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Effects of stress on the plant epigenome and its implications in plant breeding

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ABSTRACT: DNA methylation entails covalent binding of a methyl group to the fifth carbon of a cytosine nucleotide ring of a DNA molecule. In plants, it represses gene expression and maintains genome stability in differentiated reproductive tissues. The rate of formation of new allele is far too slow compared to the occurrence of different environmental stresses which leads to epigenetic mechanism where plant survival depends on the regulation of various stress responsive genes. This involves addition or deletion of epimarks like methylation of DNA, posttranslational modification of histones tails like acetylation, methylation and RNA interference. Therefore, the association of stress induced gene expression changes with the alteration in DNA methylation and histones modification will help in understanding stress induced epigenetic processes in stress tolerance of plants.
Key words: Epigenetic, Histones, Homeostasis, Biotic, Polymorphism, Methylation

INTRODUCTION

The basic genetic information which determines the properties and biological behavior of a species is found in plant genome.Also, information guiding the behavior of plant lies in the DNA sequence and alteration of it through mutation or genetic recombination results to new allele which may confer enhanced stress tolerance to the plant. The rate of formation of new allele is far too slow compared to the occurrence of different environmental stresses. Epigenetic mechanism involves addition or deletion of epimarks like methylation of DNA, posttranslational modification of histones tails like acetylation, methylation and RNA interference.

DNA methylation involves covalently binding of a methyl group to the fifth carbon of a cytosine nucleotide ring of a DNA molecule. Cytosine is linked by a phosphodiester bond to guanine and methylated cytosine accounts for more than 30% of the nucleotides in plants. In plants, DNA methylation represses gene expression and maintains genome stability and in differentiated reproductive tissues.

Information content of the genome and its expression to stress are very important for the adaptability of a genotype. Chromatin structure influence the expression of the genome and this is governed by processes often associated with epigenetic regulation. Environmental and developmental signals can induce epigenetic modification in the genome and thus the single genome in a plant cell gives rise to multiple epigenomes in response to these signals. Thus ,the association of stress induced gene expression changes with the alteration in DNA methylation and histones modification will help a lot in understanding stress induced epigenetic processes in plants.

Stress And Modification Of Plant Genomic Dna By Methylation

Pathogens and plant genomic DNA methylation

Cytosine methylation controls gene expression and genome stability thus making chromatin less accessible to various processes like transposition, transcription and DNA repair. A decrease in DNA methylation correlates with up-regulation of stress specific genes and some studies have reported the accumulation of specific abiotic or biotic stress-induced transcripts in tobacco was due to an active demethylation process (Choi & Sano, 2007).The infection of a tomato plants with a virus resulted to changes in DNA methylation at a several marker loci where most of the detected polymorphism were associated with genomic response involved in defense and stress response (Mason G, 2008).

Changes in DNA methylation induced by changes in plant Transcriptome mediated by stress could help alleviate stress effects in exposed plants. But since the same stress is likely to persist for a longer period of time than the lifetime of one generation of plants, the newly patterns of DNA methylation have important adaptive qualities if transmitted to progeny. (Verhoeven, 2010) Showed that expose of a population of apomistic dandelion to salicylic acid results to genome wide and stress specific changes in DNA methylation which can be transmitted to the immediate progeny.

Non-infected progeny of tobacco plants exposed to a compatible pathogen undergoes genome wide and locus specific changes in DNA methylation (Boyko A, 2007).The genome was hypermethylated at CpG and CpNpG sites. In contrast, methylation analysis of the n-gene like R genes using methylation-sensitive RFLP and combined bisulfate restriction has shown a number of N-gene like R-gene to be hypomethylated. (Boyko A, 2007) Argued that DNA methylation may serve as a mechanism for preventing rearrangements and genome stabilization and thus this global genome hypermethylation could prevent the deleterious reshuffling of multiple duplicated and repetitive loci spread in the plant genome. (Boyko A, 2010a) On a transgenerational effect studies following exposure to various abiotic stresses found that global genome hypermethylation in the progeny of stressed plants that was contrasted by locus-specific hypomethylation. Redistribution of DNA methylation from the nuclear centre to the nuclear periphery for the progeny of a tobacco plant infected with the virus was documented (Kathiria P, 2010).Changes in methylation coincided with the delayed appearance of viral and bacterial infection systems (Kathiria P, 2010).

