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Strategies for Rice Improvement: Utilizing Genetic Resources from Wild and Cultivated *Oryza* Species

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Abstract This study aims to explore and summarize strategies for rice improvement by utilizing genetic resources from both wild and cultivated *Oryza* species. This includes assessing genetic diversity, identifying beneficial alleles, and leveraging advanced genomic tools to enhance rice breeding programs. The results indicate that wild *Oryza* species have great potential in rice improvement, and the genetic diversity within the *Oryza* genus plays an important role in enhancing rice cultivars. The *de novo* domestication of wild allotetraploid rice also shows promise for developing new staple cereals with improved agronomic traits. Recent genomic studies have provided a deeper understanding of rice domestication, heterosis, and complex traits, which are crucial for future breeding programs. The findings underscore the importance of utilizing genetic resources from both wild and cultivated *Oryza* species to enhance rice breeding programs. The integration of advanced genomic tools and the identification of beneficial alleles from wild species can significantly broaden the genetic base of cultivated rice, leading to improved yield, quality, and sustainability. These strategies are essential for addressing the global food security challenges posed by a growing population.

Keywords Rice improvement; Srategies; *Oryza* species; Genetic diversity; Traditional breeding; Modern breeding techniques; Domestication

1 Introduction

Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population, making it one of the most crucial crops globally (Jena et al., 2017; Ahmad, 2022). The increasing global population, decreasing arable lands, and escalating threats posed by climate change necessitate continuous efforts to improve rice varieties to ensure food security (Jena et al., 2017). Traditional breeding methods have been instrumental in developing rice varieties with improved yield and stress resistance. However, the genetic diversity within cultivated rice is limited due to domestication, which has led to the loss of many beneficial alleles (Eizenga et al., 2017). Therefore, utilizing genetic resources from both wild and cultivated *Oryza* species is essential for broadening the genetic base and enhancing the resilience and productivity of rice (Zhang et al., 2022; Zhou et al., 2022).

The genus *Oryza* comprises more than 20 species, including both wild and cultivated types, which are classified into several genome groups. The AA genome group, which includes *Oryza sativa* and its wild relatives, is particularly significant for rice improvement due to its rich genetic diversity (Zhang et al., 2022). Wild species such as *Oryza nivara* and *Oryza rufipogon* have been identified as valuable sources of novel alleles for traits such as stress resistance and yield improvement (Chen et al., 2004; Eizenga et al., 2017). Interspecific hybridization and introgression between cultivated rice and its wild relatives have historically played a crucial role in enhancing the genetic diversity and adaptability of rice (Zhou et al., 2022). Modern genomic and transcriptomic techniques have further facilitated the identification and utilization of these genetic resources, enabling the development of rice varieties with improved traits (Jena et al., 2017; Ahmad, 2022).

This study aims to study strategies for improving rice by utilizing the genetic resources of wild and cultivated *Oryza* species. The research emphasizes the importance of genetic diversity in rice improvement and the role of wild *Oryza* species as reservoirs of beneficial alleles. It highlights the use of biotechnological tools and methods to harness the genetic traits of wild species and discusses case studies of successfully incorporating wild rice genes into cultivated rice. Additionally, the study identifies the challenges of integrating wild genetic resources into breeding programs and outlines future research and development directions. By addressing these objectives, the study underscores the significance of wild *Oryza* species in rice improvement and offers valuable insights for sustainable agricultural practices to enhance rice productivity and resilience.

2 Genetic Resources in the *Oryza* Genus

2.1 Wild *Oryza* species

The genus *Oryza* includes a diverse range of species, serving as a vital genetic reservoir for rice improvement. It is primarily divided into wild and cultivated rice, both of which make significant contributions to rice breeding programs. Wild *Oryza* species exhibit significant genetic diversity and are distributed across various ecological niches worldwide. The genus includes 27 species, which have evolved over 15 million years, resulting in a wide range of adaptive traits (Mussurova et al., 2020). These species are found in diverse environments, from tropical to subtropical regions, and possess different genome types, such as AA, BB, CC, and others (Ricachenevsky and Sperotto, 2016). This extensive diversity makes wild *Oryza* species a rich source of genetic variation for improving cultivated rice.

Wild *Oryza* species harbor numerous traits of interest that can be harnessed for rice improvement. For instance, *Oryza longistaminata*, a perennial wild rice, possesses traits such as rhizomatousness, disease resistance, and drought tolerance, which are valuable for enhancing the resilience of cultivated rice (He et al., 2014). Additionally, *Oryza rufipogon*, the closest wild relative of cultivated rice, has been shown to contain alleles that improve yield and other agronomic traits (Li et al., 2020). These wild species also exhibit traits related to metal tolerance and nutrient accumulation, which are crucial for improving the nutritional quality and stress tolerance of rice (Ricachenevsky and Sperotto, 2016).

2.2 Cultivated *Oryza* species

The domestication of rice began approximately 10 000 years ago, involving the selection of specific traits from wild ancestors to develop cultivated varieties. *Oryza sativa*, the most widely cultivated rice species, was domesticated from *Oryza rufipogon* (Ricachenevsky and Sperotto, 2016). The domestication process involved the selection of traits such as reduced seed shattering, increased grain size, and improved yield (Eizenga et al., 2017). Advances in genomics have provided insights into the genetic changes that occurred during domestication, revealing the loss of genetic diversity in cultivated rice compared to its wild relatives (Wambetugu et al., 2019).

There are two major subspecies of cultivated rice: *Oryza sativa* ssp. *japonica* and *Oryza sativa* ssp. *indica*. Japonica varieties, such as Dianjingyou 1 and Yundao 1, are typically grown in temperate regions, while indica varieties, such as RD23, are more common in tropical areas (Zhang et al., 2022). Additionally, African rice (*Oryza glaberrima*) is another cultivated species that has been utilized for its resistance to biotic and abiotic stresses (Wambetugu et al., 2019). These cultivated varieties have been the focus of breeding programs aimed at improving yield, disease resistance, and other agronomic traits through the introgression of beneficial alleles from wild species (Zhang et al., 2021; Zhang et al., 2022).

The genetic resources within the *Oryza* genus, encompassing both wild and cultivated species, offer a wealth of traits that can be leveraged for rice improvement. By utilizing the genetic diversity present in wild species and the advanced genomic tools available for cultivated varieties, breeders can develop rice cultivars with enhanced yield, resilience, and nutritional quality.

3 Phylogenetic Relationships and Classification

3.1 Molecular phylogenetics of *Oryza*

Molecular phylogenetics has significantly advanced our understanding of the evolutionary relationships within the genus *Oryza*. The genus comprises 27 species, providing a rich source of genetic diversity for rice improvement (Mussurova et al., 2020). High-quality genome assemblies, such as those produced for *Oryza rufipogon* using SMRT sequencing, have enabled detailed comparative genomic analyses (Mahajan and Kapoor, 2019; Li et al., 2020). These studies have identified numerous genomic variants and lineage-specific expansions of gene families that contribute to reproductive isolation and adaptation to diverse environments. The development of platinum standard reference genome sequences (PSRefSeq) for all *Oryza* species sets a new benchmark for integrating wild relatives into crop improvement programs (Mussurova et al., 2020).

3.2 Classification systems

The classification of *Oryza* species is based on morphological and genetic criteria. As more genetic and morphological data become available, the classification system of *Oryza* species continues to evolve. Traditional classification systems have relied on morphological traits, such as plant stature, leaf shape, and spikelet structure. Advances in genomics have allowed for more precise classifications based on genetic data. For instance, the construction of pan-genomes across all *Oryza* species has provided a comprehensive framework for understanding the genetic diversity within the genus (Huang et al., 2021). This approach has revealed the presence of numerous dispensable genes and large-effect mutations that are crucial for agronomic traits (Li et al., 2020; Huang et al., 2021).

