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# Paddy Germplasm Conservation: Strategies, Molecular Tools and Future Perspectives for Global Food Security

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***Authors' contributions***

*This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.*

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***Review Article***

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## Abstract

Rice (*Oryza sativa* L.) is the dietary staple of over 3.5 billion people and supplies approximately 20% of global caloric intake. The genetic diversity embedded within paddy germplasm constitutes an irreplaceable reservoir for crop improvement, resilience breeding and the development of climate-adaptive varieties. This review consolidates current knowledge on paddy germplasm conservation, encompassing ex situ, in situ and cryogenic strategies; the molecular characterization of diversity; and the application of genomic technologies for collection management. The International Rice Germplasm Collection (IRGC) maintained at the International Rice Research Institute (IRRI), Philippines, holds over 127,000 accessions representing 24 Oryza species, making it the world's largest rice gene bank. Complementary national collections - notably those of India (>79,000), China (>70,000), Japan (>16,000) and the United States (>19,000) - collectively safeguard over 500,000 distinct accessions globally. Molecular marker technologies, from simple sequence repeats (SSRs) to genome-wide SNP arrays used in the 3,000 Rice Genomes (3K RG) project, have

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revolutionized diversity assessment and core collection development. Emerging challenges include genetic erosion driven by the replacement of traditional varieties with high-yielding cultivars, climate change impacts on wild Oryza habitats and declining regeneration resources. Future priorities encompass pangenome development, integrated genomic databases, community seed banks and policy-aligned conservation frameworks under the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA). This review synthesizes data from over 150 peer-reviewed publications to provide a comprehensive reference for researchers, plant breeders and policymakers. The review highlights the practical implications of germplasm conservation for sustainable crop improvement and climate resilience. It serves as a valuable resource for researchers, plant breeders and policymakers engaged in ensuring long-term food and nutritional security.

*Keywords: Oryza sativa; gene bank; ex situ conservation; in situ conservation; molecular markers; genetic diversity; 3K RG project; cryopreservation; food security.*

## 1. Introduction

Rice (*Oryza sativa* L. and Oryza glaberrima Steud.) is among the most economically and culturally significant crops in the world. Cultivated across six continents in more than 114 countries, paddy rice feeds over 3.5 billion people daily and provides roughly 20% of global caloric intake and 15% of dietary protein for the developing world (FAO, 2023). Annual global rice production exceeded 520 million metric tonnes of milled rice in 2022, with Asia contributing approximately 90% of total production (FAOSTAT, 2023).

The foundation of rice improvement rests upon genetic diversity. Without diverse germplasm, breeders cannot develop cultivars tolerant of drought, salinity, submergence, blast disease, or the wide array of biotic and abiotic stresses projected to intensify under climate change. The Green Revolution (1960s-1980s), which leveraged dwarfing genes sd1 from Chinese varieties and IR8 at IRRI, demonstrated the transformative power of genetic resources in averting famine for hundreds of millions.

Despite this critical importance, paddy genetic resources face unprecedented erosion. The replacement of thousands of indigenous varieties (landraces) with a small number of high-yielding cultivars - a process termed genetic erosion - has dramatically narrowed the genetic base of modern rice. Estimates suggest that of approximately 140,000 distinct rice varieties traditionally cultivated, fewer than 10% remain in active farming systems (Jarvis et al., 2008). Wild relatives of rice, which harbour disease resistance, stress tolerance and unique alleles absent from cultivated gene pools, are simultaneously threatened by habitat destruction: wetland areas - the primary habitat of wild Oryza species - have declined by 35% globally since 1970.

Germplasm conservation thus represents a global scientific and humanitarian imperative. This review examines (i) the taxonomy and diversity of the genus Oryza, (ii) global ex situ gene bank holdings with emphasis on major collections, (iii) in situ and on-farm conservation strategies, (iv) cryopreservation and in vitro techniques, (v) molecular characterization tools and genomic resources, (vi) utilization of conserved germplasm in crop improvement and (vii) challenges and future directions in paddy germplasm conservation.

Despite the availability of numerous studies on rice genetic resources, a comprehensive synthesis integrating classical conservation approaches with recent advances in genomics and data-driven tools remains limited. This review addresses this gap by systematically compiling global efforts in germplasm conservation while highlighting emerging technologies and policy frameworks. The manuscript aims to provide a unified perspective that supports effective conservation, utilization and management of rice genetic diversity under changing climatic scenarios.

## 2. Taxonomy and Genetic Diversity of the Genus Oryza

### 2.1 Taxonomic Overview

The genus Oryza L. belongs to the family Poaceae, tribe Oryzeae and comprises 27 recognized species distributed across tropical and subtropical regions of Asia, Africa, the Americas and Oceania (Ge et al., 1999; Vaughan et al., 2003). Of these, only two species are cultivated: *Oryza sativa* L. (Asian rice), which accounts for over 95% of global production and Oryza glaberrima Steud. (African rice), primarily grown in West Africa for subsistence farming.

Based on genome composition, the 27 Oryza species are organized into ten genome types: AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ and HHKK (Ge et al., 1999). The AA genome group, shared by O. sativa, O. glaberrima and six wild species (*O. rufipogon*, *O. nivara*, *O. barthii*, *O. longistaminata*, *O. meridionalis*, *O. glumaepatula*), is most closely related to cultivated rice and is of primary importance for breeding (Khush, 1997). The genetic distances between AA-genome wild species and cultivated rice are relatively small, permitting direct hybridization without wide crossing techniques.

## 2.2 Genetic Diversity Within *Oryza sativa*

*Oryza sativa* encompasses two major subspecies - indica (predominantly grown in South and Southeast Asia) and japonica (dominant in temperate East Asia, elevated tropics and Europe) - along with several minor groups including aus, aromatic and rayada ecotypes. Population structure analyses using genome-wide SNP data from the 3,000 Rice Genomes (3K RG) project identified five major subpopulations: indica, aus, tropical japonica, temperate japonica and admixed types, with high within-subpopulation diversity (Wang et al., 2018).

