

## Adaptation of Maize to Various Climatic Conditions: Genetic Underpinnings

Xian Zhang, Minli Xu ✉

Hainan Provincial Key Laboratory of Crop Molecular Breeding, Sanya, 572025, Hainan, China

✉ Corresponding author email: [minli.xu@hitar.org](mailto:minli.xu@hitar.org)

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**Abstract** Maize (*Zea mays* L.) exhibits remarkable adaptability to diverse climatic conditions, a trait that has been extensively studied to understand its genetic underpinnings. This study synthesizes current research on the genetic basis of maize adaptation to various climates, focusing on key genomic regions and alleles associated with traits such as flowering time, drought tolerance, and cold resistance. Studies have highlighted the role of specific genes, such as *Dwarf8* and *Vgt2*, in facilitating adaptation through diversifying selection and polygenic selection mechanisms. The evolutionary dynamics of maize adaptation involve both short-term and long-term processes, with significant contributions from admixture and independent introductions. Additionally, landraces play a crucial role in climate change adaptation, offering a reservoir of genetic diversity that can be harnessed for breeding stress-tolerant cultivars. This study underscores the importance of integrating genomic insights with traditional breeding practices to develop maize varieties capable of thriving under future climate scenarios.

**Keywords** Maize (*Zea mays* L.); Climatic adaptation; Genetic underpinnings; *Dwarf8*; *Vgt2*

## 1 Introduction

Maize (*Zea mays* L.), commonly known as corn, is one of the most significant cereal crops globally, serving as a staple food for humans and a primary feed for livestock. It is also a crucial raw material for various industrial products, including starch, oil, protein, alcoholic beverages, food sweeteners, pharmaceuticals, cosmetics, and bio-energy production (Jodage et al., 2018; Kumar et al., 2018; Zafar et al., 2019). Maize's versatility and high genetic yield potential have earned it the title "queen of cereals" (Kumar et al., 2018). Its cultivation spans a wide range of altitudes and climatic conditions, from sea level to highland regions up to 4 000 meters above sea level (Kumar et al., 2018; Hu et al., 2022).

Climate change poses a significant threat to global agriculture, affecting crop yields and food security. Increased temperatures, altered precipitation patterns, and the frequency of extreme weather events such as droughts and floods are some of the challenges that crops, including maize, must adapt to (Moradi et al., 2014; Jodage et al., 2018; Zafar et al., 2019). These changes can lead to reduced growing seasons, increased heat stress, and water scarcity, all of which can negatively impact maize production (Moradi et al., 2014; Jodage et al., 2018).

Understanding how maize adapts to various climatic conditions is essential for developing strategies to mitigate the adverse effects of climate change on crop production. By studying the genetic mechanisms underlying maize adaptation, researchers can identify key genes and traits that enable maize to thrive in different environments. This knowledge can inform breeding programs aimed at developing climate-resilient maize varieties (Moradi et al., 2014; Brandenburg et al., 2017; Lóránt et al., 2018).

Maize's ability to adapt to diverse climatic conditions is a result of both natural selection and human-guided breeding. Genetic studies have revealed that maize has undergone significant adaptation since its domestication in Mexico, allowing it to be cultivated in a wide range of environments worldwide (Brandenburg et al., 2017; Swarts et al., 2017; Lóránt et al., 2018). For instance, ancient DNA analysis has shown that maize adapted to temperate regions through selection on standing genetic variation, enabling it to grow in shorter growing seasons (Swarts et al., 2017; Zahn, 2017). Additionally, research on highland maize has identified genes with divergent expression

patterns between highland and lowland populations, highlighting the complex genetic architecture underlying maize adaptation (Hu et al., 2022).

Research has identified several key genes and gene networks involved in maize adaptation to various climatic conditions. These include genes related to flowering time, drought and cold tolerance, plant defense, and starch properties (Brandenburg et al., 2017; Hu et al., 2022). For example, studies have shown that maize's adaptation to highland regions involves multiple genetic mechanisms, including convergent evolution at the gene expression and regulation levels (Hu et al., 2022). Similarly, the adaptation of maize to temperate climates has been linked to early flowering and other traits that enhance its performance in shorter growing seasons (Swarts et al., 2017; Zahn, 2017). Understanding these genetic underpinnings is crucial for developing maize varieties that can withstand the challenges posed by climate change, ensuring food security and agricultural sustainability (Moradi et al., 2014; Lóránt et al., 2018; Zafar et al., 2019).