Modern classification systems incorporate both genetic and morphological data, leading to a more accurate representation of the evolutionary relationships within the genus. The current classification system divides the *Oryza* genus into two main groups: the AA genome group, which includes most diploid species and is particularly important in rice breeding due to its reservoir of many beneficial alleles (Zhang et al., 2022). And the BB, CC, EE, and FF genome groups, which contain the polyploid species. This genomic classification has practical implications for rice breeding, as it helps breeders select compatible species for hybridization and gene transfer.

3.3 Evolutionary history and speciation

The evolutionary history of the *Oryza* genus is marked by complex processes of speciation, adaptation, and genome evolution. Phylogenetic studies suggest that the genus originated in Asia around 15 million years ago, with subsequent radiation into diverse ecological niches across the tropics and subtropics (Mahajan and Kapoor, 2019). Speciation within *Oryza* has been driven by both allopatric and sympatric mechanisms, resulting in the rich genetic diversity observed today.

The evolutionary history of *Oryza* is marked by significant events such as polyploidization and speciation. Cultivated rice varieties are diploid, but there is growing interest in the domestication of wild allotetraploid species like *Oryza alta*, which offers advantages in genome buffering and environmental robustness (Yu et al., 2021). The speciation process within *Oryza* has been driven by various factors, including reproductive isolation mechanisms and selection pressures. For example, the lineage-specific expansion of gene families in *Oryza rufipogon* has played a role in the evolution of mating systems and adaptation to different habitats (Li et al., 2020). Understanding these evolutionary processes is essential for harnessing the genetic potential of wild *Oryza* species for rice improvement (Li et al., 2020).

4 Geographical Migration and Domestication

4.1 Historical perspectives on rice migration

The migration and domestication of rice have been pivotal in shaping its genetic diversity and adaptability. The genus *Oryza*, which includes both wild and cultivated species, has a rich evolutionary history spanning 15 million years, contributing to the genetic reservoir available for rice improvement (Mussurova et al., 2020). The migration of rice can be traced back to the earliest agricultural practices. Initially domesticated in Asia, rice gradually spread worldwide through human migration, trade routes, and cultural exchanges.

The spread of rice cultivation followed major waterways and trade routes, such as the Silk Road, facilitating the dissemination of rice to the Middle East, Africa, and Europe. At the same time, maritime routes enabled the distribution of rice varieties to Southeast Asia, the Pacific Islands, and eventually to the Americas through the Columbian Exchange. Rice domestication is believed to have occurred independently in multiple regions, leading to the formation of various subspecies and local varieties (Zhang et al., 2021). The multi-origin model is supported by genetic evidence, showing that local variety groups are closely related to wild rice populations from the same geographical origins (Zhou et al., 2022).

4.2 Domestication events and centers

The domestication of rice has been a complex process involving multiple events and centers. The primary center of domestication for Asian rice (*Oryza sativa*) is believed to be the Yangtze River Valley in China, where evidence of rice cultivation dates back approximately 10 000 years. Two major subspecies, *indica* and *japonica*, emerged from this center, adapted to different environmental conditions. Indica varieties thrived in the tropical and subtropical regions, while *japonica* varieties were better suited for temperate climates (Zhou et al., 2022).

African rice (*Oryza glaberrima*) was domesticated independently in the Niger River basin around 3 500 years ago. This domestication event occurred in response to the distinct ecological conditions of West Africa, leading to the development of varieties with unique adaptations to local environments. The domestication process involved the selection of traits such as reduced seed shattering, increased grain size, and improved yield, which were pivotal for the success of rice as a staple crop (Wambugu et al., 2021).

The domestication process has been influenced by interspecific hybridization and introgression, which have played significant roles in enhancing the genetic diversity and adaptability of rice (Zhou et al., 2022). For instance, Domestication of wild allo-tetraploid rice (such as *Oryza alta*) has been proposed as a strategy for developing new staple crops with improved agronomic traits (Figure 1) (Yu et al., 2021). The research team developed a breeding method using gene editing technology to domesticate wild allo-tetraploid rice, resulting in a series of edited tetraploid rice lines that show significant improvements in domestication and agronomic traits. This domestication approach provides a viable strategy for creating new crops, contributing to global food security.

4.3 Impact on genetic diversity

The domestication and migration of rice have had profound impacts on its genetic diversity. The narrow genetic base of modern rice varieties, resulting from the limited number of parental lines used in breeding programs, has led to yield stagnation and vulnerability to biotic and abiotic stresses. However, the wild relatives of rice, such as *Oryza rufipogon* and *Oryza glaberrima*, possess a wealth of genetic diversity that can be harnessed for rice improvement (Wambugu et al., 2019). These wild species contain genes for resistance to various stresses and have been used to develop introgression lines with valuable agronomic traits (Zhang et al., 2022). Advances in genomics and molecular breeding technologies have facilitated the identification and transfer of these beneficial genes into cultivated rice, thereby broadening the genetic base and enhancing the resilience of rice varieties (Wambugu et al., 2019).

Understanding the historical perspectives on rice migration, the domestication events and centers, and their impact on genetic diversity is crucial for developing strategies to utilize the genetic resources from wild and cultivated *Oryza* species for rice improvement. By leveraging the genetic diversity present in wild relatives and employing advanced breeding techniques, it is possible to enhance the adaptability and productivity of rice to meet the challenges of a growing global population.

