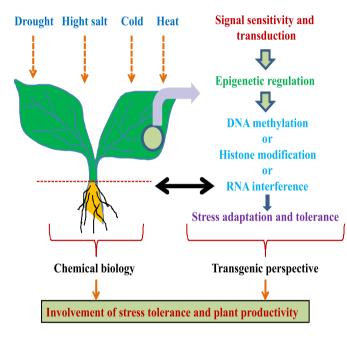
CSIR - National Botanical Research Institute, Lucknow

Plants are able to regulate their metabolism in order to respond to environmental factors. With this natural aptitude plants can face different environmental stresses such as drought, heat, salt stress, cold etc and modify themselves accordingly. Different modification to an alike stress depicts the concept of 'stress memory'.



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From:

The ENVIS Coordinator
NBRI-ENVIS Centre
Centre for "Plants and Pollution"
CSIR-National Botanical Research Institute
Rana Pratap Marg, Lucknow-226001

Plants as leading systems for epigenetics and epigenomics research

Epigenetic phenomena involve mitotically or meiotically heritable alternative gene expression states that are not due to DNA sequence differences. A number of epigenetic phenomena were discovered in plants. Nucleolar dominance describes the selective silencing of the ribosomal RNA genes inherited from one progenitor of a genetic hybrid, regardless of whether that progenitor served as the male or the female parent. Some epigenetic phenomena are plant-specific and are agriculturally important. For instance, the induction of flowering in plants in response to the experience of winter (prolonged cold) is a physiological phenomenon known as vernalization, which is now known to have an epigenetic basis. RNA-mediated DNA methylation, leading to transcriptional gene silencing, and RNA-mediated post-transcriptional silencing, involving mRNA degradation or inactivation, are principal RNA silencing mechanisms.

Plants modify their histones and execute transcriptional as well as post-transcriptional gene silencing programs as a defense against transposable elements and viruses. Like animals, plants make use of miRNAs and siRNAs; in the case of Arabidopsis, these small RNAs are generated via pathways that have been, and continue to be, genetically defined. Genome sequences for Arabidopsis, rice, poplar, maize and moss are available, facilitating genome-wide analyses of DNA methylation, histone modifications, and their relationships to coding as well as noncoding RNAs. These positive attributes of plants as model systems have helped to keep plants at the forefront of discoveries in the fields of epigenetics and epigenomics.

Source: www.plant-epigenome.org/plants-leading-systems-epigenetics-and-epigenomics-research

An integrated reaction at the cellular and gene/genome levels is considered to increase the survival chances of plant by improving the plant's tolerance to particular environmental stress. Finally, stress memory may provide a mechanism for acclimation and adaptation (Avramova 2015). Epigenetic changes do not modify DNA sequences and are consequently reversible. The major defiance for the examination of epigenetic adaptation is to recognize genomic loci that experience DNA methylation or histone modification as an adaptation to environmental stress. Sometimes epigenetic changes occur in an inherited way which improves the plant's ability to adapt to the inducing conditions (Meyer 2015).

Environmental Sensitive Epigenetics

Plants faced various environmental conditions such as elevated temperature and salt, water stress etc and try to adapt their growth and developmental processes to reduce the amount of injury. Characteristically these adaptations are temporary and reversible. The induction level of these adaptations depends on the time of that particular environmental stress. These modifications originally occur at the epigenetic level in plants. Epigenetics is defined as the heritable alteration of gene expression without changing the basic DNA sequence (Bonasio et al. 2010). These epigenetic changes like DNA methylation, histone modifications, and small RNA interference takes place in plant body and play a very important role in plants adaptation. At the time of stress these epigenetic mechanism modify gene expression pattern individually all the way through the growth and developmental stages of plants as well as protect a plant from the undesirable environmental stimuli such as abiotic and biotic stresses.

Epigenetic modifications are affecting gene expression without changing genome sequence. These changes inherited in plant species and may occur in response to biotic or abiotic stress such as drought, temperature variation, water stress etc. Epigenetic changes can modify phenotypes without changing nucleotide sequence of promoter or coding regions of a gene (Jablonka and Lamb 1998).

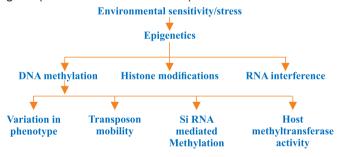


Figure: 1 Types of epigenetic changes caused by environmental sensitivity.

