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► **To cite this version:**

Sophie Brunel-muguet, Ramesh R Vetukuri, Pilar S Testillano. Epigenetics for crop adaptation to climate change. *Physiologia Plantarum*, 2022, 174, 10.1111/ppl.13835 . hal-04135902

HAL Id: hal-04135902

<https://hal.science/hal-04135902>

Submitted on 26 Jun 2023

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Epigenetics for crop adaptation to climate change

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DOI: 10.1111/ppl.13835

The environment provides all the resources that plants need (water, air, nutrients, substrates, etc.) but, as sessile organisms, they are exposed to environmental stresses that they must face to survive. Moreover, climate changes are exacerbating these constraints through increases in the intensity, duration, and frequency of abiotic stressing events (e.g., drought and heat waves), with associated effects on the biological cycles of pathogens and their recurrence throughout plants' lives. Thus, the resilience (ability to adapt to climatic and other environmental changes they will encounter) of crops and other plants is a crucial determinant of their future productivity and sustainability. Further, elucidation of the mechanisms involved in plant adaptations to environmental changes has become a major objective for various research communities. These include epigenetic mechanisms, which are receiving increasing attention since they mediate environmental effects on hereditary material without affecting DNA sequences. Hence, epigeneticists' general aim is to understand how endogenous, biotic, and abiotic factors regulate plant development and growth through transcriptional changes that occur independently of changes in genomic sequences. A recent and important research effort is the European Cost Action EpiCATCH "EPIgenetic mechanisms of Crop Adaptation To Climate cHange" (CA19125), a network that includes scientific researchers and stakeholders from more than 28 countries. Epi CATCH supports the efforts to build epigenetic-related resources. Those resources can help a broad community of plant scientists and agroforestry-industrial developers to acquire and share cutting-edge knowledge and techniques that can be applied in diverse plant adaptation contexts. Among other initiatives, EpiCATCH organized a conference in July 2021 with two major aims. One was to update knowledge on the epigenetic mechanisms (including chromatin modifications, DNA methylation, and RNA-directed mechanisms) involved in crops' adaptations to environmental stresses. The other was to promote scientific discussion on key epigenetic topics, such as standardization of methodology in studies on plant epigenetics (e.g., priming, somatic memory, inter/transgenerational memory, and epi-molecular markers). Recent advances indicate that epigenetic approaches can play key roles in improving the climatic resilience of both crop and forest species (Kakoulidou et al., 2021; Mladenov et al., 2021). Furthermore, epigenetic modulators with small molecular sizes have been successfully used to decipher epigenetic molecular pathways and enhance in vitro plant regeneration for improving and accelerating crop breeding (Berenguer et al., 2017; Ghosh et al., 2021; Testillano, 2019). Clearly, epigenetic research has a crucial impact on present and future investigations in agriculture and environment. Thus, this special issue gathers research articles and reviews that address key aspects of plant epigenetic adaptation. Epigenetic patterns are key determinants of whether specific sets of genes are switched on or off by various environmental triggers. They offer sources of phenotypic variation, in addition to classical genetic variations, that

