



Systematic Review Open Access

# Phylogenetic Patterns and Classification of *Oryza* Species: A Molecular Perspective

Xuanjun Fang 🔀

Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China

Corresponding email: <a href="mailto:xuanjunfang@hitar.org">xuanjunfang@hitar.org</a>

Rice Genomics and Genetics, 2024, Vol.15, No.3 doi: 10.5376/rgg.2024.15.0011

Received: 10 Apr., 2024 Accepted: 11 May, 2024 Published: 22 May, 2024

Copyright © 2024 Fang, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

#### Preferred citation for this article:

Fang X.J., 2024, Phylogenetic patterns and classification of *Oryza* species: a molecular perspective, Rice Genomics and Genetics, 15(3): 94-105 (doi: 10.5376/rgg,2024.15.0011)

**Abstract** This study explores the phylogenetic patterns and classification of *Oryza* species from a molecular perspective, offering key findings and insights. Major studies have found that traditional morphological methods have been enhanced by molecular techniques, such as DNA markers and next-generation sequencing (NGS), refining our understanding of *Oryza* phylogenetics, independent domestication in Asia and Africa has led to distinct genetic differences. Molecular evidence identifies key domestication genes and genomic signatures, shedding light on evolutionary adaptations, and that the distribution and genetic diversity of *Oryza* species have been shaped by natural dispersal and human-mediated migration. This study provides a detailed understanding of the phylogenetic system of the *Oryza* genus, providing profound insights into the evolutionary history and genetic diversity of rice species. Leveraging molecular phylogenetic insights can enhance taxonomy, conservation, and breeding, contributing to sustainable global rice agriculture.

Keywords Oryza genus; Phylogenetics; Molecular classification; Domestication genes; Genetic diversity

# 1 Introduction

The genus *Oryza*, commonly known as rice, is of paramount importance both economically and scientifically. It comprises 23 species, including two domesticated species, *Oryza sativa* and *Oryza glaberrima*, which are staple foods for over half of the world's population (Joshi et al., 2000). The genus is also a model system for studying molecular evolution, given its diverse genome types and the evolutionary history spanning millions of years (Stein et al., 2018). Understanding the phylogenetic relationships within the *Oryza* genus is crucial for crop improvement, conservation of genetic resources, and elucidating the mechanisms of plant evolution (Zhu et al., 2014; Joshi et al., 2000).

Molecular phylogenetics has revolutionized our understanding of evolutionary relationships by utilizing DNA sequences to reconstruct the tree of life. In the context of *Oryza*, various molecular approaches have been employed to resolve phylogenetic relationships. These include the analysis of nuclear genes, mitochondrial and chloroplast DNA sequences, and inter simple sequence repeat (ISSR) polymorphisms (Nishikawa et al., 2005; Zhu et al., 2014; Joshi et al., 2000). Phylogenomic analyses using large datasets, such as 53 nuclear genes and 16 intergenic regions, have provided high-resolution insights into the evolutionary history of *Oryza* species (Zhu et al., 2014). Additionally, the use of simple sequence repeats (SSR) and their flanking regions has offered new perspectives on the genetic diversity and phylogenetic relationships within the genus (Nishikawa et al., 2005).

This study aims to synthesize the current knowledge on the phylogenetic patterns and classification of *Oryza* species from a molecular perspective. The primary objectives are to compile and analyze the various molecular approaches used in phylogenetic studies of the *Oryza* genus, evaluate the effectiveness of these methods in resolving phylogenetic relationships and understanding genome evolution, and identify gaps in the current research and suggest future directions for comprehensive phylogenetic studies. By achieving these objectives, this study expects to provide a cohesive understanding of the molecular phylogenetics of *Oryza*, which will be instrumental for future research and practical applications in rice breeding and conservation.



http://cropscipublisher.com/index.php/rgg

# 2 Historical Overview of Oryza Classification

# 2.1 Traditional morphological classification

The traditional classification of *Oryza* species was primarily based on morphological characteristics such as plant height, leaf shape, and flower structure. This method, while useful, often led to ambiguities due to the phenotypic plasticity of plants and the influence of environmental factors on their morphology. Early taxonomists grouped *Oryza* species into complexes based on these visible traits, which sometimes resulted in misclassification and confusion regarding the evolutionary relationships among species (Wang et al., 1992).

#### 2.2 Transition to molecular classification

The advent of molecular techniques revolutionized the classification of *Oryza* species. Molecular markers such as RFLPs (Restriction Fragment Length Polymorphisms), SSRs (Simple Sequence Repeats), and ISSRs (Inter Simple Sequence Repeats) provided more reliable and precise tools for phylogenetic studies. These methods allowed researchers to analyze genetic diversity and relationships at the DNA level, leading to more accurate classifications. For instance, ISSR polymorphism has been used to determine genetic diversity and phylogenetic relationships, revealing that the genus *Oryza* may have evolved following a polyphyletic pathway (Joshi et al., 2000). Similarly, SSR markers from mitochondrial and chloroplast genomes have provided new insights into the phylogenetic relationships among *Oryza* species (Nishikawa et al., 2005).

# 2.3 Major milestones in Oryza phylogenetic research

Several key studies have marked significant milestones in the phylogenetic research of *Oryza* species. One such study used sequences from nuclear genes and MITE insertions to reconstruct the phylogeny of the A-genome group, providing evidence for the monophyletic origin of most species within this group (Zhu and Ge, 2005). Another important study utilized AFLP markers to fingerprint 23 *Oryza* species, suggesting a common ancestry and polyphyletic evolution within the genus. Additionally, the use of nuclear and mitochondrial DNA sequences has helped resolve the phylogenetic relationships among medaka fishes of the genus Oryzias, indicating the necessity for systematic taxonomic revisions (Takehana et al., 2005).