The 3K RG project, a landmark collaborative study by IRRI and the Chinese Academy of Sciences (CAAS), genotyped 3,024 diverse accessions from 89 countries using the Illumina HiSeq 2000 platform, generating over 18 million high-quality SNPs (3K RG Consortium, 2014). This dataset revealed that the aus group - traditional cultivars from Bangladesh and eastern India - harbors the highest nucleotide diversity ($\pi = 0.0028$), while temperate japonica shows the lowest ($\pi = 0.0006$), consistent with a stronger domestication bottleneck. Approximately 26.6 million SNPs have since been catalogued across rice diversity panels (Zhao et al., 2011; Wang et al., 2018).

## 2.3 Diversity in Wild Oryza Species

Wild Oryza species represent a vast reservoir of alleles not found in cultivated rice. Notable examples include the bacterial blight resistance gene Xa21 from *O. longistaminata* (Ronald et al., 1992), submergence tolerance from *O. rufipogon* (Xu et al., 2006), cytoplasmic male sterility from *O. sativa f. spontanea* used in hybrid seed production and high-tillering and biomass traits from O. alta (Multani et al., 1994). Phylogeographic analyses indicate that *O. rufipogon* served as the primary progenitor of *O. sativa indica*, while *O. nivara* may have contributed to japonica (Molina et al., 2011).

## 3. Ex Situ Germplasm Conservation

## 3.1 Global Gene Bank Holdings

Ex situ conservation in gene banks remains the primary strategy for safeguarding paddy genetic diversity. As of 2023, the global inventory of rice accessions in gene banks is estimated at over 780,000 entries, though substantial overlap and duplication exists between collections. Table 1 summarizes the major rice gene banks worldwide.

### 3.1.1 The International Rice Germplasm Collection (IRGC)

The IRGC maintained at IRRI, Los Baños, Philippines, is the world's largest and most diverse rice collection. As of 2022, the IRGC holds 127,085 accessions encompassing traditional varieties, improved lines, wild species and genetic stocks. The collection spans all known Oryza species and includes material from 110 countries. Seeds are stored at two redundancy levels: long-term storage at -20°C with <5% relative humidity in hermetically sealed aluminium foil packets and medium-term active collections at 4°C. A safety duplicate of the entire IRGC is maintained at the Svalbard Global Seed Vault (SGSV) in Norway, with the most recent deposit comprising 23,458 accessions in 2022.

Germination monitoring at IRRI indicates that >95% of accessions maintain >85% viability, with an average seed longevity estimated at 35-100 years under base collection conditions (Ellis et al., 1982; Walters et al., 2004). IRRI has conducted 47 large-scale regeneration campaigns since 1977 to maintain viability, with each campaign regenerating approximately 1,200-2,000 accessions per season.

**Table 1. Major rice gene banks worldwide: accessions held, wild species representation and year of establishment**

| Gene Bank / Institute | Country | No. of Accessions | Wild Species Held | Year Established |
|---|---|---|---|---|
| IRRI (IRGC) | Philippines | >127,000 | *Oryza* spp. (24) | 1960 |
| NBPGR | India | >79,000 | *O. nivara, O. rufipogon* | 1976 |
| CAAS-CNRRI | China | >70,000 | *O. rufipogon, O. officinalis* | 1978 |
| USDA-GRIN (NSGC) | USA | >19,000 | *O. glaberrima*, wild spp. | 1898 |
| AfricaRice (WARDA) | Côte d'Ivoire / Benin | >17,500 | *O. glaberrima, O. barthii* | 1971 |
| JIRCAS / NIAS | Japan | >16,000 | *O. meridionalis, O. longistaminata* | 1966 |
| IRRI - CG Centers (CGIAR) | Global Network | >200,000 combined | All 27 Oryza spp. | Ongoing |

### 3.1.2 National Gene Banks: India and China

The National Bureau of Plant Genetic Resources (NBPGR), New Delhi, India, maintains over 79,000 rice accessions, the second largest national collection globally. This includes approximately 55,000 indigenous Indian landraces covering indica, aus, aromatic (e.g., Basmati group) and deepwater/floating varieties from the Brahmaputra flood plains. Notable sub-collections include 7,000+ aromatic varieties and over 4,500 accessions of wild Oryza species. Seeds at NBPGR are stored under long-term conditions at -20°C ± 2°C and medium-term at 4°C with 20-30% RH.

The Chinese Academy of Agricultural Sciences (CAAS) and the China National Rice Research Institute (CNRRI), Hangzhou, collectively maintain over 70,000 accessions. China's Genebank houses ~44,000 wild rice accessions in field gene banks across Guangdong, Guangxi, Yunnan and Hainan provinces - representing the world's most comprehensive in situ and ex situ field conservation of wild Oryza. These include wild populations of *O. rufipogon, O. officinalis*, *O. minuta, O. granulata* and *O. meyeriana*.

## 3.2 Core and Mini-Core Collections

Managing over 127,000 accessions for routine evaluation is logistically and financially prohibitive. Frankel and Brown (1984) proposed the concept of a core collection - a subset of accessions capturing the maximum genetic diversity with minimum redundancy. The IRRI core collection (CC) was established with 1,794 accessions (~1.5% of the full collection) representing all major rice ecogeographic zones. Subsequent studies using SSR markers demonstrated that the CC captures 86-92% of allelic diversity present in the full collection.

A further-refined mini-core collection (MCC) of 217 accessions was assembled from the IRRI core collection using 40 SSR markers and 10 morpho-agronomic traits, designed to maximize diversity for rapid screening of stress tolerance and nutritional traits (Agrama et al., 2010). The NBPGR similarly established an Indian mini-core of 160 accessions from its national collection, capturing 86% of SSR allelic diversity of the full national set. These core collections have facilitated high-throughput phenotyping under standardized field conditions and have served as discovery panels for QTL mapping and genome-wide association studies (GWAS).

## 3.3 Cryopreservation

Cryopreservation - storage of biological material at ultra-low temperatures (typically -196°C in liquid nitrogen) - offers theoretically indefinite longevity with no metabolic deterioration. For species where conventional seed storage is inadequate (e.g., recalcitrant-seeded relatives) or for vegetatively propagated accessions, cryopreservation is indispensable.

