

Phylogenetic Insights into Cassava's Domestication: Unraveling Genetic Origins and Evolutionary Trajectories

Wenzhong Huang ✉

CRO Service Station, Sanya Tihitar SciTech Breeding Service Inc., Sanya, 572025, China

✉ Corresponding email: hitar@hitar.org

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Abstract This systematic review synthesizes current knowledge on the phylogenetic insights into cassava's domestication, tracing its genetic origins, and evolutionary trajectories. Leveraging advanced genetic markers and DNA sequencing technologies, studies have traced cassava's lineage back to its wild ancestor, *M. esculenta ssp. flabellifolia*, in the southern Amazon basin, revealing a history of singular domestication events followed by global dissemination. The review highlights the significant genetic diversity within cassava populations and elucidates how specific traits for drought resistance, yield enhancement, and pest resistance have been selected through domestication and breeding efforts. A special case study focusing on cassava's adaptation to arid climates provides unique insights into the genetic mechanisms conferring drought resistance. Furthermore, the review discusses the complexities and limitations in current phylogenetic research, and proposes future directions for research. This review aims to deepen our understanding of cassava domestication and better apply it to improve and maintain cassava cultivation for future generations.

Keywords (*Manihot esculenta* Crantz); Cassava's domestication; Phylogenetic analysis; Genetic origin; Evolutionary trajectory; Drought resistance; Agricultural sustainability

Cassava (*Manihot esculenta* Crantz), with its capacity to thrive in marginal soils and a variety of climates, stands as a cornerstone of global food security. This robust root crop is not only a primary source of carbohydrates for over half a billion people but also a staple in the diets of many in the tropics (Liu et al., 2011). Originating from the South American wild species, cassava was domesticated in the southwestern Amazon basin (Olsen and Schaal, 2001). It has since traversed continents, becoming a vital crop in Africa, Asia, and beyond, thanks to its adaptability and the ease with which it can be cultivated.

The importance of phylogenetic studies cannot be overstated, as they shed light on the genetic diversity within cassava populations, elucidate evolutionary processes, and reveal patterns of domestication that are essential for the crop's future development and adaptation (Fregene et al., 2003; Burns et al., 2010). Cassava's ability to withstand drought and poor soil conditions makes it a vital crop for food security, especially in the face of climate change.

The journey from a wild shrub to a global agricultural staple is rich with genetic and evolutionary intrigue, the exploration of which is the focal point of this review. The objectives are to delve into cassava's genetic beginnings, understand its phylogenetic relationships, and trace the evolutionary trajectories that have contributed to its current domesticated state. This includes examining the progress made in cassava domestication, molecular breeding, genetic transformation and so on (Liu et al., 2011; Pen, 2014; Ozoegwu et al., 2017). This review intends to compile and synthesize recent genetic studies and phylogenetic insights to shed light on the complexities of cassava's domestication. Through the lens of simple sequence repeat (SSR) markers, we can gain a deeper understanding of the crop's history (Fregene et al., 2003).

1 Cassava's Origin and Domestication

1.1 Geographical origin

Cassava, a staple crop with significant economic importance, is believed to have been domesticated from wild *M. esculenta* populations along the southern border of the Amazon basin. Phylogeographic studies based on the

single-copy nuclear gene glyceraldehyde 3-phosphate dehydrogenase (G3pdh) and microsatellite loci have provided insights into the crop's evolutionary origin, suggesting that the domestication of cassava did not involve multiple progenitor species or hybridization with closely related species such as *Manihot pruinosa* (Olsen and Schaal, 1999). Genetic evidence further supports the southern Amazonian origin of domestication, with phenetic analyses grouping cassava with wild populations from this region (Olsen and Schaal, 2001).

1.2 Domestication timeline

The timeline of cassava's domestication has been a subject of extensive research. Phylogenomic analyses indicate that the genus *Manihot*, to which cassava belongs, diversified around 6 million years ago, with cassava's domestication occurring much later, and found different taxa are morphologically diverse (Figure 1) (Simon et al., 2021). The genetic variation in cassava is a subset of that found in the wild *M. esculenta* subspecies, indicating that the crop was derived solely from its conspecific wild relative (Olsen and Schaal, 2001). The differentiation among wild populations is likely a result of random genetic drift following recent population divergence, which suggests a relatively recent domestication event (Olsen and Schaal, 2001). Comparative genotyping of Brazilian cassava germplasm has also provided insights into the diversification and domestication of cassava, revealing spatial genetic differentiation and gene flow patterns that contribute to the understanding of cassava's domestication history (Ogbonna et al., 2020).

