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PJBS

ISSN 1028-8880

Pakistan Journal of Biological Sciences

ANSInet
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308 Lasani Town, Sargodha Road, Faisalabad - Pakistan

Pakistan Journal of Biological Sciences 9 (3): 568-573, 2006
ISSN 1028-8880

Class III Homeodomain-leucine Zipper Genes in Plant Development

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Abstract: The homeodomain-leucine zipper (HD-Zip) genes containing both a homeodomain and a leucine zipper motif encode plant-specific transcription factors, which belong to the homeobox gene supper family. HD-Zip genes are believed to have key roles in various aspects of plant development. These transcription factors, especially the class III HD-Zip genes, involve in apical embryo patterning, postembryonic meristem initiation, organ polarity and vascular development. According to sequence conservation, HD-Zip genes can be subdivided into four subfamilies named HD-Zip I, II, III and IV. The class III HD-Zip transcription factors have become the hotspot for studying plant development in recent years. This review focuses on what is known about the function of class III HD-Zip transcription factors and of the encoded proteins.

Key words: Homeodomain-leucine Zipper (HD-Zip), plant development, transcription factor

INTRODUCTION

The homeobox, a DNA sequence motif, was first identified in a set of *Drosophila* development genes (McGinnis *et al*., 1984; Scott and Weiner, 1984) and subsequently shown to be present in evolutionary distant organisms, including animals, fungi and plants. In the plant there is a kind of special homeobox genes, which encode transcription factors including a homeodomain structurally characterized by a leucine zipper domain tightly linked to the homeodomain, which called homeodomain-leucine zipper (HD-Zip)(Baima *et al*., 1995; Carabelli *et al*., 1993; Mattsson *et al*., 1992; Schena and Davis, 1992, 1994; Sessa *et al*., 1994; Söderman *et al*., 1994). These genes have so far been found only in plants and have key roles in development of plants. According to sequence conservation, HD-Zip genes can be subdivided into four subfamilies, named HD-Zip I, II, III and IV (Sessa *et al*., 1994).

Functional data available on a subset of the class II genes and I have shown a number of them to be involved in developmental reprogramming in response to changes in environmental conditions (Anna *et al*., 2004). A number of HD-Zip I proteins have been suggested to be dependent on ABA-signaling for their transcriptional regulation. The class I genes *ATHB5*, *ATHB6* and *ATHB7* are suggested to regulate aspects of the plant response to ABA, which are implicated in the plant response to water deficit as deduced from their transcriptional induction by water deficit conditions or ABA treatment (Söderman *et al*., 1996, 1999; Lee and Chun, 1998; Johannesson *et al*., 2003). *ATHB5* also has a role in the signaling pathway that mediates the inhibitory effect of ABA on growth during early seedling establishment. The class I gene *ATHB16* is thought to mediate blue-light-responses (Wang *et al*., 2003) and *ATHB13* is suggested to have a role in sucrose signaling (Hanson *et al*., 2001). The class II genes *ATHB2* and *ATHB4* are essential for the shade avoidance response (Carabelli *et al*., 1996; Steindler *et al*., 1999; Ohgishi *et al*., 2001). Two HD-Zip genes (*CPHB-1* and *CPHB-2*, class II) isolated from *C. plantagineum* involved in regulation of dehydration responses through different branches of the dehydration-induced signaling network, ABA-independent or ABA-

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dependent. The function of *Athb-10/GL2* (HD-Zip IV) might be different in the two organs, acting as a positive regulator of trichome formation in the shoot and a negative regulator of hair formation in the root (Anna *et al*., 2004; Cristina *et al*., 1996; Rerie *et al*., 1994).

The function of class III HD-Zip genes are the most complicated among these four groups of HD-Zip family, which involve in post embryo development and have a important role in regulating apical embryo patterning, postembryonic meristem initiation, vascular development and leaf polarity (Kirsten *et al*., 2005; Prigge *et al*., 2005). There is a dramatically progress in this research area, a number of genes have been isolated. We try to introduce some recently reported certain functions of this gene subfamily.