In conclusion, the adaptation of maize to various climatic conditions is a complex process driven by both natural and human-guided selection. By exploring the genetic mechanisms underlying this adaptation, researchers can develop strategies to enhance maize's resilience to climate change, ultimately contributing to global food security.

## **2 Literature Review**

### **2.1 The origin and evolution of corn**

Maize, originated in a restricted area of Mexico and has since become one of the most widely cultivated crops globally. The domestication of maize from its wild ancestor, teosinte, involved significant genetic changes that allowed it to adapt to a variety of climatic conditions (Corral et al., 2008; Brandenburg et al., 2017). The genetic basis of maize's adaptation has been extensively studied, revealing that both natural and human-driven selection have played crucial roles in its evolution (Lóránt et al., 2018).

The evolutionary history of maize is marked by its spread from its center of origin in Mexico to diverse environments across the globe. This spread was facilitated by both natural selection and human intervention, which guided the adaptation of maize to various climatic and ecological conditions (Corral et al., 2008; Brandenburg et al., 2017). For instance, maize was introduced to temperate North America around 4 000 years ago, where it underwent significant genetic changes to adapt to shorter growing seasons and cooler climates (Swarts et al., 2017). The adaptation process involved both short-term and long-term evolutionary changes, with significant contributions from its wild relatives, the teosintes (Lóránt et al., 2018).

### **2.2 The impact of climate conditions on maize growth**

Maize growth is highly influenced by various climatic factors, including temperature, precipitation, sunshine duration, and soil conditions. These factors can significantly affect the phenology, yield, and overall health of maize plants.

Temperature plays a critical role in maize development, particularly in flowering time. Studies have shown that maize can adapt to different temperature regimes through genetic changes. For example, the *Dwarf8* gene has been associated with flowering time variation under different temperature conditions (Camus-Kulandaivelu et al., 2006). Additionally, experimental evolution studies have demonstrated that selection for flowering time can lead to rapid adaptation to new temperature conditions (Figure 1) (Choquette et al., 2023).

Water availability is another crucial factor for maize growth. Maize landraces in Mexico, for instance, have been shown to exhibit a wide range of adaptation to different precipitation levels, indicating their potential for use in breeding programs aimed at improving drought tolerance (Corral et al., 2008; Hellin et al., 2014).

The amount of sunlight received by maize plants can also influence their growth and development. Studies have shown that maize can adapt to varying photoperiods, which is essential for its cultivation in different latitudes (Choquette et al., 2023).

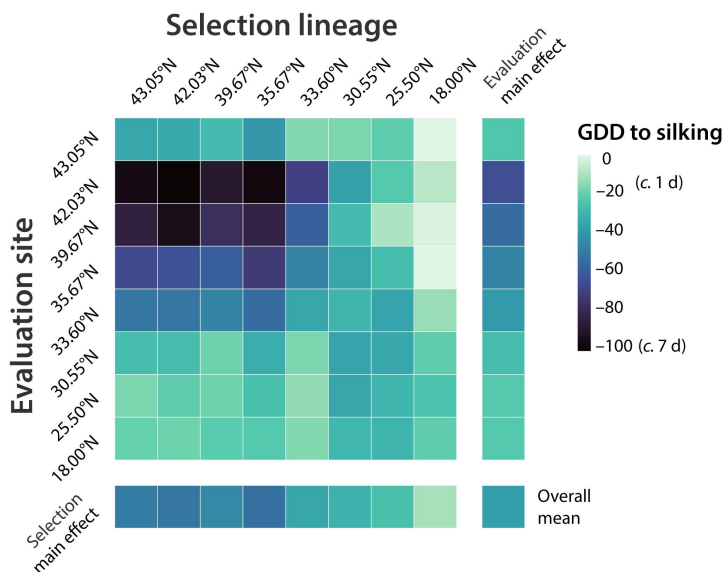


Figure 1 Selection-by-evaluation matrix of phenotypic responses to selection for early flowering time (Adopted from Choquette et al., 2023)

Soil fertility and structure can also impact maize growth. Genetic studies have identified several genes involved in nutrient uptake and stress response, which are crucial for maize adaptation to different soil conditions.