A number of epigenetic phenomena were discovered in plants, plants provide ideal systems for epigenomics research. Plants make extensive use of DNA methylation, Cytosine as an epigenetic mark; Plants modify their histones and execute transcriptional as well as post-transcriptional gene silencing programs as a defense against transposable elements and viruses. Like animals, plants make use of miRNAs and siRNAs; in the case of Arabidopsis, these small RNAs are generated *via* pathways that have been, and continue to be, genetically

defined. Importantly, plants tolerate null mutations in many chromatin regulators that are lethal in animals, despite undergoing similarly complex developmental transitions. Genome sequences for Arabidopsis, rice, poplar, maize and moss are available, facilitating genome-wide analyses of DNA methylation,

histone modifications, and their relationships to coding as well as noncoding RNAs. These positive attributes of plants as model systems have helped keep plants at the forefront of discoveries in the fields of epigenetics and epigenomics.

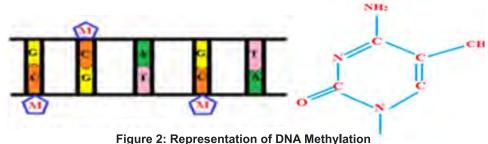
a) DNA Methylation:

DNA is surrounded by arrangement of four nucleotides which contain cytosine, guanine, thymine and adenine. An addition of a methyl (CH₃) group to the cytosine or guanine nucleotides is called DNA methylation. Sometimes this methyl group added to the fifth carbon atom of the cytosine base or the sixth nitrogen atom of the adenine base.

DNA methylation raised by environmental stress may be denoted specifically to stress-related genes. On the other hand, methylation changes may generate nonspecific/ random dissimilarities between individuals, which may have adaptive significance during times of stress (Rapp & Wendel, 2005). In plants, only significant amount of DNA methylation trail can be steadily forwarded from parents to progeny (Johannes et al. 2009).

The whole process of DNA methylation is protected by both DNA methyltransferase and DNA demethylation enzymes. Demethylation occurs in two ways i.e. passive and active. The passive demethylation may occur due to the inhibition of de novo methylation or absence of methylation of newly synthesised DNA strands (Kankel et al. 2003). On the other hand, active demethylation may occur *via* the glycosylase activity by direct removing the methyl group from DNA (Zhu et al. 2007). Both of these processes are actually important for plant facing environmental stress because they stop the formation of stable hypermethylated epialleles in plant genome (Penterman et al. 2007).

In response to environmental signal, growth as well as development; DNA methylation in plants is controlled by an RNA-directed mechanism to facilitate different genomic sites to be separately methylated (Mahfouz 2010). This process involves members of the family of PAZ (Piwi Argonaut and Zwille). Piwi domain proteins that are capable of binding to 24- to 26-nt-long RNAs transcribed from non-coding regions are called Piwi-interacting RNAs (*piRNAs*). The *PIWI/piRNA* complex is guided to specific sequences in the genome by RNA–DNA or RNA–RNA pairing recognition (Pe'lissier and Wassenegger 2000). This *PIWI* complex then attracts *DNMT3* to perform de novo methylation (Figure 3 Recently, it has also been shown that other small RNAs



Mechanisms targeting DNA Methylation:

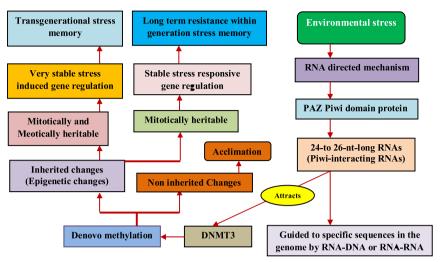


Figure 3: Mechanisms targeting DNA methylation

similarly mediate de novo DNA methylation by associating with *PIWI* proteins in plants. In these instances, siRNAs or miRNAs that arose from miRNA-coding regions guided DNA methylation at some of their generation sites and in trans at their target sites (Wu et al. 2010).