STRUCTURE OF CLASS III HD-ZIP

HD-Zip belongs to homeodomian gene super family, which contains a homeobox, a 180 bp consensus DNA sequence, encodes a 60 amino acid protein motif, the homeodomain, which folds into a characteristic DNA-binding structure composed of three K-helixes separated by a loop and a turn. Hence, the homeodomain allows the sequence-specific recognition of other genes by homeodomain containing proteins, which act as transcription factors, regulating the expression of the target genes. DNA recognition is established by helix III, which lies within the major groove of DNA and by the N-terminal fixable arm and the loop between helices II and I. Most DNA sequences that are bound efficiently by homeodomains contain the ATTA (TAAT in the complementary strand) core, which interacts with the highly conserved amino acids. HD-Zip III genes are highly conserved in land plants; >50% of the full-length amino acid sequence is conserved between the moss *PpHB10* protein and each of the *Arabidopsis* HD-Zip III proteins (Sakakibara *et al*., 2001). HD-Zip proteins may have redundant functions, such that one family member might fully or partially substitute for the loss of function of another in specific cells or tissues. Whereas highly conserved, the nonequivalence of HD-Zip III gene function is suggested by the retention of gene pairs from ancient duplication events.

ARABIDOPSIS HD-ZIP III GENES

Arabidopsis homeobox genes have been identified in studies using mutants, degenerate oligonucleotides deduced from conserved sequences, differential screening or binding to known promoters. According to sequence conservation, plant homeoboxes can be subdivided into different families, each comprising several members, till to now there were 93 homeobox genes have been submitted to gene bank (http://www.ncbi.nlm.nih.gov/), Among these genes, *REVOLUTA (REV)/ INTERFASCICULAR FIBERLESS1 (IFL1)*, *PHAVOLUTA (PHV)*, *PHABULOSA (PHB)* and *CORONA (CNA)/ ATHB 15* have a closet relationship, which belong to HD-Zip III subfamily. Theses genes play overlapping and divergent roles in *Arabidopsis* development (Prigge *et al*., 2005).

HD-ZIP III GENES REGULATE APICAL EMBRYO PATTERNING

During plant zygotic embryogenesis the cell divisions relatively evenly distributed within the embryo. The apical part of the embryo will become the shoot and the basal part the root. Postembryonic growth, however, is quite different between the two kingdoms. At this stage, plant growth is highly polarized with cell proliferation occurring almost exclusively at the two ends of the longitudinal axis: the root tip and the shoot tip. The seedling, therefore, no longer has a single 'anterior-posterior' axis. Instead it has two, oppositely oriented apical basal axes, with the base of both at the root-shoot junction (Jürgens, 2003).

In *Arabidopsis* three mutants rev phb phv have been discovered and their factions are indicated to be involved in apical embryo patterning. Genetic analysis revealed that *REVOLUTA (REV)*, *PHAVOLUTA (PHV)* and *PHABULOSA (PHB)* play the key, overlapping roles in two major processes during embryogenesis: the establishment of apical bilateral symmetry and the establishment of the shoot apical meristem (SAM) (Prigge *et al*., 2005). Rev phb double mutant plants usually displayed a shoot meristemless phenotype, characterized by the normal production of all embryonic structures, with the exceptions that the SAM was absent and cotyledons were occasionally absent or display patterning defects (Prigge *et al*., 2005) and no further postembryonic growth occurred in the double mutants. It is suggests that *REV* is required for adventitious shoot formation. Mutations in the *CNA* gene similarly enhanced the apical patterning defect of rev phb embryos such that the triple mutant developed a radially symmetric apical structure similar to that of the rev phb phv triple mutant. This indicates The *CNA* gene also plays a role in apical embryo patterning.

HD-ZIP III GENES REGULATE POSTEMBRYONIC MERISTEM INITIATION

A central feature of plant development is the continuous generation of organs throughout the plant's