### 2.3 Current research status of corn's adaptability to climate

Recent research has made significant strides in understanding the genetic basis of maize adaptation to various climatic conditions. Studies have identified key genes and genetic networks involved in traits such as flowering time, drought tolerance, and cold tolerance (Camus-Kulandaivelu et al., 2006; Brandenburg et al., 2017; Choquette et al., 2023). Additionally, the role of admixture and genetic diversity in enhancing maize's adaptability has been highlighted, with evidence showing that admixture between different maize populations has contributed to its environmental adaptation (Brandenburg et al., 2017).

Advancements in genomic, transcriptomic, and phenomic technologies have greatly enhanced our understanding of maize adaptation. High-throughput sequencing and genotyping have allowed researchers to identify genetic variants associated with adaptive traits (Brandenburg et al., 2017). Experimental evolution and association mapping studies have provided insights into the evolutionary dynamics of maize populations under different environmental conditions (Wisser et al., 2019; Choquette et al., 2023). Furthermore, the use of crop growth models and climate simulations has enabled the prediction of maize performance under future climate scenarios, aiding in the development of climate-resilient maize varieties.

## 3 Research Methods

### 3.1 Sample selection

The selection of corn varieties for this study was based on their genetic diversity and adaptability to different climatic conditions. Various studies have highlighted the importance of using a wide range of germplasm to understand the genetic underpinnings of maize adaptation. For instance, a study by Choquette et al. (2023) utilized a common population of tropical origin and performed artificial selection on flowering time across multiple geographical zones. Similarly, Brandenburg et al. (2017) sequenced 67 genomes from European and American maize to document routes of introduction and selective history, targeting germplasm directly derived from landraces to avoid confounding effects of recent breeding. Additionally, Camus-Kulandaivelu et al. (2006) evaluated collections of inbred lines and landraces representative of American and European diversity to investigate the genetic basis of maize adaptation to temperate climates.

The experimental areas were chosen to represent a wide range of climatic conditions, ensuring a comprehensive understanding of maize adaptation. For example, Lafitte et al. (1997) conducted experiments in seven tropical

environments with mean temperatures ranging from 13 °C to 28 °C. Another study by Wisser et al. (2019) focused on the adaptation of a tropical landrace of maize to a temperate environment, highlighting the importance of selecting diverse climatic conditions for experimental trials. Furthermore, Moradi et al. (2014) simulated climate change effects on maize growth and yield in Khorasan Razavi province of Iran, employing various General Circulation Models (GCMs) and scenarios to predict future climatic conditions.

### 3.2 Experimental design

Field and greenhouse trials were arranged to evaluate the performance of selected maize varieties under different environmental conditions. For instance, Hallauer and Carena (2013) utilized stratified mass selection methodology for the adaptation of tropical and temperate populations to Iowa and North Dakota environments, screening up to 25 000 genotypes per population cycle. Similarly, Teixeira et al. (2014) conducted trials across a geographical range from Wisconsin to Puerto Rico to study the adaptation process of a tropical maize population subjected to recurrent selection for early flowering.

Data collection focused on key traits such as flowering time, yield, and developmental patterns. For example, Choquette et al. (2023) jointly tested all selection lineages for the target trait (flowering time) and 23 other traits, modeling intergenerational shifts in a physiological reaction norm. Another study by Lafitte et al. (1997) measured rates of emergence, leaf appearance, anthesis, silking, final leaf number, grain yield, and yield components across different environments. Additionally, Tao and Zhang (2010) applied a super-ensemble-based probabilistic projection system to project maize productivity and evapotranspiration during the growing period, examining the relative contributions of various adaptation options.

### 3.3 Molecular biology methods

DNA extraction and sequencing were performed to identify genetic variations associated with maize adaptation. For instance, Brandenburg et al. (2017) sequenced 67 genomes with an average sequencing depth of 18x, discovering over 22 million SNPs and identifying segments with high rates of heterozygosity (Figure 2). Another study by Camus-Kulandaivelu et al. (2006) genotyped collections of inbred lines and landraces for genome-wide simple sequence repeat (SSR) markers and a specific insertion/deletion in the *Dwarf8* gene, which was associated with flowering time variation.

