Review

Understanding epigenetic effects in crop species

Joseph Onwusemu Disi, Dayong Wei, Jiaqin Mei and Wei Qian*

College of Agronomy and Biotechnology, Southwest University, Chongqing, 40076, People’s Republic of China.

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Epigenetics, which generally refers to beyond genetics, began to attract the attention of plant geneticits principally due to many biological phenomena that deviate from basic evolutionary rules and trends. Several studies past and present have attributed gene expression including both qualitative and environmentally influenced morphological changes in plants and crop species to epigenetic related activities such as DNA methylation, histone modifications, non-coding RNA mediated pathways amongst others and show that these epigenetic landmarks can be stably inherited across generations. However, the ‘ghostlike’ nature of these epigenetic activities will otherwise make steady progress in its utilization in agronomy related problems fairly slow. There are still many unknown about the ‘how’ (for example it is well known that the emergence of DNA methylation is mostly affected by growth conditions such as stress but this is not so with random mutational events) before this science can be adequately utilized in the manipulation of quantitatively controlled agronomic traits. Here, we examined the mechanisms as well as showed recent epigenetic inheritance and somaclonal variation related evidences in plant, with emphasis on a number of methylation related fingerprints in crop plants as an epigenetic marker that play key role in phenotypic variations.

Key words: DNA methylation, epigenetic inheritance, gene expression.

INTRODUCTION

Over the years, Mendelian suppositions could not continue to adequately explain the several biological phenomena such as paramutation in maize (Sikkink and Chandler, 2006), transgene silencing, somaclonal variations, transvection and transinduction, interpooly crosses and parental imprinting, transgressive behavior of interspecific hybrids among others. Epigenetics is simply defined as the study of mechanisms or pathways that initiate and maintain heritable patterns of gene expression is currently a subject of debate among plant biologists. Functionally, epigenetic systems can be grouped based on two schools of thought; namely the developmental age, from seedling to mature plant such genome defense and exaptationists. While the proponents of the “genome defense mechanism” argue that epigenetics regulatory systems evolved various repressive mechanisms to defend against deleterious transposable element activities and ensure the host genome survival (Ziberman, 2008), the exaptationists speculate that cells and sequences possess a preexisting characteristic that enhances the ability of a species to adapt to change in its environment or way of living for example, energy use efficiency as demonstrated in canola populations (Hauben et al., 2009), epigenetic histone modification of human transposable elements (Huda et al., 2010; Santangelo et al., 2007).

Attempts to understand epigenetic effects necessitated studies directed at key mechanisms controlling epigenetic phenomenon in eukaryotes. These include DNA methylation (Simmons, 2008), histone modification, nucleosome remodeling, and non-coding RNA-mediated pathways (Grant-Downton and Dickinson, 2005) in both plants and crop species. These mechanisms exert
different effects ranging from repression of gene expression to RNA-mediated gene silencing in developing cells. To broaden our understanding of these epigenetic landmarks, we presented studies in plants and crops that showed the involvement of DNA methylation, histone modification and nucleosome remodeling and non coding RNAs in the alteration of crop phenotypes. We also discussed epigenetic inheritance and somaclonal variation in crop species.

EPGENETIC MECHANISMS

DNA methylation

DNA methylation is a chemical modification of DNA molecules by covalent addition of a methyl group to cytosine bases (a member of the five nucleotides in the nucleic acids of DNA and RNA). It is involved in a number of cell development activities including the regulation of cell differentiation and function. Cytosine methylation can be split into cytosines methylated at (1) symmetric and (2) asymmetric sites (Grant and Dickinson, 2005). Regions of DNA that have high density of CpG and CpNpG sites are the symmetric sites (sequence is self complementary methylatable cytosines in pairs on opposite stands) often called CpG islands. DNA methylation occurs predominately on these CpG islands. Other unmethylated gene-rich CpG islands in plant are sites of DNA where a cytosine is followed by and linked via a phosphate to guanine. Asymmetric methylation sites, known to be rare in plants, are cytosine in any other sequence context. It has been reported that failure of DNA methylation in stressed plants usually results in cumulative developmental abnormalities. Too much or too little methylation is associated with different gene expression and some have been associated with negative gene’s function such as diseases as observed in crops (Akimoto et al., 2007) and humans (Weinhold, 2006).