Chilling and plant genomic DNA methylation

Stress causes hypermethylation or hypomethylation of DNA. In maize roots, cold induce expression of ZmMI1 which was accompanied with a decrease in DNA methylation which did not revert to a basal level even after 7days of recovery. In tobacco, salt, cold and paraquat stresses induced DNA methylation at CG nucleotides in the coding sequence of NtGPDL gene (glycerophosphodiesterase-like protein).

Transposon Tam3 in Antirrhinum majus is usually activated at low growth temperatures of 15°C permissive temperature, whereas the activity is suppressed at high growth temperature of 25°C non permissive temperature (Hashida SN, 2003). In low temperature-dependent transposition (LTDT), there is a change of the methylation state of the Tam3 sequence that parallels Tam3 behavior. The methylation levels at 15°C are markedly lower than that at 25°C (Hashida SN, 2003).The methylation state of Tam3 sequence is reversibly altered and the temperature dependent can occur during the lifetime of a single plant (Hashida SN, 2003).Such kind of rapid change in response to a change of temperature is a Tam3 feature which provides an interesting system for analyzing the effects of changes of the methylation state, especially the process involved in decreasing DNA methylation.

Effects of metallic ions on the epigenome

Epigenetic variations of plants and animals like histone modification and DNA methylation occurs due to heavy metals in the environment. Studies have shown that the treatment of heavy metals take an important role in the carcinogenesis of heavy metals like nickel, Arsenic and chromium. (Chen H, 2006) Found that nickel would increase the demethylation level in H3K4. (Klein C B, 2001) Found that nickel compounds could induce DNA methylation and chromatin variation which results in gene silencing. In addition, Nickel could lead to modification missing in histone H2A, H2B, H3 and H4 and this bring about increased demethylation of H3K9 and generally improved ubiquitination level of H2A and H2B.

(Boyko A, 2010a) Studied the genome stability under chlorine ions stress and showed that chlorine ions would influence on somatic cell and change the recombination rate. Some researchers also believed that the variation of epigenetic information is an important adaptation mechanism to adversity of environment.DNA methylation levels are inversely related to the levels of gene expression and regulation of gene expression under stress is not limited to promoter region but can also be achieved by changing the methylation status of the coding region. (Zhang X Y, 2006) Observed that genes that are methylated in their coding and promoter regions are expressed at high and low levels respectively.

Methylation-sensitive amplified polymorphism analysis (MSAP) which is the modified form of Amplified Fragment length polymorphism (AFLP) is used to analyze the epigenomic effects of metal toxicity. MSAP only reveal cytosine methylation at CG and partial CCG sites but cannot detect methylation at other sites like CAG and CTG sites which are often methylated in plant genomes (Li, ZX, Guo, & Zhang, 2009). For this reason, analysis of global genome methylation through MSAP possibly underestimates the actual levels of methylation in the genome (Lu, Rong, & Cao, 2008).

Salt/Water stress and plant genomic DNA methylation

Salt stress affects both growth and germination (Anuradha & Rao, 2001). Root, shoot length and fresh weights of plants under salt stress are affected negatively even at lower concentration (Agarwal & Pandey, 2004). During salt stress, reactive oxygen species are formed which harm macromolecules like protein, lipid and nucleic acid.DNA methylation pattern is affected by oxidative DNA damage (Franco, Schoneveid, Georgalikas, & Panayiotidis, 2008).However, this DNA damage was detected by agarose gel electrophoresis of DNA samples which may fail to show less severe damage thus making the use of molecular markers crucial. Salt stress has been reported to induce genetic modification (Guangyuan L, 2007) . Salt stress induced DNA methylation changes comprised both hypermethylation and hypomethylation events but ended up leading to net hypermethylation of the genome (Guangyuan L, 2007).

