Abiotic stress responsive *cis*-regulatory elements (CREs) in rice (*Oryza sativa* L.) and other plants

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Abstract

Capability of crop plants to adjust to the adverse environmental conditions in a spatio-temporal fashion is critical for their survival and maintaining agricultural productivity. Genetic engineering efforts for improving tolerance to diverse abiotic stresses in crop plants using well characterised stress-inducible promoter elements have proven to be advantageous. Combinatorial interactions of *cis*-acting DNA elements in the promoters with *trans*-acting protein factors are key processes governing spatio-temporal gene expression. It is becoming increasingly evident that targeted modification of molecular genetic network is feasible, for exploiting the potential of specific abiotic stress responsive element and its corresponding master regulatory genes *via* plant genetic engineering. The importance of inducible promoters in agricultural crop improvement is enormous; hence it is very crucial to characterise inducible promoters from plant genome sequence data bases on a large scale. We will briefly discuss here abiotic stress responsive *cis*-acting elements and their role in abiotic stress regulated gene expression.

Introduction

Due to their sessile life style, plants are only able to survive by their ability to build up fast and highly adaptive responses to diverse environmental stresses. These adaptive mechanisms involve a complex network for perception and transmission of stress signals to initiate cellular responses by changes in enzyme activity, gene expression, and transport of molecules across membranes (Boyer, 1982; Mittler, 2006). Abiotic stress tolerance in plants involves diverse genetic mechanisms and versatile molecular adaptive processes (Bohnert et al., 1995). Therefore, capability of crop plants to adjust to the adverse environmental conditions in a

spatio-temporal fashion is critical for their survival and maintaining agricultural productivity. The greatest challenge for humanity in the next few decades will be to increase and sustain agricultural productivity without degrading the ecosystem. Deep understanding about abiotic stress responses in crop plants is vital for the continuous development of rational precision breeding programs as well as for devising transgenic strategies for developing improved stress tolerant crops plants. During the last two decades, tremendous advancement in recombinant DNA technology has enabled us to introduce traits of agronomic importance into the crop plants. However, it is still difficult to introduce a complex trait such as drought tolerance regulated by multiple genes. Some unique regulatory genes (transcription factor encoding genes) controlling several downstream cellular responses have been successfully integrated into some of the plant species to improve tolerance to environmental stresses including drought.

Plant genetic engineering efforts for improving tolerance to diverse abiotic stresses in crop plants using well characterised stress-inducible promoter elements and master regulatory genes (transcription factors) have proven to be advantageous (Bhatnagar-Mathur et al., 2008; Yamaguchi-Shinozaki and Shinozaki, 2005). We mainly discuss here functional characterization of ABA responsive *cis*-acting elements (ABREs) in plant species.

Cis-elements: Driving Gene Expression

Cis-regulatory elements basically include core promoter elements, proximal promoter elements, and long range regulatory elements. RNA polymerase II, its other subunits and different *trans*-acting protein factors (transcription factors) recognise the core promoter elements and other functional DNA sequences to initiate transcription in response to internal and external cues. TATA box, the initiator element and other downstream promoter elements are well characterised components of the core promoter element. A promoter becomes non-functional if the orientation and the distance between the core elements and the transcription start sites altered. However, the enhancer elements, classified under long range regulatory elements will still (but not always) have the ability to activate gene expression. Apart from these *cis*-elements, the insulators function as long-range regulatory elements and may function as boundary mark between heterochromatin and euchromatin or may function for blocking enhancer activity to regulate the accurate expression of the adjacent genes (Burgess-Beusse et al., 2002).

Based on the nature of promoters, they are basically divided into three types:

i.) Constitutive promoters ii.) Tissue-specific promoters iii.) Inducible promoters

Among these three groups of promoters, inducible promoters up-regulate the corresponding gene expression in response to internal and external signals. The interest of researchers in inducible systems of promoters is increasing for two reasons: (i) to understand the precise functional role of genes under stress and (ii) to allow crop plants to have “auto-regulatory” expression of trans-genes under versatile environmental conditions (Reynolds, 1999). However, in some instances, the ectopic expression (leaky expression) and pleiotropic expression of genes negatively affect the use of inducible promoters (Aoyama, 1999). The importance of inducible promoters in agricultural crop improvement is enormous; hence it is very crucial to characterise inducible promoters from plant genome sequence data bases on a large scale. Complete understanding of the functional elements within the inducible promoters responsible for driving gene expression is very crucial to engineer synthetic promoters of interest to drive expression of the potential transgenes (Venter, 2007).

Abiotic Stress Responsive Transcriptional Gene Regulation

Transcription factor is a protein that binds to specific *cis*-regulatory element (CRE) and thereby regulates transcription of genetic information from DNA to primary RNA transcript (Latchman, 1997). Molecular genetic analysis and genetic engineering for abiotic stress tolerance during the past one-decade revealed that transcriptome engineering (use of master switch genes such as signaling proteins and transcription factors) is a viable option for enhancing abiotic stress tolerance of crop plants. Due to the complex and versatile nature of abiotic stress response of plants, multiple stress receptors rather than a single receptor, are more likely to be responsible for perception of the stress. One of the important lessons learnt is that the regulons and sub-regulons of master regulators vary from species to species and thus determine the differential sensitivity of these species to abiotic stresses. Hence, master-regulatory genes from closely related species appear to be better candidate genes rather than that from distant species.