Recent advancements in phylogenomics have further refined our understanding of *Oryza* evolution. For example, a comprehensive phylogenomic analysis of AA-genome species by Zhu et al. (2014) using over 60 kb of nuclear genes and intergenic regions successfully resolved their phylogenetic relationships and divergence times. Another study highlighted the genetic conservation, turnover, and innovation across the genus *Oryza* by analyzing 13 reference genomes, providing a detailed view of genome evolution and species diversification (Stein et al., 2018).

These molecular approaches have not only clarified the evolutionary history of *Oryza* species but also identified potential genetic resources for crop improvement, such as new haplotypes for disease resistance (Stein et al., 2018). The integration of molecular data with traditional morphological classification continues to enhance our understanding of the complex phylogenetic relationships within the genus *Oryza*.

# 3 Molecular Phylogenetics of Oryza

# 3.1 DNA markers and genomic tools used in phylogenetic studies

Chloroplast DNA (cpDNA) markers have been extensively used in phylogenetic studies of the *Oryza* genus due to their maternal inheritance and relatively conserved nature. Studies have utilized various cpDNA regions to resolve phylogenetic relationships among *Oryza* species. For instance, the trnL-trnF and trnK/matK regions have been commonly employed, although their resolution at lower taxonomic levels can be limited (Bouillé et al., 2011). Additionally, cpDNA restriction patterns have been used to distinguish between different *Oryza* species, revealing significant diversity within species with histories of introgression and allotetraploidization. The use of noncoding cpDNA sequences has also been highlighted for their variability and utility in phylogenetic and phylogeographic studies (Shaw et al., 2014).

Nuclear DNA markers, such as internal transcribed spacer (ITS) sequences of ribosomal DNA, have been used alongside cpDNA markers to provide a more comprehensive understanding of phylogenetic relationships. These

http://cropscipublisher.com/index.php/rgg

markers often exhibit higher sequence divergence compared to cpDNA, making them useful for resolving relationships at both inter- and intraspecific levels. Random amplified polymorphic DNA (RAPD) markers and cleaved amplified polymorphic sequence (CAPS) analysis have also been employed to study nuclear DNA polymorphisms in *Oryza*, aiding in the classification and phylogenetic analysis of different species (Buso et al., 2001).

Next-generation sequencing (NGS) technologies have revolutionized phylogenetic studies by enabling the sequencing of entire genomes or large genomic regions. These technologies facilitate the identification of numerous genetic markers across the genome, providing high-resolution data for phylogenetic analysis. NGS has been particularly useful in identifying variable regions within the chloroplast genome and developing universal cpDNA markers for phylogenetic studies (Yang et al., 2017). The application of NGS has also allowed for the comprehensive analysis of nuclear and organellar genomes, enhancing our understanding of the evolutionary history and relationships among *Oryza* species.

# 3.2 Phylogenetic relationships among Oryza species

The primary gene pool of *Oryza* includes species that are closely related to the cultivated rice, *Oryza sativa*, and can readily interbreed with it. Phylogenetic studies using cpDNA and nuclear DNA markers have shown that species within the primary gene pool, such as *O. rufipogon* and *O. nivara*, share a close evolutionary relationship with *O. sativa* (Buso et al., 2001). These species are often used in breeding programs to introduce desirable traits into cultivated rice.

Secondary and tertiary gene pool species are more distantly related to *O. sativa* and exhibit greater genetic divergence. These species include *O. glumaepatula*, *O. alta*, *O. grandiglumis*, and *O. latifolia*, which belong to the *O. officinalis* complex (Buso et al., 2001). Phylogenetic analyses have indicated that these species diverged from the primary gene pool species approximately 20 million years ago. The secondary and tertiary gene pool species are valuable for studying the broader evolutionary history of the *Oryza* genus and for identifying novel genetic resources for rice improvement.

# 3.3 Evolutionary divergence and speciation

Molecular clock estimates have been used to date the divergence times of various *Oryza* species. These estimates are based on the accumulation of genetic mutations over time and provide insights into the timing of speciation events. For example, the divergence of American diploid and tetraploid species from the primary gene pool species has been estimated to have occurred around 20 million years ago (Buso et al., 2001). Such estimates are crucial for understanding the evolutionary timeline and the factors driving speciation in the *Oryza* genus.

Divergence of *Oryza sativa* and *Oryza glaberrima*: The wild progenitors of *Oryza sativa* and *Oryza glaberrima* diverged from a common ancestor approximately 2~3 million years ago. This divergence occurred due to geographical and ecological isolation, leading to the development of distinct gene pools in Asia and Africa. *Oryza sativa* was domesticated from its wild relatives *Oryza nivara* and *Oryza rufipogon* in the Yangtze River basin of China around 8 000 ~ 9 000 years ago. *Oryza glaberrima* was domesticated from its wild ancestor *Oryza barthii* in the Niger River basin of West Africa around 3 000~3 500 years ago. Adam et al. (2023) found significant differences in genomic structure between Asian rice and African rice, particularly in regions related to panicle structure. The results showed that *Oryza glaberrima* had fewer branches, while *Oryza sativa* exhibited complex panicle shapes and more branches (Figure 1).

Formation of *Oryza nivara* and *Oryza rufipogon*: The common ancestor of *Oryza nivara* and *Oryza rufipogon* diverged from other *Oryza* species approximately 2~3 million years ago. This divergence was driven by geographical isolation and ecological differentiation, leading to the establishment of distinct genetic lineages. Xu et al. (2020) found the differences in flowering times between *O. rufipogon* and *O. nivara* contribute significantly to reproductive isolation. *O. nivara* flowers much earlier than *O. rufipogon*, maintaining species divergence despite potential hybrid viability.