How DNA Methylation processes relate to many qualitative and quantitative traits in plant and crop species alike were initially not well understood. Thanks to the discovery of several methylation detection tools which has made it possible to explore methylation-related epiallelic diversity among individual plants including how these methylation patterns relate to phenotypes. In the past one or two decades, these techniques have been employed singly or combined to monitor methylation-related gene expression status in crop species. Methylation variations affecting phenotypes detected by methylation-sensitive amplification polymorphism (MSAP) have been reported in crop species.

Zhao et al. (2011) studied the levels and patterns of methylation-polymorphism at CCGG sites in 48 accessions of allotetraploid flue-cured tobacco (Nicotinia tabacum). The study showed that high level of methylation and distinct patterns of geography-specific groups among accessions suggesting that methylation also play roles in the expression of qualitative traits. Other studies include drought tolerance in rice (Wang et al., 2010), epigenetic modification of genome evolution and domestication in soybean (Zhong et al., 2009), phenotypic variability due to high structural genome plasticity in Brassica oleracea (Salmon et al., 2008), genomic variations, and loss and gain of cytosine methylation in resynthesized allopolyploid Brassica napus (Gaeta et al., 2007; Lukens et al., 2006), and polyploidy i.e gene doubling effect in cotton (Keye et al., 2006).

Nakamura and Hosaka (2010) have applied the new generation sequencing technologies to demonstrate the possible role of DNA methylation in the regulation of heterosis in diploid inbred lines of potatoes. Their study suggested that since DNA methylation suppresses gene expression acting as regulatory factors, homozygosity/heterozygosity of methylated DNA may be involved in inbreeding depression/heterosis. In a study involving epigenetic modifications of distinct sequences of the p1 regulatory gene expression patterns in maize, Sekhon et al. (2008), suggest that distinct regulatory sequences in the P1-wr promoter and intron 2 regions undergo independent epigenetic modifications to generate tissue-specific expression patterns. Other tissue specific regulation gene expression attributable to developmental changes in cytosine methylation were reported (Sekhon and Chopra, 2009; Bao et al., 2004 and Kinoshita et al., 2004). Interplay between DNA methylation, histone methylation, and gene expression in epigenetic modifications of the rice genome have been uncovered (Li et al., 2008). Bender (2004), work on plants revealed that aberrant RNA signals direct DNA methylation to target sequences, which appropriately or inappropriately leads to no clear consequences. Aceituno et al. (2008), demonstrate that in Arabidopsis transcriptome, a novel functional role for DNA methylation is a prominent aspect of epigenetic mechanisms in the regulation of gene expression in plants and that this DNA methylation is largely established during development thereby making plant genome comparatively stable during periods of external perturbations.

Epigenetic processes especially mechanisms of DNA methylation and histone modifications responsible for the protection of somatic cells and inheritance of stress memories have been extensively reviewed (Boyko and Kovalchuk, 2008; Tariq and Paszkowski, 2004). Global analysis of genetic, epigenetic and transcriptional polymorphisms in Arabidopsis thaliana using whole genome tiling arrays revealed extensive genetic and epigenetic polymorphisms between Arabidopsis accessions and suggested a possible relationship between natural CG methylation variation and gene expression variation (Zhang et al., 2008). Demethylation
by DEMETER-LIKE (DML) DNA glycosylases has been shown to edit the patterns of DNA methylation within the Arabidopsis genome to protect genes from potentially deleterious methylation (Penterman et al., 2007). It has been shown in many studies that DNA methylation decreases as cells age (Sedivy et al., 2008; Fraga and Esteller, 2007). This is followed by changes in phenotypes, a development that is attributed to the dynamic nature of chromatin, which is subject to extensive developmental and age-associated remodeling. A correlation between gene activity and DNA methylation; differential epigenetic modifications with changes in transcript levels among hybrids and parental lines have also been reported in two rice subspecies (He et al., 2010). A similar study in our laboratory (Xiong et al., unpublished) show that heterosis in Brassica does not correlate directly with genome-wide changes in DNA methylation since the alterations that occurred during development in Brassica investigated were not random but a function of genomic structure and gametophyte type. Study shows that environmental heterogeneity may be associated with CpG-methylation changes.