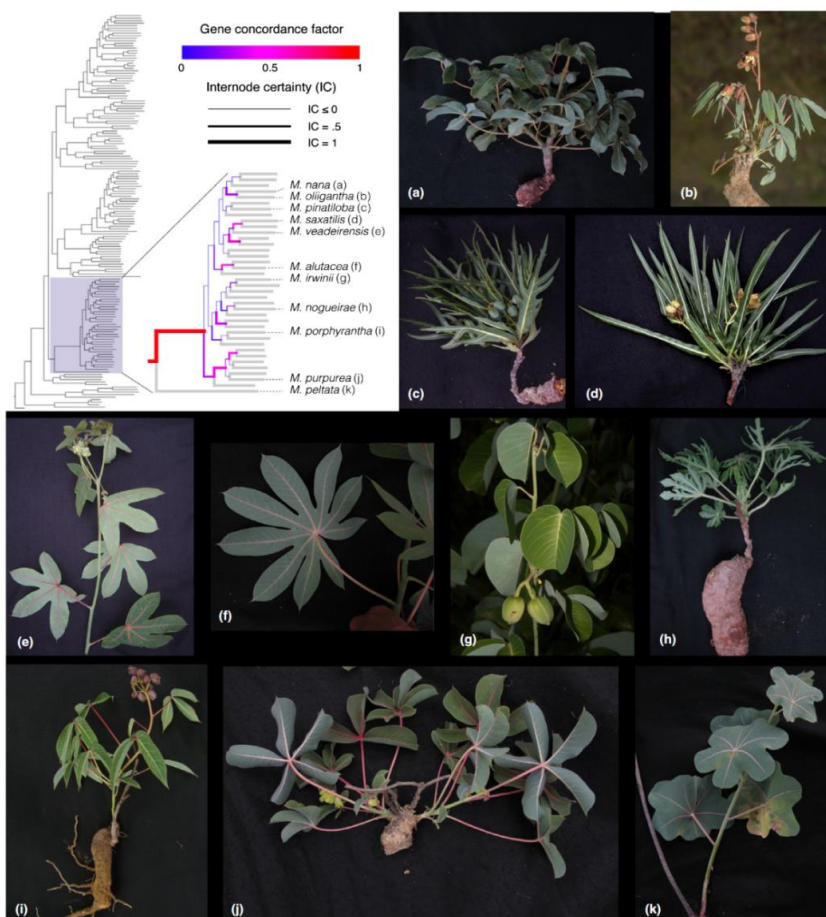


Figure 1 Representative species within the Cerrado radiation clade show high morphological diversity in spite of low phylogenetic differentiation (Photo credit: Simon et al., 2021)

Image caption: Forms include the following: (a–d, h–j) subshrubs <30 cm tall growing annually from thick woody underground structures; (e–g, k) shrubs with slender stems up to 3 m tall; (d) unilobed leaves; (f) multilobed leaves with entire lobes; (c) pinnately lobed leaves; (c, d) short petiolate rosette-like leaves; (c, h) multilobed leaves with dissected lobes; (g) leaves with naviculate lobes; and (a, e, f, j, k) peltate leaves; flowers arranged along an extended axis (b, i) above the foliage or (d, j) immersed within the foliage. Most species within this clade are narrow endemics restricted to one or few localities within the Cerrado (Adopted from Simon et al., 2021)

Simon et al. (2021) highlights the significant morphological diversity present within the Cerrado radiation clade, illustrating various growth forms, leaf structures, and flower arrangements. This diversity is notable given the low phylogenetic differentiation among these species, suggesting that significant phenotypic variation can occur even with limited genetic divergence. This phenomenon is particularly evident in the narrow endemic species restricted to specific localities within the Cerrado, emphasizing the adaptive versatility of these plants in different ecological niches. The detailed morphological descriptions alongside the phylogenetic tree provide valuable insights into the evolutionary processes driving diversification in this clade.

1.3 Early cultivators and cultivation practices

The domestication of cassava was influenced by the cultural and agricultural practices of early cultivators. The transition from wild species to cultivated cassava involved changes in morphological traits and gene expression associated with the domestication syndrome (Carvalho et al., 2018). For instance, seedling morphology has evolved under domestication, with domesticated cassava exhibiting epigeal germination and photosynthetic cotyledons, traits that confer high initial growth rates in agricultural habitats (Pujol et al., 2005). Proteomic analysis between cultivated cassava and its wild relatives has revealed differences in photosynthesis and starch accumulation, which are critical for the selection in domestication syndrome phenomena (An et al., 2016). Additionally, the domestication process has been characterized by selection for traits such as high carbohydrate production, adaptability to diverse environments, and reduced cyanogenic glucoside accumulation.

It can be seen that cassava's domestication is rooted in the southern Amazon basin, with genetic evidence pointing to a single wild ancestor. The domestication process has been shaped by natural selection and human cultivation practices, leading to the crop's adaptation to agricultural environments and its current genetic diversity (Olsen and Schaal, 2001; Pujol et al., 2005; An et al., 2016; Carvalho et al., 2018; Ogbonna et al., 2020).

2 Phylogenetic Analysis Techniques Used in Cassava Research

2.1 Genetic markers and DNA sequencing

In cassava research, genetic markers such as single nucleotide polymorphisms (SNPs) are widely used due to their abundance and high-throughput detection capabilities. Additionally, because of the high heterozygosity of the cassava genome, it serves as an excellent system for studying diallelic differentiation. For instance, Hu et al. (2021) performed whole-genome sequencing on the cassava variety SC205, which is widely used as a breeding parent in China. They estimated the genome size of SC205 to be 770.3 Mb using flow cytometry (Figure 2). The study found that two haplotypes were assembled in the heterozygous regions of the genome and revealed allelic differentiation during the evolutionary process of cassava.