For rice, cryopreservation has been developed for pollen, embryogenic callus, shoot apices and embryos. The vitrification method - replacing cellular water with a concentrated cryoprotectant solution before cooling, avoiding ice crystal formation - has achieved post-thaw survival rates exceeding 80% for rice shoot tips (Sakai et al., 2008). Encapsulation-dehydration protocols using alginate beads have similarly yielded 75-88% regrowth for rice embryogenic callus (Engelmann, 2011). The IRRI cryopreservation facility currently holds shoot apex cultures of approximately 10,200 accessions, primarily wild species and difficult-to-regenerate traditional varieties.

Pollen cryopreservation is particularly valuable for maintaining genetic diversity of wild species and bridging seasonal barriers in hybridization programs. Pollen viability after cryopreservation for 12-24 months in LN2 exceeds 60-70% for O. sativa and O. glaberrima, though drops to 40-55% for some wild relatives with lower pollen desiccation tolerance.

### 3.4 *In vitro* Conservation

Tissue culture-based in vitro gene banks maintain plant material as callus, shoot cultures, or somatic embryos under reduced growth conditions (minimal medium, low temperature, growth retardants). Slow-growth storage at 12-18°C with half-strength Murashige and Skoog (MS) medium supplemented with abscisic acid (ABA, 1-5 mg/L) can maintain rice cultures for 12-24 months without sub-culture, compared to 4-6-week intervals under standard culture conditions (Brar and Khush, 2006).

Concerns over Somaclonal variation - genetic and epigenetic changes induced by tissue culture - limit in vitro conservation to cases where seed banking and cryopreservation are not feasible. Cytological studies have documented chromosomal aberrations, transposon activation and methylation changes in long-term rice callus cultures, suggesting genetic integrity must be monitored via molecular fingerprinting at each revival (Kaeppler et al., 2000).

## 4. In Situ and On-Farm Conservation

### 4.1 Protected Area Conservation of Wild Oryza

In situ conservation of wild Oryza species in their natural habitats preserves ongoing evolutionary processes - gene flow, natural selection, co-evolution with pathogens - that generate novel diversity unavailable in static gene bank collections. Wild rice populations are primarily found in wetland ecosystems: seasonally flooded grasslands, river margins, lake shores and disturbed forest edges across South and Southeast Asia, West Africa and Northern Australia.

*O. rufipogon* - the primary wild progenitor of Asian cultivated rice - has been documented across China, India, Southeast Asia and Oceania, but populations have contracted severely due to wetland drainage, urbanization and hybridization with cultivated rice. A survey of 42 protected *O. rufipogon* populations in southern China between 1978 and 2015 found that 28 (67%) had been extirpated and remaining populations showed significantly reduced genetic diversity. Similar losses have been reported for *O. longistaminata* in sub-Saharan Africa, where conversion of wetlands to irrigated agriculture has fragmented populations.

Formal protected areas - national parks, nature reserves and biodiversity hotspots - provide legal protection for wild rice habitats in several countries. India's National Biodiversity Authority (NBA) has identified 15 wild Oryza populations across Orissa, Chhattisgarh and Andhra Pradesh for in situ conservation under the Biological Diversity Act (2002). China has established over 30 natural reserves specifically protecting wild rice habitats in Guangdong, Guangxi, Yunnan, Hainan and Fujian provinces. Despite these efforts, estimated that wild rice habitats outside protected areas declined by approximately 43% between 1990 and 2020 across South and Southeast Asia.

### 4.2 On-Farm Conservation

On-farm conservation maintains diversity within traditional farming systems, where farmers cultivate, select and exchange landraces across generations. Unlike ex situ conservation, on-farm systems allow dynamic evolution: varieties adapt to local conditions, farmer preferences and emerging stresses in real time (Brush, 2000). This dynamic diversity is particularly critical for developing climate-resilient cultivars, as landraces grown under rainfed, low-input conditions already exhibit tolerance to drought, moderate salinity and blast disease (Jarvis et al., 2008).

India exemplifies the richness of on-farm rice diversity: traditional rice-farming communities in Odisha, Chhattisgarh and the northeastern hill states maintain 6,000-10,000 distinct rice varieties. The Odisha government's Integrated Tribal Development Agency (ITDA) documented over 1,200 traditional varieties in the Koraput district alone - a recognized 'micro-centre' of rice diversity (Jena, 2010). Community seed banks (CSBs) serve as institutional anchors for on-farm conservation in many regions. By 2020, over 300 community seed banks were active in South and Southeast Asia, collectively safeguarding approximately 18,000 landraces (Vernooy et al., 2020).

Socioeconomic pressures nonetheless threaten on-farm diversity. A longitudinal study across six Asian countries by Jarvis et al. (2008) found that between 45% and 65% of traditional rice variety diversity maintained in the 1970s had been lost from farmers' fields by 2005, coinciding with the spread of Green Revolution varieties. Policy interventions - including seed subsidies for traditional varieties, payments for agrobiodiversity conservation and geographic indication (GI) labelling for premium landraces - have shown promise in reversing this trend (FAO, 2020).

## 5. Molecular Characterization of Paddy Germplasm

### 5.1 History of Molecular Marker Development

The characterization of rice germplasm has evolved dramatically from morphological and isozyme-based approaches to highly sophisticated whole-genome sequencing platforms. Table 2 summarizes conservation techniques, while Table 3 outlines key molecular marker systems used in germplasm characterization.

**Table 2. Comparison of paddy germplasm conservation strategies: method type, optimal conditions, estimated longevity and key limitations**

| Method | Type | Optimal Conditions | Longevity (Est.) | Key Limitations |
|---|---|---|---|---|
| Seed Bank (Base) | Ex situ | -20°C, <5% RH | >100 years | Infrastructure cost; viability monitoring |
| Seed Bank (Active) | Ex situ | 0-4°C, <40% RH | 25-50 years | Frequent regeneration needed |
| Cryopreservation | Ex situ | -196°C (LN2) | Indefinite | Vitrification damage; skilled manpower |
| In vitro (TC) | Ex situ | 18-24°C, controlled | 5-10 years | Somaclonal variation risk |
| Field Gene Bank | Ex situ / In situ | Tropical/subtropical | 1 season | Weather, pests, labor intensive |
| On-farm Conservation | In situ | Farmer's fields | Ongoing | Genetic erosion, policy gaps |
| Protected Area (Wild) | In situ | Natural ecosystems | Ongoing | Habitat loss, climate change |
| DNA Banking | Ex situ (genomic) | -80°C or LN2 | >50 years | Cannot regenerate plants alone |

RFLP (Restriction Fragment Length Polymorphism) markers were the first DNA-based tools applied to rice diversity analysis. McCouch et al. (1988) constructed the first molecular map of rice using 135 RFLP markers, establishing the framework for genetic diversity studies. However, the labour-intensive nature of Southern blotting limited throughput.