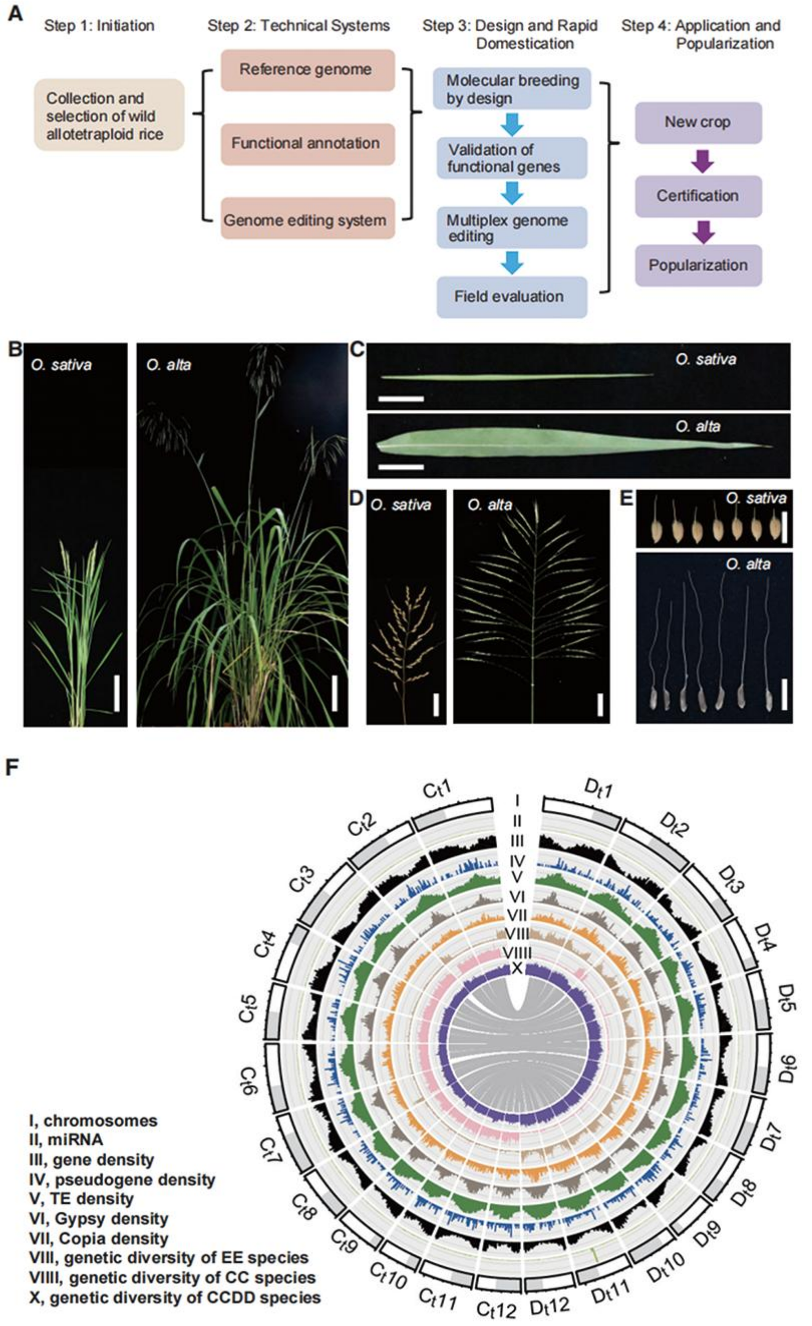

Figure 1 Roadmap of *de novo* domestication of *O. alta* and its structures and genomic features (Adopted from Yu et al., 2021)

Image caption: The figure details the domestication route of wild allotetraploid rice. A: The domestication route from wild allotetraploid rice to new crops is divided into four steps. This route includes the establishment of a reference genome, functional gene annotation, development of efficient transformation and gene editing systems, application of multiplex gene editing technology, and the certification and promotion of new crops; B: A comparison of the whole plants of cultivated rice (*O. sativa*) and wild rice (*O. alta)*. The plant height of *O. alta* exceeds 2.7 meters, significantly taller than *O. sativa*, demonstrating its wild characteristics; C: The leaves of *O. alta* are wider and longer compared to *O. sativa*, reflecting the morphological traits of wild rice; D: A comparison of the panicles of *O. alta* and *O. sativa*. The panicle length of *O. alta* exceeds 48 centimeters with sparse spikelets, whereas *O. sativa* has relatively shorter panicles with dense spikelets; E: A comparison of the seeds of the two rice types. *O. alta* has smaller seeds with a thousand-grain weight of approximately 8.79 grams and awns longer than 4 centimeters; F: Various features of the *O. alta* genome, including the distribution of chromosomes, miRNA, gene density, and Gypsy and Copia elements. The results demonstrate significant differences in morphological and genomic characteristics between wild allotetraploid rice and cultivated rice, highlighting the feasibility and advantages of using gene editing technology for the rapid domestication of wild rice (Adapted from Yu et al., 2021)

5 Genetic Diversity and Its Utilization

5.1 Assessing genetic diversity in *Oryza*

The assessment of genetic diversity in *Oryza* species has been significantly advanced by the development of various genomic tools and techniques. High-throughput sequencing technologies, such as RADSeq and SLAF-seq, have enabled the detailed analysis of genetic variation across different *Oryza* species. For instance, RADSeq was used to assess the genetic diversity of *Oryza longistaminata* in Ethiopia, revealing high genetic diversity and regional differentiation (Melaku et al., 2019). Similarly, SLAF-seq facilitated the development of a genome-wide SNP array for *Oryza rufipogon*, which was used to genotype 110 accessions and assess their genetic structure (Zhang et al., 2020). Advances in DNA sequencing technologies have also led to the creation of platinum standard reference genome sequences (PSRefSeq) for all *Oryza* species, setting a new benchmark for integrating wild relatives into crop improvement programs (Mussurova et al., 2020). Moreover, Techniques like genome-wide association studies (GWAS) and quantitative trait locus (QTL) mapping have proven invaluable in uncovering the genetic basis of traits such as disease resistance, yield, and stress tolerance.

Several case studies highlight the genetic diversity present in wild and cultivated *Oryza* species. For example, Melaku et al. (2019) studied the genetic diversity and regional differentiation of African wild rice (*Oryza longistaminata*) in Ethiopia. Using SSR markers on 360 samples and RADSeq analysis on 87 early-maturing samples, they found high genetic diversity (PIC=76.5%) and regional genetic differentiation (Fst=0.08) in the wild rice populations (Figure 2). The results indicate that genetic relationships among these populations are primarily based on their geographic origins. The high genetic diversity and regional differentiation suggest that these wild rice populations are valuable genetic resources for rice improvement projects (Melaku et al., 2019). Another study on *Oryza rufipogon* in Guangdong Province, China, used a 79,422-SNP array to reveal significant genetic differentiation among accessions from different agroclimatic zones (Zhang et al., 2020). Additionally, the genetic diversity of African rice (*Oryza glaberrima*) has been explored through whole genome re-sequencing, providing insights into its domestication process and potential for breeding climate-resilient rice varieties (Wambugu et al., 2019).

5.2 Conservation of genetic resources

The conservation of genetic resources in *Oryza* species is crucial for maintaining their genetic diversity and potential for crop improvement. In-situ conservation involves preserving wild rice populations in their natural habitats, which helps maintain their ecological interactions and evolutionary processes. Ex-situ conservation, on the other hand, involves the collection and storage of genetic material in germplasm banks and repositories. For instance, the genetic diversity of *Oryza rufipogon*, an endangered species due to habitat loss, has been assessed to inform conservation strategies. The establishment of chromosome segment substitution lines (CSSLs) from wild rice species also contributes to ex-situ conservation by preserving valuable genetic traits for future breeding programs (Yuan et al., 2020).

Germplasm banks and repositories play a vital role in the conservation and utilization of genetic resources from wild and cultivated *Oryza* species. These facilities store genetic material, such as seeds and DNA samples, which can be used for breeding and research purposes. For example, Zhang et al. (2022) developed an introgression library of agronomic traits from all AA genome *Oryza* species, providing a valuable resource for rice improvement. The construction of *Oryza* pan-genomes, which include high-quality genome assemblies from both cultivated and wild rice populations, further enhances the accessibility and utilization of genetic diversity for future rice research and improvement (Huang et al., 2021).

The assessment and conservation of genetic diversity in *Oryza* species are essential for the sustainable improvement of rice. Advances in genomic tools and techniques, along with effective conservation strategies, provide a strong foundation for utilizing the genetic resources of wild and cultivated *Oryza* species in rice breeding programs.