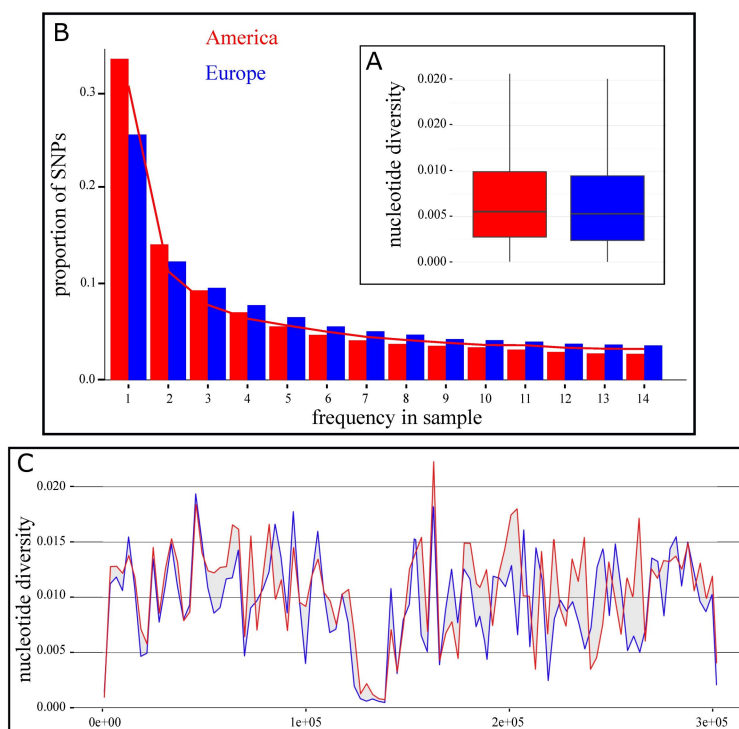


Figure 2 Genome-wide patterns of nucleotide diversity of American and European samples (Adopted from Brandenburg et al., 2017)

Genomic analysis focused on identifying key genes and gene networks involved in maize adaptation to different climatic conditions. For example, Wisser et al. (2019) highlighted several key genes driving the phenotypic response to selection for flowering time in a tropical landrace of maize adapted to a temperate environment. Similarly, Brandenburg et al. (2017) combined differentiation- and diversity-based statistics to identify genes involved in flowering time, drought and cold tolerance, plant defense, and starch properties.

## 4 Results and Analysis

### 4.1 Growth performance of corn under different climatic conditions

The growth performance of maize under various climatic conditions, including growth rate, yield, and resistance to pests and diseases, has been extensively studied. For instance, maize cultivars in Iran showed a significant reduction in days to anthesis (DTA) and anthesis period (AP) under climate change scenarios, with grain yields decreasing by 6.4% to 42.15% over the next 100 years (Moradi et al., 2014). Similarly, maize production in the North China Plain is projected to decrease by 13.2% to 19.1% without adaptation strategies, although the use of high-temperature tolerant varieties could mitigate these losses (Tao and Zhang, 2010). In tropical environments, maize cultivars exhibited varying responses to temperature fluctuations, with some cultivars showing stable yields across a range of temperatures from 13 °C to 28 °C, while others were more specific in their adaptation (Lafitte et al., 1997). These findings highlight the importance of selecting appropriate maize varieties to optimize growth performance under different climatic conditions.

### 4.2 Genetic basis of maize adaptation to climate

The genetic basis of maize adaptation to different climates involves several key genes. The *Dwarf8* (*D8idp*) gene, for example, has been associated with flowering time variation and is subject to diversifying selection, particularly in temperate climates (Camus-Kulandaivelu et al., 2006). Additionally, genomic studies have identified numerous single nucleotide polymorphisms (SNPs) and gene networks involved in traits such as drought and cold tolerance, plant defense, and starch properties (Brandenburg et al., 2017).

Gene expression studies have revealed that maize varieties with enhanced root growth ratios under low temperatures are more tolerant to chilling stress. For instance, the transcriptomic response of maize primary roots to low temperatures identified 64 differentially expressed genes in cold-tolerant varieties, suggesting that these genes play a crucial role in cold adaptation. Moreover, the evolutionary dynamics of polygenic architectures have been shown to condition rapid environmental adaptation, with key genes driving phenotypic responses to selection (Wisser et al., 2019).