Impacts of DNA Methylation and demethylation in plants:

- Flowering stage of plants are highly affected by 1. different environmental stresses. Flowering stage determines the gross yield of plant and disturbance in this stage disturbs the whole life cycle as well as next generation too. In stressed conditions plants tend to flower earlier than plants growing under standard environmental conditions. Early flowering helps plants to complete their life cycle in less time and also reduces their exposure period to adverse conditions (Yaish 2013). At the time of stress DNA methylation controls the expression of those genes which are involved in the process of flowering. Transformation in global DNA methylation can modify the flowering time in plants. For example mutations within the Methyltransferase1 gene (MET1) guided the late flowering in Arabidopsis plant. According to some studies AtMBD8 gene has been shown to control flowering in the Arabidopsis vernalization-responsive C24 ecotype. Mutation of AtMBD8 leads to a delay in flowering under both long and short-day photoperiods (Yaish et al. 2009).
- 2. DNA methylation helps plants to tolerate salt stress conditions also. In a study, loss of DNA methylation reduced the ability of *Arabidopsis* plants to tolerate salt stress conditions. For example; met1-3 mutants are hypersensitive to salt stress and the failure in cytosine methylation in a putative small RNA target region causes loss in met1-3 functioning which lowers the expression of the sodium transporter gene (*AtHKT1*), which is essential for salt tolerance (Baek et al. 2011).

- In Arabidopsis, low temperature (around 15°C) generally linked with DNA demethylation, along with other plant species such as maize (Steward et al., 2002), snapdragon (Hashida et al., 2003), and wheat (Sherman and Talbert 2002).
- 4. Water deficit (water stress was imposed by withholding irrigation from 53 DAS for a period of 10 days) led to specific cytosine hyper methylation (CCGG) in the pea genome (Labra et al. 2002) as well as in lowland rice cultivars (Suji and John 2010).
- As an adaptation, for hightemperature (25°C to 55°C) Cork oak leaves showed interplay between specific DNA methylation and histone H3 acetylation (Correia et al.

2013).

- In soybean, salinity stress (45 of 49 transcription factors) treatment induced the reduction of DNA methylation and transcriptional activation in genes that encoded salt stress-responsive transcription factors (Song et al. 2012).
- 7. DNA methylation and transcriptional suppression in two positive regulator genes for stomatal development i.e. *SPCH* (speechless) and *FAMA*, were reported to be induced by low relative humidity stress (45±5%) in Arabidopsis (Tricker et al. 2012).
- 8. In rice, drought stress increases DNA methylation in a genotypic-specific fashion and only 70% of the total changes in DNA methylation are reorganize even after restoration in non-drought conditions (Wang et al. 2010).
- 9. Reduction of DNA methylation in ddm1 and met1-1 mutant lines causes late flowering in Columbia and Landsberg erecta ecotypes (Kankel et al. 2003) and promoted flowering in the vernalization-responsive Arabidopsis ecotype C24.

b) Histone modification:

They are the chief protein components of chromatin. acting as spools around which DNA winds, and play a role in gene regulation. Five major families of histones exist: H1/H5, H2A, H2B, H3 and H4 (Bhasin et al. 2006). Histones H2A, H2B, H3 and H4 are known as the core histones (Zhou et al. 2013), while histones H1 and H5 are known as the linker histones. Histone modifications are wide variety of posttranslational modifications including, Ivsine acetylation, Ivsine and arginine methylation, serine and threonine phosphorylation, and lysine ubiquitination and sumoylation (Vasquero et al. 2003). Principally these modifications take place insight the histone aminoterminal tails, stick out from the surface of the nucleosome and on the globular core region (Cosgrove et al. 2004). Comparable to DNA methylation, histone modification is also regulated by environmental stress (Kim et al. 2012).

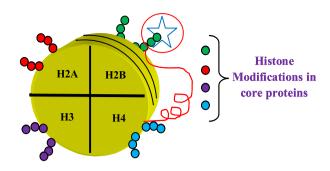


Figure 4: Diagram showing Histon modifications in H2A, H2B, H3 and H4 proteins

Impacts of Histone modification in plants:

