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Epigenetics: An Unexplained Variability

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SUMMARY

Whole phenotypic variation found in plant cannot be explain by sequence variability of genome, one more factor affecting this variation is epigenetics an unexplained heritability also termed as missing heritability. The variation explained by epigenetics shows two types of inheritance via mitotic and meiotic inheritance. This phenomenon plays an important role in regulation of different plant phenology as well as provides better adaptation to different environmental stimulus. The epigenetics can be better exploited by plant breeders to develop commendable climate resilient varieties.

INTRODUCTION

Epigenetic phenomenon is important for developmental gene regulation, environmental response, and natural variation in gene expression levels. Although Waddington invented the term "epigenetic" to describe the methods by which genes interact to regulate phenotype, molecular scientists have adopted it to characterise the study of heritable information that is not entirely explained by DNA sequence variation (Haig, D. 2004). The memory of gene expression states imposed during development or by environmental factors (mitotic inheritance; facultative heterochromatin) and the transgenerational memory of gene expression states are two potentially distinct topics of epigenetics (meiotic inheritance; constitutive heterochromatin). Long-term memory of gene expression states that is passed down across generations is less likely to vary throughout tissues. During reproduction, however, embryonic programming of gene expression must be reset. Transgene behaviour is frequently influenced by epigenetic control, which might be utilised to create new epialleles for breeding purposes. The complete spectrum of phenotypic variety found in plants cannot be described by sequence variability of genes affecting agronomical variables, and there is still a considerable fraction of unexplained heritability, referred to as "missing heritability". New disruptive techniques are clearly needed to expand the sources of heritable phenotypic variants, not only for better control of agronomically important traits, but also for crop adaptation to rising environmental restrictions in the face of global climate change.

Mitotic inheritance of epigenetic information

Even in the absence of the appropriate transcription factors, chromatin alterations are frequently used to maintain epigenetic memory of differentiation and normal gene expression levels. These chromatin changes are most likely involved in the generational reset of facultative heterochromatin. Crop relies heavily on mitotically stable epigenetic information. Similar to transcription factors, chromatin modifications influence plant morphology and responses to the environment, and knowing these mechanisms could lead to greater control over characteristics. Stable transmission of histone PTMs through mitosis was first revealed by the vernalization process, a period of cold necessary for flowering in some arabidopsis (*Arabidopsis thaliana*) ecotypes and other winter annuals. The priming response provides additional proof of environmentally driven epigenetic memory mediated by histone PTMs. Given the importance of facultative heterochromatin in cellular differentiation, mitotically persistent epigenetic information is anticipated to be vital for the regeneration of plantlets from cell culture as well as the capacity to influence reproductive behaviours such as apomixis (the ability to reproduce without fertilization).

Transgenerational inheritance of epigenetic information

Several studies indicate that DNA methylation has a role in transgenerational epigenetic memory (transgenerational epigenetic inheritance; TEI). This was illustrated by the observation that small interfering (si)RNA production involved in RNA-directed methylation (RdDM, Box 2) was necessary for the transgenerational memory of herbivory attack, although a direct impact of DNA methylation patterns was not investigated. There is increasing evidence of heritable natural diversity in DNA methylation patterns across members of the same species. There are various examples of spontaneously produced epialleles in plants that modify characteristics. Epigenetic variations can be very stable over hundreds of years, but they can still reverse. This would allow natural or artificial selection to increase the frequency of a certain epigenetic state without preventing fixation.

It can be difficult to separate the relative contributions of genetic and epigenetic variation in natural variation investigations. Epialleles can have variation that is entirely epigenetic or variation that is partially due to both genetic and epigenetic changes. Structure rearrangements and TE insertions have been shown to cause chromatin alterations that result in epigenetic control for specific haplotypes. Gene interactions with neighbouring TEs may account for a significant percentage of epigenetic regulation. The presence of stable epigenetic variations that impact plant properties, such as the peloric mutant in Linaria [23], a tomato ripening variant [36], and melon sex determination [37], demonstrates that epigenetic variation may play a role in natural phenotypic variation.

It is possible that epigenetic variation, rather than genetic variation, is responsible for some of the quantitative trait loci (QTLs) used by breeders. In order to determine how to merge epigenetics with crop development, a better understanding of the rules regulating epigenetic variation is required. Knowing that specific QTLs are the consequence of epigenetic modifications may have an impact on how they are tracked and used in breeding operations. Understanding the usefulness and possible additional value of epigenomic profiling for crop development will require determining the amount of epigenetic variation that is not captured by local SNPs.

Role of epigenetics in Plant phenology and in Environmental Responses

Epigenetic information is mediated by DNA methylation and histone PTMs, the so-called **chromatin marks** that together with chromatin remodeling, small RNAs, and histone variants, determine the conformational state of chromatin and, thus, also its transcriptional state.