A study by Lira-Medeiros et al. (2010), revealed that individuals of L. racemosa plant grown in salt marsh and riverside presented little genetic but abundant DNA methylation differentiation, suggesting that epigenetic variation in natural plant populations has an important role in helping individuals cope with different environments. If this is true as the study indicates, it could also explain why individual plants such as those from doubled haploid lines with similar genetic profiles may show divergent epigenetic profiles that were characteristic of the population in a particular environment. Evidence of within-plant heterogeneity of meiotic behavior of telocentric trisomics of rye also exists (Sybenga et al., 2008). Similar development has been reported in Arabidopsis disease resistance (Stokes et al., 2002) as well as maize genes (Makarevitch et al., 2007). Studies applying the new generation sequencing technologies in characterization of genes and genes' functions may explain the effects of methylation changes on phenotypes.

**Histone modification and nucleosome remodeling**

Histone, a globular proteins (H1, H3, H4, H2A, and H2B), is a complex of DNA and proteins that makes up chromosomes. DNA and small basic proteins called histones complexly packaged into the nucleus of a cell is known as chromatin. The nucleosome is the structurally repeating unit of chromatin. Histones influence how tightly or loosely packed the chromatin is during the phase when gene transcription occurs, thus, determining whether genes can be transcribed. The packaging of the chromatin is achieved by histone modification- acetylation and methylation. These chemical processes add either an acetyl or methyl group to the amino acid lysine that is located in the histone. Histone acetylation or deacetylation can lead to two different ends- active chromatin (euchromatin), if chromatin fibres are not in a compact form and inactive chromatin (heterochromatin), if chromatin fibres are compact and highly condensed. While the euchromatin is a region where DNA sequences can be transcribed, the heterochromatin is known to be poor in transcribed coding genes which are rich in repetitive DNA sequences and are also known to possess high functional values such as suppressed recombination rates (Simmons, 2008; Grant-Downton and Dickinson, 2005; Egger et al., 2004; Anderson and Stack, 2002 and Murata, 2002).

Are there evidences of histone modification involvement in epigenetic control of gene expression in plant and crop species? Changes in methylation and acetylation including genome-wide gene expression status are throwing more lights on the relationship between Histone modification and changes in plant cell functions. Histone modification studies of many crop species including maize (Rossi et al., 2007) and rice (Zhou and Hu, 2010) show that functional relationship exist between histone modification and gene regulation. Zhou and Hu (2010) reported several rice genes encoding histone deacetylases and histone methyltransferases and demethylases that reveal specific regulators involved in transposon repression, development regulation, and responses to environmental conditions. These rice genes were observed to play tissue specific functions that are different from those of A.thaliana. The rice histone acetyltransferases and histone deacetylases (HDAC) gene SRT701, are involved in transcriptional activation of many transposons (Qin et al., 2010; Zhou and Hu, 2010; Huang et al., 2007). Studies show that acetylated H3K9 needs to be deacetylated by HDAC before methylation, suggesting that SRT701 and Suv(var) 3-9 homologs (SUVH) genes are important component of transposon and retrotransposon silencing in plants. It indicates that histone modification seems to also play a primary role in retrotransposon repression in rice. Downregulation and overexpression of the maize Rpd3-type hda101 histone deacetylase gene have induced morphological and developmental defects (Rossi et al., 2007). Arias et al. (2006), show that inducible expression and/or suppression of the genes that control the cell cycle and development, by altering chromatin structure and exerting epigenetic control of gene expression. These, it is believed have the potential to substantially improve competence for transformation and/or regeneration, thus eliminating the instability associated with genetic transformation and regeneration of majority of transgenic plant species. Paszkowski and others worked on the role of mCpGs marks in epigenetic inheritance in Arabidopsis
strain mutated in maintenance of mCpG. Apparently, the complete removal of CpG methylation leads to depletion, not only at transcriptionally reactivated templates but also at heterochromatic loci, which remained transcriptionally silent despite being demethylated. The findings of the research supported a self-reinforcing system contributing to the formation of silent heterochromatin in vivo in which CpG methylation plays the role of a central scaffold directing histone methylation and acetylation, and perhaps further chromatin modifications. Aceituno et al. (2008) demonstrated that Arabidopsis transcriptome is largely established during development and is comparatively stable when faced with external perturbations. This suggests a novel functional role for DNA methylation in the transcribed region as a key determinant capable of restraining the capacity of a gene to respond to internal/external cue. This also suggests a prominent role for epigenetic mechanisms in the regulation of gene expression in plants. Epigenetic developmental mechanisms including histone modification and nucleosome remodeling in plants was extensively discussed in (Habu et al., 2001). Minor changes of chromatin properties and other nuclear features in response to intraspecific hybridization in Arabidopsis thaliana have been reported (Moghaddam et al., 2009).