- Under strong drought conditions (percentage of the fully turgid water content (H - D), the histone modifications H3K4me3 and H3K9ac on drought stress-up regulated genes, such as RD20 and RD29A, were more highly enriched than under moderate drought conditions (Kim et al. 2012).
- 2. In response to drought stress, the histone acetylation level increased on the drought-responsive genes, such as *RD20*, *RD29A*, and *RD29B* (Kim et al. 2008)
- In rice, drought stress significantly induced four HAT genes (OsHAC703, OsHAG703, OsHAF701, and OsHAM701 (Fang et al. 2014) and enhanced acetylation of H3K9, H3K18, H3K27, and H4K5 under drought stress conditions was found by western blotting analysis.
- As a response of high salinity (200 mM NaCl) the up regulation of cell wall-related genes, such as ZmEXPB2 and ZmXET1, has been associated with increased H3K9 acetylation in the promoter and coding regions, of maize roots (Hui et al. 2014).
- Arabidopsis mutants for HDAC proteins such as HD2C, histone deacetylase 6 (HDA6), and histone deacetylase 19 (HDA19), which should increase histone acetylation, showed hypersensitivity to salt (150 mM NaCl) (Luo et al. 2012).
- In Arabidopsis, the expression of HDA 6 was induced by long-term low temperature treatments and a mutation in this gene resulted in sensitivity to freezing stress (To et al. 2011).
- 7. In maize, histone acetylation in cold (4°C) responsive genes such as *ZmDREB1* and *ZmCOR* 413 was found to be increased (Hu et al. 2011).
- 8. In rice, histone acetylation of *OsDREB1b* was induced by cold stress (4°C) (Roy et al. 2014).
- In Brachypodium, the impairment of H2A.Z deposition reduced grain yield under heat stress (22/17°C (night) or 27/22°C (day) conditions (Boden et al. 2013).
- In Arabidopsis histone H3 Lys4 methylation (H3K4) patterns vigorously act in response to dehydration stress (relative water content (RWC of 65%) (Van Dijk et al. 2010).

c) RNA interference:

RNA interference (RNAi) is a naturally occurring

mechanism that leads to the "silencing" of genes. Double stranded RNA (dsRNA) acts as an igniter in RNA interference and activate the homologous mRNAs to inhibit its translation and transcription to silence the susceptible genes (Almeida and Allshire 2005). Plant miRNAs have been shown to be involved in various abiotic stress responses such as drought, salinity, temperature, cold (chilling), and other abiotic stress (Kumar 2014). These abiotic stresses are the main source for crop destruction with respect to loss in quality and quantity as well as in yield (Tardieu and Tuberosa 2010). In plants, several classes of small RNAs with specific sizes and dedicated functions have evolved through a series of pathways (table 1). The major classes of small RNAs include microRNAs (miRNAs) and small interfering RNAs (siRNAs), which differ in their biogenesis.

Table 1. Types of Small RNA and their role:

RNA		F	unction
Small RNA (RNAs)		(RNAs)	mall RNAs play important role in plant stress responses by nodifying their gene expression through the activity of small NAs
Types of Small RNA (sRNA)			
	S.No.	RNAs type	Function
→	1	MicroRNAs (miRNAs)	Control the expression of cognate target genes by binding to reverse complementary sequences, resulting in cleavage or translational inhibition of the target RNAs
	2	Small interfering RNAs (siRNAs)	

Source: Khraiwesh et al. 2012

Impacts of RNA interference in plants:

- 1. *miR393* was unregulated by cold (0°C for 24 h), dehydration (seedlings in agar plates were exposed to dry air), salinity treatments (300-mM NaCl) (Sunkar and Zhu 2004, Khraiwesh et al 2012).
- 2. *miR389a*, was down regulated by all of the stress treatments. (Sunkar and Zhu 2004, Khraiwesh et al. 2012).
- 3. 48 miRNA sequences from the Populus genome target developmental and stress/defense-related genes (Lu et al 2005).
- 4. miRNAs such as *miR168*, *miR171*, and *miR396* were found to be responsive to high salinity (300 mM NaCl), drought, and cold stress (4°C) in *Arabidopsis* (Liu et al. 2008).
- 5. In Arabidopsis, miR396, miR168, miR167, miR165, miR319, miR159, miR394, miR156, miR393, miR171, miR158, and miR169 were shown to be drought responsive (Liu et al. 2008).
- In rice, miR169g was strongly up regulated by drought while miR393 was transiently induced by drought (Zhao et al. 2007).
- 7. Populus, miR171I-n, miR1445, miR1446a-e, and miR1447 were found to be drought-responsive (Lu et al. 2008).
- 8. In *Populus*, *miR168a*, *b* and *miR477a*,*b* were up regulated while *miR156g-j*, *miR475a*,*b*, and *miR476a* were downregulated under cold stress (4°C) (Lu et al. 2008).

 miR172 was significantly decreased, and miRNAs (including miR156, miR159, miR160, miR166, miR168, miR169, miR393 and miR827) were up regulated under heat stress (40°C) (Xin et al. 2010).