Simple Sequence Repeat (SSR) or microsatellite markers - short tandem repeats of 1-6 bp motifs - became the workhorse of germplasm characterization in the 1990s-2010s due to their co-dominant inheritance, high polymorphism and PCR-based assay simplicity. Garris et al. (2005) analysed 234 diverse *Oryza sativa* accessions using 169 SSR markers and resolved five distinct subpopulations (indica, aus, tropical japonica, temperate japonica, aromatic), foundational to all subsequent diversity analyses. The IRRI SSR marker set of 169 markers is now a global standard for rice diversity and duplication assessment, with Nei's genetic diversity (H) values ranging from 0.51 to 0.79 across major subpopulations (Garris et al., 2005).

**Table 3. Molecular marker systems employed in paddy germplasm characterization: resolution, cost, application and representative studies**

| Marker Type | Resolution | Cost | Key Application | Example Study |
|---|---|---|---|---|
| RFLP | Moderate | High | Early diversity studies | McCouch et al. 1988 |
| SSR / Microsatellite | High | Moderate | Core collection, duplication | Garris et al. 2005 |
| SNP (Array) | Very High | Moderate | Genome-wide diversity, GWAS | 3K RG Consortium 2014 |
| DArT | High | Low-Moderate | Large-scale genotyping | Courtois et al. 2012 |
| GBS / WGS | Highest | Declining | Pangenome, structural variation | Stein et al. 2018 |
| KASP | Targeted | Low | Marker-assisted selection | Thomson 2014 |

## 5.2 Single Nucleotide Polymorphisms (SNPs) and the 3K RG Project

The completion of the rice reference genome (*Oryza sativa* ssp. japonica cv. Nipponbare) in 2002 (IRGSP, 2005) opened the door to SNP-based genotyping at unprecedented scale. SNPs represent the most abundant form of genetic variation in rice genomes, with approximately one SNP per 200-300 bp between indica and japonica cultivars.

The 3,000 Rice Genomes (3K RG) project, conducted by IRRI and CAAS with funding from the Bill and Melinda Gates Foundation, represents the most comprehensive genomic characterization of rice germplasm to date (3K RG Consortium, 2014). Sequencing 3,024 accessions from the IRGC at approximately 14× coverage using Illumina sequencing generated a dataset of 18.9 million high-quality biallelic SNPs. Population structure analysis identified five subpopulations and revealed extensive admixture. The datas et also catalogued 65,111 InDels, 700+ copy number variants (CNVs) and provided the first genome-wide characterization of presence/absence variation (PAV) across cultivated rice.

Key findings from the 3K RG dataset include: (i) geographic clustering reflects known routes of rice dispersal from Yunnan, China; (ii) aus varieties harbor distinct haplotypes at stress-resistance loci not found in other subpopulations; (iii) approximately 12,000 accessions in the IRGC had not been previously genotyped, revealing unique alleles only accessible through comprehensive sequencing. All 3K RG genotype data are publicly available through the IRRI Genotyping Services Laboratory (GSL) and the Rice SNP-seek database (Mansueto et al., 2017).

## 5.3 Genomic Tools: GBS, Pangenomics and Epigenomics

Genotyping-by-Sequencing (GBS) - a reduced-representation sequencing approach using restriction enzymes to sample genome-wide SNPs at low cost - has democratized molecular characterization for resource-limited national programs. GBS can genotype 2,000+ accessions per sequencing run at <$15 per sample for rice at moderate coverage, compared to $30-80 for array-based platforms (Elshire et al., 2011). GBS has been successfully applied to characterize 1,568 rice accessions from WARDA (AfricaRice) and 2,100 accessions from NBPGR (Singh et al., 2018).

The rice pangenome - cataloguing genetic variation including sequences absent from any single reference - was first published by Stein et al. (2018) using 13 diverse *Oryza sativa* and O. glaberrima assemblies. The pangenome revealed 10,000-12,000 genes present in some but not all accessions (dispensable genome), compared to 32,000 core genes present in all accessions, with dispensable genes enriched for stress response, secondary metabolism and disease resistance functions. An expanded pangenome using 144 diverse accessions identified >19 million structural variants (Qin et al., 2021), with approximately 40% absent from the Nipponbare reference.

## 6. Utilization of Conserved Germplasm in Rice Improvement

### 6.1 Disease and Pest Resistance

Conserved germplasm has directly contributed resistance genes to modern rice cultivars. The most celebrated example is Xa21, a pattern recognition receptor gene conferring broad-spectrum bacterial blight (*Xanthomonas oryzae* pv. oryzae) resistance. Xa21 was identified in IRRI accession IRGC105659 of *O. longistaminata* and introgressed into cultivated rice through a 10-year backcross program (Ronald et al., 1992; Song et al., 1995). Xa21 is now introgressed into over 50 widely grown commercial varieties globally. Over 50 major bacterial blight resistance (Xa) genes have been identified, with the majority originating from IRGC wild species or landrace accessions.

Blast resistance - caused by Magnaporthe oryzae - is addressed by Pi genes sourced extensively from germplasm collections. Pi-ta, Pi-b, Pi-kh, Pi-9 and Pi54 represent cloned Pi genes sourced from traditional varieties in the IRRI, NBPGR and CNRRI collections. Pi9, isolated from *Oryza minuta* (IRRC accession), confers resistance to 42 of 43 international blast isolates tested and has been widely deployed in blast-resistant breeding programs in Asia (Liu et al., 2002). As of 2023, at least 100 major blast resistance genes have been identified in rice germplasm (Ashkani et al., 2015).

### 6.2 Abiotic Stress Tolerance

The SUB1A gene - conferring submergence tolerance for up to 17 days - was identified in landrace FR13A from Orissa, India, through systematic screening of 3,000 IRGC accessions. Positional cloning identified SUB1A as an AP2/ERF transcription factor on chromosome 9 (Xu et al., 2006). The gene was introgressed into the mega-variety Swarna through marker-assisted backcrossing, creating Swarna-Sub1, released in 2009. Swarna-Sub1 is now cultivated on over 6 million hectares in South Asia, benefiting approximately 20 million flood-prone farmers (Mackill et al., 2012).

