**Genetic Significance of IR64: Exploring Diversity and Traits in Modern Rice Breeding**

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**Abstract**   
In the 1960s and 1970s, the International Rice Research Institute (IRRI) and other organizations developed rice varieties that had high yields. These varieties were beneficial for farmers and the general public since they increased the amount of rice produced and reduced its price for consumers. Despite these advantages, early high-yielding varieties lacked the cooking quality of traditional counterparts. A breakthrough occurred in 1985 with IRRI's release of IR64, an indica rice variety in the Philippines. IR64 not only exhibited high yield, early maturity, and disease resistance but also matched the excellent cooking quality of traditional varieties. Rapidly adopted, IR64 was cultivated on over 10 million hectares within two decades. Featuring characteristics such as moderate amylose content, gelatinization temperature, and a pleasant flavour, it demonstrated resistance to blast, bacterial blight, and the brown planthopper. In addition to being cultivated, IR64 received significant attention in scientific research and underwent comprehensive genetic analysis. Through backcross breeding, valuable genes were introduced, making it crucial in thousands of crosses. Although the cultivation area of IR64 has declined in the last decade, it has been surpassed by a new generation of superior varieties, many of which are either descendants or closely related to IR64. The ongoing research on IR64 and its related varieties has the potential to reveal complex genetic pathways that govern the desirable features highly prized by rice producers and consumers.

**Introduction**

Rice is a staple food that requires significant irrigation water and is consumed by more than half of the population (Shekhar et al. 2018; Verma et al. 2023a, 2023b, 2023c). Notably, in November 2016, the 50th anniversary of the introduction of IR8 marked a pivotal moment for the International Rice Research Institute (IRRI) and collaborators, signifying the inception of the Green Revolution in rice (http://irri.org/ir8). IR8, the institute's inaugural variety, laid the foundation for the widespread cultivation of high-yielding varieties (HYVs) across major rice-growing regions. Despite its notable high grain yield, IR8 exhibited critical drawbacks, including subpar grain quality, susceptibility to diseases and pests, and delayed maturity. Subsequent varieties developed and released in the following two decades made significant strides in overcoming these limitations (Khush 1999).

In the early 1980s, IR36 emerged as a prominent choice among farmers (Shekhar et al. 2017, 2018, 2019, 2020, 2021a, 2021b, 2021c, 2022, 2023a, 2023b; Shekhar 2022). Boasting disease and insect resistance, it achieved a high yield within a shorter growth period of 111 days, a notable improvement compared to the 130 days required by IR8 (Khush and Virk 2005). IR36 gained swift popularity, reaching cultivation on more than 10 million hectares during the 1980s. Despite these advancements, IR36 still fell short of the quality standards set by pre-Green Revolution varieties in the Philippines and Indonesia.

A breakthrough came with the release of IR64 in 1985 in the Philippines, marking a significant advancement by combining outstanding cooked rice palatability with the desirable traits of earlier IRRI HYVs. IR64 quickly supplanted IR36 as the preferred choice for top-notch rice, much sought after by the rice sector due to its extensive versatility, early maturation, and enhanced quality. The indica variety's popularity led to its widespread use as a representative strain in scientific investigations. Moreover, IR64 served as a pivotal progenitor in breeding initiatives and in the formation of populations for genetic scrutiny. This article delves into the evolution of IR64, elucidating its key developmental aspects, and explores its pivotal contributions to ongoing breeding efforts and rice research.

**History of breeding, assessment, and release**

Khush and Virk (2005) provide a breeding history of IR64 that begins with the IRRI careful attempts to create a variety that combines a number of desirable qualities for farmers. IRRI's Genetic Evaluation and Utilization (GEU) program, which was founded in 1977 in partnership with Khush and Coffman, was essential in incorporating features such as increased grain quality, early maturity, tolerance to biotic and abiotic stressors, and high yield.