The role of nucleosome remodeling in gene regulation is currently receiving attention in many molecular biology centers across the world. Earlier report (Jaskelioff, 2000) indicates that remodeling of mononucleosomes or nucleosomal arrays does not lead to an accumulation of novel nucleosomes that maintain an accessible state in the absence of continuous ATP hydrolysis, however a recent view (Blosser et al., 2009) shows that ATP-dependent chromatin assembly and remodeling factor (ACF) always function to generate regularly spaced nucleosomes, which are required for heritable gene silencing. The individuality of three classes of nucleosome remodeling factors: the SWI/sucrose non-fermentable (SWI/SNF)-type complexes, the ISWI/SNF2L-containing machines, and the CHD containing complexes are well documented (Becker and Horz, 2002). This has been demonstrated in dynamic remodeling of individual nucleosomes across a eukaryotic genome in response to transcriptional perturbation (Shivaswamy et al., 2008). The ISWI-containing protein complex (nucleosome remodeling factor) that facilitates nucleosome mobility and transcriptional activation in an ATP-dependent manner has been reported in Drosophila (Mizuguchi et al., 2001). The dynamic nature of chromatin is subject to extensive developmental and age-associated remodeling in the nucleus of the eukaryotes. Age-related epigenetics consequences such as cancerous growths have been reported in humans (Sedivy et al., 2008; Fraga and Esteller, 2007). It is evident that genomic DNA methylation levels have been shown to increase with developmental age, from seedling to mature plant such as in A. thaliana (Ruiz-García et al., 2005).

Non-coding RNAs

The eukaryotic genomes are now known to posses several classes of small RNAs (miRNAs, siRNAs, snoRNAs, and piRNAs) of approximately 21 to 30 nucleotides long. These small RNAs, coupled with their known simple messenger role, play crucial regulatory roles at different development stages as well as mechanisms that have to do with response to stress and/or environmental changes (Bonnet et al., 2006). They are involved in cell activities such as translation, transcription, genome defense, and sometimes play key roles in turning on and off functional genes. Heterochromatin formation, histone modifications and DNA methylation are suggested RNAs machineries associated with gene expression (Moazed, 2009).

