induced by abiotic stress

S.No	Corresponding gene	Inducer	Organism	References
1	HSP1&2	Thermal shock	*Arabidopsis thaliana*	Takahashi *et al*., (1992)
2	Rd29	Osmotic stress	*Arabidopsis thaliana*	Yamaguchi-Shinozaki and Shinozaki (1993)
3	Adh	Dehydration and cold stress	*Arabidopsis thaliana*	Dolfreus *et al*., (1994)
4	rbcS-3A	Light	*Pisum sativum*	Kuhlemeier *et al*., (1989)
5	Chn48	Ethylene	*Nicotiana tabacum*	Shinshi *et al*., (1995)
6	HVADhn45	Drought stress	*Hordeum vulgare*	Xiao and Xue (2001)
7	PtDrl02	Methyl jasmonate	*Populus sp*	Zheng *et al*., (2011)

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