Plants respond to environmental cues at molecular level by altering expression of different sets of genes (Qureshi et al., 2007; Tran et al., 2007). Expressions of such genes are mainly regulated through transcriptional control process, while post-transcriptional and post-translational processes also play a crucial role. Transcriptional control machinery appears to be conserved among plant species (Hakimi et al., 2000; Hirt et al., 1990). It is well established from different experiments over past decades that promoters containing a particular *cis*-element respond to a specific trigger (Viswanathan and Zhu, 2002)

(Chinnusamy et al., 2003; Viswanathan and Zhu, 2002; Yamaguchi-Shinozaki and Shinozaki, 2005; Zhou et al., 2007). Combinatorial interactions of *cis*-acting DNA elements in the promoters with *trans*-acting protein factors are key processes governing spatio-temporal gene expression (Bustos et al., 1991; Hartmann et al., 2005; Hauffe et al., 1993). At an organism level, vast array of molecular genetic networks are operational in a very complex and dynamic mode. Complete understanding of the molecular genetic networks is a long cherished goal of system biologists (Chinnusamy et al., 2004; Li et al., 2006). Till today, several groups of abiotic stress inducible transcription factor families have been characterised from crop plants; these primarily include AP2/ERF, bZIP, MYB and MYC, Zinc-finger proteins, HD-ZIP, NAC, etc. In order to dissect out regulatory activity of promoters in response to abiotic stresses, deep understanding of various transcription factors and their sub-regulons are indispensable.

Occurrence of specific abiotic stress responsive *cis*-regulatory element is the hallmark of abiotic stress responsive promoter element. It is becoming increasingly evident that targeted modification of molecular genetic network is feasible, for exploiting the potential of specific abiotic stress responsive element and its corresponding master regulatory genes *via* plant genetic engineering.

Abiotic Stress Responsive *cis*-Acting Elements

Promoters regulate gene expression by specific *cis*-regulatory elements either by enhancing (enhancers) or repressing (repressors) the transcription efficiency in response to environmental stresses. Several abiotic stress responsive *cis*-acting elements are well characterised in different plant species, such as ABA responsive element (ABRE) in response to ABA and drought responsive element/C-repeat sequence (DRE/CRT) receptive to high salinity, dehydration and low temperature (Yamaguchi-Shinozaki and Shinozaki, 2005).

ABA Responsive *cis*-Acting Elements (ABRE)

The ABRE *cis*-element was originally discovered in *EmBP-1b* promoter of wheat (*Triticum aestivum*) as 8-base pair (bp) sequence (CACGTGGC) (Guiltinan et al., 1990). Subsequently, several stress-inducible promoters have been characterised having ABRE with a conserved core element -ACGT. Molecular dissection experiments like deletion and linker scanning analysis have pinpointed the ABA responsive elements (ABREs), also termed as G-box, C-box or G-box/C-box hybrids within promoters of the ABA responsive genes. The ACGT core nucleotide sequence within ABRE, acts as a binding site for bZIP family transcription factors

governing transcriptional regulation of ABA responsive genes (Guiltinan et al., 1990; Hattori et al., 2002; Mundy et al., 1990; Ross and Shen, 2006; Shen and Ho, 1995). ABREs are also coupled to the non-ACGT coupling elements like CE1, CE3, DRE, O2S, motif III or ACGT core containing ABRE itself (Hobo et al., 1999; Shen et al., 1996; Singh, 1998). Table-1 summarises the list of ACGT and non-ACGT core containing ABA responsive elements validated by various wet-lab experiments. We identified and validated the rice specific ABRE (CGMCACGTGGB) using integrated partial interactive methods and expectation maximization algorithm (MEME) as our top prediction for ABA responsive element (Lenka et al., 2009). Non ACGT core containing ABREs have also been reported (Abe et al., 1997), and named as MYBR and MYCR. These *cis*-elements act like weak enhancer elements responsible for ABA responsive induction in promoters of *RD22* genes. Hence, all these ABA responsive components listed in Table-1 are significant hardware of ABA-dependent pathway and are sensitive to various abiotic stresses and ABA treatment in rice.