Hu et al., (2021) provided a comprehensive analysis of the cassava SC205 genome, focusing on biallelic differentiation and expression profiles. The comparison with the AM560 genome (Panel A) and Hi-C data (Panel B) ensures the robustness of the assembly. Panels C through F highlight the expression dynamics of bialleles, revealing tissue-specific and developmental stage-specific expression patterns. Panel G's analysis of sequence divergence and Panel H's investigation into the relationship between K_a/K_s ratios and expression divergence offer deeper insights into the evolutionary pressures and functional differentiation of bialleles. This detailed genomic and expression analysis is crucial for understanding the genetic basis of important traits in cassava.

2.2 Phylogenetic tree construction

To infer the evolutionary relationships among different cassava varieties and their wild relatives, researchers commonly use phylogenetic tree construction methods such as Maximum Likelihood (ML) (Simon et al., 2021) and Bayesian Inference (BI) (Yonis et al., 2020). These methods are employed to infer evolutionary relationships among different cassava genotypes by analyzing genetic marker data. ML is a statistical method that estimates the tree topology with the highest likelihood given the observed data, while BI uses probability distributions to estimate the uncertainty of phylogenetic trees.

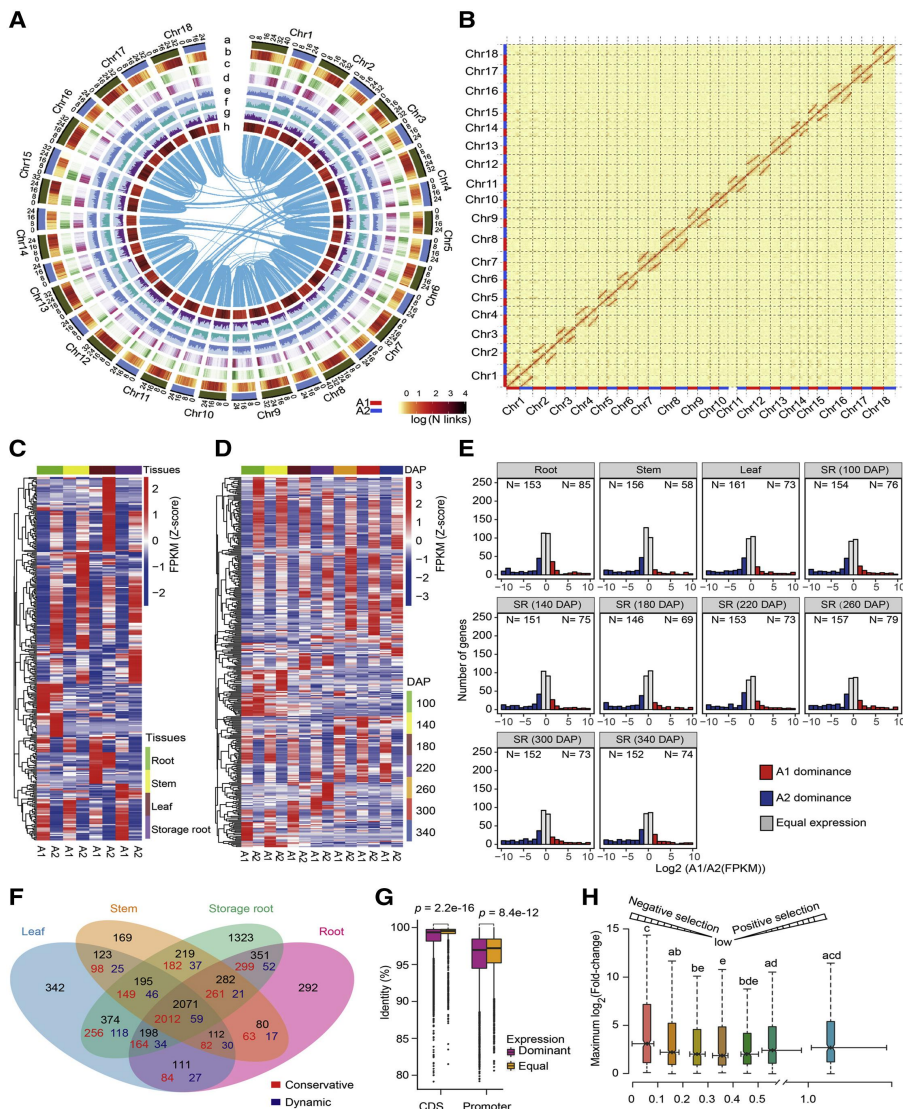


Figure 2 Assembly and biallelic differentiation of the cassava genome SC205 (Photo credit: Hu et al., 2021)

Image caption: (A) Comparison of the cassava SC205 and previously assembled AM560 genomes. (B) Assessment of the homologous chromosomes assembly based on frequencies of intrachromosomal interactions using Hi-C. (C and D) Allelic expression profiles of divergent bialleles on chromosome 3 in various tissues (C) and developmental stages of storage roots (D). (E) Histograms of biallelic expression of divergent alleles on chromosome three among different tissues and developmental stages of storage roots (SR). (F) Comparison of expression dominance of divergent bialleles in different tissues. (G) Sequence divergence between promoter regions and between the coding DNA sequence (CDS) of bialleles (Wilcoxon signed-rank test, $P < 0.01$). (H) Relationship between median values for K_a/K_s subsets and the maximum observed biallelic expression divergence for each divergent biallele pair with 0.95 confidence (Adapted from Hu et al., 2021)

