

Stress-induced epigenetic modifications: how plants fit into their environments

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The mechanisms of evolution, such as natural selection and genetic drift, are strongly associated to the random variation generated by DNA mutations. Changes in the nucleotide sequence have potentially the power to create altered versions of living organisms able to live and reproduce based on how they fit into their environments. Several factors in the environment are thought to influence the rate of mutations but are not generally thought to influence the direction of them. These elements of our current biological thinking are being challenged by recent work in the field of epigenetics. Indeed, a number of studies have shown that something other than DNA can affect the phenotype and, mostly important, can arise in direct response to external environmental cues. Biotic and abiotic stresses during plant growth are proven to induce epigenetic changes in plants so that, in addition to mutations that create the genetic variation underlying phenotypic traits, epimutations produce a new source of variation for selection (Figure 1). To date, three mechanisms are recognized as the main players capable to alter gene activity without changes in the underlying DNA sequences, namely DNA methylation, histone modifications and RNA interference. Among them, the only epigenetic mark for which the mechanism of inheritance has been well established is DNA methylation. Indeed, methylation is not reset during reproduction and, therefore it may be inherited across mitotic or even meiotic cell divisions over many generations (transgenerational epigenetic inheritance). Therefore, this mark has been considered the main driving force for epiallelic variation with significant implications in plant breeding. In plant, DNA methylation occurs

in three nucleotide contexts: symmetrical CG and CNG and asymmetric CNN sites (where N is A, T or C)¹ and may lead both to transcriptional and post-transcriptional gene silencing.

The link between DNA methylation and biotic stress was proved by Choi and Sano¹ who found, in tobacco, that aluminum treatments induced DNA demethylation of NtGPDH gene (encoding a glycerophosphodiesterase like protein) and, consequently, its

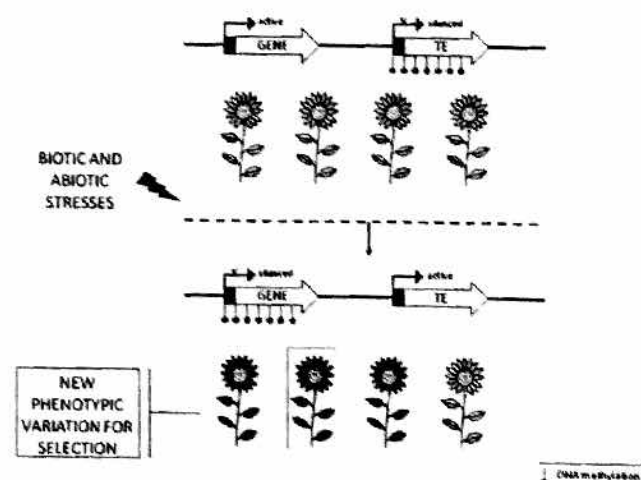


Figure 1.—Generation of phenotypic variation through alteration of DNA methylation patterns. Epigenetic changes are triggered by environmental stresses leading to new source of phenotypic variation available for breeding.

ectopic expression. Similarly, DNA hypomethylation of the nucleosome core was observed in maize in response to cold stress. By contrast, DNA hypermethylation was found to be induced in a cause-effect relationship by osmotic and drought stresses in pea and tobacco, respectively. In addition, it has been observed that in *Mesembryanthemum crystallinum* L. a change in CNG hypermethylation of satellite DNA triggers a switch from C₃ to CAM photosynthesis, in response to drought and salt stresses.

Most of these stresses-induced modifications are reset to the basal level once the stress is relieved, while some of the modifications may be carried forward as "stress memory" and may be inherited in the next generations. Epigenetic stress memory may play a crucial role for the adaptability of a genotype to a new challenging environment, helping plants to more effectively cope with subsequent stresses. The adaptive value of stress-induced epigenetic plasticity was studied by Akimoto and colleagues², who used the DNA methyltransferase inhibitor 5-aza-2'deoxyctidine to obtain hypomethylated progenies of rice. The authors demonstrated that loss of methylation at the Xa21G locus was stably inherited and conferred an adaptive advantage against the bacteria *Xanthomonas oryzae* pv. *oryzae*. This form of adaptive response to stress resembles McClintock's model, which bridges activation of transposable elements (TEs) to genetic and environmental triggers. Several researches reported on stress-responsive TEs whose mobility was responsible for a decreased genome stability. Ito *et al.*³ found that a copia-type retrotransposon named ONSEN responded to specific environmental stimuli (e.g. heat stress). Interestingly, the activation of transposable elements and their insertion in gene-rich chromosome regions can influence the expression of neighboring genes and increase the complexity of the regulatory networks. TEs can generate small interfering RNAs (siRNAs) capable to regulate stress-related genes or mediate silencing upon stress. For instance, Hilbricht and colleagues⁴ analyzed the activation of the unusual *Craterostigma desiccation tolerant* gene (*CDT-1*), which belongs to a family of retroelements, under stress conditions. They showed that *CDT-1* directs the synthesis of a double-stranded 21-bp short interfering RNA (siRNA), which opens the metabolic pathway

for desiccation tolerance capacity of *Craterostigma plantagineum*.

Recently, it has been also reported that transposable elements might contain binding sites for transcription factors similar to those of resistance genes. Therefore, there may be one or more classes of transposable elements preferentially activated by a particular stress. In rice, a LTR retrotransposon named "Renovator" contributed to the evolution of the resistance gene *Pit*, which conferred race-specific resistance against the fungal pathogen *Magnaporthe grisea*⁴. The data by Woodrow *et al.*⁵ suggested that transposon-mediated transcriptional activation might play an important role in the functionalization of additional "sleeping" R genes in the plant genome.

In conclusion, the prevailing view that variation in a species is simply the result of a DNA program locked off from the environment and altered only through random DNA mutations is now too limited. The studies on epigenetics showed that the life and the evolution are dynamic processes, based on the complex back-and-forth relationship between organism and their entire environment. Such epigenetic variants could have significant implications in plant breeding. Indeed, the phenotypic plasticity induced by adverse conditions and controlled by epigenetic buffering could be used, in the future, to improve those plants where genetic resources appear to have reached their limits.

References

1. Choi C. S. and Sano H. Abiotic-stress induces demethylation and transcriptional activation of a gene encoding a glycerophosphodiesterase-like protein in tobacco plants. *Molecular Genetics & Genomics* 2007; 277: 589-600.
2. Akimoto K., Katakami H., Kim H. J., Ogawa E., Sano C. M., Wada Y. and Sano H. Epigenetic inheritance in rice plants. *Annals of Botany Company* 2007; 100:205-217.
3. Ito H., Gaubert H., Bucher E., Mirouze M., Vaillant I. and Paszkowski J. An siRNA pathway prevents transgenerational retrotransposition in plants subjected to stress. *Nature* 2011; 472:115-119.
4. Hilbricht T., Varotto S., Sgaramella V., Bartels D., Sakamini F. and Furini A. Retrotransposons and siRNA have a role in the evolution of desiccation tolerance leading to resurrection of the plant *Craterostigma plantagineum*. *New Phytologist* 2008; 179:877-887.
5. Woodrow P., Pontecorvo G., Fantaccione S., Fuffi A., Kafantaris I., Parisi D. and Carillo P. Polymorphism of a new Ty1-copia retrotransposon in durum wheat under salt and light stresses. *Theor. Appl. Genet.* 2010; 121:311-322.