DNA methylases and demethylases, HATs, HDACs, proteins of the Trithorax group and PcG (Trx-G), and histone demethylases, were documented [e.g., arabidopsis, maize (Zea mays)], suggesting that epigenomes are remodeled in plants under stress. Plants adapted to contrasting environments have evolved different epigenomes, suggesting that they have long-term adaptation. They are involved in the control of flowering time, seed and endosperm development, parental imprinting, fruit ripening, symbiotic nodule organogenesis, and cell fate maintenance and reprogramming. For example, in arabidopsis, Polycomb Groups were shown to control the transition between developmental phases, including seed and endosperm development, inhibition of central cell division before fertilization, stem cell identity and differentiation, and transition from vegetative growth to reproductive development, in addition to their role in the memory of cold. Similarly, chromatin marks also mediate plant responses to environmental stimuli, thereby contributing to plant phenotypic plasticity.

Behavior and segregation of epigenetic information in crosses

Paramutation is an example of unanticipated behavior of epigenetic information in crosses in which a paramutagenic allele can direct alterations to a paramutable allele when present together in a heterozygote. In Arabidopsis thaliana, the rate of spontaneous changes in DNA methylation is significantly larger than the rate of spontaneous genetic alterations. Studies shows low levels of spontaneous change during inheritance of DNA methylation patterns in plants that had been self-pollinated for many generations. However, there is evidence that epigenetic information may become unstable in wide crosses or in recently formed polyploids. Also, epigenetic interactions between loci in the two parents limit the capacity of some traits to introgress into specific genetic backgrounds. Unlike genetic mutagenesis, which almost always results in loss-of-function alleles, epigenetic mutagenesis can commonly result in gain-of-function variations due to the removal of epigenetic silencing. Changes in epigenetic patterns could lead to new combinations of (epi)alleles within linkage blocks without the need for recombination, perhaps resulting in advantageous haplotypes.

Epigenetic responses to environmental variation

Short-term (mitotic) and long-term (meiotic) changes in response to stress could be caused by epigenetic responses to environmental stimuli. Vernalization is one of the most well-studied examples of mitotically heritable environmental epigenetic reactions. Vernalization, or prolonged exposure to cold, is required by many plant species to commence the growth of reproductive organs. A series of complex experiments in maize (*Zea mays*) on the paramutable R locus, which controls expression of genes in the anthocyanin biosynthesis pathway, discovered that light regimes experienced at the seedling growth stage can impact the expression and epigenetic state of the R gene [66]. Selection might work on the variation to raise or reduce the frequency of a certain epigenetic state within a population if the epigenetic state was altered in germline cells and passed down to next generations. It's also crucial to understand the stability and heritability of epigenetic variation in order to evaluate if it can be captured effectively in breeding programmes or if it's too unstable to be useful. Epigenetic regulation affects transgenic integration, expression, and stability, in addition to its potential function in regulating natural variation.

Exploiting Epigenetic Variations for Crop Improvement

Exploitation of epigenetic variation in crop improvement clearly relies on their transmission features and on the plant propagation strategies. For example DNA methylation 5mC patterns can be transmitted through mitosis as well as meiosis and hence could be useful in all crops, irrespective of their propagation mode. While, histone PTMs are likely to be erased following meiosis, their relevance is more in clonally propagated crops, such as perennial fruit crops as new epigenetic patterns could be simply maintained in meristems or ramets over years. Because the epigenetic state of genes under epigenetic control is expected to be reset at meiosis, limiting their potential trans-generational inheritance, epigenetic regulations as a whole are unlikely to be useful targets for plant improvement. Although, epigenetic regulatory mechanism provides new opportunities for plant improvement as it can be subjected to quantitative variation among varieties by itself transmitting to the progeny. For example, combination of sequence polymorphism at *FLC locus* influencing the accumulation of H3K27me3 in *FLC* of Arabidopsis results in quantitative variations in cold requirements for flowering by epigenetic silencing of *FLC*.

Epigenetics for Plant Improvement: Current Knowledge and Modeling Avenue

Plant developmental processes and phenotypic plasticity, including adaptive responses to environmental challenges, are influenced by epigenetic information. This has prompted scientists to rethink the relationship between genotype and phenotype, utilising natural or produced epigenetic alterations demands that these differences are stable or heritable, two properties of primary importance for potential transfer to the progeny.

Exploiting epigenetic variations for breeding applications, whether they control developmental processes or contribute to adaptation to various environments, clearly relies on their transmission features and on the plant propagation strategies (sexual versus clonal). For example, because 5mC patterns can be transmitted after mitosis and meiosis, DNA methylation marks could be useful in all crops, irrespective of their propagation mode. By contrast, because histone PTMs are more likely to be erased following meiosis, they would be of little benefit to breeding applications in sexually propagated crops. However, they could be relevant for clonally propagated crops, such as perennial fruit crops, because new epigenetic patterns could be simply maintained in meristems or ramets over years.

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