2.3 Role of bioinformatics

Bioinformatics plays a pivotal role in cassava phylogenetic analysis by providing the software and computational tools necessary for handling and analyzing large-scale genetic data. For example, genomic selection models that incorporate spatial kernels, such as Power, Spherical, and Gaussian, are used to account for spatial variation in field experiments, thereby increasing the accuracy of breeding value estimations (Elias et al., 2017). Additionally, genome-wide association analysis (GWAS) is facilitated by bioinformatics tools that can handle the complex data derived from image phenotyping protocols, as demonstrated in the study of root characteristics in cassava (Yonis et al., 2020). These tools are essential for the high-throughput methods applied in cassava research, enabling the identification of significant quantitative trait loci (QTL) and the prediction of genomic selection accuracies.

3 Genetic Insights from Phylogenetic Studies

3.1 Genetic diversity in cassava

Phylogenetic studies have provided significant insights into the genetic diversity present within cassava populations, which is crucial for understanding its history of domestication. Studies have shown that the genetic variation in domesticated cassava (*Manihot esculenta subsp. esculenta*) is a subset of that found in its wild relatives, indicating that the domesticated variety was derived solely from its conspecific wild relative, *M. esculenta subsp. flabellifolia* (Olsen and Schaal, 2001). This is further supported by the presence of shared alleles between domesticated cassava and a specific geographical subset of wild *Manihot* populations, suggesting a single domestication event from *M. esculenta subsp. flabellifolia* in the southern Amazon basin (Olsen, 2004). Simon et al. (2021) estimated ancestral states for habitat type and geographic region throughout our concatenated nuclear genomic tree after pruning tips to remove species replicates (Figure 3). Additionally, traditional farming practices, such as the incorporation of volunteer seedlings from sexual reproduction into the stock of varieties grown, have been shown to maintain a high level of genetic diversity within cassava populations (Elias et al., 2000).

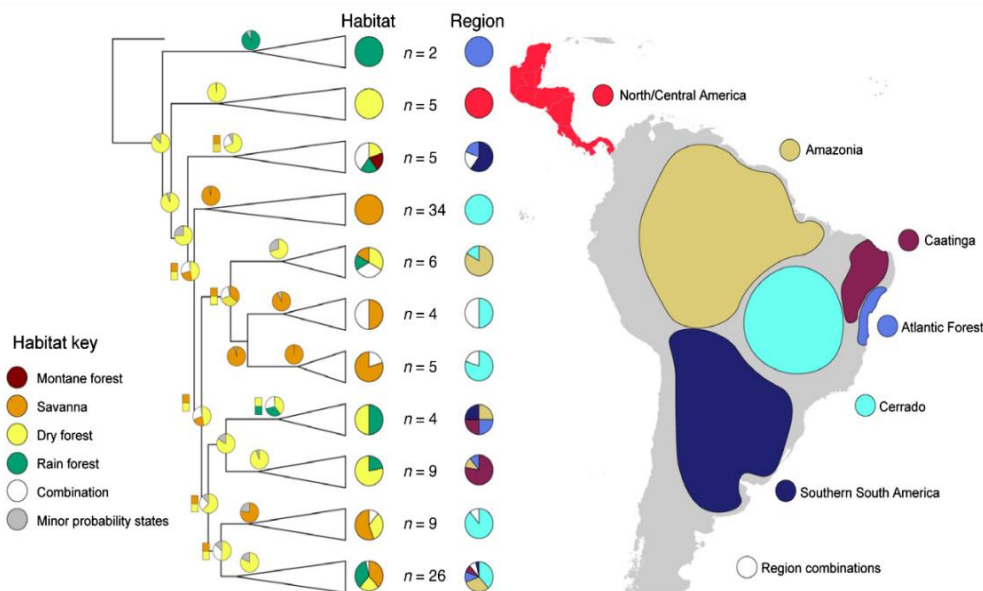


Figure 3 Ancestral state reconstruction (ASR) of habitat during *Manihot* diversification (Photo credit: Simon et al., 2021)

Image caption: ‘Habitat’ pies show the fraction of taxa within each clade corresponding to each habitat type, and ‘Region’ pies show the fraction of taxa corresponding to the geographic zones on the map. ‘Combination’ habitats on internal nodes with $\geq 25\%$ probability have their contributing habitats shown with bars to the left (Adopted from Simon et al., 2021)

This figure drawn by Simon et al. (2021) provides a detailed visual representation of the ancestral habitats and geographic regions associated with *Manihot* diversification. The use of pie charts to represent habitat and region fractions offers a clear and concise way to visualize the ecological and geographical distribution of these taxa. The figure underscores the complexity and diversity of *Manihot* species' habitats, highlighting how different environmental conditions have influenced their evolutionary trajectories. The comprehensive approach to ASR, including the removal of species replicates, ensures accurate and meaningful insights into the evolutionary history of this genus.