lifespan. The capacity to generate new aboveground organs post-embryonically is a property of shoot meristems. Within shoot meristems reside stem cells that are maintained at a constant number while giving rise to organ primordia and ultimately all of the differentiated cells of organs and tissues (Steeves and Sussex, 1989). In this way, shoot meristems have the capacity to balance perpetual differentiation of cells while replenishing the pool of undifferentiated, pluripotent cells. Genetic screens have identified several key regulators of shoot meristem development (Barton and Peothig, 1993; Clark *et al*., 1993; Laux *et al*., 1996; Pogany *et al*., 1998; Yu *et al*., 2000). The *WUSCHEL* (*WUS*) gene encodes a homeodomain protein, which is an important regulator of stem cell identity (Mayer *et al*., 1998; Schoof *et al*., 2000). Loss-of-function wus mutants fail to organize functional shoot meristems. After germination, wus mutants sporadically generate adventitious shoots, which form only a few organs before termination (Endrizzi *et al*., 1996; Laux *et al*., 1996). Expression of *WUS* within the meristem appears to be sufficient for establishing stem cell identity. When *WUS* was ectopically expressed, transgenic seedlings accumulate undifferentiated stem cells (Schoof *et al*., 2000).

Three *CLAVATA* genes (*CLV1*, *CLV2* and *CLV3*) promote the differentiation of stem cells. Loss-of-function *CLV1*, *CLV2* and *CLV3* mutants accumulate undifferentiated cells in shoot and floral meristems, resulting in meristems that are significantly larger than the wild type and in flowers with increased numbers of floral organs (Clark *et al*., 1993, 1995; Jeong *et al*., 1999). The *CLV1*, *CLV2* and *CLV3* loci encode signal transduction components: a receptor kinase (Clark *et al*., 1997), a receptor-like protein (Jeong *et al*., 1999) and a small secreted protein (Fletcher *et al*., 1999), respectively. *WUS* is a key target of the *CLV* signal transduction pathway (Brand *et al*., 2000; Schoof *et al*., 2000). In wild-type plants, the domain of *WUS* expression is normally restricted to a small, centrally located subset of cells beneath the three outermost cell layers (Mayer *et al*., 1998; Schoof *et al*., 2000). In clv3 mutant meristems, the *WUS* expression domain expands laterally and apically into the topmost cells of the L3 layer (Brand *et al*., 2000; Schoof *et al*., 2000). Conversely, plants overexpressing *CLV3* recreate the wus phenotype and do not appear to express *WUS* mRNA (Brand *et al*., 2000), indicating that the *CLV* signaling pathway limits stem cell number by restricting the size of the *WUS* expression domain. Overexpression of *WUS* through promoter fusions can also lead to ectopic stem cell accumulation (Schoof *et al*., 2000). Interestingly, transcripts of *CLV3* are found on the periphery of stem cell masses formed by *WUS* overexpression, whereas in the meristems of wild-type plants, *CLV3* expression is restricted to the center of the shoot meristem (Fletcher *et al*., 1999; Schoof *et al*., 2000). These expression analyses indicate that while the *CLV* signaling pathway targets *WUS* and restricts its activity, *WUS* activity is also sufficient to induce transcription of *CLV3*. This regulatory feedback loop may act to maintain strict control of the number of stem cells. Organogenesis at the shoot meristem requires a delicate balance between stem cell specification and differentiation. In *Arabidopsis thaliana*, *WUSCHEL* (*WUS*) is a key factor promoting stem cell identity, whereas the *CLAVATA* (*CLV1*, *CLV2* and *CLV3*) loci appear to promote differentiation by repressing *WUS* expression. In a screen for mutations modifying clv1 mutants, a novel regulator named *CORONA* (*CNA*) has been identified, which controls meristem's development. clv cna double mutants develop massively enlarged apices that display early loss of organogenesis, misexpression of *WUS* and *CLV3* and eventual differentiation of the entire apex. The *CNA* gene was isolated by positional cloning and found to encode a class III homeodomain leucine zipper protein. A missense mutation resulting in the dominant-negative cna-1 allele was identified in a conserved domain of unknown function and a likely null allele was shown to display a similar but weaker phenotype. *CNA* is expressed in developing vascular tissue, diffusely through shoot and flower meristems and within developing stamens and carpels. Analysis of *WUS* expression in wild type, clv, clv and cna plants revealed that contrary to current models, *WUS* is neither necessary nor sufficient for stem cell specification and that neither *WUS* nor *CLV3* is a marker for stem cell identity. It is suggested that *CNA* functions in parallel to the *CLV* loci to promote organ formation (Kirsten *et al*., 2005). Besides *CAN* there are several other genes also regulating postembryonic meristem initiation. *REV* is required for the formation of lateral shoot meristems (LSM) and floral meristems (FM) as well as adventitious shoots (Otsuga *et al*., 2001; Prigge *et al*., 2005), rev mutants are characterized by rosette and cauline leaves with barren axils and flowers lacking full meristematic activity, although these phenotypes are variably expressive (Otsuga *et al*., 2001; Prigge *et al*., 2005; Talbert *et al*., 1995). The *PHV* gene appears to play a lesser role in LSM function . *CNA* and *ATHB8* play roles antagonistic to *REV*, *PHB* and *PHV* in the formation of LSM, with *CNA* and *ATHB8* promoting meristem activity (Prigge *et al*., 2005).