The interaction between genes and the environment is critical for maize adaptation. For example, the genetic analysis of highland and lowland tropical maize revealed significant line  $\times$  environment interactions for traits such as biomass, grain yield, and flowering time. These interactions were reflected in systematic changes in trait values and genomic composition across different thermal environments (Jiang et al., 1999). Furthermore, the adaptation of tropical maize germplasm to temperate environments has been achieved through stratified mass selection, indicating that a few major genes are responsible for most of the flowering date expression.

### 4.3 Comparison between different varieties

Genetic diversity among maize varieties is substantial, with studies documenting high levels of variation in climatic adaptation and ecological descriptors among Mexican maize races (Corral et al., 2008). The genetic structuring and historical splits of European and American maize have revealed five genetic groups and two independent European introductions, highlighting the role of admixture in environmental adaptation (Brandenburg et al., 2017).

The differences between maize varieties can be attributed to their genetic backgrounds and the specific selection pressures they have undergone. For instance, tropical maize cultivars selected for broad thermal adaptation exhibited unique developmental responses to temperature, resulting in stable grain yields across a wide range of temperatures (Lafitte et al., 1997). In contrast, highland-derived alleles showed little effect at lowland sites, while lowland-derived alleles exhibited broader adaptation (Jiang et al., 1999). These differences underscore the importance of understanding the genetic basis of adaptation to optimize maize breeding programs for diverse

climatic conditions.

## 5 Discussion

Research has identified several key genes that contribute significantly to maize adaptability under various climatic conditions. For instance, the *Dwarf8* (*D8idp*) gene has been associated with flowering time variation, which is crucial for maize adaptation to temperate climates. The deletion allele of *D8idp* is linked to earlier flowering, which is advantageous in temperate regions with shorter growing seasons (Camus-Kulandaivelu et al., 2006). Additionally, genomic studies have highlighted the role of polygenic architectures in rapid environmental adaptation. Specific alleles have been shown to shift in frequency in response to selection pressures, contributing to phenotypic changes such as reduced flowering time (Wisser et al., 2019). Furthermore, genes involved in drought and cold tolerance, plant defense, and starch properties have been identified as critical for maize adaptation through admixture and selection processes (Brandenburg et al., 2017).

Maize performance under varying climatic conditions is influenced by both genetic and environmental factors. Studies have shown that maize can adapt to a wide range of altitudinal and climatic conditions, surpassing those of its wild ancestor, teosinte (Corral et al., 2008). The adaptation mechanisms include changes in phenology, such as shortened days to anthesis and anthesis period under climate change scenarios, which help mitigate the adverse effects of high temperatures (Moradi et al., 2014). Additionally, transcriptomic responses to low temperatures have revealed differentially expressed genes that contribute to cold tolerance, particularly in the root systems of maize seedlings (Fenza et al., 2017). These genetic adaptations enable maize to maintain productivity and resilience in diverse environmental conditions.

The findings from various studies on maize adaptation show both consistencies and differences. Consistently, research highlights the importance of genetic diversity and selection in enhancing maize adaptability. For example, the role of the *Dwarf8* gene in flowering time adaptation is supported by multiple studies (Camus-Kulandaivelu et al., 2006; Brandenburg et al., 2017). However, differences arise in the specific genetic mechanisms and environmental factors considered. Some studies focus on the genomic basis of short-term evolution and the role of polygenic architectures (Wisser et al., 2019), while others emphasize the importance of local adaptation and the role of admixture in environmental adaptation (Brandenburg et al., 2017). Additionally, the impact of climate change on maize phenology and yield varies across different regions and scenarios, reflecting the complexity of environmental interactions (Tao and Zhang, 2010; Moradi et al., 2014).

The research methods employed in these studies have their respective advantages and disadvantages. Genomic and transcriptomic analyses provide detailed insights into the genetic basis of adaptation, allowing for the identification of specific genes and alleles involved (Fenza et al., 2017; Wisser et al., 2019). However, these methods can be resource-intensive and may not capture the full complexity of environmental interactions. Simulation models, such as those used to predict climate change impacts on maize growth and yield, offer valuable projections and adaptation strategies (Tao and Zhang, 2010; Moradi et al., 2014). Yet, these models rely on assumptions and may not fully account for local variations and unforeseen climatic events. Field experiments and phenotypic evaluations provide practical insights but can be limited by environmental variability and the scale of study (Camus-Kulandaivelu et al., 2006).