3.2 Wild relatives and ancestral species

The wild relatives of cassava, particularly *M. esculenta subsp. flabellifolia*, have been identified as the closest wild relative and likely the progenitor species of domesticated cassava (Olsen and Schaal, 2001). Phylogenetic studies using microsatellite loci and single-copy nuclear genes like G3pdh have provided evidence that cassava was domesticated from wild populations along the southern border of the Amazon basin (Olsen and Schaal, 1999). Contrary to previous beliefs, cassava does not appear to be derived from multiple progenitor species or from hybridization with closely related species such as *M. pruinosa* (Olsen and Schaal, 1999).

3.3 Adaptive traits and selection

The process of domestication has led to the selection of certain adaptive traits in cassava. For instance, domesticated cassava exhibits epigeal germination and photosynthetic cotyledons, which confer high initial growth rates in agricultural habitats, contrasting with the hypogeal germination of its wild relatives that is more suited to their savanna environment (Pujol et al., 2005). These traits are likely the result of selection pressures in agricultural environments favoring rapid growth.

Moreover, throughout its domestication, more specific traits in cassava have been emphasized to meet human needs and environmental challenges. Traits such as increased yield, enhanced drought resistance, and improved pest resistance have been particularly crucial. Phylogenetic and genomic research has identified several adaptive traits that were selected during the domestication process:

- 1) Yield: Selection for higher yield is reflected in the genetic modifications that enhance root bulk, starch content and root-rot resistance. Hohenfeld et al. (2024) analyzed the transcriptome of two contrasting genotypes (BRS Kiriris/resistant and BGM-1345/susceptible) using RNA-Seq to understand the molecular response and identify candidate genes for resistance (Figure 4).

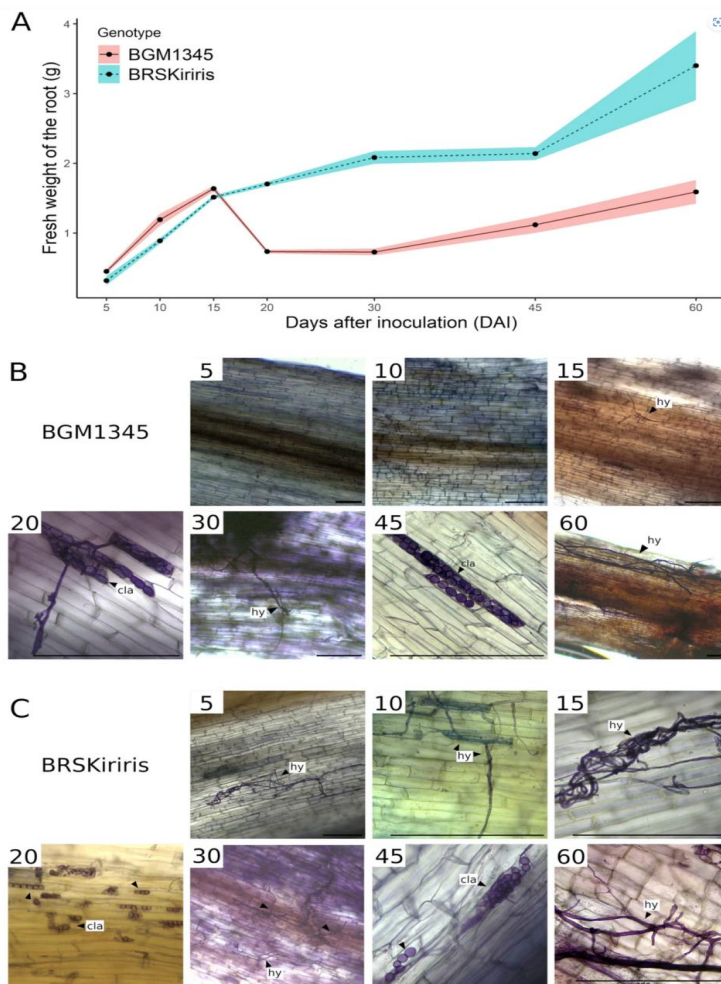


Figure 4 Fresh root weight (g) and staining of fungal structures across collection time-periods (Photo credit: Hohenfeld et al., 2024)
 Image caption: (A) Fresh root weight (g) of resistant (BRS Kiriris) and susceptible (BGM-1345) cassava genotypes grown in soil infested with root rot pathogens between 5 and 60 days after planting. (B) Clarification of root fragments and staining of fungal structures of the cassava genotype BGM-1345 at seven collection time-periods after planting in infested soil (5, 10, 15, 20, 30, 45, 60 days after planting). (C) Clarification of root fragments and staining of fungal structures of cassava genotype BRS Kiriris at seven collection time-periods after planting in infested soil (5, 10, 15, 20, 30, 45, 60 days after planting). hy = hyphae; cla: chlamydo-spore (Adopted from Hohenfeld et al., 2024)

- 2) **Drought Resistance:** Cassava's ability to withstand periods of drought is a critical trait that has been enhanced through selective breeding. Genetic studies have pinpointed alleles involved in water retention and stress response, which are now targets for genetic improvement (Okogbenin et al., 2012; Oliveira et al., 2017).
- 3) **Pest Resistance:** As cassava spread across different continents, it faced diverse pest pressures, leading to the selection of pest-resistant varieties. Genetic markers linked to resistance against common pests like the cassava mosaic virus and cassava green mite are particularly valuable for developing resilient cassava strains (Ntui et al., 2023).