The breeding process involved rigorous assessment of plants and breeding lines in dedicated nurseries to ensure the incorporation of multiple desirable traits into a single variety. The cross between IR5657-33-2-1 and IR2061-465-1-5-5 in 1977 yielded IR18348, with the female parent contributing good cooking quality and salinity tolerance, and the male parent being a high-yielding breeding line associated with varieties like IR28, IR29, and IR34. The origin of IR64 from 19 conventional rice varieties is shown in the whole pedigree (Fig. 1).

Illustrated in a comprehensive pedigree, IR64's derivation involves 19 traditional rice varieties. The F2 population was evaluated in 1978, and the F3 and F4 populations using the pedigree approach in 1979. Originating from the bulk harvest of an F5 family in 1980, the breeding line IR18348-36-3-3 exceeded IR36 by 21% in yield testing conducted at IRRI and the Philippine National testing between 1981 and 1983. After being released as 'IR64' in 1985 by the Philippine Seed Board, this variety is still known by that name (IRRI 1986).

Before IR64, early rice varieties from IRRI excelled in yield, disease, and insect resistance but lacked the grain quality of benchmark varieties. BPI-76 and its counterpart BPI-121, originating from the Fortuna/Seraup Besar 15 cross, set the grain quality standard in the Philippines. C4-63, derived from Peta/BPI-76, was esteemed for its quality before IR64. The short-statured breeding line BPI-121-407, known for superior quality, significantly contributed to IR64's pedigree alongside BPI-76. Taste panels were employed during the evaluation of IR18348-36-3-3 at IRRI to ensure the capture of BPI-76 quality. These taste panels also played a crucial role in the data collection for the variety's release in the Philippine government's rice program (Juliano et al. 1989; Yoshida 1981; Dalrymple 1978; Cada and Escuro 1972).