High salt concentration usually causes osmotic pressure and restricts absorption of water by plants and this explains the water deficit which usually accompanies salt stress. Rice is one of the salt-sensitive cereal crops and their sensitivity varies among different genotypes. Rice portrays uniqueness in genetic makeup and regulatory architecture where some genotypes have ability to adapt to toxic levels of salt stress whereas others can't. Differences in methylation pattern and epigenetic responses in contrasting rice varieties under salinity stress have been underexplored. (Ratna Karen, 2012) Using methyl sensitive amplification polymorphism(MSAP) technique observed that the influence of methylation or demethylation status to the expression pattern of stress related genes under salinity stress in the rice genotypes shows the role of epigenetic mechanism in stress adaptation and extent and pattern of DNA methylation has nothing to do with natural genetic variability in salinity tolerance. (Mhajan S, 2005), There is little information about the genetic and epigenetic effects of salinity in plants even after a lot of effort of studying the biochemical and physiological effects of salinity together with the mechanism of stress and tolerance been reviewed.

Implications of DNA methylation variation under stress.

Tissue culture-induced genomic changes have been associated with several mutagenic mechanisms (Kaeppler SM, 2000). Wounding during explants isolation and cell wall hydrolases are associated with tissue culture stress and this is used in isolation of protoplasts by digesting cell wall prior to culturing. Wounding contributes to Transposon activation but activation can be as a result of exposure to hormones in the culture medium (Kubis S E, 2003). Thus, there is a link between tissue culture and trasnspositional activation with a decrease of DNA methylation being observed. Tissue culture compromises the epigenetic homeostasis of plants genomes and can results in secondary genomic effects.

Infections by pathogens like fungi and bacteria are stressful to plants and results in genomic responses. Bacterial pathogens manipulate the host cell for the pathogen advantages by secreting proteins that interact with host cell components (Greenberg JT, 2003). Studies have identified proteins that interact with plasma membrane, chloroplast or mitochondrion. (Szurek B, 2001) Shows it's possible that some of the secreted proteins may target the genome or epigenetic regulation and candidates with nuclear targets have been emerging. Thus, pathogens can induce genomic remodeling and regulatory changes.

Abiotic stress results not only in well programmed physiological stress responses but also in genome–wide changes. This stress induced genomic responses includes transposon activation, transposition and structural genome changes. Transposon mediated alterations in transcriptional activity of affected genes lead to avoidance or tolerance of the stress.

Expressions of some genes involved in flowering are controlled by DNA methylation and thus flowering times in plants can be changed from DNA methylation. Late flowering in Arabidopsis is caused by mutation within methyltransferase1 gene (MET1).Improper auxin gradient, seed viability, abnormal cell division and embryonic malformation are caused by mutation in MET1 and chromomethylase3 (cmt3). (Xiao W, 2006). DNA methylation controls the plant requirements for cold temperatures during the vernalization process.

The DNA methylation process is accepted for a genome protective mechanism against unfavorable factors which may alter a DNA sequence. Methylation levels within the genome are rapidly affected by environmental changes. Mesembryanthemum crystallinum L is a halotype plant that switches from C3 to CAM photosynthesis system. DNA methylation at the CCWGG satellites sequences play a role in salt adaptation and ability to switch from C3 to CAM in plants (Dyachenko OV, 2006).This process results in an alteration in chromatin structure and leads to global gene expression changes.

In some plants like rice, drought stress increases DNA methylation and only 70% of the total DNA methylation reset to normal level after recovery in non-drought conditions (Wang WS, 2010).Reducing DNA methylation results to plant inability to tolerate environmental stresses. Cold temperature decreases the amount of DNA methyltransferase and reduces DNA methylation by 10% in corn roots (Steward N, 2002).Stresses produced

by heavy metals like nickel and chromium have varied effects on plants in terms of global DNA methylation. DNA methylation depends on the type of heavy metal and the plant species.