Hohenfeld et al. (2024) effectively illustrates the comparative resistance of two cassava genotypes to root rot pathogens. The growth data (Panel A) clearly indicates that BRS Kiriris maintains better growth in infested soil compared to BGM-1345. The microscopic analysis (Panels B and C) provides a visual confirmation of the resistance and susceptibility observed, showing less fungal colonization in BRS Kiriris roots. This comprehensive approach, combining growth metrics and microscopic examination, offers valuable insights into the mechanisms of disease resistance in cassava. Such findings are crucial for breeding programs aimed at enhancing cassava resilience against root rot pathogens, ensuring better crop yields.

The understanding gained from these phylogenetic studies not only sheds light on the past selection pressures and adaptations but also guides current genetic improvement efforts. By identifying the genetic bases of key adaptive traits, researchers can employ modern biotechnological tools to enhance these characteristics in cassava, ensuring its sustainability and productivity in the face of global change.

4 Case Study: Genetic Adaptation of Cassava to Arid Climates

4.1 Introduction to the specific case study region and its significance

Cassava (*Manihot esculenta*) is a staple crop that plays a crucial role in the food security of millions of people in arid and semi-arid regions. Its ability to produce adequate yields under drought conditions makes it an ideal crop for marginal environments where other crops might fail (Okogbenin et al., 2012). The genetic adaptation of cassava to arid climates is of paramount importance for maximizing productivity potential in these drought-prone areas (Okogbenin et al., 2003). This case study focuses on the genetic traits associated with drought resistance in cassava and the phylogenetic analysis of cassava varieties from arid and non-arid regions, providing insights into the evolutionary trajectories and implications for future breeding programs.

4.2 Genetic traits associated with drought resistance

Drought resistance in cassava is a complex, multigenic trait that poses significant challenges for breeding programs. Studies have identified several mechanisms and traits that contribute to drought tolerance, such as early stomatal closure, reduction in photosynthetic proteins, and changes in root morphology (Figure 5) (Zhao et al., 2015; Orek et al., 2020). Additionally, genotypic variability has been observed in cassava's response to drought stress, with certain varieties demonstrating stronger genetic bases for phenotypic differences in traits like fresh root yield, dry matter content, and harvest index (Okogbenin et al., 2003). A single nucleotide polymorphism in the phytoene synthase gene has been associated with increased provitamin A accumulation in cassava roots, which may also contribute to the crop's adaptability to arid conditions (Kurniawati et al., 2020).

The model drawn by Orek et al. (2020) effectively delineates the complex molecular mechanisms plants use to respond to drought stress. By highlighting the roles of various genes and proteins in both ABA-dependent and ABA-independent pathways, the model provides a comprehensive overview of how plants manage water stress. Understanding these pathways is crucial for genetic and breeding programs aimed at enhancing drought resistance in crops. The clear division between the two pathways and the detailed labeling of involved components make this model a valuable resource for researchers studying plant stress responses.

4.3 The implications of genetic findings for future breeding

The genetic insights gained from studying cassava's adaptation to arid climates have significant implications for breeding programs aimed at improving drought tolerance. The identification of drought-responsive genes and alleles provides targets for both conventional breeding and genetic modification (Lokko et al., 2007; Welsch et al., 2010; Okogbenin et al., 2012). For instance, the discovery of a PSY gene allele that enhances carotenoid production offers a means to improve provitamin A content in cassava roots (Welsch et al., 2010). Additionally, understanding the genetic basis of traits associated with drought tolerance can inform the selection of varieties specifically adapted to drought-prone environments (Okogbenin et al., 2003). The development of molecular markers from EST datasets enriched for drought-responsive genes will further facilitate the dissection of complex traits like drought tolerance and accelerate the breeding of improved varieties (Lokko et al., 2007).