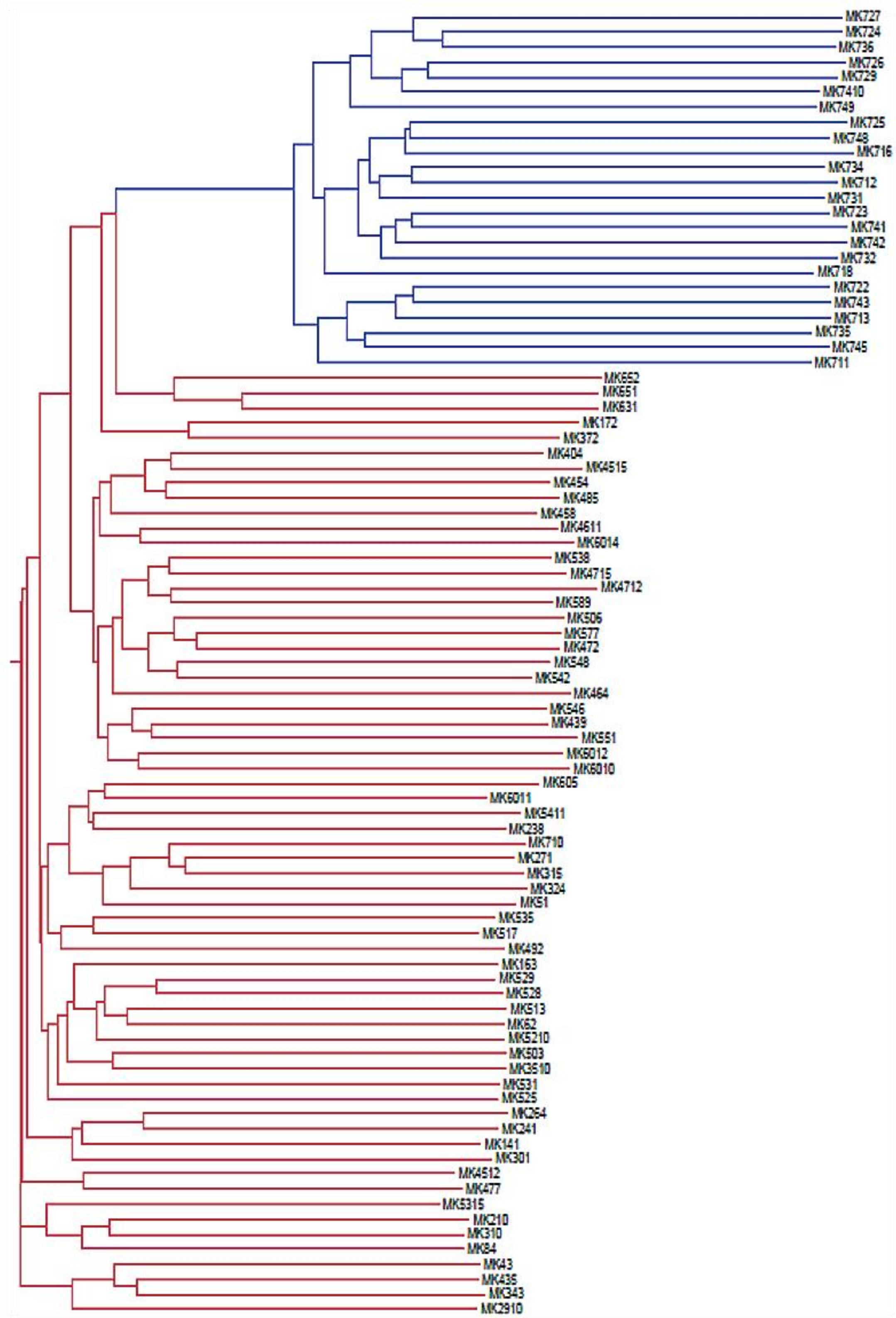

Figure 2 30 256 RAD Tag SNPs based phylogenetic tree of 87 *O. longistaminata* accessions of Ethiopia (Adopted from Melaku et al., 2019)

Image caption: The figure shows that samples from the Amhara region (blue branches) are clearly separated from those from the Gambella region (red branches), indicating significant genetic differentiation between the two regions. The Amhara samples form a distinct cluster, while the Gambella samples exhibit more genetic admixture. This result further supports the geographical and genetic differentiation between the populations of this species (Adapted from Melaku et al., 2019)

6 Breeding Strategies and Techniques

6.1 Traditional breeding methods

Selection and hybridization are foundational techniques in traditional rice breeding. These methods involve selecting parent plants with desirable traits and cross-breeding them to produce offspring that combine these traits. Selection involves choosing plants with desirable traits such as high yield, disease resistance, and stress tolerance, and using them as parents in breeding programs (Xu et al., 2021). Hybridization, or cross-breeding, combines the genetic material from two different parent plants to produce offspring with improved characteristics. This approach has been instrumental in developing high-yielding and disease-resistant rice varieties. For instance, interspecific hybridization has played a significant role in the diversification and improvement of Asian cultivated rice, leading to the development of subgroups like indica and japonica, which are adapted to various environmental conditions (Zhou et al., 2022).

Mutation breeding involves inducing genetic mutations to create new genetic variations. This can be achieved using physical agents like radiation or chemical agents such as ethyl methanesulfonate (EMS). These mutations can result in new traits that may be beneficial for rice improvement. This method has been used to develop rice varieties with improved yield, disease resistance, and stress tolerance. For example, mutation breeding has been employed to enhance traits such as drought resistance and grain quality in rice (Zhang et al., 2022).

6.2 Modern breeding techniques

Marker-assisted selection (MAS) is a modern breeding technique that uses molecular markers to select plants with desirable traits at the seedling stage, thus speeding up the breeding process. MAS has been effectively used to introduce quantitative trait loci (QTLs) associated with yield, drought tolerance, and other complex traits into rice varieties. For example, MAS has been employed to enhance grain number and yield-related traits in rice by incorporating QTLs such as Gn1a and Dep1 (Gouda et al., 2020). Additionally, MAS has been used to pyramid QTLs for moisture and heat stress tolerance, resulting in rice lines with significantly improved yields under stress conditions (Withanawasam et al., 2022).

Genetic engineering and CRISPR-Cas9 are cutting-edge techniques that allow precise modifications of the rice genome. These methods have been used to introduce beneficial genes from wild rice species into cultivated varieties, enhancing traits such as yield, stress tolerance, and disease resistance. For instance, CRISPR has been used to edit genes in wild allotetraploid rice, leading to the rapid improvement of agronomically important traits (Yu et al., 2021). Genetic engineering has also facilitated the development of rice varieties with enhanced resistance to biotic and abiotic stresses by incorporating genes from wild progenitors like *Oryza rufipogon* (Li et al., 2020).

6.3 Integrating wild genetic resources

The genetic diversity found in wild *Oryza* species offers a valuable reservoir of traits that can be harnessed to improve cultivated rice. Integrating these wild genetic resources into breeding programs is essential for broadening the genetic base and enhancing the resilience of rice varieties. Introgression breeding involves the incorporation of genes from wild rice species into cultivated varieties to enhance genetic diversity and improve traits. This method has been used to develop introgression lines (ILs) that carry valuable alleles from wild species, such as *Oryza rufipogo*n, which contribute to traits like drought resistance and grain quality (Zhang et al., 2022). The development of chromosome segment substitution lines (CSSLs) from wild rice has also facilitated the fine mapping of QTLs and the discovery of new genes for rice improvement (Yuan et al., 2020).

Pre-breeding and base broadening involve the initial steps of incorporating genetic diversity from wild species into breeding programs. This process helps to create a broader genetic base for future breeding efforts. For example, the *de novo* domestication of wild allotetraploid rice has been proposed as a strategy to develop new rice varieties with enhanced genome buffering and environmental robustness (Yu et al., 2021). Additionally, the genomic analysis of wild and cultivated *Oryza* species has provided insights into the genetic basis of important traits, facilitating the identification of genes for rice improvement (Chen et al., 2019). By integrating traditional and modern breeding techniques with the genetic resources from wild and cultivated *Oryza* species, significant advancements can be made in rice improvement, ensuring food security and sustainability for the growing global population.