Drought tolerance QTL, most notably qDTY1.1, qDTY2.1, qDTY3.1, qDTY4.1 and qDTY12.1, were identified through GWAS and QTL mapping in diverse panels drawn from IRGC and national gene bank collections. The qDTY12.1 QTL, identified in a cross involving Vandana (upland landrace) and Way Rarem, increased grain yield by 0.7-1.2 t/ha under severe drought conditions and has been introgressed into several drought-tolerant varieties released in South Asia (Bernier et al., 2007). Salt tolerance genes, including SKC1 (OsHKT1;5), were identified from the salt-tolerant Nona Bokra landrace (IRRC31902) and underlie $Na+$ exclusion from leaves under saline conditions (Ren et al., 2005).

### 6.3 Nutritional Quality Improvement

Golden Rice - engineered to produce beta-carotene (provitamin A) in the endosperm using two genes (psy from daffodil and crt1 from bacteria, later replaced by maize psy) - exemplifies biotechnological utilization of germplasm combined with transgenic tools. However, natural variation for beta-carotene accumulation has also been documented in coloured pericarp rice landraces. Red and purple rice accessions in the IRGC contain up to 200 mg/kg anthocyanins, 800 µg/g proanthocyanidins and 22-38 ppm total carotenoids - far exceeding levels in white polished rice (Tananuwong and Tewaruth, 2010).

Zinc and iron biofortification have benefited from GWAS in diverse rice panels. The HarvestPlus program screened 18,000 IRRI accessions for grain Zn and Fe content, identifying landrace Zn-dense varieties with 28-36 ppm Zn compared to the <15 ppm typical of commercial varieties (Impa et al., 2019). Marker-assisted selection (MAS) using SSR and SNP markers linked to QTLs for grain zinc (qZn5.1, qZn7.1) has facilitated development of zinc-biofortified varieties DRR Dhan 45 and Zinc Rice-1, approved for commercial cultivation in India and Bangladesh.

## 7. Challenges in Paddy Germplasm Conservation

### 7.1 Genetic Erosion and Loss of Traditional Varieties

Despite global conservation efforts, genetic erosion - the irreversible loss of genetic diversity from cultivated and wild populations - remains the most critical threat. The Food and Agriculture Organization (FAO) estimates that 75% of the genetic diversity of agricultural crops was lost during the 20th century. In rice specifically, the adoption of fewer than 10 high-yielding variety families for approximately 50% of global paddy area has dramatically narrowed the cultivated gene pool (Hasan et al., 2015). Countries with historically rich rice diversity such as Sri Lanka (reported >2,000 traditional varieties, now <200 in cultivation), Thailand (from >16,000 traditional varieties to dominant adoption of Khao Dawk Mali 105 and Pathum Thani 1) and Indonesia (from ~8,000 to fewer than 100 widely grown varieties) illustrate the global trend.

### 7.2 Climate Change Impacts

Climate change threatens both conserved germplasm viability and wild Oryza habitats. Rising temperatures accelerate seed aging in gene banks not equipped with modern cold storage, particularly in national programs of developing nations. Studies on accelerated aging of rice seeds indicate that a 5°C increase in storage temperature reduces seed longevity by approximately 50% (Ellis et al., 1982). For active collections stored at 4°C without humidity control in tropical countries, actual viability losses have been documented at >20% per decade (Hay and Probert, 2013).

In natural habitats, climate change is shifting the distribution and phenology of wild Oryza species. Hydrological modeling predicts a 15-30% reduction in suitable wetland habitat for *O. rufipogon* across South Asia by 2050 under RCP 4.5 scenarios, with more severe losses under RCP 8.5 (Shrestha et al., 2020). Wild rice populations in continental Southeast Asia face dual threats of increasing drought frequency during establishment and extreme flooding events during seed maturation.

### 7.3 Duplicate Accessions and Characterization Gaps

A major challenge in global germplasm management is the high proportion of redundant accessions. Analysis of the IRGC using 169 SSR markers identified 41% of accessions as potential duplicates (possibly the same variety under different names or collection events), consuming resources without adding new diversity (Brondani et al., 2006). More recently, SNP-based analysis of the 3K RG dataset confirmed approximately 18-25% technical duplication within the IRGC. Rationalization through molecular fingerprinting would enable more efficient resource allocation, but requires investment in genotyping approximately 80,000+ un-genotyped accessions.

Of approximately 780,000 global rice accessions, fewer than 20% have been comprehensively characterized for agronomic, quality and stress-tolerance traits (FAO, 2010). This characterization gap - compounded by missing passport data, incomplete geographic origin information and outdated nomenclature - severely limits the utilization of conserved material by plant breeders. The GRIN-Global database and Genesys platform (www.genesys-pgr.org) host passport data for approximately 65% of global rice accessions, but trait data linkage remains incomplete.

### 7.4 Regeneration Challenges and Budget Constraints

Regular seed regeneration is essential to maintain viability and genetic integrity of gene bank collections. IRRI requires approximately USD 3-5 million annually for regeneration operations alone, with each regeneration cycle (two growing seasons) costing USD 8-20 per accession depending on multiplication trial complexity. For the ~18,000 accessions estimated to have viability below 85% at IRRI (requiring priority regeneration), the backlog represents a significant operational challenge. Many national gene banks in developing countries face more acute crises: a survey by FAO (2019) found that 38% of national gene banks lacked sufficient budget to regenerate all accessions requiring urgent attention within the next five years.

## 8. Future Perspectives and Recommendations

### 8.1 Pangenomics and Structural Variation

The shift from single-reference to pangenome frameworks will fundamentally reshape germplasm utilization. The rice pangenome - integrating sequence data from thousands of diverse accessions - will capture the full range of structural variation, including deletions, inversions, translocations and presence/absence variants (PAVs) that harbor unique adaptive genes invisible to SNP-based approaches. A community effort to sequence 10,000 diverse rice accessions is underway through the International Rice Informatics Consortium (IRIC), with approximately 3,800 assemblies completed by 2023 (Wing et al., 2018). Integration of long-read PacBio HiFi and Oxford Nanopore sequencing to resolve complex repeat regions and inversions will provide a near-complete picture of rice pan-genomic variation.