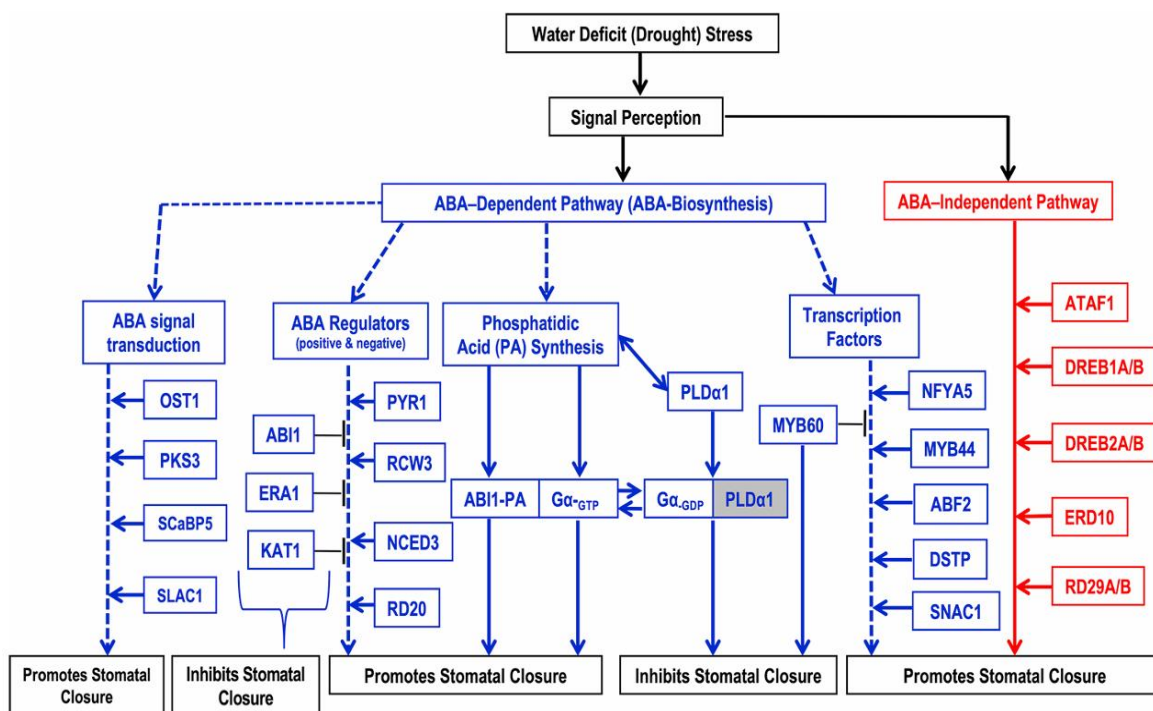


Figure 5 A model adopted and modified from Shinozaki and Yamaguchi-Shinozaki (2007) (Photo credit: Orek et al., 2020)

Image caption: A model represents selected Drought Responsive Genes (DRGs) profiled in cassava and categorized into either ABA-D or ABA-I molecular pathways. ABA-D refers to ABA-Dependent; ABA-I refers to ABA-Independent (Adapted from Orek et al., 2020)

5 Evolutionary Trajectories and Domestication Pathways of Cassava

5.1 Migration and spread

Cassava, a staple food crop with significant economic importance, is believed to have originated in the southern Amazon basin. Genetic analyses using SNPs (single nucleotide polymorphisms) and SSR (simple sequence repeat) variation have traced cassava's evolutionary and geographical origins, suggesting that it was likely domesticated from a single wild species, *M. esculenta ssp. flabellifolia*, rather than from multiple hybridizing species (Olsen, 2004). The crop's spread from its place of origin to other parts of the world involved the migration of people and the exchange of planting materials. As cassava was introduced to new environments, it underwent genetic changes, including adaptations to different climates and agricultural practices. The genetic diversity in cassava is a subset of that found in its wild relatives, indicating that the domesticated varieties were derived from their conspecific wild relatives (Ding et al., 2016).

5.2 Impact of human intervention

Human cultivation practices have had a profound impact on the evolutionary pathways of cassava. The practice of incorporating seedlings from sexual reproduction into planting stocks has exposed cassava to selection pressures favoring rapid growth in agricultural environments (Pujol et al., 2005). This has led to morphological changes, such as the reversion to epigeal germination and the development of photosynthetic cotyledons, which confer high initial growth rates in cultivated habitats (Pujol et al., 2005).

Meanwhile, selecting traits that can improve agricultural productivity and resilience also significantly affects the genetic structure of cassava, which has been shaped to enhance yield, improve drought resistance, and increase pest resistance (Okogbenin et al., 2012; Oliveira et al., 2017; Ntui et al., 2023). For instance, the selection for larger root size and higher starch content has led to varieties that are vastly more productive than their wild counterparts. Similarly, in response to the challenge of variable water availability, especially in regions like Northeast Brazil and sub-Saharan Africa, cultivars with enhanced drought tolerance have been developed. These traits are not only the result of direct selection but also of sophisticated breeding techniques, including hybridization and, more recently, genetic engineering. The modifications in genetic traits have also had ecological impacts, such as changes in plant architecture and root system depth, which in turn affect soil health and agricultural sustainability.

5.3 Comparative analysis

Comparing cassava's domestication trajectory with that of other staple crops reveals both unique and common patterns of domestication. Like many other crops, cassava has undergone selection for traits favored by humans, such as increased palatability and yield, while experiencing a reduction in genetic diversity due to selective sweeps and genetic bottlenecks (Smýkal et al., 2018). Unlike some other crops, cassava's clonal propagation has allowed for the effective exploitation of nonadditive genetic effects, such as dominance and epistasis, particularly for traits like root yield and disease resistance (Elias et al., 2000). This contrasts with crops that are primarily sexually reproduced, where additive genetic effects are more commonly selected.

6 Challenges and Limitations in Current Research

6.1 Gaps in phylogenetic data

Despite advancements in genetic sequencing and phylogenetic analysis, significant gaps remain in the phylogenetic data available for cassava. One major limitation is the incomplete representation of wild and ancestral varieties in genetic studies, which are crucial for understanding the full phylogenetic landscape of cassava. This lack of comprehensive sampling can lead to biased interpretations of cassava's evolutionary history and its domestication process. Additionally, many existing phylogenetic studies rely on limited genetic markers, which may not provide a complete picture of the genetic diversity and evolutionary relationships within the *Manihot* genus (Simon et al., 2021). Expanding the types of genetic markers used, such as incorporating more single nucleotide polymorphisms (SNPs) and whole-genome sequencing data, could greatly enhance the resolution and accuracy of phylogenetic trees.