Other Abiotic Stress Responsive *cis*-Acting Elements in Rice

ABRE is also responsive to other categories of abiotic stresses like drought and salinity. In case of rice *rab16A-D*, the ABRE (RTACGTGGCR) was reported to be desiccation stress responsive (Mundy et al., 1990). Among the other prominent groups of abiotic stress responsive *cis*-elements which can activate gene expression in the absence of ABA are termed as DRE/CRT, originally identified in *Arabidopsis RD29A/COR78/LTI78* promoter (Table-2). This CRE is responsive to high salinity, drought and low temperature (Yamaguchi-Shinozaki and Shinozaki, 2006). The regulatory activity of DRE/CRT elements was also found to be conserved in rice. The OsDREB1A protein binds to GCCGAC core of the DRE/CRT element more preferentially than to the ACCGAC, whereas the DREB1A protein binds to both GCCGAC and ACCGAC efficiently (Dubouzet et al., 2003). The cold responsive hexamer motif sequence (ACGTCA) was reported to be present in *LIP19* promoters of rice (Table-2) to which *OBF1* that encodes a bZIP protein (OsOBF1) interacts and regulates low-temperature responsive gene expression (Shimizu et al., 2005). CORE (coordinate regulatory element for antioxidant defence) was found to play an important role in response to oxidative stress in rice (Tsukamoto et al., 2005). The core sequence of the OsIRO2-binding sequence (CACGTGG) occurred more frequently in the upstream regions of Fe deficiency-inducible genes than in the corresponding regions of non-inducible genes. *OsIRO2* is a putative basic helix-loop-helix (bHLH) transcription factor encoding gene,

which was strongly expressed in both roots and shoots during Fe deficiency stress (Ogo et al., 2006).

Conclusions

Abiotic stress responsive *cis*-elements are important regulators of transcriptional gene regulation and therefore important hallmark of abiotic stress inducible promoters. Well characterised abiotic stress inducible promoter elements have tremendous potential for engineering crop plants with improved tolerance to adverse environmental factors.

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Table-1 ABA responsive *cis*-acting elements containing ACGT/non ACTG sequence

Sequence of the ABA responsive <i>cis</i> -element	Promoter(s)	Reference
ACGT <u>ACGT</u> GTCG	<i>emp1</i>	Morris et al.1990
RT <u>ACGT</u> GGCR	<i>rab16</i>	Mundy et al.1990
ACAT <u>ACGT</u> GGCGG	<i>rab16c</i>	Yamaguchi-Shinozaki et al. (1990)
ACGT <u>ACGT</u> GGCGC	<i>rab16d</i>	Yamaguchi-Shinozaki et al. (1990)
CAGT <u>ACGT</u> GGCAG	<i>rab16b</i>	Yamaguchi-Shinozaki et al. (1990)
CCGT <u>ACGT</u> GGCGC	<i>rab16a</i>	Yamaguchi-Shinozaki et al. (1990)
GT <u>ACGT</u> GGCGC	<i>rab16 and alpha-amylase genes</i>	Skriver et al. (1991)
<u>ACGT</u> G-containing sequences	<i>Osem</i>	Hattori et al.(1995)
CC <u>ACGT</u> GG	<i>rgal</i>	Seo et al. (1995)
AGT <u>ACGT</u> GGC	<i>rab16b</i>	Ono et al. (1996)
GCCGCGTGGC	<i>rab16b</i>	Ono et al. (1996)
CACATG	<i>rd22</i>	Abe et al. (1997)
TGGTTAG	<i>rd22</i>	Abe et al. (1997)
TGCT <u>ACGT</u> GTCCC	<i>lea</i>	Moons et al. (1997)
TTCT <u>ACGT</u> GGCCA	<i>lea</i>	Moons et al. (1997)
<u>ACGT</u> SSSC	<i>rab21</i>	Busk and Pages (1998)
CT <u>ACGT</u> GGCCA	<i>amy3d</i>	Hwang et al. (1998)
CCCT <u>ACGT</u> GGCCG	<i>wsi18</i>	Joshee et al.(1998)
AACGCGTGTC	<i>Vp1</i>	Hobo et al. (1999)
ACGTGKC	<i>Osem</i>	Hattori et al. (2002)
CTCC <u>ACGT</u> GGCAC	similar to <i>Hva22</i>	Zhang et al. (2004)
TACC <u>ACGT</u> GGCAT	<i>tb2/dp1 Hva22</i>	Zhang et al. (2004)
<u>ACGT</u> GGC	<i>Hva1</i> rice orthologue	Ross and Shen (2006)
CGMC <u>ACGT</u> TGB	genome wide	Lenka et al. (2009)

Table-2 Abiotic stress responsive elements other than ABRE

Sequence of different abiotic stress responsive <i>cis</i> -elements	Motif/Promoter name	Abiotic Stress Condition	Reference
RTACGTGGCR	<i>rab16A-D</i>	Desiccation	Mundy et al. (1990)
GCCGAC	<i>DRE/CRT</i>	Drought-, high salt- and cold	Dubouzet et al. (2003)
ACGTCA	<i>LIP19</i>	Cold	Shimizu et al. (2005)
AAKAATWYRT AWATAAAAM TTTTATWTA	<i>CORE</i>	Oxidative stress	Tsukamoto et al. (2005)
CACGTGG	<i>OsIRO2</i> -binding sequence	Fe deficiency stress	Ogo et al. (2006)