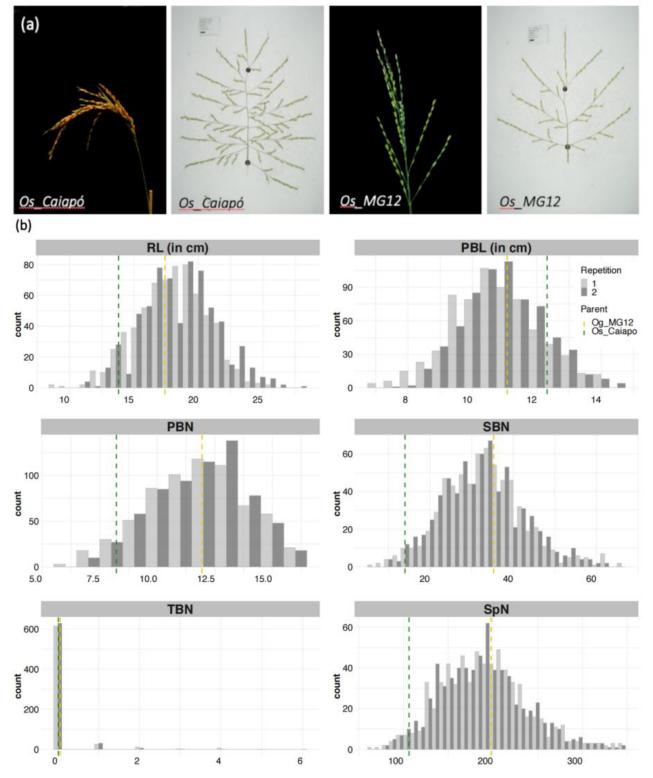


Figure 1 Panicle structure and morphological panicle trait values in *O. sativa cv. Caiapó* (referred to as  $Os\_Caiapó$  hereafter) and *O. glaberrima cv. MG12* (referred to as  $Os\_MG12$  hereafter) and the 60 BC3DH CSSLs (Adopted from Adam et al., 2023)

Image caption: (a) Panicle architecture contrasts between the two parental lines ( $Os\_Caiapó$  and  $Os\_MG12$ ). (b) Distribution of panicle trait values in the 60BC3DH CSSLs. Dashed vertical lines correspond to the mean values of each parent (green for  $Os\_MG12$  and yellow for  $Os\_Caiapó$ ). Values for repetitions 1 and 2 are shown in light gray and dark gray, respectively. Abbreviations: RL, Rachis Length; PBN, Primary Branch Number; PBL, Primary Branch Length; SBN, Secondary Branch Number; TBN, Tertiary Branch Number; SpN, Spikelet Number (Adopted from Adam et al., 2023)

http://cropscipublisher.com/index.php/rgg

Radiation of Australian *Oryza* Species: The formation of *Oryza australiensis* began with the divergence from a common ancestor shared with other *Oryza* species. This divergence likely occurred due to geological events and climatic changes that led to the isolation of populations. Over time, the isolated populations of *Oryza* in Australia adapted to the local environmental conditions, including the arid and semi-arid climates, soil types, and ecological interactions with other native flora and fauna. These adaptations involved changes at the genetic level, which contributed to the development of specific traits that are unique to *Oryza australiensis*. Matthew et al. (2021) found that Oryza australiensis exhibited higher leaf photosynthetic efficiency compared to *Oryza sativa* (Figure 2).

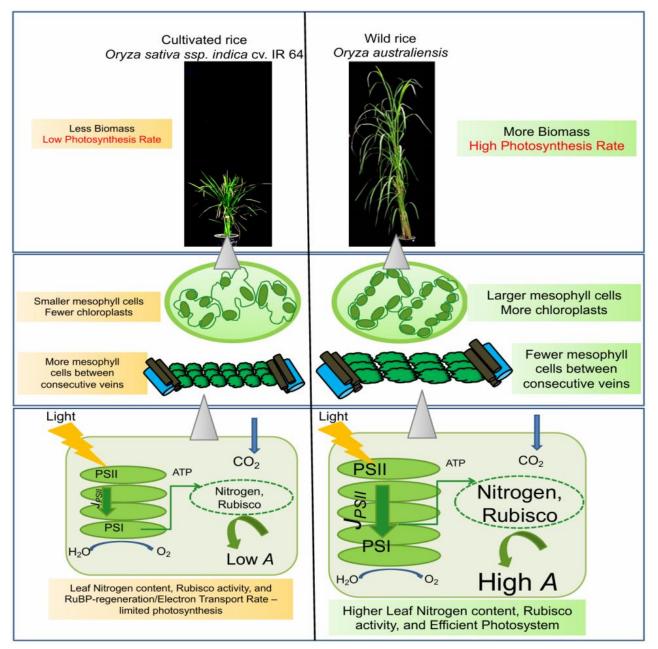


Figure 2 Leaf developmental, photochemical, and biochemical traits contributing towards photosynthetic differences between two extreme genotypes: *Oryza sativa ssp. indica cv.* IR 64 and *Oryza australiensis* (Adopted from Mathan et al., 2021)

Image caption: Wider leaf, larger mesophyll cells, larger veins, fewer number of mesophyll cells between two consecutive veins, more chloroplasts, efficient Electron Transport Rate along with higher leaf nitrogen content and Rubisco activity facilitate higher leaf photosynthesis per unit area in the wild rice species *Oryza australiensis* compared to the cultivated variety *Oryza sativa* ssp. *indica* cv. IR 64 (Adopted from Mathan et al., 2021)



http://cropscipublisher.com/index.php/rgg

# 4 Geographical Distribution and Migration Patterns

# 4.1 Historical biogeography of Oryza

The genus *Oryza*, which includes both wild and cultivated rice species, has a complex evolutionary history marked by significant biogeographical events. The origin of *Oryza* is traced back to approximately 24 million years ago (MYA) during the Miocene epoch, with the deepest split within the genus occurring around 15 MYA (Tang et al., 2010). The early diversification of the AA-genome species, a major group within *Oryza*, is estimated to have occurred around 2.93 MYA (Zhu et al., 2014). This period of diversification was characterized by rapid radiation events, which have posed challenges in resolving the phylogenetic relationships within the genus.

