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TRICHOME: Role of Promoter and *Cis*-Regulatory Elements, and Effect of Gamma Radiation, UV Radiation, Methylation, Phosphorylation

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ABSTRACT

Trichomes are hair-like structure that originated from aerial epidermis cells and are found in most plant species, trichomes exposed to various adverse conditions including gamma radiations and ultra violet radiations and herbivore attack insects and pests. Trichome initiation, formation, and development is regulated by some specific group of gene, transcription factors, promoters and cis-regulatory elements which performs as positive regulators, and negative regulators during trichome gene expression, external application of gamma radiations results in reduced or enhanced trichome numbers depending of doses and genotypes. Trichome growth and development is also effected by methylation, UV radiation and phosphorylation.

Key word: *Trichome, Cis-regulatory elements, Gamma radiation, UV radiation, Methylation, and phosphorylation.*

INTRODUCTION

Plants are sessile organism, they are exposed to different environmental stresses some plants naturally developed a physical structures to protect from different biotic and abiotic stresses, trichomes are epidermal cell structures found in different parts of plants parts such as leaf, stem, seed, flower parts in various plant species such as tomato, tobacco, arabidopsis, cotton (*Gossypium spp*) and Salix, produce seed trichomes. Trichomes are believed to protect plants against insects, microbes, herbivores, and abiotic damages and to assist seed dispersal. In general, plant trichomes are categorized, into two groups, glandular and non-glandular[1]. Trichomes are dedicated cell structure occurs in wide range in form, length and thickness [2]. Endoreplication plays crucial role in trichome development and branching, mutants with greater endoreplication shows enhanced trichomes with more branching, mutants with lower endoreplication shows shorten trichomes and few branches[3]. SIAMESE, (SIM) production level is crucial role in the transition to endoreplication during trichome growth stages[4].

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Trichome development is regulated under few specific genes, transcription factors; both positive regulators or activators and negative regulators or repressors play a crucial role in up regulation or down regulation expression of trichome in plants. Positive regulators are GLABRA1 (GL1), (GLABRA2 (GL2), ENHANCER OF GLABRA3 (EGL3) and TRANSPARENT TESTA GLABRA1 (TTG1)[5,6,7]. Negative regulator or repressor are ENHANCER OF TRY AND CPC1 (ETC1), ENHANCER OF TRY CPC 2 (ETC2), CAPRICE (CPC), and TRIPTYCHON (TRY)[8,9,10]. Trichome development is regulated by complex network of transcription factors (TFs), encoded by major three groups, R2R3 MYBs, WD40, and bHLH factors[11]. To investigate role of differential expression levels of transcription factor family in three different cells such as trichome, basal and pavement cells of *A. thaliana*[12]. Phytohormones also have their own important role in trichome development in *Arabidopsis*[13]. Phytohormones, such as Cytokinin, Gibberellin acid, and Jasmonic acid, play central roles in regulating a extensive plant growth and development. Gibberellin acid plays essential role in trichome development identified by several mutants' studies during signaling pathways in *Arabidopsis*, DELLA proteins comprise RGA, and GAI play major roles in trichome formation. Mutations in *RGA* and *GAI* reestablish trichome initiation in the *ga1-3* mutant[14]. Derivative of cytokinin phytohormone (6-benzylaminopurine) (BAP) acts positive regulator of trichome development in *Arabidopsis*[15].

Brassinosteroids (BR), mutants shows role in trichome formation, *bls*1 mutant, shows altered response of brassinosteroids (BR), may cause lesser numbers trichome developments on both surface of leaf[16]. Trichome have multiple role for survival in harsh environmental condition, for instance in Arabidopsis trichome cell specific analysis revealed that enzymes which influences in sulfur metabolism and detoxification process[17]. In transgenic birch due to *BpMYB106* over expression results changes in trichome density on both surfaces of birch leaf, enhanced growth rate and height, and higher photosynthetic rate[18]. Trichome acts as a physical support to plant aerial surface helps in capable to reduce water loss water absorbent from leaf surfaces helps in adjusting, water deficit conditions, coping with water scare supply adopt epiphytic environment[19]. Four genotypes of wheat, two are drought sensitive and two drought tolerant subjected to two cycles of drought treatment at anthesis. Observed change in the frequency of stomata, and trichomes was considerably greater on the adaxial leaves surface on all four genotypes[20]. In this review we discussed of role of different *cis*-regulatory elements and gene promoter trichome regulating expression in trichome. Methylation, gamma radiation and UV-radiation and phosphorylation also impacts on trichome growth and development.