HD-ZIP III GENES REGULATE LEAF POLARITY

Based on gain-of-function alleles, HD-Zip III Genes are most important for patterning in lateral organs, especially *PHB* and *PHV*. Gain-of-function mutations in HD-Zip III Genes affected a sterolbinding domain that is conserved in these proteins, suggesting that they act as receptors for a sterol signal from the meristem (McConnell *et al*., 2001). Subsequently, however, these mutations were shown to prevent microRNA (miRNA)-directed mRNA cleavage (Bartel, 2004) that restricts HD-Zip expression to the adaxial side of the leaf primordium (Tang *et al*., 2003). A loss of miRNA-mediated negative regulation could account for both the spatial expansion and the increase in expression levels, although positive autoregulation cannot be discounted (McConnell *et al*., 2001). The control of polarity in the leaves and stem vasculature by the same mechanism (i.e., by HD-Zip genes that are downregulated on the abaxial side by miRNAs and by *KANADI* genes) has been confirmed (Emery *et al*., 2003; McHale and Koning, 2004).

ROLES OF HD-ZIP III GENES IN VASCULAR DEVELOPMENT

Vascular development involves the formation of provascular cells that give rise to the procambium and after specific events of cytodifferentiation, to both conducting tissues (Steeves and Sussex, 1989). The histological analysis of transgenic plants suggests that *ATHB-8* is likely to act as a differentiation-promoting transcription factor regulating the activity of procambial and cambial cells. The expression of *ATHB-8* is modulated by auxin. As a positive regulator, auxin activates the provascular cells, which stimulate the expression of the *ATHB-8* gene and subsequently, cell division and cyto-differentiation toward the formation of the vascular tissue. Through the transgenic tobacco experiment (Baima *et al*., 1995), it is suggested that *ATHB-8* is involved in revascularization processes caused by wounding.

CONCLUSIONS

In the plant lifespan post-embryogenesis is important and complex, which relates to a precise order of events ensuring the correct relative positioning of embryonic organs the shoot and root stem-cell systems (i.e., meristems), cotyledons and the hypocotyl and the correct arrangement of different cell types within each organ. Apical embryo patterning, postembryonic meristem initiation, leaf polarity and vascular development have been found to be regulated by a series of genes and plant hormones, among which HD-Zip III genes are research hot spots in last three years. Class III HD-Zip genes are found to be involved in the processes during embryogenesis: the establishment of apical bilateral symmetry and the establishment of the shoot apical meristem (SAM). *CAN* (Class III HD-Zip) can promote differentiation by repressing *WUS* expression and keep the balance between stem cell specification and differentiation and regulates the postembryonic meristem initiation. Class III HD-Zip transcription factors also involve in auxin mediated polarity. Class III HD-Zip genes downregulated on the abaxial side by miRNAs and by *KANADI* can specify adaxial development. Finally *ATHB-8* modulated by auxin, as a differentiation-promoting transcription factor regulates the activity of procambial and cambial cells and promotes formation of the vascular tissue.

By suppression subtractive hybridization (SSH), we isolated a class III HD-Zip gene *GbHB1* (NCBI *AY966446*). Transformation study showed that it could partially recover the type ifl1 mutant of *Arabidopsis*, suggesting that *GbHB1* has a role in vascular development (data not shown). Although dramatically progress has been made in this area, there is still a long way to unveil the precise mechanism of class III HD-Zip genes in plant development.

ACKNOWLEDGMENTS

This research is financially supported by the National Basic Research Program (973) of China (No.2004CB117300) and China Ministry of Education.

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