The distribution of *Oryza* species is widespread, encompassing various continents and regions. The AA-genome species, for instance, are distributed worldwide, with significant populations in Asia, Africa, and Australia. The biogeographical history of *Oryza* suggests that long-distance dispersal played a crucial role in the genus's diversification. This is supported by evidence of trans-oceanic dispersal events, which facilitated the spread of *Oryza* species across different continents (Tang et al., 2010). The genus's ability to adapt to diverse ecological niches has further contributed to its extensive geographical distribution.

# 4.2 Contemporary migration and gene flow

Natural dispersal mechanisms have significantly influenced the contemporary migration patterns of *Oryza* species. These mechanisms include water-mediated seed dispersal, which is particularly effective in wetland habitats where many *Oryza* species thrive. Additionally, the presence of specific morphological traits, such as awns and buoyant seeds, enhances the ability of these species to disperse over long distances (Tang et al., 2010). The role of natural dispersal is evident in the genetic diversity observed within and between *Oryza* populations, which reflects historical and ongoing gene flow.

Human activities have also played a pivotal role in the migration and distribution of *Oryza* species. The domestication of rice, particularly *Oryza sativa*, has led to extensive human-mediated migration, resulting in the widespread cultivation of rice across various continents. This process has facilitated gene flow between wild and cultivated rice species, contributing to the genetic diversity observed in contemporary *Oryza* populations (Stein et al., 2018). The introduction of rice to new regions through trade and agricultural practices has further expanded the geographical range of the genus, highlighting the significant impact of human intervention on the distribution patterns of *Oryza* (Spano et al., 2018; Torke et al., 2021). The geographical distribution and migration patterns of *Oryza* species are shaped by a combination of historical biogeographical events, natural dispersal mechanisms, and human-mediated migration. These factors have collectively contributed to the extensive and diverse distribution of *Oryza* species across the globe.

# 5 Domestication and Evolution of Cultivated Rice

# 5.1 Domestication centers and early cultivation

The domestication of rice, one of the most significant agricultural developments in human history, has been a subject of extensive research and debate. The origins of cultivated rice (*Oryza sativa*) are traced back to specific regions in Asia. Genetic evidence suggests that *Oryza sativa japonica* rice was first domesticated from a population of *O. rufipogon* in the middle area of the Pearl River in southern China. Subsequently, Oryza sativa indica rice developed from crosses between japonica rice and local wild rice as the initial cultivars spread into South East and South Asia (Huang et al., 2012). Additionally, African rice (*Oryza glaberrima*) was independently domesticated along the Niger River, indicating a separate domestication event from its Asian counterpart (Wang et al., 2014).

### 5.2 Genetic evidence of domestication

The domestication of rice involved the selection of specific genes and traits that were advantageous for cultivation. Studies have identified numerous domestication-associated traits through high-resolution genetic mapping. These traits include changes in plant architecture, seed shattering, and flowering time, which were crucial for the transition from wild to cultivated forms (Huang et al., 2012). Comparative genomic analyses have revealed that



# http://cropscipublisher.com/index.php/rgg

both Asian and African rice underwent convergent yet independent selection of a common set of genes during their domestication processes (Wang et al., 2014).

Genome-wide analyses have identified several selective sweeps that occurred during the domestication of rice. For instance, 55 selective sweeps were identified in the genome of *Oryza sativa*, highlighting regions that underwent strong artificial selection (Huang et al., 2012). Similarly, population genomics analyses of *Oryza glaberrima* and its wild progenitor *Oryza barthii* have detected evidence for artificial selection at a genome-wide scale, further supporting the theory of independent domestication in African rice (Figure 3) (Wang et al., 2014). These genomic signatures of selection provide insights into the evolutionary pressures that shaped the domesticated rice varieties.

The figure from Wang et al. (2014) illustrates the phylogenetic relationships and geographical distribution of *Oryza glaberrima* and its wild progenitor *Oryza barthii*. Panel (a) indicates that *O. glaberrima* shares a close genetic relationship with *O. barthii* from the OB-V group, suggesting that *O. glaberrima* was domesticated from *O. barthii* within this genetic group. Panel (b) maps the geographical distribution of *O. barthii* accessions, supporting the hypothesis that *O. glaberrima* was domesticated in this region. This phylogeographic pattern underlines the significance of West Africa as the center of domestication for *O. glaberrima* and provides insights into the spread of genetic diversity within the species. The findings emphasize the role of geographical isolation and local adaptation in the domestication process.