TRICHOME RELATED PROMOTERS AND *CIS*-REGULATORY ELEMENTS

Plant gene expression is under control of many components as externally or internally, *cis*-regulatory (*cis*-acting) elements and trans-regulatory (trans-acting) elements regulate gene. Different transcription factor binds to particular region on DNA and regulates by enhancing or repressing the transcription. Promoter is regulated by RNA polymerase and other *cis*-regulatory elements, many transcription factors binds helps in expression at particular tissue or organ in plants. Understanding gene regulation its regulatory elements at molecular level which are at expressing at specific tissue or traits related to agronomic importance helps in crop improvement.

A rice (*Oryza sativa*) gene known as homeodomain-leucine zipper (HD-Zip) and its Oshox1 its promoter fused with GUS reporter gene transferred in Arabidopsis, transgenic Arabidopsis (Oshox1-GUS) shows expression only in trichome, where as in rice expression was noticed in trichomes, stomata, and pollen. Further Oshox1 promoter 5′ deletion series analysis reveals sequence from –1,621 and –898 of Oshox1 promoter is contains a auxin and sucrose sensitivity, *cis*-regulatory elements -896 to +1 and -528 to +1 deletion fragments showed expression in trichome structure[21]. Genes which are greatly

expressed in trichome initial cell contains several putative MYB sites, MYBCOREATCYCB1, CURECORECR and SURECOREATSULTR11 *cis*-acting elements, in promoters region[22]. GaMYB2 promoter fragment 360 bp contains major *cis*-regulatory elements which contributes mainly trichome specific gene expression, further studies reveals that 17 bp DNA sequence which occurs between -230 and -214 crucial role in triggering the GaMYB2 promoter, and T/G-box is supposed to be *cis*-acting element conferring promoter action in trichomes[23]. Sequence analysis of cotton seed trichome gene, RD22-like1 (RDL1), promoter region contains an L1 box (TGCATTTA) and MYB motif (CAGTTG). Mutation in L1 box and MYB motif by altering nucleotides results in reduced activity in promoter[24]. OASA1 gene which highly expressed in trichome, obtained upstream regulatory promoter region fused with reporters GFP and GUS gene. High GUS activity specifically detected in various parts in leaf trichomes and a very little activity in epidermal cells. Sequential deletions of 5´and 3´reveals that –269 to –66 contain the regulatory elements essential for trichome expression. At 3´end a domain from +112 to +375 that is also critical for trichome expression[25]. Two promoters AaGL2 (PAaGL2) and AaMIXTALike1 (PAaMIX1), obtained from *Artemisia annua.* Sequence analysis reveals a putative numerous MYB sites at positions in AaGL2 promoter, E-box, S-box, heat stress responsive element (HSE), B-box, W-box, and two G-boxes. Where as in, AaMIXTA-Like1 promoter contains diverse *cis*-acting regulatory elements were identified such as Gibberellin responsive element (GARE motif), skn-1motifs, ARE motif, MYB binding site, I-box, GT-1motif, Abscisic acid responsive element (ABRE). Both promoters showed GUS expression completely noticed in the trichome cells of Arabidopsis and *Artemisia annua*[27]. Cotton glucuronosyl transferase gene (*GhGlcAT1*) expressed during fibre elongation stage. Their upstream region of 1647 bp was obtained and investigated for putative *cis*-elements regulatory elements showed amylase-box, E-box, CARE, GARE, GCN4-motif, ACGT motif and AACA motif. The 5' upstream fragment was fused with *GUS* gene, *GUS* gene expression observed in the trichomes, seed coat, and pollen grains[28]. Tobacco (*Nicotiana sylvestris*) NsCBTS-2a gene highly expressed in glandular trichomes, its 5' flanking region was obtained 1100 bp, contains two essential *cis*-acting regulatory elements, activator elements -589 to -479 from the transcription initiation site and repressor element located between -279 to -119 were identified key regulator during gene expression of trichome[29]. *A. thaliana* L-Cysdesulfhydrase1 (DES1) promoter was ligated to GFP reporter gene a strong GFP expression was also observed inside the trichomes, sequence analysis of promoter region showed light responsive elements, drought responsive, defense and stress related, ABA and Auxin-related regulatory elements and leaf development and senescence *cis*-regulatory elements[30]. Three 5' flanking fragments were isolated from two genes one from lignin biosynthetic gene *BdPMT* another cellulose synthase genes *BdCESA7* and *BdCESA8* obtained from *Brachypodium distachyon, all* were fused with reporter genes all reporter expression were also noticed in trichome macrohairs[31]. Genome-wide investigation performed to understand variation at transcripts level between two contrasting trichome producing closely related desert species of poplar, further investigated upstream region of candidate genes suggests dissimilarities in the number and types of elements such as gibberellin response elements (GAREs), pyrimidine box (P-box), abscisic acid response elements (ARE), and W box elements MYB-binding sites (MBS), these may be cause in difference in gene regulation between two contrasting trichome desert species of poplar[32].