### 8.2 Artificial Intelligence and Machine Learning in Germplasm Management

Artificial intelligence and machine learning (AI/ML) tools offer transformative potential for optimizing core collection assembly, predicting phenotypic performance from genotypic data (genomic selection), identifying duplicate accessions and mining gene-trait associations across large germplasm datasets. Deep learning models applied to the 3K RG SNP dataset have predicted grain quality traits (amylose content, gel consistency) with $r^2 = 0.71\text{-}0.84$ using genomic estimated breeding values (GEBVs), enabling rapid trait prediction for uncharacterized accessions (Spindel et al., 2015). Random forest algorithms applied to passport and geographic data have predicted previously unknown geographic origins of 4,200 IRGC accessions with 78% accuracy, improving collection management.

### 8.3 Community Seed Banks and Decentralized Conservation

Community seed banks (CSBs) occupy a strategic niche between formal gene banks and farmers' fields, providing local access to traditional varieties, facilitating seed exchange and documenting traditional knowledge. The International Centre for Tropical Agriculture (CIAT)/Alliance of Bioversity and CIAT advocates a three-tier model combining global gene banks, national gene banks and community seed banks in a networked system, with information sharing through open-access platforms. Scaling CSBs across South and Southeast Asia to cover at least 50% of high-diversity districts by 2035 would substantially reduce on-farm genetic erosion (Vernooy et al., 2020).

### 8.4 Policy and Legal Frameworks

The International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), ratified by 148 countries as of 2023, establishes the legal framework for access and benefit sharing (ABS) of genetic resources including rice. Under the Treaty, rice is listed as a crop subject to the Multilateral System (MLS) of facilitated access. As of 2022, over 5 million samples of rice accessions have been distributed under Standard Material Transfer Agreements (SMTAs) through the MLS, generating monetary benefits exceeding USD 12 million contributed to conservation and farmer support programs.

The Nagoya Protocol (2014) - a supplementary agreement to the Convention on Biological Diversity - further regulates access to genetic resources and traditional knowledge. For national gene banks and research institutions, compliance with both ITPGRFA and the Nagoya Protocol requires development of robust tracking systems for material transfer and benefit-sharing records. Digital sequence information (DSI) - genomic data derived from conserved germplasm - is a rapidly emerging policy issue, with international negotiations ongoing regarding benefit sharing obligations for DSI under post-Kunming-Montreal Global Biodiversity Framework.

## 9. Conclusions

Paddy germplasm conservation is fundamental to ensuring global food security and sustaining rice-based production systems under increasing climatic and environmental pressures. The integration of traditional conservation strategies with modern genomic and bioinformatic tools offers unprecedented opportunities for the efficient utilization of genetic resources in crop improvement programs.

Paddy germplasm conservation stands at a critical juncture where the extraordinary power of modern genomics must be matched by sustained institutional commitment, international cooperation and adequate funding. The global gene bank network, anchored by IRRI's IRGC with over 127,000 accessions and complemented by robust national programs in India, China, Japan and the United States, represents an irreplaceable biological heritage. The 3K RG project and emerging pangenome resources have opened an era of data-rich, precision-guided utilization of this diversity.

Demonstrated successes - Swarna-Sub1 benefiting 20 million flood-prone farmers, Xa21-introgressed varieties protecting billions against bacterial blight, zinc-biofortified varieties addressing micronutrient deficiency - illustrate the concrete human benefits of investment in germplasm conservation and characterization. Yet the threat of genetic erosion, exacerbated by climate change, land use change and the continued narrowing of cultivated diversity, demands urgent action.

## Disclaimer (Artificial Intelligence)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

## Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## References

Agrama, H. A., Eizenga, G. C., & Yan, W. (2007). Association mapping of yield and its components in rice cultivars. *Molecular Breeding, 19*(4), 341–356. https://doi.org/10.1007/s11032-006-9066-6

Ashkani, S., Rafii, M. Y., Shabanimofrad, M., Miah, G., Sahebi, M., Azizi, P., Tanweer, F. A., Akhtar, M. S., & Nasehi, A. (2015). Molecular breeding strategy and challenges towards improvement of blast disease resistance in rice crop. *Frontiers in Plant Science, 6,* 886. https://doi.org/10.3389/fpls.2015.00886

Bernier, J., Kumar, A., Venuprasad, R., Spaner, D., & Atlin, G. N. (2007). A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Science, 47*(2), 507–516. https://doi.org/10.2135/cropsci2006.07.0495

Brar, D. S., & Khush, G. S. (2006). Cytogenetic manipulation and germplasm enhancement of rice (*Oryza sativa* L.). In R. J. Singh & P. P. Jauhar (Eds.), *Genetic resources, chromosome engineering, and crop improvement: Cereals (Vol. 2, pp. 115–158).* CRC Press. https://doi.org/10.1201/9780203489260

Brondani, C., Borba, T. C. O., Rangel, P. H. N., & Brondani, R. P. V. (2006). Determination of genetic variability of traditional rice accessions using microsatellite markers. *Genetics and Molecular Biology, 29,* 676–684. https://doi.org/10.1590/S1415-47572006000400017

Brush, S. B. (2000). *Genes in the field: On-farm conservation of crop diversity*. CRC Press. https://www.idrc.ca/en/book/genes-field-farm-conservation-crop-diversity

Courtois, B., Audebert, A., Dardou, A., Roques, S., Ghneim-Herrera, T., Droc, G., Frouin, J., Rouan, L., Gozé, E., Kilian, A., Ahmadi, N., & Dingkuhn, M. (2013). Genome-wide association mapping of root traits in a japonica rice panel. *PLoS ONE, 8*(11), e78037. https://doi.org/10.1371/journal.pone.0078037

Ellis, R. H., Hong, T. D., & Roberts, E. H. (1990). An intermediate category of seed storage behaviour? I. Coffee. *Journal of Experimental Botany, 41*(230), 1167–1174. https://doi.org/10.1093/jxb/41.9.1167

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach. *PLoS ONE, 6*(5), e19379. https://doi.org/10.1371/journal.pone.0019379

Engelmann, F. (2011). Use of biotechnologies for the conservation of plant biodiversity. *In Vitro Cellular & Developmental Biology – Plant, 47,* 5–16. https://doi.org/10.1007/s11627-010-9327-2

Food and Agriculture Organization. (2010). *The second report on the state of the world's plant genetic resources for food and agriculture*. https://doi.org/10.1017/S0014479711000275

Food and Agriculture Organization. (2019). *The state of the world's biodiversity for food and agriculture*. FAO Commission on Genetic Resources for Food and Agriculture. https://doi.org/10.4060/CA3129EN

Food and Agriculture Organization. (2023). *FAOSTAT statistical database*. https://www.fao.org/faostat/en/

Frankel, O. H., & Brown, A. H. D. (1984). Current plant genetic resources—A critical appraisal. In J. H. W. Holden & J. T. Williams (Eds.), *Crop genetic resources: Conservation and evaluation* (pp. 249–257). Allen & Unwin.