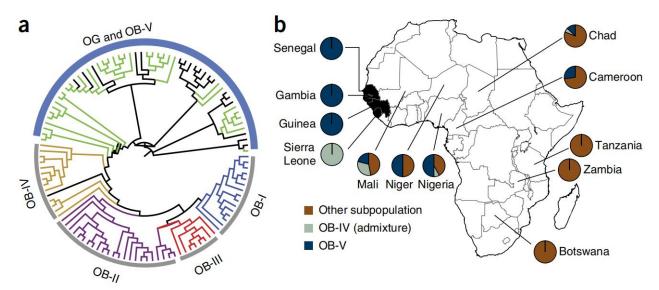


Figure 3 Identification of the domestication center of O. glaberrima (Adopted from Wang et al., 2014)

Image caption: (a) NJ phylogenetic tree of 20 O. glaberrima and 94 O. barthii accessions. All but one of the O. glaberrima accessions (black) are clustered with O. barthii accessions from group OB-V (green). (b) The proportion of each group of O. barthii accessions originating from different countries in Africa. All O. barthii accessions collected from the countries in the proposed domestication center (highlighted in black) are from the OB-V and OB-IV admixture groups. The proportion of O. barthii from the OB-V and OB-IV admixture groups found in each country decreased with distance from the domestication center, whereas the O. barthii accessions from other subgroups showed the opposite trend (Adopted from Wang et al., 2014)

#### 5.3 Impact of domestication on phylogenetic structure

Comparative genomic studies between wild and cultivated rice species have elucidated the impact of domestication on the phylogenetic structure of the genus *Oryza*. The analysis of 13 reference genomes spanning the *Oryza* species tree has shown that despite few large-scale chromosomal rearrangements, rapid species diversification is mirrored by lineage-specific emergence and turnover of many novel elements, including transposons and potential new coding and noncoding genes. This comparative approach has resolved controversial areas of the *Oryza* phylogeny and highlighted the complex history of introgression among different chromosomes in the young 'AA' subclade containing the two domesticated species (Stein et al., 2018).

http://cropscipublisher.com/index.php/rgg

Hybridization and introgression have played significant roles in the evolution of cultivated rice. The domestication of *Oryza sativa* indica involved hybridization between japonica rice and local wild rice, leading to the development of new cultivars as the initial domesticated varieties spread into new regions (Huang et al., 2012). Additionally, the study of whole chloroplast genome sequences has provided a well-resolved phylogeny of the AA genome *Oryza* species, revealing the evolutionary relationships and hybridization events among wild and domesticated rice species (Wambugu et al., 2015). These findings underscore the importance of hybridization and introgression in the diversification and adaptation of cultivated rice.

# 6 Genetic Diversity and Conservation

# 6.1 Levels and patterns of genetic diversity

Intraspecific variation within *Oryza* species has been extensively studied using various molecular markers. For instance, a study utilizing inter simple sequence repeat (ISSR) polymorphism revealed significant genetic diversity within *Oryza* species, identifying 87 putative genome/species-specific molecular markers (Joshi et al., 2000). Another study focused on nucleotide variation in *Oryza officinalis* and its close relatives, showing that these species harbor relatively low levels of nucleotide diversity compared to other plant species, which could be attributed to their smaller historic effective population sizes (Zhang and Ge, 2006). Additionally, a detailed study of molecular diversity in *Oryza sativa* and its wild relatives using 176 SSR markers demonstrated significant genetic discrimination among accessions, with a mean of 16 alleles per SSR marker (Agrama and Eizenga, 2008).

Interspecific variation among *Oryza* species has been highlighted through various phylogenetic and genomic studies. For example, the analysis of 13 reference genomes spanning the *Oryza* species tree revealed rapid species diversification and the emergence of novel genetic elements, including transposons and new coding and noncoding genes (Stein et al., 2018). Another study using ISSR markers suggested that the genus *Oryza* may have evolved following a polyphyletic pathway, with *Oryza brachyantha* being the most divergent species (Joshi et al., 2000). Furthermore, phylogenetic analyses based on nuclear genes and intergenic regions have successfully reconstructed the relationships among AA-genome species, indicating that *Oryza meridionalis* is the earliest divergent lineage (Zhu et al., 2014).

# 6.2 Conservation strategies for wild Oryza species

In situ conservation strategies are crucial for preserving the genetic diversity of wild *Oryza* species in their natural habitats. A study on the endangered wild species *Oryza granulata* in Yunnan, China, highlighted the importance of rescuing and conserving core populations for in situ conservation. The field survey showed that 44% of natural populations have become extinct over the last 30 years, emphasizing the need for immediate conservation efforts (Wu et al., 2004). Additionally, the genetic diversity analysis within populations of *Oryza granulata* revealed higher genetic variation among populations than within populations, suggesting that in situ conservation should focus on maintaining multiple populations to preserve overall genetic diversity (Wu et al., 2004).

Ex situ conservation strategies involve preserving genetic material outside of its natural habitat, which is essential for safeguarding genetic resources against habitat loss and other threats. The study on *Oryza granulata* proposed sampling and preserving more populations with fewer individuals from each population for ex situ conservation (Wu et al., 2004). Moreover, the establishment of genomic databases, such as OryzaGenome, which integrates genotype and phenotype information, provides a valuable resource for ex situ conservation efforts. This database includes genotype information for various *Oryza* species, facilitating the preservation and study of genetic diversity (Ohyanagi et al., 2015). Additionally, the release of a complete long-read assembly of IR 8 'Miracle Rice' marks a significant milestone in modern rice research, contributing to the ex situ conservation of important genetic resources (Stein et al., 2018). By combining in situ and ex situ conservation strategies, we can ensure the preservation of genetic diversity within the genus *Oryza*, which is vital for future crop protection and the sustainable use of these genetic resources.



http://cropscipublisher.com/index.php/rgg

# 7 Future Directions in *Oryza* Phylogenetics

# 7.1 Advances in molecular techniques and their implications

Recent advancements in molecular techniques have significantly enhanced our understanding of the phylogenetic relationships within the genus *Oryza*. The use of whole genome sequencing, as demonstrated by the comprehensive analysis of 13 domesticated and wild rice relatives, has provided detailed insights into genetic conservation, turnover, and innovation across the genus. These techniques have resolved controversial areas of the *Oryza* phylogeny, particularly within the AA genome species, by elucidating the complex history of introgression among different chromosomes (Stein et al., 2018). Additionally, the development of chloroplast genomic resources has enabled more accurate species discrimination and phylogenetic analysis, highlighting the potential of chloroplast DNA barcodes for species identification (Song et al., 2017). The integration of these advanced molecular techniques will continue to refine our understanding of *Oryza* phylogenetics and facilitate the discovery of novel genetic elements that can be leveraged for crop improvement.