7 Case Studies of Successful Rice Improvement

7.1 Disease resistance

Disease resistance is a critical aspect of rice improvement, as diseases can significantly reduce yield and quality. Several successful case studies illustrate how genetic resources from wild and cultivated *Oryza* species have been used to develop disease-resistant rice varieties. Bacterial blight (BB), caused by *Xanthomonas Oryzae* pv. *Oryzae* (Xoo), poses a major threat to rice production (Kumar et al., 2020). To enhance rice resistance to BB, researchers have adopted various strategies such as utilizing wild rice genes, marker-assisted breeding, and genome-wide association studies. Angeles-Shim et al. (2020) identified a new locus from the wild rice species *Oryza latifolia* that confers race-specific resistance to PXO339 (Philippine *Xoo* race 9A).

The study showed that this locus was transmitted through two introgression lines (WH12-2252 and WH12-2256) and exhibited resistance to the PXO339 strain. Genotypic analysis and phenotypic segregation ratios indicated that this resistance is controlled by a single recessive gene (Figure 3). Further genomic analysis narrowed down the candidate region to a 1 817 kb segment on chromosome 12 and identified potential candidate genes regulating this resistance. The findings underscore the importance of wild rice species as a valuable source of new resistance genes and suggest integrating these genes into rice breeding programs to improve crop disease resistance (Angeles-Shim et al., 2020).

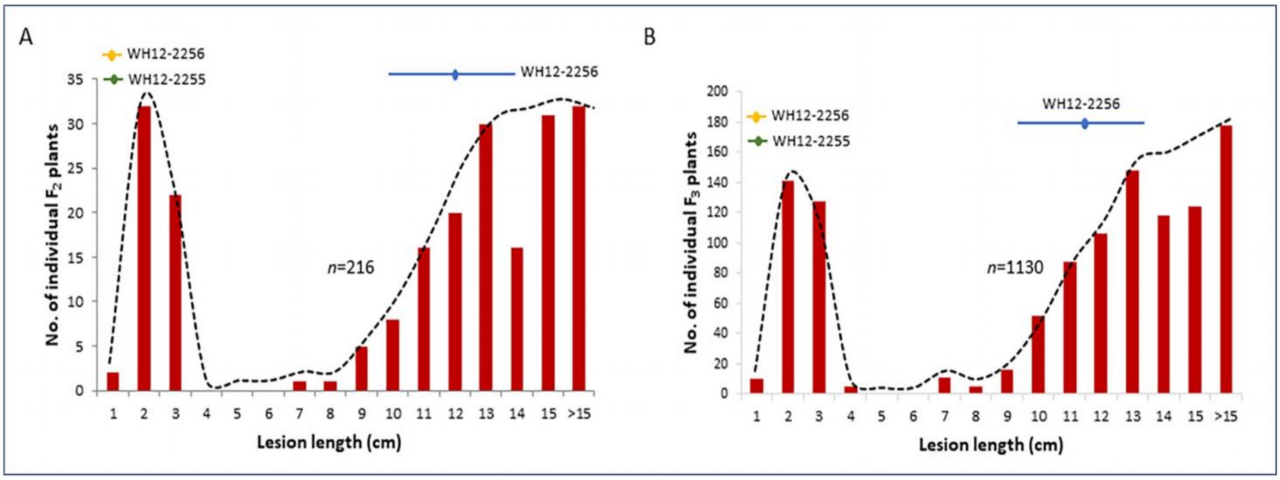

Figure 3 Phenotype distribution in segregating populations (Adopted from Angeles-Shim et al., 2020)

Image caption: The figure shows the distribution of lesion lengths in F2 and F3 segregating populations after inoculation with PXO339. In the F2 population, the lesion length exhibits a bimodal distribution, separating into resistant and susceptible phenotypes. Resistant plants have lesion lengths less than 4 cm, while susceptible plants have lesion lengths greater than 6 cm. The F3 population shows a similar bimodal distribution, with resistant plants having lesion lengths less than 5 cm and susceptible plants having lesion lengths greater than 6 cm. The lesion length distribution in the F2 population indicates a clear segregation of resistant and susceptible plants, consistent with a Mendelian 3:1 segregation ratio, and the F3 population displays a similar pattern. These results collectively support the conclusion that PXO339 resistance is controlled by a single recessive gene (Adapted from Angeles-Shim et al., 2020)

Rice blast, caused by the fungus *Magnaporthe Oryzae*, is another major biotic stress affecting rice. The use of genes from wild and traditional rice varieties has successfully achieved resistance to rice blast. For instance, the study used marker-assisted backcrossing to improve the Indian elite rice variety ‘Krishna Hamsa’, making it resistant to bacterial blight (BB) and blast disease (Badri et al., 2022). Additionally, researchers have developed an introgression library that includes agronomic traits from all AA genome *Oryza* species, which encompasses traits for rice blast resistance. This provides a valuable resource for future breeding programs (Zhang et al., 2022).

7.2 Abiotic stress tolerance

Abiotic stresses such as drought and salinity can severely impact rice production. Developing varieties with enhanced tolerance to these stresses is essential for ensuring food security in the face of climate change. Drought stress significantly affects rice yield, and drought tolerance is a crucial trait for rice cultivation in water-scarce regions. Strategies to improve drought tolerance include multiparent-derived introgression and genomic and transcriptomic approaches. The disease-resistant introgression lines developed for 'Krishna Hamsa' also contain QTLs for drought tolerance. These lines not only exhibit resistance to BB and blast disease but also show improved drought tolerance. The study utilized a multi-locus introgression strategy, integrating multiple disease resistance genes and drought tolerance QTLs into 'Krishna Hamsa', ultimately developing 196 introgression lines with different gene/QTL combinations (Figure 4). This research demonstrates the potential for rapidly developing multi-resistant rice varieties through selective multiparent crosses combined with marker-assisted selection (Badri et al., 2022). Advances in genomics and transcriptomics have identified numerous QTLs, genes, and transcription factors involved in the drought response of rice, providing a genetic foundation for developing drought-tolerant rice varieties (Ahmad, 2022).