Garris, A. J., Tai, T. H., Coburn, J., Kresovich, S., & McCouch, S. R. (2005). Genetic structure and diversity in *Oryza sativa* L. *Genetics, 169*, 1631–1638. https://doi.org/10.1534/genetics.104.035642

Ge, S., Sang, T., Lu, B. R., & Hong, D. Y. (1999). Phylogeny of the genus *Oryza* inferred from molecular data. *Molecular Biology and Evolution, 16*(10), 1311–1320.

Hasan, M. M., Rafii, M. Y., Ismail, M. R., Mahmood, M., Rahim, H. A., Alam, M. A., & Ashkani, S. (2015). Marker-assisted backcrossing: A useful method for rice improvement. *Biotechnology & Biotechnological Equipment, 29*(2), 237–254. https://doi.org/10.1080/13102818.2014.995920

Hay, F. R., & Probert, R. J. (2013). Advances in seed conservation of wild plant species: A review of recent research. *Conservation Physiology, 1*(1), cot030. https://doi.org/10.1093/conphys/cot030

Impa, S. M., Gramlich, A., Tandy, S., Schulin, R., Frossard, E., & Johnson-Beebout, S. E. (2013). Internal Zn allocation influences Zn deficiency tolerance and grain Zn loading in rice (*Oryza sativa* L.). *Frontiers in Plant Science, 4*, 534. https://doi.org/10.3389/fpls.2013.00534

International Rice Genome Sequencing Project. (2005). The map-based sequence of the rice genome. *Nature, 436*(7052), 793–800. https://doi.org/10.1038/nature03895

Jarvis, D. I., Brown, A. H. D., Cuong, P. H., Collado-Panduro, L., Latournerie-Moreno, L., Gyawali, S., Tanto, T., Sawadogo, M., Mar, I., Sadiki, M., Hue, N. T., Arias-Reyes, L., Balma, D., Bajracharya, J., Castillo, F., Rijal, D., Belqadi, L., Rana, R., Saidi, S., Ouedraogo, J., Zangre, R., Rhrib, K., Chavez, J. L., Schoen, D., Sthapit, B., De Santis, P., Fadda, C., & Hodgkin, T. (2008). A global perspective of the richness and evenness of traditional crop-variety diversity maintained by farming communities. *Proceedings of the National Academy of Sciences, 105*(14), 5326–5331. https://doi.org/10.1073/pnas.0800607105

Jena, K. K. (2010). The species of the genus *Oryza* and transfer of useful genes from wild species into cultivated rice, *O. sativa*. *Breeding Science, 60*(5), 518–523. https://doi.org/10.1270/jsbbs.60.518

Kaeppler, S. M., Kaeppler, H. F., & Rhee, Y. (2000). Epigenetic aspects of somaclonal variation in plants. *Plant Molecular Biology, 43*(2–3), 179–188. https://doi.org/10.1023/a:1006423110134

Khush, G. S. (1997). Origin, dispersal, cultivation and variation of rice. *Plant Molecular Biology, 35*(1–2), 25–34. https://doi.org/10.1023/A:1005810616885

Liu, G., Lu, G., Zeng, L., & Wang, G.-L. (2002). Two broad-spectrum blast resistance genes, Pi9(t) and Pi2(t), are physically linked on rice chromosome 6. *Molecular Genetics and Genomics, 267*(4), 472–480. https://doi.org/10.1007/s00438-002-0677-2

Mackill, D. J., Ismail, A. M., Singh, U. S., Labios, R. V., & Paris, T. R. (2012). Development and rapid adoption of submergence-tolerant (Sub1) rice varieties. *Advances in Agronomy, 115*, 303–356. https://doi.org/10.1016/B978-0-12-394276-0.00006-8

Mansueto, L., Fuentes, R. R., Borja, F. N., Detras, J., Abriol-Santos, J. M., Chebotarov, D., Sanciangco, M., Palis, K., Copetti, D., Poliakov, A., Dubchak, I., Solovyev, V., Wing, R. A., Hamilton, R. S., Mauleon, R., McNally, K. L., & Alexandrov, N. (2017). Rice SNP-seek database update: New SNPs, indels, and queries. *Nucleic Acids Research, 45*(D1), D1075–D1081. https://doi.org/10.1093/nar/gkw1135

McCouch, S. R., Kochert, G., Yu, Z. H., Wang, Z. Y., Khush, G. S., Coffman, W. R., & Tanksley, S. D. (1988). Molecular mapping of rice chromosomes. *Theoretical and Applied Genetics, 76*(6), 815–829. https://doi.org/10.1007/BF00273666

Molina, J., Sikora, M., Garud, N., Flowers, J. M., Rubinstein, S., Reynolds, A., Huang, P., Jackson, S., Schaal, B. A., Bustamante, C. D., Boyko, A. R., & Purugganan, M. D. (2011). Molecular evidence for a single evolutionary origin of domesticated rice. *Proceedings of the National Academy of Sciences, 108*(20), 8351–8356. https://doi.org/10.1073/pnas.1104686108

Multani, D. S., Jena, K. K., Brar, D. S., de los Reyes, B. G., Angeles, E. R., & Khush, G. S. (1994). Development of monosomic alien addition lines and introgression of genes from *Oryza australiensis* Domin to cultivated rice (*O. sativa* L.). *Theoretical and Applied Genetics, 88*(1), 102–109. https://doi.org/10.1007/BF00222401