Applications of epigenome modification in plant breeding

Genetic variation and phenotypic diversity are materials for the selection and improvement of breeding programs. Change in DNA methylation produces phenotypic variations in plants. The extensive methylation of the two direct repeats in the 5'-region of the imprinted fwa gene caused the late flowering phenotype (Kinoshita T, 2004).The basic DNA sequences of both the wild-type and the fwa line are the same. Mutation in the methylation maintenance gene MET1 causes hypermethylation which results to fwa mutant line showing lower level of ectopic gene expression in the vegetative tissue. (Kinoshita Y, 2007). In tomato, hypermethylation of an SBP-box gene at the colorless non-ripening (Cnr) locus results in colorless fruits with substantial loss of cell to cell adhesion (Manning K, 2006).

DNA methylation alterations results to epialleles which yields phenotypic variations. This epialleles represents two or more genetically identical genes that are epigenetically distinct due to methylation. The variants from epialleles based phenotypic are used in breeding programs to improve plant tolerance to stresses. DNA methylation can be stable where it persists even in absence of triggering environmental factors or unstable where the variation disappears when the environmental conditions are normalized. When DNA methylation variation takes place randomly and vanishes in the same way, it's difficult to use this type of variation to produce plants with a novel trait (Zhao X, 2007).

Epigenetic modification leads to adaptive mechanism in plants where DNA methylation at specific locus can be inherited through meiosis and shows gene expression diversity within the individuals of the same plant species when grown under diverse environmental conditions (Bender, 2004).

Challenges for the exploitation of stress induced methylation variations in breeding applications

DNA methylation modification has flexible and dynamic features which require breeders to accurately determine the time points at which observations were made but due to errors, results concluded may differ. Observations at multiple time points and repeated analysis under different types of stresses are required to determine whether the variations in methylation are reversed after removal of stress. Quantitative differences in methylation variation under stress can also be detected and quantitative analysis is complex than qualitative one and techniques like that of bisulfate sequencing and southern blot are commonly used and they are very tedious and expensive which makes their application to breeding practice difficult.

Methylated alleles are not commonly used in breeding program and instead most programs involves treatment with 5-azacytidine to induce a decrease in plant methylation levels and produce novel phenotypes that are explored in various breeding studies like that of resistance to blight pathogen in rice (Hai & Jing, 2009). The use of 5-azacytidine has some limitations where the whole genome is affected thus favorable phenotypes are inevitably linked to the unfavorable ones and this weakens the plants and thus its limitation in breeding programs.

Molecular linkage maps provides platform for molecular-assisted selection and the analysis of gene function. This linkage maps for some crops have been constructed and are used in gene mapping and cloning which allows association of the DNA sequence, gene function and phenotype. This has been done in Arabidopsis thaliana where a high resolution methylation map was constructed (Zhang X Y, 2006).This method focuses more on the DNA sequence and less on the influence of DNA methylation on genetics and evolution and this marks one of its drawback. Also, lack of suitable methods of genomic methylation mapping limits the application of the method in breeding programs. Microarrays which could be the solution are not available for most plant species including crops thus its limitation to breeding programs.

CONCLUSION

The binding of a methyl group to DNA cytosine through DNA methylation controls gene expression.DNA methylation can be affected by environmental cues or be inherited as epialleles and often associated with tolerance for abiotic and biotic stresses. Epialleles are mostly useful in plant tolerance improvement programs but the molecular control of DNA methylation and the inheritance of epigenes are not manageable using the available technology and knowledge. Thus, better understanding of epigenetic mechanisms will facilitate future research through controlling the pattern of gene expression together with the epigenetic inheritance of stress tolerance phenotypes in plants.

Though published work indicates that DNA methylation is capable of being altered upon stress exposure, these studies are usually limited by low resolution and non comprehensive approaches. Future unbiased and

genome wide approaches should reveal unique aspects of dynamic DNA methylation as the correlation between stresses induced differential methylation, inductions of specific smRNAs and proximal genes. Moreover, the response to stress does not result in methylation changes at a few target genes but consists of a multitude of genome-wide changes that together alter transcriptional programs. Future prospects should provide analysis aimed at how dynamic methylation changes are executed. Also strategy of engineering pathogen-resistant crops strains through manipulation of DNA methylation at some loci.

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