# 7.2 Integration of molecular and ecological data

The integration of molecular data with ecological information is crucial for a holistic understanding of *Oryza* phylogenetics. Studies utilizing inter simple sequence repeat (ISSR) polymorphism have revealed significant genetic diversity and phylogenetic relationships among *Oryza* species, suggesting a polyphyletic evolutionary pathway (Joshi et al., 2000). Furthermore, the use of whole chloroplast genome sequences has provided insights into the geographical differentiation and long-distance dispersal patterns of AA genome species, which are essential for understanding their evolutionary history and ecological adaptation (Wambugu et al., 2015). By combining molecular data with ecological and geographical information, researchers can gain a more comprehensive understanding of the evolutionary processes shaping the diversity within the genus *Oryza*.

#### 7.3 Potential for crop improvement and sustainable agriculture

The phylogenetic insights gained from molecular studies have significant implications for crop improvement and sustainable agriculture. The identification of functionally coupled disease resistance genes and new haplotypes in wild and domesticated rice relatives offers valuable genetic resources for enhancing disease resistance in cultivated rice (Stein et al., 2018). Additionally, the detailed phylogenetic relationships and genetic diversity revealed by various molecular markers, such as SSR and AFLP, provide a foundation for the targeted use of wild genetic resources in rice breeding programs (Nishikawa et al., 2005). The integration of these phylogenetic insights into breeding strategies can lead to the development of rice varieties with improved traits, contributing to sustainable agricultural practices and food security.

# **8 Concluding Remarks**

Traditional morphological classification methods have laid the groundwork for understanding *Oryza* diversity, but molecular techniques have significantly refined and enhanced our understanding of phylogenetic relationships within the genus. Advances in molecular markers and genomic technologies, including cpDNA, nuclear DNA, and next-generation sequencing (NGS), have revolutionized *Oryza* phylogenetics, providing high-resolution insights into genetic relationships and evolutionary processes. The independent domestication events of *Oryza sativa* in Asia and *Oryza glaberrima* in Africa have led to significant genetic differentiation and adaptations, with molecular evidence revealing the key domestication genes and genomic signatures of selection.

The geographical distribution and migration patterns of *Oryza* species, shaped by natural dispersal mechanisms and human-mediated migration, have contributed to the genetic diversity and evolutionary history of the genus. The genetic diversity within and between *Oryza* species is critical for the resilience and adaptability of rice. Conservation strategies, both in situ and ex situ, are essential for preserving this diversity and ensuring the availability of genetic resources for future breeding programs. Ongoing advancements in molecular techniques, the integration of ecological data, and the focus on sustainable agriculture and climate change adaptation underscore the dynamic nature of *Oryza* phylogenetics and its potential for driving innovations in rice breeding.

# Rice Genomics and Genetics 2024, Vol.15, No.3, 94-105 http://cropscipublisher.com/index.php/rgg



Molecular phylogenetic studies provide a more accurate and detailed understanding of the evolutionary relationships within Oryza, leading to a more robust and scientifically grounded classification system. This improved taxonomy can aid in the identification and characterization of species and subspecies, facilitating biodiversity studies and conservation efforts.

The conservation of genetic diversity in wild *Oryza* species is essential for maintaining the evolutionary potential and adaptability of rice. In situ conservation efforts, such as protecting natural habitats and promoting sustainable land-use practices, are complemented by ex situ strategies like gene banks and living collections. Together, these approaches ensure the preservation of genetic resources for future research and breeding.

The genetic diversity within wild *Oryza* species offers valuable traits for improving cultivated rice varieties. Molecular phylogenetic insights can guide the selection of wild relatives and specific genetic loci for breeding programs, enhancing disease resistance, stress tolerance, and yield. Additionally, understanding the genetic basis of domestication and adaptive traits can inform the development of new rice varieties that are better suited to changing environmental conditions and agricultural needs.

While significant progress has been made, comprehensive genomic studies involving more species and genome types are needed to fully elucidate the evolutionary history and relationships within the genus Oryza. This includes the use of advanced sequencing technologies and integrative approaches combining nuclear, chloroplast, and mitochondrial genomes.

Future research should focus on the functional characterization of newly identified genetic elements and their roles in rice adaptation and domestication. This includes studying the regulatory mechanisms of transposons and the functional implications of novel coding and noncoding genes. There is a need for more in-depth studies on the genetic diversity and population structure of wild rice species to inform conservation strategies. This includes assessing the impact of habitat loss and climate change on genetic diversity and developing in situ and ex situ conservation plans.

Breeding Applications: Translating phylogenetic and genomic findings into practical breeding applications remains a key challenge. Future research should aim to integrate molecular markers and genomic information into breeding programs to develop rice varieties with improved agronomic traits and resilience to biotic and abiotic stresses. The molecular phylogenetic studies of Oryza species have provided a robust framework for understanding the evolutionary dynamics and genetic diversity of rice. Continued research in this field will not only enhance our knowledge of rice biology but also contribute to the sustainable conservation and improvement of this vital crop.