The theory that small RNAs play vital roles in the targeting of epigenetic marks is becoming clearer. Zhai et al. (2008), in his study of small RNA-directed epigenetic natural variation in Arabidopsis thaliana revealed that small interfering RNA (siRNA) is involved in both the initiation and maintenance of gene silencing by directing DNA methylation and/or histone methylation in plants. The report stated that a cluster of approximately 24 nt siRNAs found at high levels in the ecotype of (Landsberg erecta (Ler) could direct DNA methylation and heterochromatinization at a hAT element adjacent to the promoter of FLOWERING LOCUS C (FLC), whereas the same hAT element in ecotype Columbia (Col) with almost identical DNA sequence, generates a set of low abundance siRNAs that do not direct these activities. This suggests that small RNA can direct epigenetics differences between two closely related Arabidopsis ecotypes. Other RNA-directed epigenetic natural variations abound in literature (Cuzin et al., 2008; Chandler, 2007; Alleman et al., 2006; Chandler and Stam, 2004). A study revealed that silencing of RNA-directed RNA polymerase 1 (RdR1) makes Nicotiana attenuata highly susceptible to insect herbivores (Pandey et al., 2008). This suggests that defense elicitation is under the direct control of small-RNAs (smRNAs). MicroRNA involvement in regulation of many developmental processes, including post-transcriptional regulation of gene expression in plants during abiotic stress is well documented (Floris et al., 2009; Dugas and Bartel, 2004). Rangwala and Richards (2007) demonstrated potential impact of differential epigenetic regulation within an Arabidopsis retroposon family on the stability of silencing in natural populations. RNA-related transgene silencing by the host genome defense have been reported (Matzke et al., 2000).
EPIGENETIC INHERITANCE

Epigenetic heritability in plants has drawn the attention of many plant genetics and evolutionists. Plants are incapable of moving from place to place to escape biotic and abiotic stress such as the ones caused by tissue culture. Exposure to stress normally leads to genome instability and changes in DNA methylation. Research has shown that plants possess plastic epigenetic systems that permit sensitive as well as rapid gene expression changes developed de novo from somatic tissues. This, as Grant-Downton and Dickinson (2006) note, “allows the opportunity for any stable epigenetics information acquired by the chromatin–DNA structures of the somatic tissues to be transmitted to the next generation, provided no epigenetic resetting system that deletes such acquired information is active.” It was reported that abiotic and biotic stress responses of plants are transgenerational and this was demonstrated when Viral infection of tobacco plants and exposure of Arabidopsis thaliana plants to UVC and flagellin show potentiality of inducing transgenerational increases in homologous recombination frequency. Histone methylation studies in Arabidopsis have shown that vernalisation often times require epigenetics silencing of flowering time gene FLC, a phenomenon that explains how plants’ memory extends from one generation to another (Bastow et al., 2004). Dominant epigenetic trait inheritance involving both the maternal and the paternal crossing partner has been reported in Arabidopsis (Molinier et al., 2006). Based on this, although not many studies have been reported in this area, it is now clear that plants, unlike animals, retain some memory of stress information passed from one generation to the other.