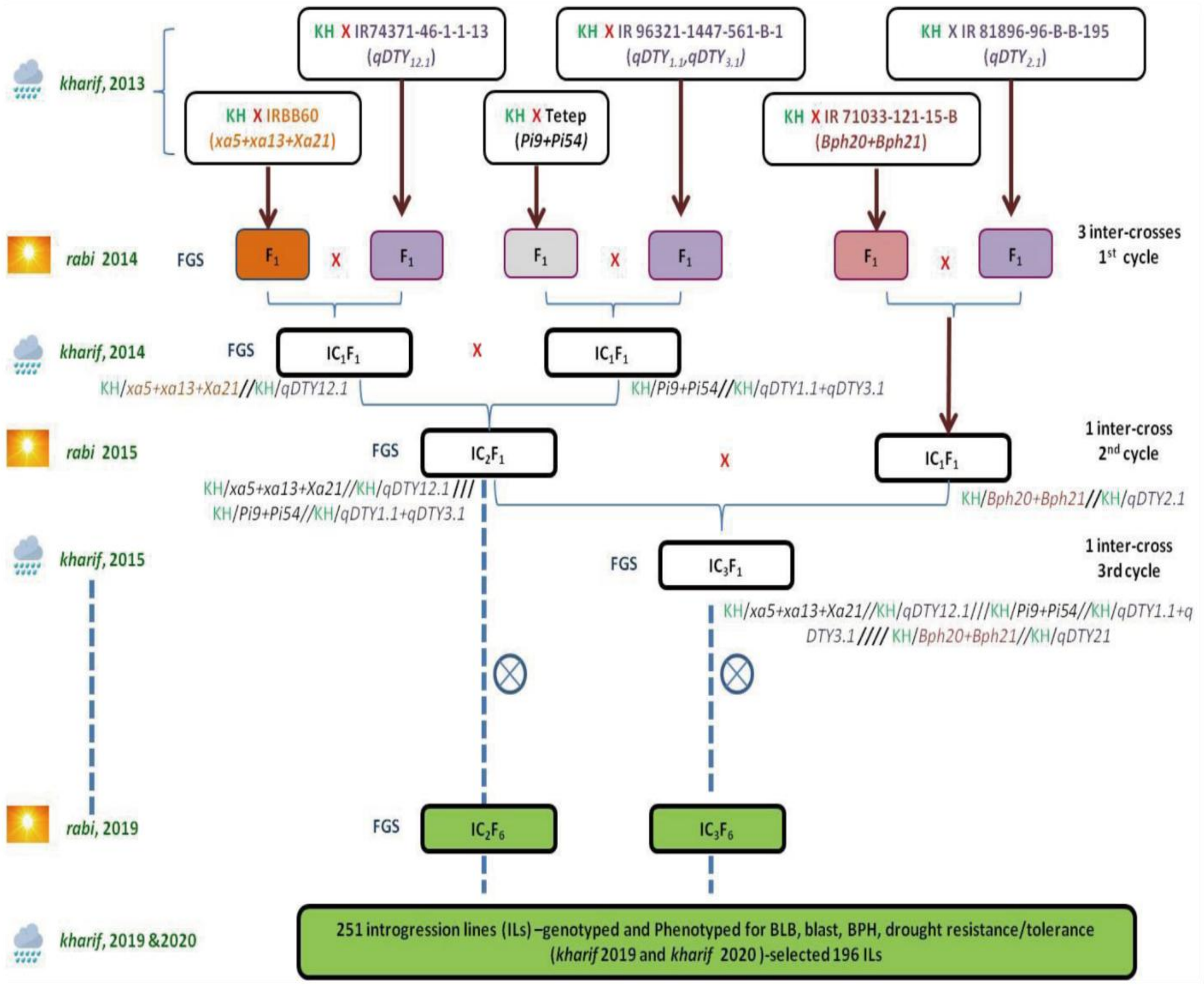

Figure 4 Introgression scheme involving elite recurrent parent, 'Krishna Hamsa', and six donor parents for biotic and abiotic traits (Adopted from Badri et al., 2022)

Image caption: The figure describes the process of crossing and selfing with six donor parents, each carrying genes for resistance to bacterial blight (BB), blast disease (Blast), and brown planthopper (BPH) (such as xa5, xa13, Xa21, Pi9, Pi54, Bph20, and Bph21), as well as drought tolerance QTLs (qDTY1.1, qDTY2.1, qDTY3.1, qDTY12.1). Through three rounds of selective crossing and selfing, combined with foreground selection and phenotypic evaluation, 196 introgression lines (ILs) were developed. These ILs exhibit resistance to various biotic and abiotic stresses (Adapted from Badri et al., 2022)

The salt-tolerant line DJ15, derived from a cross between Dongxiang wild rice and a cultivated variety, showed improved salinity tolerance. QTL mapping identified key QTLs and candidate genes responsible for this trait (Quan et al., 2018). Wild *Oryza* species, such as *O. rufipogon*, *O. coarctata*, *O. latifolia*, and *O. alta*, have been identified as valuable sources of salinity tolerance traits. The results showed that these species possess mechanisms for efficient Na^+ sequestration and K^+ retention, which are crucial for salinity tolerance (Solis et al., 2020).

7.3 Yield and quality enhancement

Developing high-yielding varieties has always been a primary focus of breeding programs. During the Green Revolution, the introduction of semi-dwarf varieties like IR8 significantly increased rice yields. The success of IR8 lay in its vigorous growth, high fertilizer response, and yield that was markedly higher than traditional varieties, benefiting rice-producing countries worldwide. In recent years, the integration of genes from wild rice species has further enhanced yield potential. The introgression gene pool of AA genome *Oryza* species includes high-yield traits such as grain size and thousand-grain weight, providing genetic resources for developing high-yielding rice varieties (Zhang et al., 2022). Wild species like *Oryza rufipogon* also offer rich genetic diversity for yield-related traits.

Pre-breeding methods and molecular breeding techniques are used to transfer these valuable genes into cultivated varieties. Pre-breeding involves creating intermediate germplasm to introduce beneficial genes from wild rice into cultivated rice, laying the foundation for further improvement. Molecular breeding techniques, such as marker-assisted selection (MAS) and genome editing technologies like CRISPR-Cas9, significantly accelerate the introduction and integration of these genes (Badri et al., 2022; Gautam et al., 2023). MAS utilizes molecular markers to quickly identify and select individuals carrying target genes, enhancing breeding efficiency and accuracy. Genome editing technologies allow breeders to precisely modify or insert specific genes, further boosting the potential for rice variety improvement.

Improving the nutritional quality of rice is crucial for addressing malnutrition. Progress has been made in enhancing the nutritional content of rice by utilizing genetic resources from wild and traditional rice varieties. The development of Golden Rice, which is rich in vitamin A (β-carotene), involved the introduction of genes from maize and a common soil bacterium. This biofortified rice aims to tackle vitamin A deficiency in developing countries. Similarly, by incorporating genes from wild and traditional varieties, high-iron and high-zinc rice varieties have been developed, providing a more nutritious staple food for populations deficient in these micronutrients. By leveraging the genetic resources from wild and cultivated *Oryza* species, significant improvements in disease resistance, abiotic stress tolerance, yield, and nutritional quality of rice can be achieved. These strategies are essential for sustainable rice production and global food security.

8 Future Prospects and Challenges

8.1 Emerging technologies in rice improvement

The future of rice improvement is closely tied to the advancement of emerging technologies. Genome editing tools, particularly CRISPR/Cas9, have revolutionized the field by enabling precise modifications in the rice genome to enhance desirable traits such as yield, stress tolerance, and disease resistance (Zafar et al., 2020). Recent developments in genome editing, including CRISPR-directed evolution and base editors, have further expanded the potential for crop improvement by allowing more efficient and accurate genetic modifications (Mishra et al., 2018).

High-throughput phenotyping platforms, utilizing drones, sensors, and imaging technologies, allow for rapid and accurate assessment of phenotypic traits in large breeding populations. These platforms facilitate the collection of detailed data on plant growth, development, and response to environmental stresses, accelerating the selection process for desirable traits. Additionally, the concept of *de novo* domestication of wild allotetraploid rice presents a novel approach to developing new rice varieties with enhanced genome buffering and environmental robustness (Yu et al., 2021). The integration of these advanced technologies with traditional breeding methods holds great promise for the future of rice improvement.

8.2 Addressing climate change and sustainability

Climate change poses significant challenges to rice production, necessitating the development of climate-resilient rice varieties. African rice (*Oryza glaberrima*) and other wild relatives of rice harbor a wealth of genetic diversity that can be harnessed to improve climate resilience in cultivated rice (Wambugu et al., 2019). The use of genetic resources from wild species, such as *Oryza rufipogon*, can provide valuable traits for biotic and abiotic stress tolerance, which are crucial for sustaining rice production under changing climatic conditions. The construction of *Oryza* pan-genomes, which encompass the genetic diversity of both cultivated and wild rice species, offers a comprehensive foundation for future rice research and improvement (Huang et al., 2021). These efforts are essential for ensuring the sustainability of rice production in the face of global climate challenges.