GAMMA RADIATIONS AND ULTRA VIOLET RADATIONS

Plant growth and development depends mainly on energy derived from light, in nature sun generates different types of energy and rays and reaches to land plants some are useful and some are harmful to living organisms, among them gamma rays, visible light, ultraviolet and X-rays, are all belongs to electromagnetic radiation. Gamma rays are ionizing radiation

and acts on atoms or molecules to generate free radicals in cells. These radicals can injure or alter essential components of plant cells during different metabolism processes depending on the exposure irradiation level. Low dose of gamma irradiation induces cell division and high-dose stops cell division because of free radicals and DNA damage system[33]. Under supplementary UV-B radiation exposure leads reduced plant growth and development characters, increased antioxidants enzymatic activities was observed in medicinal plant called *Phyllanthus amarus*[34]. There is difference in UV absorbance between trichome layer and lamina surfaces of six olive cultivars (*Olea europaea)* leaves; due to higher wax content per unit leaf surface of the trichome surface to the lamina surface[35]. Flavonoids production generally occurs in glandular trichomes of *Phillyrea latifolia* leaves, differential productions of different flavonoids and trichome numbers occurs between plants which are exposed to full solar radiation compared to shade plants in *Phillyrea latifolia*[36]. Two ecotypes of Arabidopsis *Columbia* (Col) and *Landsberg erecta* (Ler) were subjected to gamma radiation doses (1–3 kilograys) from cobalt-60, an increased in trichome number on adaxial leaf surface were noticed than control plants[37]. Gamma radiations enhanced trichome density but lessened in overall trichome quantities, showed negative impact on photosynthesis, total protein content. Up regulation *TTG1*, *GL2* and *CPC* genes crucial player in trichome developmental stages from 14 to 21 days of exposure, CPC gene expressed greatly among three genes[38]. Arabidopsis mutant's exo70H4 phenotype exhibits thin and fragile trichome cell wall thickening during development stage. Increased cell wall thickening in wild type arabidopsis and no effect on exo70H4 mutants when both are exposed to UV-B irradiation only, when both exposed to UV and MeJA simultaneously, there is increase in cell wall thickness in both wild and mutant exo70H4 Arabidopsis[39]. Ultraviolet-B radiation exposure on *vigna unguiculata* results in altered leaf morphological characteristics, hard and necrosis tissue, fragmented trichomes, malformed stomata, but improved trichome occurrence on both leaf surfaces, leaves shows plentiful cracked trichome generally on adaxial side of leaves[40]. Different rate of application of gamma rays (Gy) have different impacts on cotton genotypes, which leads to increase or decrease in trichome size numbers and densities its helps in keeping the jassid population control on leaf surface, cotton mutant line SP (150) is highly prone to jassid shows less numbers of trichomes and density on leaf surface, another cotton mutant line SB (250 Gy) showed highly tolerant against jassid population showing higher trichome size and density[41]. To understand influence of UV-B radiation on plant growth development and trichome in plants, used mutants with trichome overexpression, trichome reduced expression and wild type as control[42], after investigation they concluded that substantial difference in sensitivity was observed in trichome mutants and the wild when exposed to UV-B radiation, mutants with more trichomes is less sensitive compared to mutants with few trichomes would be more sensitive to the UV-B radiation, real time reveals that few reduced trichome phenotype shows increased expression of trichome initiation positive regulator gene GL3 during UV-B radiation, exposure compared to control treatment[42].

METHYLATION

DNA methylation is an essential mechanism of epigenetic gene expression control that can be transferred from one generation to next generations. Generally cytosine methylation of DNA event main means of gene expression control. In plants, it occurs naturally at CpG residues but can also occur often at CHG and CHH sites (H=adenine or thymine or cytosine). Methylation which occurs within gene promoter regions is believed to hamper regulatory protein binding and negative impacts on transcription (and can also silence transposable elements), however methylation at introns and exons is interrelated with highly expressed genes. Recently, however, the knowledge of DNA methylation in regulating agronomical traits importance has role in responses to various stresses[43]. ENHANCER OF TRY AND CPC1 (ETC1) gene play essential role in trichome and root hair cell