breeders and (epi-)geneticists must exploit to enable cultivated plants to withstand environmental fluctuations, especially as previous intense breeding programs have largely contributed to the erosion of genetic diversity. The articles in this special issue address plants' acclimation to environmental stresses, biotic or abiotic, through mechanisms that improve their stress tolerance or induce stress priming (which enhances plants' adaptive responses to subsequent stress exposures). The contributions of three epigenetic mechanisms (DNA methylation, histone post-translational modifications, and enzymatic regulation) are also described and discussed. The reported studies aimed to describe how plants acclimate to abiotic environmental constraints (Alves et al., 2022), including low temperature and drought in early stages of winter wheat seedling establishment (Hidvégi et al., 2022), frost risks in budbreak and flowering stages of apple crops (Lempe et al., 2022), chronic heavy metal contamination in hyperaccumulating plants (Karalija et al., 2022) or flax (Jopčič et al., 2022) in the radioactive Chernobyl area, and biotic stresses such as powdery mildew caused by *Plasmopara viticola* in grapevine (Azevedo et al., 2022). Most also discussed the contributions of epigenetic regulations in acclimation processes or their evolution under continuous climate change generally, and/or in specific taxa, such as members of the Fagaceae family (Alves et al., 2022). Azevedo et al. (2022) investigated epigenetic features that promote tolerance of, or susceptibility to, powdery mildew in grapevine. They found that tolerance of infection by *Plasmopara viticola* was negatively associated with 5-mC DNA methylation levels, suggesting that this epigenetic form of methylation plays a key role in plant immune defense systems. Moreover, they detected differential regulation of genes involved in chromatin and histone modification, small RNA biogenesis, and DNA damage and repair processes, suggesting that these processes are also involved in defensive responses to the pathogen. Deciphering the epigenetic regulation of the infection responses is important as it offers new approaches for improving tolerance to powdery mildew in grapevine and reducing the massive current and recurring use of chemicals. Abiotic constraints, at any time from early stages of crop establishment to late stages of fruit or grain development, also greatly reduce crop yields. To counter such losses, Hidvégi et al. (2022) explored the effects of ultrasonication on wheat seeds to assess its potential value as a priming technique promoting seedling growth and development under frequently encountered stresses, for example, low temperature and soil drought. They found that ultrasonication of seeds prior to sowing induced hypomethylation, thereby modifying DNA methylation levels and transcriptomic patterns in young seedlings. They also found that the treatment increased both the length and weight of roots and shoots, as well as clear indications of the mechanisms involved. These included shifts in expression patterns of genes involved in starch biosynthesis, auxin synthesis, and the TCA cycle, including upregulation of differentially expressed genes (DEGs) associated with higher DNA hypomethylation in CHG and CHH sequence contexts. This study provides the first whole genome-level insights into the epigenetic and transcriptomic landscape of young wheat seedlings after ultrasonic treatment. It also indicates that ultrasonication has promising potential to improve early seedling growth as a substitute for chemicals or bioagents. However, before applying this treatment, the potential effects of the treatment on other epigenetic marks (e.g., histone post-translational modifications, small RNAs, and long noncoding RNAs), which also influence gene expression patterns, should be investigated. Lempe et al. (2022) explored the potential of epigenetic variation as a novel approach for breeding climate-resilient apple varieties. This is important because increases in winter and spring temperatures may impair developmental controls of phenological cycles involving dormancy in winter, followed by budbreak and flowering in spring (among other processes). Such impairments could include flowering when temperatures are still unpredictably fluctuating and there are substantial risks of frost damage. As noted by Lempe et al. (2022), epigenetic variations have high potential utility in breeding strategies because they are inducible by environmental cues, they can have strong phenotypic effects, and (in the absence of further environmental triggers) they can be stably inherited across generations. To illustrate the first of these advantages, they provide evidence of