Conclusion:

Plants act together with their surroundings and accordingly change their physiological activities. These modifications are related with transformation in DNA methylation, histone modifications such as acetylation and methylation, along with production of specific miRNA molecules. These epigenetic changes motivate some physiological or biochemical changes in plant body which are essential for survival under a variety of stress conditions. These adaptations are highly important for the production of genetically fertile crop species that can stand up in a warmer world.

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ABSTRACTS

Chromatin changes in response to drought, salinity, heat, and cold stresses in plants

Jong-Myong Kim, Taku Sasaki, Minoru Ueda, Kaori Sako and Motoaki Seki

Front Plant Sci. 114 (2015)

Chromatin regulation is essential to regulate genes and genome activities. In plants, the alteration of histone modification and DNA methylation are coordinated with

changes in the expression of stress-responsive genes to adapt to environmental changes. Several chromatin regulators have been shown to be involved in the regulation of stress-responsive gene networks under abiotic stress conditions. Specific histone modification sites and the histone modifiers that regulate key stressresponsive genes have been identified by genetic and biochemical approaches, revealing the importance of chromatin regulation in plant stress responses. Recent studies have also suggested that histone modification plays an important role in plant stress memory. In this review, we summarize recent progress on the regulation and alteration of histone modification (acetylation. methylation, phosphorylation, and SUMOylation) in response to the abiotic stresses, drought, high-salinity, heat, and cold in plants.

Immediate and Transgenerational Regulation of Plant Stress Response through DNA Methylation

A. R. Khan, S. M. Shah, M. Irshad

Journal of Agricultural Science 7 (2015)

Epigenetics refers to the heritable changes in gene activity without altering the DNA sequence. DNA methylation along with other epigenetic mechanisms is involved in the chromatin remodeling. This remodeling, especially in plants, plays an important role in the activation or silencing of specific genes as well as other genomic regions in response to the developmental and environmental clues. Environmental clues, biotic and abiotic stresses trigger the shift in the site specific as well as genome wide DNA methylation patterns which influences the plant response to these situations through gene regulation. Therefore, it is of prime importance to analyze variation in the DNA methylation pattern under stress conditions. This review summarizes the topic of DNA methylation by providing the basic/conceptual knowledge and some cases of DNA methylation shift due to stresses.

Stress-induced chromatin changes in plants: of memories, metabolites and crop improvement

Ce'cile Vriet, Lars Hennig, Christophe Laloi

Cell. Mol. Life Sci. 72 (2015) 1261-1273

Exposure of plants to adverse environmental conditions leads to extensive transcriptional changes. Genome-wide approaches and gene function studies have revealed the importance of chromatin-level control in the regulation of stress-responsive gene expression. Advances in understanding chromatin modifications implicated in plant stress response and identifying proteins involved in chromatin-mediated transcriptional responses to stress are briefly presented in this review. We then highlight how chromatin-mediated gene expression changes can be coupled to the metabolic status of the cell, since many of the chromatin-modifying proteins involved in transcriptional regulation depend on cofactors and metabolites that are shared with enzymes in basic metabolism. Lastly, we discuss the stability and heritability of stress-induced chromatin changes and the potential of chromatin-based strategies for increasing stress tolerance of crops.

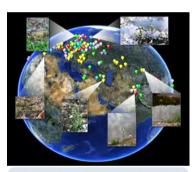
NEWS

Epigenetics unveils how plants may adapt to environments throughout the world

Scientists at the Salk Institute for Biological Studies have identified patterns of epigenomic diversity that not only allow plants to adapt to various environments, but could also benefit crop production and the study of human diseases.

Published March 6 in Nature, the findings show that in addition to genetic diversity found in plants throughout the world, their epigenomic makeup is as varied as the environments in which they are found. Epigenomics is the study of the pattern of chemical markers that serve as a regulatory layer on top of the DNA sequence. Depending on where they grow, the plants' epigenomic differences may allow them to rapidly adapt to their environments. Epigenomic modifications alter gene expression without changing the letters of the DNA alphabet (A-T-C-G), providing cells with an additional tool to fine-tune how genes control the cellular machinery. These changes occur not only in plants, but in humans as well.