8.3 Policy and regulatory considerations

The successful implementation of advanced genetic technologies in rice improvement requires careful consideration of policy and regulatory frameworks. The deployment of genome editing technologies, such as CRISPR/Cas9, raises safety concerns that must be addressed to gain public acceptance and regulatory approval (Mishra et al., 2018; Zafar et al., 2020). It is crucial to establish clear guidelines and regulations that ensure the safe and responsible use of these technologies while promoting innovation in rice breeding. Additionally, policies that support the conservation and utilization of genetic resources from wild and cultivated *Oryza* species are essential for maintaining the genetic diversity necessary for future rice improvement (Wambugu et al., 2019; Mussurova et al., 2020). Collaborative efforts between researchers, policymakers, and stakeholders are needed to create an enabling environment for the sustainable advancement of rice improvement strategies.

The future of rice improvement lies in the integration of emerging technologies, the utilization of genetic resources from wild and cultivated *Oryza* species, and the establishment of supportive policy and regulatory frameworks. By addressing these key areas, we can enhance the resilience and sustainability of rice production to meet the growing global food demand.

9 Concluding Remarks

The utilization of genetic resources from wild and cultivated *Oryza* species presents a promising strategy for rice improvement. The genus *Oryza*, comprising 27 species, offers a rich reservoir of adaptive traits such as biotic and abiotic resistances that can be harnessed to enhance cultivated rice varieties. Strategies like conventional crossing, genetic transformation, and gene editing have been employed to introduce these traits into cultivated rice. Additionally, the concept of neodomestication, which involves domesticating wild relatives with desirable traits, has been proposed as an alternative approach. The development of genomic resources, such as platinum standard reference genome sequences (PSRefSeq) and chromosome segment substitution lines (CSSLs), has facilitated the identification and utilization of valuable genetic variations for rice improvement. Furthermore, advances in molecular breeding techniques, including marker-assisted selection and CRISPR/Cas9 genome editing, have significantly contributed to the progress in rice breeding programs.

Future research should focus on expanding the genomic resources available for all *Oryza* species to ensure comprehensive utilization of their genetic potential. The establishment of PSRefSeqs for every *Oryza* species will set a new standard for integrating crop wild relatives into improvement programs. Additionally, the development of efficient tissue culture, transformation, and genome editing systems for wild rice species will be crucial for their *de novo* domestication and subsequent breeding efforts. Research should also aim to systematically evaluate and utilize the genetic diversity present in wild and cultivated rice species to identify novel allelic variations and quantitative trait loci (QTLs) associated with important agronomic traits. Moreover, the integration of advanced molecular techniques, such as next-generation sequencing and CRISPR/Cas9, into breeding programs will enhance the precision and efficiency of trait introgression and gene discovery.

The genetic resources from wild and cultivated *Oryza* species hold immense potential for addressing the challenges of sustainable rice production and food security. By leveraging the genetic diversity and adaptive traits present in these species, researchers and breeders can develop rice varieties that are more resilient to biotic and abiotic stresses, thereby ensuring stable and increased yields. The continued advancement in genomic technologies and molecular breeding techniques will play a pivotal role in unlocking the full potential of these genetic resources. Collaborative efforts among scientists, breeders, and policymakers will be essential to translate these research findings into practical applications that benefit global rice production and contribute to food security for the growing population.

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

References

Acevedo-Siaca L., Dionora J., Laza R., Quick W., and Long S., 2021, Dynamics of photosynthetic induction and relaxation within the canopy of rice and two wild relatives, Food and Energy Security, 10(3): e286.
https://doi.org/10.1002/fes3.286

Ahmad M., 2022, Genomics and transcriptomics to protect rice (*Oryza sativa* L.) from abiotic stressors: -pathways to achieving zero hunger, Frontiers in Plant Science, 13: 1002596.
https://doi.org/10.3389/fpls.2022.1002596

Angeles-Shim R., Shim J., Vinarao R., Lapis R., and Singleton J., 2020, A novel locus from the wild allotetraploid rice species *Oryza* latifolia Desv, confers bacterial blight (*Xanthomonas Oryzae* pv. *Oryzae*) resistance in rice (*O. sativa*), PLoS One, 15(2): e0229155.
https://doi.org/10.1371/journal.pone.0229155

Badri J., Lakshmidevi G., JaiVidhya L., Prasad M., Laha G., Lakshmi V., Isetty S., Padmashree R., Balakrishnan D., Varanasi Y., Jukanti A., Singh U., Singh V., Kumar A., Ram T., Rao L., and Sundaram R., 2022, Multiparent-derived marker-assisted introgression lines of the elite Indian rice cultivar 'Krishna Hamsa' show resistance against bacterial blight and blast and tolerance to drought, Plants, 11(5): 622.
https://doi.org/10.3390/plants11050622

Chen E., Huang X., Tian Z., Wing R., and Han B., 2019, The genomics of Oryza species provides insights into rice domestication and heterosis, Annual Review of Plant Biology, 70(1): 639-665.
https://doi.org/10.1146/annurev-arplant-050718-100320

Chen L., Lee D., Song Z., Suh H., and Lu B., 2004., Gene flow from cultivated rice (*Oryza* sativa) to its weedy and wild relatives, Annals of Botany, 93(1): 67-73.
https://doi.org/10.1093/AOB/MCH006

Eizenga G., Sanchez P., Jackson A., Edwards J., Hurwitz B., Wing R., and Kudrna D., 2017, Genetic variation for domestication-related traits revealed in a cultivated rice Nipponbare (*Oryza sativa* ssp. *japonica*)×ancestral rice *O.*, *nivara* mapping population, Molecular Breeding, 37: 1-22.
https://doi.org/10.1007/s11032-017-0734-5

Gautam R., Singh P., Sakthivel K., Venkatesan K., Rao S., Srikumar M., Vijayan J., Rakesh B., Ray S., Akhtar J., Meena B., Langyan S., Ali S., and Krishnamurthy S., 2023, Marker-assisted enhancement of bacterial blight (Xanthomonas *Oryza*e pv., *Oryza*e) resistance in a salt-tolerant rice variety for sustaining rice production of tropical islands, Frontiers in Plant Science, 14: 1221537.
https://doi.org/10.3389/fpls.2023.1221537

Gouda G., Gupta M., Donde R., Mohapatra T., Vadde R., and Behera L., 2020, Marker-assisted selection for grain number and yield-related traits of rice (*Oryza sativa* L.), Physiology and Molecular Biology of Plants, 26: 885-898.
https://doi.org/10.1007/s12298-020-00773-7

He R., Salvato F., Park J., Kim M., Nelson W., Balbuena T., Willer M., Crow J., May G., Soderlund C., Thelen J., and Gang D., 2014, A systems-wide comparison of red rice (*Oryza longistaminata*) tissues identifies rhizome specific genes and proteins that are targets for cultivated rice improvement, BMC Plant Biology 14: 1-21.
https://doi.org/10.1186/1471-2229-14-46

Huang C., Chen Z., and Liang C., 2021, *Oryza* pan-genomics: A new foundation for future rice research and improvement, Crop Journal, 9(3): 622-632.
https://doi.org/10.1016/J.CJ.2021.04.003

Jena K., and Nissila E., 2017, Genetic improvement of rice (*Oryza sativa* L.), Genetic Improvement of Tropical Crops, 2017: 111-127.
https://doi.org/10.1007/978-3-319-59819-2_4