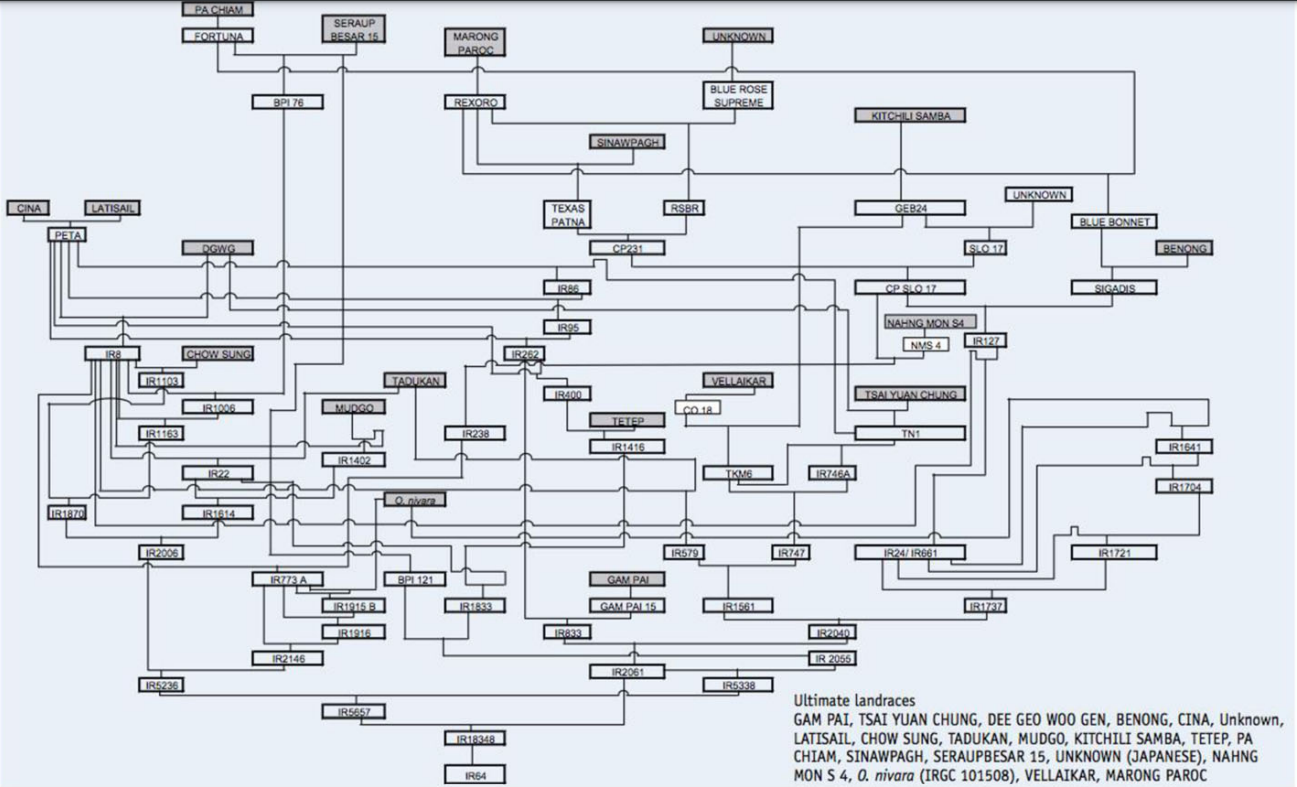


Fig. 1. The lineage of IR64 displaying the highest landraces in its lineage (Khush and Virk 2005)

**Adoption and impact**

The Philippine government introduced IR64 in 1985, which is a notable improvement as it combines the high yield, disease and pest resistance of previous IRRI types with better grain quality similar to BPI-76 and C4-63. Bhutan, Burkina Faso (as FKR42), Cambodia, China, Ecuador (as NIAP11), Gambia, India, Indonesia, Mauritania, Mozambique, and Vietnam (as OM89) were among the many nations that adopted IR64 (Khush and Virk 2005). IR64 shown extraordinary adaptability, thriving in West Africa's Sahelian areas as well as Southeast and South Asia (Devries et al. 2011; Julia and Dingkuhn 2013).

By 1995, IR64 covered an estimated 8 million hectares, surpassing 10 million hectares in the early 2000s. According to Champagne et al. (2010), its exceptional eating quality had a significant role in its lasting appeal. In the Philippines, however, cultivation witnessed a gradual decline from 2000 to 2007, partly due to tungro disease pressure (Laborte et al. 2015). Over 40% of Indonesia's total rice-growing land was covered by IR64 for a period of approximately ten years, and the crop was still widely used in 2009 (Brennan and Malabayabas 2011). India also embraced IR64, contributing significantly to breeder seed production, with an annual cultivation estimated at 2–3 million hectares during 1998–2015.

Though the specific impact on farmer incomes is not precisely quantified, however, in terms of cultivable area, IR64 is recognized as the most widely used cultivar, especially in tropical Asia. Its widespread adoption not only increased yields but also improved harvest quality, leading to higher market prices. Its early maturity facilitated higher cropping intensity. Importantly, IR64's seeds were freely given to researchers and farmers, following the example set by earlier IRRI cultivars, without requesting intellectual property protection for either the original variety or its offspring.

**Principal attributes and comprising essential features**

Indica rice variety IR64 is semi-dwarf and grows to a mature height of around 100 cm on average in the Philippines. It matures rather early, taking about 117 days to fully flower (Khush and Virk 2005). Carrying loss-of-function alleles for Hd1 and Ehd1, it inherits the semi-dwarf sd1 allele from Dee-geo-woo-gen, resulting in early duration and photoperiod insensitivity (Wei et al. 2016).