candidate genes involved in winter dormancy and flowering phenology modifications (such as Dormancy-associated MADS-box, DAM, genes), whose expression is likely regulated by environmentally induced epigenetic changes. To illustrate the second advantage, they note the phenotypic variation associated with epigenetic variation of developmental traits linked to the FLC (Flowering Locus C) gene, which controls flowering time. Regarding the third advantage, they note that the inheritance and stability of epigenetic variations can be particularly strong in clonally derived specimens, as clonal propagation is more likely to prevent the erasure of epigenetic marks than sexual propagation. They conclude that epigenetic variations have very high potential utility in breeding-adapted apple cultivars, highlight their advantages, and discuss scientific and technological challenges that must be addressed to exploit them fully in practice. Two articles in the special issue address the chronic contamination of soil by cadmium (Cd), one focused on flax growing in the Chernobyl area (Jopćik et al., 2022) and the other on “phytomining” approaches to extract Cd from contaminated soils (Karalija et al., 2022). Jopćik et al. (2022) analyzed the genomes and epigenomes of sixth consecutive generations of flax plants growing in the radioactive Chernobyl area to measure the extent of their changes and whether they have led to plant adaptation nearly three decades after the Chernobyl nuclear power plant accident. Through proteomic analysis, they detected very limited effects of ionizing radiation on the seed proteome but modification of several enzymes involved in antioxidant defenses. They also conducted amplified fragment length polymorphism (AFLP) and methylation-sensitive amplification polymorphism (MSAP) analyses to catch genetic variability and changes in DNA methylation. These analyses detected a correlation between mutation processes in the flax genome and ongoing adaptation, as well as differences in methylation variants recognized by the MspI restriction enzyme. However, genomes of flax plants in the radioactive part of the study area were neither hypo- nor hyper methylated relative to those of plants grown in a remediated area. Collectively, these results suggest that the flax population has not strongly adapted to chronic radiation stress, as only minor genomic adjustments (mutations and changes in epigenetic patterns) were detected. Karalija et al. (2022) focused on mechanisms that enhance Cd stress tolerance in hyperaccumulating plants to enhance the utility of phytoextraction for cleaning up soil and/or obtaining metal. The described processes rely on plants' ability to be primed, that is, to develop more rapid, more sensitive, stronger, or modified responses to stress after exposure to a priming agent. The priming agent may be similar or different from the following stress (Lämke & Bäurle, 2017). Some remediation strategies discussed involve priming with external agents that promote Cd solubilization (e.g., EDTA and other organic acids), thus enhancing Cd absorption. Others involve the addition of substances, such as micronutrients and phytohormones, that enhance plant growth with consequent increases in sink size (biomass) and accumulation. A third type involves bacterial strains (e.g., plant growth-promoting rhizobacteria, PGPR) to solubilize insoluble forms of Cd, enhance plant growth, or improve Cd uptake. Karalija et al. (2022) emphasize the importance of priming, as epigenetic contributions have been firmly established and plants' stress tolerance is a major constraint of efficient phytoextraction. Alves et al. (2022) performed an *in silico* study to identify gene sequences of epigenetic regulators in several tree species of the Fagaceae family with high economic and environmental interest. This involved searches for orthologs of DNA methyltransferases (DNMTs), demethylases (DDMEs), and histone modifiers involved in acetylation (HATs), deacetylation (HDACs), methylation (HMTs), and demethylation (HDMTs) in *Fagus*, *Quercus*, and *Castanea* genera (for which relevant information is still sparse). Protein analysis showed that most of them have the putative characteristic domains of these protein families, suggesting that they have highly evolutionary conserved functions. The characterization of protein sequences and domain predictions presented in this study provide new tools for studying the evolution of the focal epigenetic regulators that have enabled them to meet the needs of each species and cope with the environmental conditions in their respective ecosystems. Overall, future directions have been proposed and discussed that indicate

groundbreaking approaches that could promote the following: tolerance of powdery mildew caused by the biotrophic oomycete *Plasmopara viticola* in grapevine (Azevedo et al., 2022); acclimation to stressful conditions during sowing and seedling establishment in wheat (Hidvégi et al., 2022); phenological adjustment of budbreak and flowering in apple (Lempe et al., 2022); and adaptation to both chronic heavy metal contaminations (Jopčík et al., 2022; Karalija et al., 2022) and continuous climate change (Alves et al., 2022).

In conclusion, there is increasing evidence that epigenetic mechanisms have strong effects on diverse phenotypic traits. Thus, they have substantial potential for applications in plant breeding, forestry, and agriculture. However, despite the enormous growth of epigenetic findings in recent years, many plant epigenetic mechanisms remain unexplained, which massively limits biotechnological applications of epigenetic research in agriculture and forestry sectors. Future research efforts should address knowledge gaps in this field, particularly epigenetic regulation in non-model species, to establish a productive and efficient knowledge-driven bio-economy that enables new applications of epigenetics in crop improvement and adaptation to climate change.

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