6.2 Complexities in interpreting data

The interpretation of genetic and phylogenetic data in cassava is compounded by the complexity of its genome. Cassava possesses a highly heterozygous genome, which presents challenges for genetic assembly and accurate variant calling. This heterozygosity can obscure phylogenetic signals and complicate efforts to identify clear genetic relationships among different cassava varieties and their wild counterparts. Furthermore, cassava's genome shows evidence of past polyploidy events, adding another layer of complexity to genetic analyses (Bredeson et al., 2016; Chen et al., 2021). These polyploidy events can result in multiple copies of genes, which may undergo independent evolutionary paths, thus complicating phylogenetic interpretations and functional genomic studies.

Additionally, environmental adaptations and artificial selection pressures have led to convergent evolutionary traits in cassava, which can be mistaken for close genetic relationships in phylogenetic analyses. Distinguishing between convergence due to adaptive traits and genuine phylogenetic closeness requires careful genomic and phenotypic characterization, which is often limited by the current methodologies and data availability.

7 Future Directions in Cassava Phylogenetic Research

7.1 Emerging technologies and techniques

The field of cassava phylogenetics stands on the cusp of transformation, driven by emerging technologies and innovative research techniques. Advances in high-throughput sequencing technologies promise to further reduce costs and increase the accessibility of whole-genome sequencing, enabling more comprehensive genomic studies on a wider range of cassava varieties and its wild relatives (Thomson, 2014). Additionally, CRISPR/Cas genome editing offers exciting possibilities for functional genomics in cassava, allowing researchers to directly test the phenotypic effects of genetic variations identified in phylogenetic studies (Odipio et al., 2017).

Bioinformatics tools and computational models are also evolving rapidly, providing new ways to analyze complex genomic data and construct more accurate phylogenetic trees (Yu and Reva, 2018). Artificial intelligence and machine learning applications are beginning to play a role in predicting evolutionary patterns and identifying genetic markers linked to important traits (Sekaran and Sudha, 2020). These technologies could greatly enhance our understanding of the genetic basis of cassava's adaptability and resilience.

7.2 Conservation and sustainable use

Conservation of genetic resources is a critical component of sustaining the agricultural potential of cassava. Preserving a wide array of cassava genetic diversity, including its wild relatives, is essential for future breeding efforts, particularly in response to climate change and evolving pest and disease pressures. Conservation strategies should focus on both in-situ conservation of cassava in its natural habitats and ex-situ conservation in gene banks, which safeguard genetic material for future use.

Sustainable agricultural practices can be informed and improved by phylogenetic insights, which help identify varieties best suited to particular environments or stressors. These practices not only support the resilience of cassava crops in the face of environmental challenges but also contribute to the overall sustainability of agricultural ecosystems.

7.3 Integration of phylogenetic data with other disciplines

Integrating phylogenetic insights with ecological, archaeological, and anthropological studies can provide a more holistic view of cassava's domestication and its role in human societies over time. For example, Daemo et al. (2023) revealed the interaction between cassava and its environment through ecological research, evaluated cassava genotypes tested in multiple environments, and revealed the significant impact of different growth environments on the performance of cassava genotypes. Archaeological findings can provide historical context that informs phylogenetic analyses, such as the timing and pathways of cassava's spread.

Anthropological research can uncover the cultural practices surrounding cassava cultivation, which may influence the selection pressures and evolutionary trajectories observed genetically. This interdisciplinary approach not only enriches our understanding of cassava's past but also informs its future use and conservation strategies.

8 Concluding Remarks

8.1 Summary of key points

This review has explored the phylogenetic insights into cassava's domestication, detailing the genetic origins, relationships, and evolutionary trajectories that have shaped this vital crop. Key findings highlight cassava's origin in South America and its adaptation through centuries of cultivation, which has led to the vast genetic diversity observed today. The integration of advanced genomic technologies has shed light on the complex genome of cassava, revealing the impacts of selection pressures and environmental adaptations.

We have discussed the significant role of phylogenetic studies in identifying the genetic markers linked to desirable traits such as disease resistance and drought tolerance. These studies are crucial for the ongoing efforts in molecular breeding, aimed at enhancing cassava's yield and resilience.

8.2 Final thoughts

Phylogenetic studies of cassava are not merely academic exercises; they are essential undertakings that preserve

and enhance cassava's utility as a food resource. As climate change poses increasing threats to global food production, understanding the genetic basis of cassava's adaptability becomes ever more critical. These insights empower breeders to develop varieties that can withstand environmental stresses while meeting the needs of diverse cultures and economies.

As this review suggests, the future of cassava research lies in harnessing emerging technologies and fostering interdisciplinary collaborations. Such approaches will enhance our understanding of cassava's past and present, guiding its sustainable use as a crop for the future. In conclusion, the journey of cassava from a wild species to a cornerstone of food security illustrates the power of phylogenetic research in unlocking the genetic potential of crops to address global challenges. This body of work not only contributes to our historical knowledge but also paves the way for innovations that will sustain cassava as an indispensable resource for generations to come.

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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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