DNA methylation appears to be a principal component of epigenetic inheritance. Kakutani (2002) showed that epigenetics landmarks can be inherited in plants through epialleles over many generations. Messeguer et al. (1991) demonstrated that cytosine methylation in tomato nuclear DNA can be inherited in a Mendelian fashion and do co-segregate with the methylation target site. Takeda and Paszkowski (2006), demonstrated that the maintenance of CpG methylation (mCpG) appears to play a central role, guiding the distribution of other epigenetic signals such as histone H3 methylation and non-CpG DNA methylation. Johannes et al. (2009) confirmed the above report. However, they pointed out that numerous epialleles across the genome can be stable over many generations in the “absence of selection or extensive DNA sequence variation” thus highlighting the need to integrate epigenetics information into population genetics studies. Excellent review on the role of chromatin marks such as the methylation of DNA and the posttranslational modification of histones can be found (Henderson and Jacobsen, 2007). Zhang et al. (2008) suggested a possible relationship between natural CG methylation variation and gene expression variation in genetic and epigenetic polymorphisms between Arabidopsis accessions. A stress-induced transgenerational response in Arabidopsis was suggested to depend on altered DNA methylation and smRNA silencing pathways indicating their importance in cell differentiation and development (Boyko et al., 2010). A number of evidence on the inheritance of acquired traits abound in crop plants. Using MSAP screening in rice, Akimoto et al. (2007) showed that both hypomethylation and pathogen resistant (Xanthomonas oryzae pv. Oryzae) can be stably inherited up to eight generation or more. Similar genome-wide scan in rice has also implicated DNA demethylation in response to drought adaptation (Wang et al., 2010). Phenotypic variations observed in Jatropha curcas L. collected from five different countries in Asia and Africa and grown in the same environment proved that agronomic traits are less dependent on genetic diversity but more of epigenetic diversity (Yi et al., 2010). These instances point to the fact that the extent to which methylation varies among individuals and effect of these differentials as generators of epialleles and its relationship with phenotypic variations are becoming more lucid. Yi et al. (2010) have shown that most epigenetic variation inheritance such as epialleles often follow mendelian segregation patterns. In a study to determine the fate of DNA methylation patterns that could affect naturally occurring new asexual triploid lineages of dandelions involving a ploidy level change, Salmon and Ainouche (2010) also demonstrate stably transmitted DNA methylation changes that lead to unique DNA methylation patterns in each newly formed lineage. Several other works (Adams et al., 2004; Wendel and Cronn, 2003) are indicative of epigenetic changes that follow polyploid formation and cross generational inheritance stability of epigenetic modifications spanning over many years. Transgressive segregation observed in hybrid polyploids may be linked to epigenetics characteristics that are suggested to enable the hybrid to survive environmental conditions outside the range of either of its parents (Hegarty et al., 2008; Rieseberg et al., 2003; Moore, 1977). Chromosome instability and DNA methylation was observed among F1 hybrids from intergeneric hybridization between Raphanus sativus L. and Brassica alboglabra Bailey (Li et al., 2010). Early generations chromosome instability was evident with later generations reverting to euploidy. Variations in DNA methylation between genetically stable and unstable generations also point to the role of epigenetic mechanisms in maintaining genetic stability of the allopolyploids. This seems to confirm earlier concerns by several other reviewers about the potential for a population to revert to former morphological state before the stress (in this case the genome stress induced by polyploidization) that brought epigenetic mechanisms into play if the stress is reduced. Transgenerational epigenetics...
instability in the form of altered cytosine methylation and its associated transposable element activity has been reported in rice (Wang et al., 2009). Since heritable phenotypic variation within populations has always been the basis for selection and breeding, genome instability in polyploidy (Li et al., 2010) and transgenic plant and crop species remains a challenge.

The epigenetic impacts (genome instability and change in phenotypes) that results from harmful DNA, activation, excision and translocation of transposon elements dates back to McClintock report on chromosome organization and genic expression some decades ago. As a result, the 80s to early 21st century witnessed lots of reports on maize transposon (reviewed in Weil, 2005). Examining the impacts of mobile transposons, (Kato et al., 2004) show that inheritance of epigenetic gene silencing (endogenous Arabidopsis transposon CACTA) over generations indicates that transgenerational genome defense mechanism against deleterious movement of transposons depends on maintenance of transposon silencing over generations. A contrary report now suggests the possibility that a position effect (local chromatin environments) on the heritability of epigenetic silencing may have the capacity to erase previously established epigenetic marks. Singh et al. (2008) implicated DNA methylation for the position effect that is associated with the reversal of epigenetic silencing.

SOMACLONAL VARIATION

High throughput assays are aiding in the identification and differentiation of genetics and epigenetics variations, especially in plants. Before the report by (John and Amasino, 1989) little was known of the relationship between T-DNA methylation and phenotypic variation. Tissue culture has made it possible to circumvent normal growth circles via off-season opportunities it presents as well as in development of planting materials (clones) especially for plants that are not propagated by seed. Somaclonal variation is a common phenomenon associated with tissue cultures. Somaclonal variation was defined as phenotypic and DNA variation among putative plant clones (Kaeppler et al., 2000). This variation may be a reflection of response to cellular stress in other situations resulting in either hypo or hypermethylation of cytosine molecules. Evidence of tissue-culture induced variation abounds in literature. A study to investigate variation in DNA methylation patterns of grapevine somaclones (Vitis vinifera L.) using methylation-sensitive amplification polymorphism (MSAP) demonstrate that different digestion patterns in grapevine somaclones revealed different methylation status, especially different levels of demethylation (Schellenbaum et al., 2008), indicating a consequence of the in vitro culture. This variation noticed here may be attributable to genome induced stress often found in regenerated plants. A similar result has been demonstrated in tissue-culture-derived plants of Doritaenopsis (Park et al., 2009). Another DNA methylation report shows that leaves of ‘late regenerants’ from cultured Theobroma cacao exhibited significant less genetic and epigenetic divergence from source leaves than those exposed to short periods of callus growth which is suggestive of progressive erosion of genetic and epigenetic variation in callus-derived cocoa plants (Lopez et al., 2010). Genetic and epigenetic variations in barley calli cultures have been linked to tissue culture-induced variation as well as cytosine methylation alterations (Temel et al., 2008).