"We looked at plants collected from around the world and found that their epigenomes are surprisingly different," says senior author Joseph R. Ecker, a professor in Salk's Plant Biology Laboratory and holder of the Salk International Council Chair in "This Genetics. additional diversity may create a way for plants to rapidly adapt to diverse environments



This graphic depicts a collection of wild Arabidopsis thaliana from around the world that have adapted to their local environment. This collection of plants was used to understand the patterns of population epigenomic diversity within a species

without any genetic change in their DNA, which takes a very long time. "By understanding epigenomic alterations in plants, scientists may be able to manipulate them for various purposes, including biofuels and creating crops that can withstand stressful events such as drought. That knowledge of epigenomic changes in crop plants could tell producers what to breed for and could have a huge impact on identifying plants that can survive certain conditions and adapt to environmental stressors, says Ecker, who is also a Howard Hughes Medical Institute and Gordon and Betty Moore Foundation Investigator.

Using MethylC-Seg, a method for mapping epigenomic changes developed by Ecker, the researchers analyzed methylation patterns from a population of Arabidopsis thaliana, a modest mustard weed that has become to plant biology what laboratory mice are to animal biology. The plants were from a variety of climates in the Northern Hemisphere, from Europe to Asia and Sweden to the Cape Verde Islands. Ecker's team examined the genomes and methylomes of A. thaliana, the makeup of their entire genetic and epigenomic codes, respectively, which is the first step toward understanding the impact of epigenetic changes on the plants' physical characteristics and ability to adapt to their environment.

Source: www.phys.org

Researchers obtain precise estimates of the epigenetic mutation rate

University of Groningen scientists have obtained the first precise estimates of how often epigenetic marks that influence gene activity appear or disappear in the plant Arabidopsis thaliana, a model organism in plant biology. This paves the way to a deeper understanding of the importance of epigenetic changes in plant evolution. The work is published in the week of 11 May in the online Early Edition of the journal Proceedings of the National Academy of Sciences.

Epigenetic marks do not change the DNA sequence. but can affect the activity of genes. Although in most animals, including humans, these marks are believed to be completely reset in gametes, in plants they can be stably inherited for many generations.

It is as yet not known how important epigenetic marks are in plant evolution. One way to assess this is to look for 'signatures' of natural selection on these marks. However, for this to work it is necessary to know the precise epigenetic mutation rate, which is the rate with which these marks appear and disappear spontaneously at a specific site over generations. In close collaboration Arabidopsis thaliana with researchers from the European



Research Institute for the Biology of Ageing (University of Groningen and University Medical Center Groningen) and the University of Georgia (USA), the Johannes group used material from an inbred line of the plant Arabidopsis thaliana (thale cress), which is often used in genetic research. They analysed material from up to 32 generations and checked the entire genome for one specific epigenetic mark: the methylation of cytosine nucleotides.

Epigenetic mutation rate: 'We chose this mark because we know it is heritable between generations and can affect gene expression', Johannes explains. When this task was complete, mathematical modelling was used to estimate the epigenetic mutation rate. 'Basically, our analysis shows that epigenetic mutations are about 100,000 times more likely than DNA sequence mutations. We have also seen that not all cytosine nucleotides are created equal: some are more prone to lose than to gain methylation, while other cytosines 'prefer' methylation gain over loss. While much of this is consistent with what was already known, we are now in a position to quantify these dynamics precisely on a genome-wide scale.

Plant breeders: Another striking feature of the new paper that Johannes wants to stress is the fact that the first author, Adriaan van der Graaf, participated in the project as an undergraduate. 'He came to do a Bachelor's research project and was very curious and showed lots of initiative. In the end, he did most of the bioinformatics analysis needed to nail down the epigenetic mutation rate.' Van der Graaf, who was appointed as a research assistant in the Johannes group for a short period after his graduation in order to finish work on the paper, is now pursuing a Master's degree at the University of Groningen, with a strong emphasis on bioinformatics.

Source: www.phys.org

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Chromatin and Epigenetics (C2)

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Columbia, Canada **Date:** 20-24 March 2016

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Chromatin Structure & Function

Venue: Les Diablerets, Switzerland

Date: 22-27 May 2016

Website: http://www.grc.org/programs.aspx?id=11783

Conference on Life Sciences Research - 2015

Venue: Islamabad, ICT, Pakistan Date: 4-6 September 2015 Website: http://www.clsr.com.pk/

5th International Conference on Emerging Trends in

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NBRI Director

Dr. C.S. Nautiyal director@nbri.res.in

NBRI-ENVIS Coordinator

Dr. Nandita Singh n.singh@nbri.res.in

Editors

Dr. Nandita Singh and Dr. Pankai K. Srivastava

Compiled & designed by

Dr. Shivani Srivastava, Deepmala Yadav and Yashpal Singh

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