Kumar A., Kumar R., Sengupta D., Das S., Pandey M., Bohra A., Sharma N., Sinha P., Sk H., Ghazi I., Laha G., and Sundaram R., 2020, Deployment of genetic and genomic tools toward gaining a better understanding of rice-*Xanthomonas Oryza*e pv. *Oryza*e interactions for development of durable bacterial blight resistant rice, Frontiers in Plant Science, 11: 1152.
https://doi.org/10.3389/fpls.2020.01152

Li W., Li K., Huang Y., Shi C., Hu W., Zhang Y., Zhang Q., Xia E., Hutang G., Zhu X., Liu Y., Liu Y., Tong Y., Zhu T., Huang H., Zhang D., Zhao Y., Jiang W., Yuan J., Niu Y., Gao C., and Gao L., 2020, SMRT sequencing of the *Oryza rufipogon* genome reveals the genomic basis of rice adaptation, Communications Biology, 3(1): 167.
https://doi.org/10.1038/s42003-020-0890-8

Mahajan R., and Kapoor N., 2019, Molecular breeding strategies for genetic improvement in rice (*Oryza sativa* L.), advances in plant breeding strategies, Cereals, 5: 317-341.
https://doi.org/10.1007/978-3-030-23108-8_8

Melaku G., Labroo M., Liyu H., Shilai Z., Guangfu H., Jing Z., Tesfaye K., Haileselassie T., and Hu F., 2019, Genetic diversity and differentiation of the African wild rice (*Oryza longistaminata* chev., et roehr) in Ethiopia, Scientific African, 6: e00138.
https://doi.org/10.1016/j.sciaf.2019.e00138

Mishra R., Joshi R., and Zhao K., 2018, Genome editing in rice: recent advances challenges and future implications, Frontiers in Plant Science, 9: 1361.
https://doi.org/10.3389/fpls.2018.01361

Mussurova S., Al-Bader N., Zuccolo A., and Wing R., 2020, Potential of platinum standard reference genomes to exploit natural variation in the wild relatives of rice, Frontiers in Plant Science, 11: 579980.
https://doi.org/10.3389/fpls.2020.579980

Quan R., Wang J., Hui J., Bai H., Lyu X., Zhu Y., Zhang H., Zhang Z., Li S., and Huang R., 2018, Improvement of salt tolerance using wild rice genes, Frontiers in Plant Science, 8: 2269.
https://doi.org/10.3389/fpls.2017.02269

Ricachenevsky F., and Sperotto R., 2016, Into the wild: *Oryza* species as sources for enhanced nutrient accumulation and metal tolerance in rice, Frontiers in Plant Science, 7: 974.
https://doi.org/10.3389/fpls.2016.00974

Solis C., Yong M., Vinarao R., Jena K., Holford P., Shabala L., Zhou M., Shabala S., and Chen Z., 2020, Back to the wild: on a quest for donors toward salinity tolerant rice, Frontiers in Plant Science, 11: 323.
https://doi.org/10.3389/fpls.2020.00323

Tarang A., Kordrostami M., Kumleh A., Chaleshtori M., Saravani A., Ghanbarzadeh M., and Sattari M., 2020, Study of genetic diversity in rice (*Oryza sativa* L.) cultivars of Central and Western Asia using microsatellite markers tightly linked to important quality and yield related traits, Genetic Resources and Crop Evolution, 67: 1537-1550.
https://doi.org/10.1007/s10722-020-00927-2

Wambugu P.W., Ndjiondjop M., N., and Henry R., 2021, Genetics and genomics of African rice (*Oryza glaberrima* Steud) domestication, Rice, 14(1): 6.
https://doi.org/10.1186/s12284-020-00449-6

Wambugu P., Ndjiondjop M., and Henry R., 2019, Advances in molecular genetics and genomics of African rice (*Oryza glaberrima* Steud), Plants, 8(10): 376.
https://doi.org/10.3390/plants8100376

Wang D., Kantar M., Murugaiyan V., and Neyhart J., 2023, Where the wild things are: genetic associations of environmental adaptation in the *Oryza rufipogon* species complex, Genes Genomes Genetics, 13(8): jkad128.
https://doi.org/10.1093/g3journal/jkad128

Withanawasam D., Kommana M., Pulindala S., Eragam A., Moode V., Kolimigundla A., Puram R., Palagiri S., Balam R., and Vemireddy L., 2022., Improvement of grain yield under moisture and heat stress conditions through marker-assisted pedigree breeding in rice (*Oryza sativa* L.), Crop and Pasture Science, 73(4): 356-369.
https://doi.org/10.1071/CP21410

Xu Y., Ma K., Zhao Y., Wang X., Zhou K., Yu G., Li C., Li P., Yang Z., Xu C., and Xu S., 2021, Genomic selection: a breakthrough technology in rice breeding, The Crop Journal, 9(3): 669-677.
https://doi.org/10.1016/J.CJ.2021.03.008

Yu H., Lin T., Meng X., Du H., Zhang J., Liu G., Chen M., Jing Y., Kou L., Li X., Gao Q., Liang Y., Liu X., Fan Z., Liang Y., Cheng Z., Chen M., Tian Z., Wang Y., Chu C., Zuo J., Wan J., Qian Q., Han B., Zuccolo A., Wing R., Gao C., Liang C., and Li J., 2021, A route to *de novo* domestication of wild allotetraploid rice, Cell, 184(5): 1156-1170.
https://doi.org/10.1016/j.cell.2021.01.013

Yuan R., Zhao N., Usman B., Luo L., Liao S., Qin Y., Nawaz G., and Li R., 2020, Development of chromosome segment substitution lines (CSSLs) derived from Guangxi wild rice (*Oryza rufipogon* Griff.) under rice (*Oryza sativa* L.) background and the identification of QTLs for plant architecture agronomic traits and cold tolerance, Genes,11(9): 980.
https://doi.org/10.3390/genes11090980

Zafar K., Sedeek K., Rao G., Khan M., Amin I., Kamel R., Mukhtar Z., Zafar M., Mansoor S., and Mahfouz M., 2020, Genome editing technologies for rice improvement: progress prospects and safety concerns, Frontiers in Genome Editing, 2: 5.
https://doi.org/10.3389/fgeed.2020.00005

Zhang F., Wang C., Li M., Cui Y., Shi Y., Wu Z., Hu Z., Wang W., Xu J., and Li Z., 2021., The landscape of gene-CDS-haplotype diversity in rice (*Oryza sativa* L.): properties population organization footprints of domestication and breeding and implications in genetic improvement, Molecular Plant, 14(5): 787-804.
https://doi.org/10.1016/j.molp.2021.02.003

Zhang J., Sun B., Li C., Chen W., Jiang L., Lv S., Fan Z., and Pan D., 2020, Molecular diversity and genetic structure of wild rice accessions (*Oryza rufipogon* Griff.) in Guangdong Province China as revealed by SNP markers, Genetic Resources and Crop Evolution, 68: 969-978. https://doi.org/10.1007/s10722-020-01038-8

Zhang Y., Zhou J., Xu P., Li J., Deng X., Deng W., Yang Y., Yu Y., Pu Q., and Tao D., 2022, A Genetic resource for rice improvement: introgression library of agronomic traits for all AA genome *Oryza* species, Frontiers in Plant Science, 13: 856514. https://doi.org/10.3389/fpls.2022.856514

Zhou J., Yang Y., Lv Y., Pu Q., Li J., Zhang Y., Deng X., Wang M., Wang J., and Tao D., 2022, Interspecific hybridization is an important driving force for origin and diversification of Asian cultivated rice *Oryza sativa* L., Frontiers in Plant Science, 13: 932737. https://doi.org/10.3389/fpls.2022.932737