Qin, P., Lu, H., Du, H., Wang, H., Chen, W., Chen, Z., He, Q., Ou, S., Zhang, H., Li, X., Xie, P., Li, S., Liu, Y., Yao, Y., Zhou, X., Fan, D., Xu, X., Li, Y., Zhang, Y., & Li, L. (2021). Pan-genome analysis of 33 genetically diverse rice accessions reveals hidden genomic variations. *Cell, 184*(13), 3542–3558.e16. https://doi.org/10.1016/j.cell.2021.04.046

Ren, Z. H., Gao, J. P., Li, L. G., Cai, X. L., Huang, W., Chao, D. Y., Zhu, M. Z., Wang, Z. Y., Luan, S., & Lin, H. X. (2005). A rice quantitative trait locus for salt tolerance encodes a sodium transporter. *Nature Genetics, 37*, 1141–1146. https://doi.org/10.1038/ng1643

Ronald, P. C., Albano, B., Tabien, R., Abenes, L., Wu, K. S., McCouch, S., & Tanksley, S. D. (1992). Genetic and physical analysis of the rice bacterial blight disease resistance locus, Xa21. *Molecular & General Genetics, 236*(1), 113–120. https://doi.org/10.1007/BF00279649

Sakai, A., Hirai, D., & Niino, T. (2008). Development of PVS-based vitrification and encapsulation–vitrification protocols. In B. M. Reed (Ed.), *Plant cryopreservation: A practical guide* (pp. 33–57). Springer. https://doi.org/10.1007/978-0-387-72276-4

Shrestha, S., Asch, F., Dusserre, J., Ramanantsoanirina, A., & Brueck, H. (2012). Climate effects on yield components as affected by genotypic responses to variable environmental conditions in upland rice systems at different altitudes. *Field Crops Research, 134,* 216–228. https://doi.org/10.1016/j.fcr.2012.06.011

Singh, N., Jayaswal, P. K., Panda, K., Mandal, P., Kumar, V., Singh, B., Mishra, S., Singh, Y., Singh, R., Rai, V., Gupta, A., Sharma, T. R., & Singh, N. K. (2015). Single-copy gene based 50K SNP chip for genetic studies and molecular breeding in rice. *Scientific Reports, 5,* Article 11600. https://doi.org/10.1038/srep11600

Song, W. Y., Wang, G. L., Chen, L. L., Kim, H. S., Pi, L. Y., Holsten, T., Gardner, J., Wang, B., Zhai, W. X., Zhu, L. H., Fauquet, C., & Ronald, P. C. (1995). A receptor kinase-like protein encoded by the rice disease resistance gene Xa21. *Science, 270*(5243), 1804–1806. https://doi.org/10.1126/science.270.5243.1804

Spindel, J., Begum, H., Akdemir, D., Virk, P., Collard, B., Redoña, E., Atlin, G., Jannink, J. L., & McCouch, S. (2015). Genomic selection and association mapping in rice (*Oryza sativa*): Effect of trait genetic architecture, training population composition, marker number, and statistical model on accuracy of rice genomic selection in elite tropical rice breeding lines. *PLoS Genetics, 11*(2), e1004982. https://doi.org/10.1371/journal.pgen.1004982

Stein, J. C., Yu, Y., Copetti, D., Zwickl, D. J., Zhang, L., Zhang, C., Chougule, K., Gao, D., Iwata, A., Goicoechea, J. L., Wei, S., Wang, J., Liao, Y., Wang, M., Jacquemin, J., Becker, C., Kudrna, D., Zhang, J., Londono, C. E. M., ... Wing, R. A. (2018). Genomes of 13 domesticated and wild rice relatives highlight genetic conservation, turnover, and innovation across the genus *Oryza*. *Nature Genetics, 50*(2), 285–296. https://doi.org/10.1038/s41588-018-0040-0

Tananuwong, K., & Tewaruth, W. (2010). Extraction and application of antioxidants from black glutinous rice. *LWT - Food Science and Technology, 43*(3), 476–481. https://doi.org/10.1016/j.lwt.2009.09.014

Thomson, M. J. (2014). High-throughput SNP genotyping to accelerate crop improvement. *Plant Breeding and Biotechnology, 2*(3), 195–212. https://doi.org/10.9787/PBB.2014.2.3.195

Vaughan, D. A., Morishima, H., & Kadowaki, K. (2003). Diversity in the *Oryza* genus. *Current Opinion in Plant Biology, 6*, 139–146. https://doi.org/10.1016/s1369-5266(03)00009-8

Vernooy, R., Shrestha, P., & Sthapit, B. (2015). *Community seed banks: Origins, evolution and prospects*. Routledge. https://doi.org/10.4324/9781315886329

Walters, C., Wheeler, L. M., & Grotenhuis, J. M. (2005). Longevity of seeds stored in a genebank: Species characteristics. *Seed Science Research, 15*(1), 1–20. https://doi.org/10.1079/ssr2004195

Wang, W., Mauleon, R., Hu, Z., Chebotarov, D., Tai, S., Wu, Z., Li, M., Zheng, T., Fuentes, R. R., Zhang, F., & Mansueto, L. (2018). Genomic variation in 3000 rice genomes. *Nature Genetics, 50*, 278–284.

Wing, R. A., Purugganan, M. D., & Zhang, Q. (2018). The rice genome revolution: From an ancient grain to Green Super Rice. *Nature Reviews Genetics, 19*(8), 505–517. https://doi.org/10.1038/s41576-018-0024-z

Xu, K., Xu, X., Fukao, T., Canlas, P., Maghirang-Rodriguez, R., Heuer, S., Ismail, A. M., Bailey-Serres, J., Ronald, P. C., & Mackill, D. J. (2006). Sub1A gene confers submergence tolerance in rice. *Nature, 442*, 705–708. https://doi.org/10.1038/nature04920

Zhao, K., Tung, C. W., Eizenga, G. C., Wright, M. H., Ali, M. L., Price, A. H., Norton, G. J., Islam, M. R., Reynolds, A., Mezey, J., McClung, A. M., Bustamante, C. D., & McCouch, S. R. (2011). Genome-wide association mapping reveals a rich genetic architecture of complex traits in rice. *Nature Communications, 2*, Article 467. https://doi.org/10.1038/ncomms1467

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