### Acknowledgments

The author extends sincere thanks to two anonymous peer reviewers for their feedback on the manuscript, whose evaluations and suggestions have contributed to the improvement of the manuscript.

### **Conflict of Interest Disclosure**

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

# References

Adam H., Gutierrez A., Couderc M., Sabot F., Ntakirutimana F., Serret J., Orjuela J., Tregear J., Jouannic S., and Lorieux M., 2023, African rice (Oryza glaberrima) genomic introgressions impacting upon panicle architecture in Asian rice (O. sativa) lead to the identification of key QTLs, bioRxiv, 3: 51. https://doi.org/10.1101/2023.04.25.538245

Agrama H., and Eizenga G., 2008, Molecular diversity and genome-wide linkage disequilibrium patterns in a worldwide collection of Oryza sativa and its wild relatives, Euphytica, 160: 339-355.

https://doi.org/10.1007/s10681-007-9535-v

Ammiraju J., Fan C., Yu Y., Song X., Cranston K., Pontaroli A., Lu F., Sanyal A., Jiang N., Rambo T., Currie J., Collura K., Talag J., Bennetzen J., Chen M., Jackson S., and Wing R., 2010, Spatio-temporal patterns of genome evolution in allotetraploid species of the genus Oryza, The Plant Journal: For Cell and Molecular Biology, 63(3): 430-442.

https://doi.org/10.1111/j.1365-313X.2010.04251.x

http://cropscipublisher.com/index.php/rgg

Bouillé M., Senneville S., and Bousquet J., 2011, Discordant mtDNA and cpDNA phylogenies indicate geographic speciation and reticulation as driving factors for the diversification of the genus Picea, Tree Genetics and Genomes, 7: 469-484.

https://doi.org/10.1007/s11295-010-0349-z

Buso G., Rangel P., and Ferreira M., 2001, Analysis of random and specific sequences of nuclear and cytoplasmic DNA in diploid and tetraploid American wild rice species (*Oryza* spp.), Genome, 44(3): 476-494.

https://doi.org/10.1139/G01-019

Dally A., and Sécond G., 1990, Chloroplast DNA diversity in wild and cultivated species of rice (Genus *Oryza*, section *Oryza*). Cladistic-mutation and genetic-distance analysis, Theoretical and Applied Genetics, 80: 209-222.

https://doi.org/10.1007/BF00224389

Huang X., Kurata N., Wei X., Wang Z., Wang A., Zhao Q., Zhao Y., Liu K., Lu H., Li W., Guo Y., Lu Y., Zhou C., Fan D., Weng Q., Zhu C., Huang T., Zhang L., Wang Y., Feng L., Furuumi H., Kubo T., Miyabayashi T., Yuan X., Xu Q., Dong G., Zhan Q., Li C., Fujiyama A., Toyoda A., Lu T., Feng Q., Qian Q., Li J., and Han B., 2012, A map of rice genome variation reveals the origin of cultivated rice, Nature, 490: 497-501.

https://doi.org/10.1038/nature11532

Joshi S., Gupta V., Aggarwal R., Ranjekar P., and Brar D., 2000, Genetic diversity and phylogenetic relationship as revealed by inter simple sequence repeat (ISSR) polymorphism in the genus *Oryza*, Theoretical and Applied Genetics, 100: 1311-1320.

https://doi.org/10.1007/s001220051440

Mathan J., Singh A., Jathar V., and Ranjan A., 2021, High photosynthesis rate in the selected wild rice is driven by leaf anatomy mediating high Rubisco activity and electron transport rate, Journal of Experimental Botany, 3(6): 31-56.

https://doi.org/10.1093/jxb/erab313.

Nishikawa T., Vaughan D., and Kadowaki K., 2005, Phylogenetic analysis of *Oryza* species, based on simple sequence repeats and their flanking nucleotide sequences from the mitochondrial and chloroplast genomes, Theoretical and Applied Genetics, 110: 696-705.

https://doi.org/10.1007/s00122-004-1895-2

Ohyanagi H., Ebata T., Huang X., Gong H., Fujita M., Mochizuki T., Toyoda A., Fujiyama A., Kaminuma E., Nakamura Y., Feng Q., Wang Z., Han B., and Kurata N., 2015, *Oryza Genome*: genome diversity database of wild *Oryza* species, Plant and Cell Physiology, 57: e1. https://doi.org/10.1093/pcp/pcv171

Shaw J., Shaw J., Shafer H., Leonard O., Kovach M., Schorr M., and Morris A., 2014, Chloroplast DNA sequence utility for the lowest phylogenetic and phylogeographic inferences in angiosperms: the tortoise and the hare IV, American Journal of Botany, 101(11): 1987-2004. https://doi.org/10.3732/ajb.1400398

Song Y., Chen Y., Lv J., Xu J., Zhu S., Li M., and Chen N., 2017, Development of chloroplast genomic resources for *Oryza* species discrimination, Frontiers in Plant Science, 8:69.

https://doi.org/10.3389/fpls.2017.01854

Spano C., Häussermann V., Acuña F., Griffiths C., Seeb L., and Gomez-Uchida D., 2018, Hierarchical biogeographical processes largely explain the genomic divergence pattern in a species complex of sea anemones (Metridioidea: Sagartiidae: Anthothoe), Molecular Phylogenetics and Evolution, 127: 217-228. https://doi.org/10.1016/j.ympev.2018.05.022