Upon its release, IR64 gained recognition for its resistance to various pests and diseases. IRRI (1986) highlighted its resilience to bacterial blight, grasty stunt virus, brown planthopper (BPH) biotypes 1 and 3, green leafhopper (GLH), white-backed planthopper (WBPH), and low resistance to blast, BPH biotype 2, and stem borer. Setting itself apart, IR64 was the first IRRI variety to combine intermediate gelatinization temperature (GT) with an intermediate amylose concentration.

Although IR64 has a high yield, particularly when compared to IRRI cultivars published previously, its yields are not as great as those of later varieties like as IR72 (Peng et al. 2000). IR64 has a high grain filling percentage, a high grain weight, and a comparatively low number of spikelets per m2. Its strong grain yields are attributed to important genes, such as the narrow-leaf gene (NAL1) and the GS3 gene for grain size (Ujiie et al. 2016).

In contrast to new plant type cultivars, which have smaller tiller and panicle sizes but higher tillering rates, IR64 is a high-tillering indica type cultivar (Okami et al. 2015). The main gene Bph1 is responsible for its resistance to brown planthoppers (BPH), but other quantitative trait loci (QTLs) for BPH resistance also contribute to its resistance, allowing it to withstand the disease for a longer period of time (Alam and Cohen 1998).

Exceptional resistance to blast disease is a hallmark of IR64, involving major-gene and partial resistance, with several identified resistance genes (Bastiaans and Roumen 1993; Grand et al. 2012; Roumen 1992; Sallaud et al. 2003). Additionally, IR64 exhibits resistance to bacterial blight (BB) disease, carrying the major gene Xa4 (Adhikari et al. 1994; Khush and Virk 2005), known for conferring additional agronomic benefits (Hu et al. 2017).

IR64, which thrives in irrigated rice cultivation, is vulnerable to drought stress and was not designed with abiotic stress tolerance in mind, resulting in significant yield decreases (Anantha et al. 2016). IR64 is often grown in more favorable rainfed conditions and on somewhat unfavorable soils despite its vulnerability to abiotic stressors. During blooming, it exhibits heat sensitivity and a moderate tolerance to high temperatures (Jagadish et al. 2008).

While not prevalent in current production environments, IR64 is susceptible to iron toxicity, anaerobic germination, and low temperatures at the vegetative stage. It lacks the P deficiency gene PSTOL1 and is sensitive to low phosphorus conditions (Gamuyao et al. 2012; Mori et al. 2016; Vejchasarn et al. 2016). Moreover, Impa et al. (2013) found that IR64 is disproportionately susceptible to zinc deprivation. When in the vegetative stage, IR64 shows a modest resistance to submergence since it does not have the SUB1 submergence tolerance allele (Singh et al. 2010; Singh et al. 2013). These traits collectively define IR64's agronomic characteristics and adaptability in diverse environments.

**Grain and market characteristics**

IR64 stands out for its remarkable physical appearance, characterized by long-grain structure, leading to a high head rice yield (IRRI 1986). IR64 is a trailblazing variety that is the first IRRI variety to have an intermediate gelatinization temperature (GT) and an intermediate amylose concentration. These characteristics are essential for obtaining the right cooked rice texture and satisfying South and Southeast Asian rice consumers' tastes. Despite the significance of intermediate amylose content and GT for cooking quality, the superior attributes of IR64's cooking quality were identified through taste panels, revealing the limitations of existing evaluation methods (Concepcion et al. 2015).