patterning, which produces a transcription factor MYB highly up-regulated under Pi deficiency which further increases H3K4me3 levels at the promoter of the (ETC1) gene[7]. GL2-EXPRESSION MODULATOR (GEM) controls GL2 expression levels, gem mutants displays abundant trichomes. GEM was found to regulate histone modifications, i.e. methylation, and acetylation around genes involved in trichome patterning[44]. Epigenetic trans-generational traits transfer of parental leaf damage to its offspring of *Mimulus guttatus* plant, may induces DNA methylation patterns difference or abundance at MgMYBML8 gene position, or gene upstream region from MgMYBML8 will affect trichome densities in progenies[45]. Rice SET Domain Group Protein 714 (SDG714) codes for H3K9-specific methyltransferase, mutants of SDG714 showed decline in histone methylation and DNA methylation, further absence of macro trichomes in glumes, culms, and leaves surface, when compared to control Arabidopsis plants[46]. Glabrous Rice 1 (GLR1) plays critical role in trichome development in rice. Morphological difference were observed between near isogenic lines (NIL) of glabrous rice (NIL^{GLR1}) and knock down of (GLR1) (NIL^{glr1}), (NIL^{glr1}) display smooth leaf surface with no or less numbers of micro and macro hairs (trichomes) on leaves surface, further upstream analysis reveals that there is a difference in DNA methylation patterns between two rice genotype[47]. An investigation were performed to identify DNA methylation in cotton fibre at various fiber developmental stages from ovules (0 DPA) (0 day post anthesis (DPA) and fibres (10 DPA, 20 DPA and 30 DPA), observed difference in CG, CHG and CHH methylated cytosines at DNA level of fiber development stages. DNA methylation play crucial role during cotton fibre elongation and secondary cell wall synthesis[48].

PHOSPHORYLATION

Phosphorylation is a one of important post-translational modification process in which an specific amino acid is phosphorylated by a enzyme called protein kinase by the addition of a phosphate group to target amino acid. Generally the amino acids phosphorylated are serine, threonine, and tyrosine and histidine, phosphorylation also play essential roles in signaling pathways and metabolism, by interacting with other signal components like phosphorylation in plant systems in response to a variety of stresses. Drought stress was regulated by interlinked coordinated interaction between water channel aquaporin and bimodal trichomes, phosphorylation plays an essential role in controlling TiPIP2a (*Tillandsia ionantha* plasma membrane intrinsic protein (PIP) family) protein which acts as aquaporin in *Tillandsia ionantha* plant[18]. *GLABROUS1* (*GL1)* gene up regulated in young leaf of developing trichomes, *GL1* promoter was regulated by cis and trans regulatory elements such as transcription factors E2F, E2F play critical role in trichome gene expression, RETNOBLASTOMA *RELATED* (RBR) protein bind to E2F and interact by repressing it, phosphorylation of (RBR) protein allowed E2F freely expression of trichome related genes[49]. Cotton CDPK gene (GhCPK1) was a functional calcium dependent protein kinase, it subjected to autophosphorylation and involved in phosphorylation of histone III-S substrate, moreover presumed role in signalling pathway of cotton fiber growth, fiber cell elongation[50]. Glandular trichomes of sweet basil were investigated through transcriptomics, proteomics, metabolomics approaches and results confirmed the presence of posttranslational modifications (PTMs) of numerous proteins such as differential phosphorylation of enzymes occurs during MEP/terpenoid and shikimate/phenyl propanoid pathways were identified[51]. It was noted that the AtCDT1a promoter is active in developing trichomes found in early leaf primordial. Over expression AtCDT1a and AtCDC6a transgenic lines shows 5-6 folds enhanced branching of trichomes and less numbers of abnormal trichomes when compared with control. AtCDT1a contains seven possible CDK phosphorylation sites. AtCDT1a undergo phosphorylation, in vivo

with CDK, phosphorylates AtCDT1a then under goes degradation by the proteasome[52].

CONCLUSION

Trichome is an external appendages structure originated from epidermal cell in plants, it has versatile capabilities to survive in harsh environmental stresses. Trichome is highly regulated by few transcription factor gene families, and phyto hormones, although a vast information related to genetic and molecular analyses of trichome development already known, however knowledge of the trichome gene promoter and *cis*-regulatory networks will helps in development of synthetic promoter constructs, metabolic engineering to generate commercially demanded phytochemicals, Undoubtedly manipulation of trichomes to improve natural product established host resistance, to alter endogenous phytochemical properties and to assist in biomolecular farming. Gamma rays plays immense role in increase or decrease trichome production based on doses. Depending upon the, wax content, cell wall thickness and trichome densities unit per area covered on surface of plant parts genotypes were assumed to be tolerant UV radiation. Genome wide analysis of methylation patterns helps in distinguishing tolerant and susceptible genotypes. Phosphorylation also plays role in the different trichome development stages.

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