The practical application of these research findings lies in the breeding of maize varieties with enhanced adaptability to diverse climatic conditions. Breeding programs can leverage the identified key genes, such as *Dwarf8* and those involved in drought and cold tolerance, to develop varieties that are better suited to specific environments (Camus-Kulandaivelu et al., 2006; Brandenburg et al., 2017). The use of genomic selection and marker-assisted breeding can accelerate the development of these adaptable varieties, ensuring food security in the face of climate change (Guo, 2024).

To improve maize stress resistance, breeding strategies should focus on both genetic and phenotypic traits. Incorporating genes associated with stress tolerance, such as those identified in transcriptomic studies, can enhance resilience to abiotic stresses like drought and low temperatures (Fenza et al., 2017). Additionally,

selecting for early maturing cultivars can mitigate the adverse effects of high temperature stress, as demonstrated in climate change impact studies (Moradi et al., 2014). Integrating formal and informal seed systems can also enhance adaptive capacity by ensuring the availability and adoption of improved and local varieties that possess desirable traits. These strategies will contribute to the development of maize varieties that can thrive under changing climatic conditions, supporting sustainable agriculture and food security.

## 6 Concluding Remarks

The research on the adaptation of maize to various climatic conditions has yielded significant insights into the genetic underpinnings that enable this adaptability. Key achievements include the identification of specific genetic factors and alleles that contribute to maize's ability to thrive in diverse environments. For instance, studies have highlighted the role of the *Dwarf8* gene in flowering time variation, which is crucial for adaptation to temperate climates. Additionally, the evolutionary dynamics of polygenic architectures have been shown to condition rapid environmental adaptation, as evidenced by the shifts in allele frequencies in response to selection pressures.

Moreover, the adaptation of maize to climate change has been explored through various simulation models, revealing that early maturing cultivars can mitigate adverse effects of high temperature stress. The role of admixture and independent introductions in the adaptation of European and American maize has also been documented, emphasizing the importance of genetic diversity and historical selection processes. Overall, these findings underscore the complex interplay between genetic factors and environmental conditions in shaping maize adaptability.

Despite the significant advancements, several limitations were encountered in the research process. One major issue is the reliance on simulation models and projections, which, while informative, may not fully capture the complexities of real-world conditions. Additionally, the genetic studies often focus on specific genes or alleles, potentially overlooking other important genetic factors that contribute to adaptation. The data used in these studies are sometimes limited by the availability of high-quality genomic sequences and the representativeness of the sampled populations.

Furthermore, the methodologies employed, such as the use of SSR markers and specific gene deletions, may not provide a comprehensive view of the genetic landscape. There is also a need for more extensive field trials and longitudinal studies to validate the findings from controlled experiments and simulations. These limitations highlight the need for more robust and integrative approaches to studying maize adaptation.

Future research should focus on expanding the genetic and environmental datasets to include a wider range of maize varieties and climatic conditions. This can be achieved through large-scale genomic sequencing projects and the development of more sophisticated simulation models that incorporate a broader array of environmental variables. Additionally, there is a need to explore the potential of underutilized genetic resources, such as landraces and wild relatives, which may harbor valuable traits for climate adaptation.

Improving the methodologies for studying genetic adaptation is also crucial. This includes the use of advanced genomic tools and techniques, such as CRISPR-Cas9 for targeted gene editing, to better understand the functional roles of specific genes and alleles. Integrating phenotypic data with genomic information through approaches like genome-wide association studies (GWAS) can provide deeper insights into the genetic basis of adaptation.

Finally, collaborative efforts between researchers, breeders, and farmers are essential to ensure that the findings from scientific studies are translated into practical applications. This includes the development of new maize cultivars that are resilient to climate change and the implementation of effective adaptation strategies in agricultural practices. By addressing these future research directions, we can enhance our understanding of maize adaptation and improve its resilience to changing climatic conditions.

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### Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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