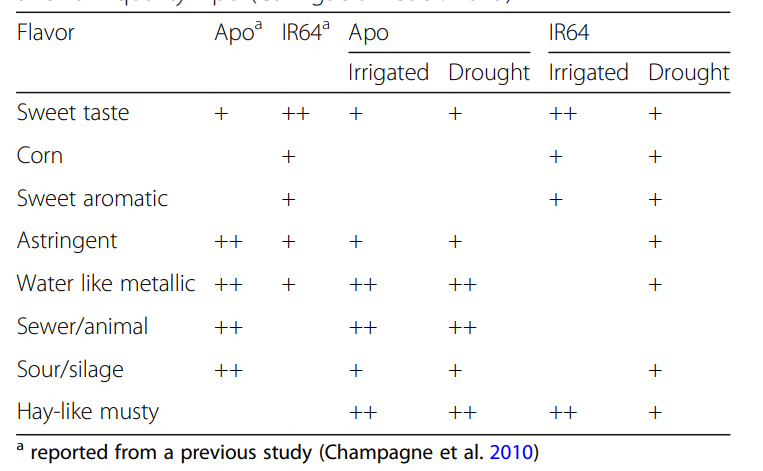
Rice texture is primarily controlled by the Wxin allele of the waxy locus (Wx) on chromosome 6, which indicates an intermediate amylose concentration in IR64 (Zhang et al. 2012). IR64 has the (CT)17 allele, which is linked to intermediate amylose content and soft to medium hardness, according to an analysis of the sequence properties of the Wx gene, including CT repeats and certain SNPs (Roferos et al. 2008; Teng et al. 2012). According to Chen et al. (2010), intermediate amylose types have a common haplotype represented by the SNPs at the Wx gene.

Comparative analysis with Azucena, another variety with intermediate amylose and GT, revealed genetic differences despite similar amylose content and GT. Using a doubled haploid population from the Azucena/IR64 hybrid, QTL identification was performed for a variety of grain quality-related variables, including properties of starch as determined by the Rapid Visco Analyzer (RVA) (Bao et al. 2002).

The higher quality of IR64 is reflected in its better taste characteristics, which include notes of maize and sweetness (Calingacion et al. 2015; Champagne et al. 2010). Comparison tests with the inferior IRRI-132 highlighted decreased yellowing, enhanced mouthfeel, texture, and greater "sweet" flavour in IR64 (Champagne et al. 2010) (Table 1). According to Calingacion et al. (2015), metabolomics research showed that IR64 has different profiles from the inferior variety Apo.

Calingacion et al. (2014) conducted a study on the preferences for grain quality in various nations and areas. The survey focused on the most popular kinds in each location and revealed dynamic consumer choices. Notably, in countries where IR64 dominates, such as Indonesia and the Philippines, diverse preferences exist, emphasizing the evolving nature of consumer choices over time.

Table 1: Comparing the taste characteristics of low-quality Apo and high-quality IR64 (Mackill and Khush 2018)



**Characteristics of the genome and genetics**

IR64 has played a pivotal role in genetic studies of rice, serving as a high-yielding and high-quality indica variety well-suited for tropical lowland growing conditions. One significant mapping population in these studies comprises about 146 lines, a doubled haploid population derived from the cross IR64/Azucena (Guiderdoni et al. 1992). This population was first used by Huang et al. (1997) to map important agronomic features, and then Wu et al. (1997) used it to map iron (Fe) toxicity tolerance. A recombinant inbred line (RIL) population of 171 families that resulted from a cross with the wild cousin O. rufipogon has been produced, and it is used to map tolerance to aluminum (Al) toxicity, among other mapping populations that use IR64 as a parent (Nguyen et al. 2003). Furthermore, to investigate the inheritance of grain structure, reciprocal chromosomal segment substitution lines (CSSL) were generated in IR64 and Koshihikari backgrounds (Nagata et al. 2015).

Although the japonica variety Nipponbare was used in the first rice genome sequencing (IRGSP 2005), further research has used IR64 in genetic analysis. IR64 was one of 20 distinct varieties that covered 100 Mb of the unique genomic fraction in the first resequencing analysis of several rice varieties (McNally et al. 2009). Along with Nipponbare and DJ123, Schatz et al. (2014) provided an extensive whole-genome de novo assembly for IR64. 37,758 genes were revealed by the 88.5% genome coverage. IR64 was found to have 381 genes that were not present in the other two types, while DJ123 and Nipponbare contained 297 and 786 unique genes, respectively.

