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THE PLANT CELL

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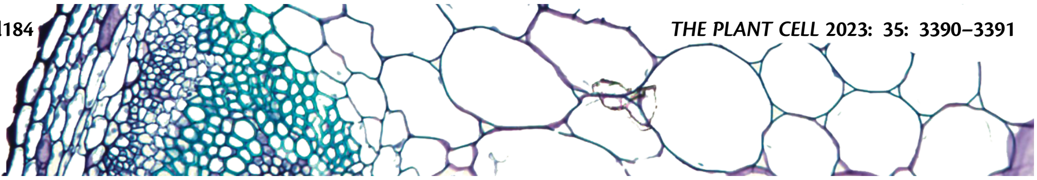

A domestication journey told by DNA methylation

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Rice (*Oryza sativa*) was first domesticated about 9,000 years ago in Asia and since then has become a staple food for more than one-third of the human population (Fornasiero et al. 2022). There are several genetically distinct subspecies of rice, including broadly cultivated groups such as Japonica or "sticky rice," found in high-latitude northeast Asia and upland areas of South Asia; and Indica or "non-sticky rice," found in lowlands of tropical Asia (Molina et al. 2011). Natural selection can return cultivated crops to a "wild-like" state in a process called de-domestication. This is the case for weedy rice, considered a weed in rice fields because it resembles cultivated rice but lacks its agronomically interesting traits. But what are the changes that rice undergoes during domestication and de-domestication? DNA methylation (the presence of a methyl group on cytosine) appears as a contributor to this process. DNA methylation is an epigenetic mark in most eukaryotes, essential for the maintenance of genome stability and regulation of gene expression (Zhang et al. 2018), and can often be linked to desired traits in domesticated crops.

In new work, **Shuai Cao, Kai Chen, and colleagues (Cao et al. 2023)** dissect the genetic and epigenetic changes associated with rice domestication and de-domestication. They focus on DNA methylation in the CG context (mCG). High levels of mCG are associated with transcriptional silencing in transposable elements and transcriptionally active states in genic regions (Zhang et al. 2018). The authors generated DNA methylation profiles for 95 rice accessions to discover that domestication and de-domestication are associated with decreased and increased mCG, respectively. However, most changes in mCG do not occur in the same regions, suggesting that de-domestication is not just a reversion to the original wild state.

mCG outside genic regions is often associated with heterochromatin, which is poorly accessible to transcriptional factors and consequently transcriptionally inactive. Focusing on cultivated rice, the authors combined their methylome and chromatin accessibility (ATAC-seq) data with previously published rice data on histone modification (ChIP-seq) and chromosomal conformation (Hi-C) (Liu et al. 2017). They found that a decrease in mCG in specific regions is associated with transcriptional changes of nearby and distant genes. This work shows how adding information about long-range interactions may aid the challenging task of connecting mCG changes to gene expression.

The authors discovered epigenetic differences among the cultivated genotypes, supporting the hypothesis that they evolved independently after the common domestication event (Molina et al. 2011). These epigenetic differences may be behind the phenotypic diversity among the cultivated rice subgroups. For example, cultivated genotypes Japonica and Aro have shorter grain, whereas Indica and Aus subgroups have longer grain. Short grain can be produced by high levels of *SHORT GRAIN 1* (SG1) (Nakagawa et al. 2012). A hypomethylated region 1.4 Kb upstream SG1 correlates with high expression in Japonica and Aro, whereas the heavily methylated region is associated with transcriptional silencing of SG1 and longer grains in Indica and Aus (see Fig.).

During de-domestication, there is a global increase in methylation that does not resemble the original wild rice epigenome. The regions affected are related to photosynthesis and defense responses that could be the consequence of weedy rice adapting to harsh natural environmental conditions. This suggests that de-domestication is a linear progression rather than a circular process back to the original wild rice.

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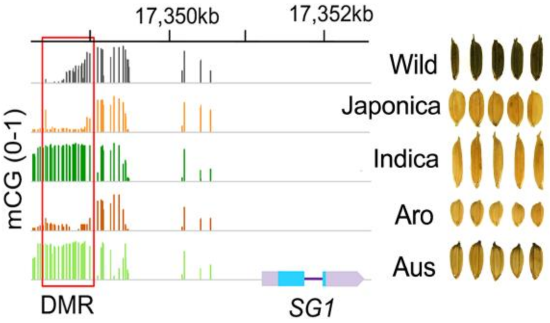

Figure. Epigenetic regulation of SHORT GRAIN 1 (SG1) varies among cultivated rice genotypes. Hypomethylation in CG context (scale 0 to 1) in a differentially methylated region (DMR) upstream of SG1 (left) is correlated with round rice grain in genotypes Japonica and Aro compared to long grains for Indica and Aus (right). Wild rice grains for comparison. Adapted from Cao et al (2023), Figures 1 and 3.

The impressive collection of DNA methylomes presented by Cao, Chen, and colleagues illustrates the role of DNA methylation during rice domestication and de-domestication. The authors also provide examples of epigenetic variations associated with valuable agronomical traits such as grain length. Future work could include the analysis of DNA methylation in non-CG contexts and the integration of long-read sequencing to study epigenetic variation in highly repetitive genomic regions. Besides expanding our evolutionary understanding of de-domestication, the insight gained on epigenetic variation during de-domestication could be used in crop breeding programs.

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