Other somaclonal variation evidences in plant are well documented. Plant E2F–Rb pathway’s relation with epigenetics control study Shen (2002), shows that plant E2F–Rb pathway communicates with chromatin-remodelling factors in the control of transcription and cell-cycle progression. Some studies demonstrated cytological aberrations and gene silencing related epigenetic variation in tobacco (Krizova et al., 2009). Pischke et al. (2006) has shown that a transcriptome-based analysis of a well established habituated Arabidopsis cell culture line can provide answers for genome-wide expression changes underlying the phenomenon of habituation which as proposed in (Moore, 1977) often makes hybrids more fit in new habitat than their parental habitat. Wu et al. (2009) showed the role of transposon activities in somaclonal variation in rice. As contained in the report, callus culture have been suggested to play an important role in destabilizing the rice endogenous long terminal repeat (LTR), however retrotransposon Tos17 was found to be transpositionally activated only in transgenic calli and their regenerated plants produced by biolistic transformation in rice (Oryza sativa L. ssp. japonica cv Matsumae) indicating not just the direction towards transpositional activation, but that biolistic transformation is the direct causal factor. It is no longer a supposition that in-vitro propagated plants show variations different from explants. Rather than finding out what the fate of cultured plants should be, cytogenetics and other cell biologists should focus on manipulating this epigenetic phenomenon for agronomic advantages.

CONCLUSION AND RECOMMENDATION

The subject of epigenetics has received extensive contribution from acclaimed plant biologists. Early epigenetic studies on crops were on maize transposon elements. Ever since Dooner et al. (1991) reported on maize element activator (Ac), the element has been confirmed in many crop species including tobacco. DNA methylation control of both qualitative and quantitative traits among many plants and crop species shows correlation between methylation and phenotypes (Zhao et
Lumping together of genes either through inter-intraspecific or intergenic hybridization creates complex metabolic effects in plants. These metabolic forces may account for the observed variation (for example, activate genes) among crop species. However, studies are needed to fully understand all metabolic forces at play in developing cells since increased variation of dosage-regulated gene effects (metabolic effects) especially in polyploids has always been the basis for selection and breeding.

Epigenetics studies at present still rotate around mechanisms of the phenomenon and may remain at this level for a decade or so to come. Aspects of breeding and evolutionary biology remain at testing whether acquired trait is stably passed on from one generation to another as well as whether traits can be fixed. Despite nearly two decades of gene expression studies on quantitative traits loci (QTL), epigenetic silencing in transgenic plants amongst others, research efforts are yet to be fully directed on utilizing epigenetic marks in marker-assisted-breeding (MAB) for crop species. Thorough understanding of gene expression, DNA and Histone modification and small RNAs may be a step further in utilizing epigenetic information. We believe there is urgent need to facilitate the application of epigenetic in agriculture but considering the time lag in utilizing marker-assisted-selection in breeding programs one issue remains unclear. How soon will epigenetic marks be manipulated for agronomic advantages? A quick resolve in this aspect by focusing researches in this direction may see a super green revolution era that could again save the world from looming hunger caused by climate change. The challenge though, is that many genes that are said to be epigenetic are yet to be characterized. Intensification in the application of new generation sequencing technologies in genes characterization and genes’ functions analyses of crop species may explain the effects of methylation changes and other mechanistic regulators of crop phenotypes.

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