Stein J., Yu Y., Copetti D., Zwickl D., Zhang L., Zhang C., Chougule K., Gao D., Iwat A., Goicoechea J., Wei S., Wang J., Liao Y., Wang M., Jacquemin J., Becker C., Kudrna D., Zhang J., Londono C., Song X., Lee S., Sanchez P., Zuccolo A., Ammiraju J., Talag J., Danowitz A., Rivera L., Gschwend A., Noutsos C., Wu C., Kao S., Zeng J., Wei F., Zhao Q., Feng Q., Baidouri M., Carpentier M., Lasserre E., Cooke R., Farias D., Maia L., Santos R., Nyberg K., McNally K., Mauleon R., Alexandrov N., Schmutz J., Flowers D., Fan C., Weigel D., Jena K., Wicker T., Chen M., Han B., Henry R., Hsing Y., Kurata N., Oliveira A., Panaud O., Jackson S., Machado C., Sanderson M., Long M., Ware D., and Wing R., 2018, Genomes of 13 domesticated and wild rice relatives highlight genetic conservation, turnover and innovation across the genus *Oryza*, Nature Genetics, 50: 285-296. https://doi.org/10.1038/s41588-018-0040-0

Takehana Y., Naruse K., and Sakaizumi M., 2005, Molecular phylogeny of the medaka fishes genus *Oryzias* (Beloniformes: Adrianichthyidae) based on nuclear and mitochondrial DNA sequences, Molecular Phylogenetics and Evolution, 36(2): 417-428.

https://doi.org/10.1016/J.YMPEV.2005.01.016

Tang L., Zou X., Achoundong G., Potgieter C., Sécond G., Zhang D., and Ge S., 2010, Phylogeny and biogeography of the rice tribe (*Oryzeae*): evidence from combined analysis of 20 chloroplast fragments, Molecular Phylogenetics and Evolution, 54(1): 266-277. <a href="https://doi.org/10.1016/j.ympev.2009.08.007">https://doi.org/10.1016/j.ympev.2009.08.007</a>

Torke B., Cardoso D., Chang H., Li S., Niu M., Pennington R., Stirton C., Xu W., Zartman C., and Chung K., 2021, A dated molecular phylogeny and biogeographical analysis reveals the evolutionary history of the *trans*-Pacifically disjunct tropical tree genus *Ormosia* (Fabaceae), Molecular Phylogenetics and Evolution, 3: 107329.

https://doi.org/10.1016/j.ympev.2021.107329

Wambugu P., Brozynska M., Furtado A., Waters D., and Henry R., 2015, Relationships of wild and domesticated rices (*Oryza* AA genome species) based upon whole chloroplast genome sequences, Scientific Reports, 5: 11-29.

https://doi.org/10.1038/srep13957



http://cropscipublisher.com/index.php/rgg

Wang M., Yu Y., Haberer G., Marri P., Fan C., Goicoechea J., Zuccolo A., Song X., Kudrna D., Ammiraju J., Cossu R., Maldonado C., Chen J., Lee S., Sisneros N., Baynast K., Golser W., Wissotski M., Kim W., Sanchez P., Ndjiondjop M., Sanni K., Long M., Carney J., Panaud O., Wicker T., Machado C., Chen M., Mayer K., Rounsley S., and Wing R., 2014, The genome sequence of African rice (*Oryza glaberrima*) and evidence for independent domestication, Nature Genetics, 46: 982-988.

https://doi.org/10.1038/ng.3044

Wang Z., Sécond G., and Tanksley S., 1992, Polymorphism and phylogenetic relationships among species in the genus *Oryza* as determined by analysis of nuclear RFLPs, Theoretical and Applied Genetics, 83: 565-581.

https://doi.org/10.1007/BF00226900

Wu C., Cheng Z., Huang X., Yin S., Cao K., and Sun C., 2004, Genetic diversity among and within populations of *Oryza granulata* from Yunnan of China revealed by RAPD and ISSR markers: implications for conservation of the endangered species, Plant Science, 167: 35-42. https://doi.org/10.1016/J.PLANTSCI.2004.02.022

Xu X., Meng Q., Geng M., Ren N., Zhou L., Du Y., Cai Z., Wang M., Wang X., Wang X., Han J., Jiang S., Jing C., Liu R., Zheng X., Yang Q., Zhang F., and Ge S., 2020, Divergence in flowering time is a major component contributing to reproductive isolation between two wild rice species (*Oryza rufipogon* and *O. nivara*), Science China Life Sciences, 63: 1714-1724.

https://doi.org/10.1007/s11427-019-1678-6

Yang J., Vázquez L., Chen X., Li H., Zhang H., Liu Z., and Zhao G., 2017, Development of Chloroplast and Nuclear DNA Markers for Chinese Oaks (Quercus Subgenus Quercus) and Assessment of Their Utility as DNA Barcodes, Frontiers in Plant Science, 8: 66. https://doi.org/10.3389/fpls.2017.00816

Zhang L., and Ge S., 2006, Multilocus analysis of nucleotide variation and speciation in *Oryza officinalis* and its close relatives, Molecular Biology and Evolution, 24(3): 769-783.

https://doi.org/10.1093/MOLBEV/MSL204

Zhu Q., and Ge S., 2005, Phylogenetic relationships among A-genome species of the genus *Oryza* revealed by intron sequences of four nuclear genes, The New Phytologist, 167(1): 249-265.

https://doi.org/10.1111/J.1469-8137.2005.01406.X

Zhu T., Xu P., Liu J., Peng S., Mo X., and Gao L., 2014, Phylogenetic relationships and genome divergence among the AA- genome species of the genus *Oryza* as revealed by 53 nuclear genes and 16 intergenic regions, Molecular Phylogenetics and Evolution, 70: 348-361.

https://doi.org/10.1016/j.ympev.2013.10.008



#### Disclaimer/Publisher's Note

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.