Jain et al. (2014) achieved an 84.5% coverage of IR64's genome in whole-genome sequencing efforts, alongside Pokkali and N22. Methylation patterns were explored in IR64, comparing it with the japonica variety Dianjingyou1 and two wild ancestors (Li et al. 2012). IR64 has served as a model variety in gene expression studies, contributing to the identification of functional roles of genes. Notable investigations include drought-responsive genes (Ray et al. 2011), gene expression changes during different developmental stages (Sharma et al. 2012), and salinity tolerance (Wang et al. 2016).

**Important progeny**

High-yielding and superior indica strain that thrives in tropical lowlands, IR64 has been a mainstay in rice genetic research. Around 146 lines, a doubled haploid population obtained from the cross IR64/Azucena, make up a critical mapping population used in these investigations (Guiderdoni et al. 1992). Huang et al. (1997) used this population to map important agronomic features, while Wu et al. (1997) used it to map iron (Fe) toxicity tolerance. The mapping of resistance to aluminum (Al) toxicity has been accomplished by other mapping populations that have been formed using IR64 as a parent. For example, a recombinant inbred line (RIL) population including 171 families was created by a cross with the wild cousin O. rufipogon (Nguyen et al. 2003). In addition, Nagata et al. (2015) developed reciprocal chromosomal segment substitution lines (CSSL) in IR64 and Koshihikari backgrounds to investigate the inheritance of grain morphology.

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In the genome sequencing efforts by Jain et al. (2014), an 84.5% coverage of IR64's genome was achieved, alongside Pokkali and N22. The exploration of methylation patterns in IR64, comparing it with the japonica variety Dianjingyou1 and two wild ancestors, added another layer to its genetic characterization (Li et al. 2012). IR64 has served as a model variety in gene expression studies, contributing to the identification of functional roles of genes. Salinity tolerance (Wang et al. 2016), gene expression alterations throughout distinct developmental stages (Sharma et al. 2012), and drought-responsive genes (Ray et al. 2011) are a few notable studies.

In summary, IR64's significance in genetic studies is underscored by its involvement in mapping populations, resequencing efforts, and whole-genome assemblies. Its genomic contributions have expanded our understanding of crucial traits, paving the way for advancements in rice breeding and cultivation practices.

**Conclusions**

This concise review seeks to highlight the significance of the IR64 rice variety in the realms of rice breeding and genetics, recognizing that the available information is extensive and cannot be fully encapsulated here. At one point, IR64 was estimated to be cultivated on 9–10 million hectares annually (Laird and Kate 1999). Over roughly two decades, it has been a staple, providing high-quality rice to hundreds of millions of consumers, akin to other mega varieties like Swarna and Samba Mahsuri in India. Nonetheless, breeders have adeptly leveraged this variety to propel further advancements.

For instance, in most parts of the Philippines and Indonesia, IR64 has been succeeded by new varieties possessing similar quality attributes but enhanced agronomic traits such as disease resistance and higher grain yield. The continual evolution of rice breeding necessitates the replacement of existing varieties with improved ones over time. Even though IR64 is becoming less popular, especially in India where better kinds are progressively taking over its land, it still exists because of its offspring that are being grown or tested all throughout the region. This excellent variety has developed as a result of many important factors:

1. Broad Breeding Program: A comprehensive breeding program with a large number of yearly crossings and widely separated populations.
2. Well-Defined Objectives: Well-defined goals that emphasize essential characteristics, such as desired quality qualities.
3. Systematic Screening: Sophisticated researchers use a methodical screening process to find and include necessary qualities.
4. Use of Sensory Data Confirmation: This method uses sensory data to verify the cooked rice's quality.
5. Effective Evaluation Program: Early in the breeding phase, a proper evaluation program should be implemented to assess yield.
6. Outreach Effort: A successful outreach initiative that guarantees seed availability and the evaluation of advanced selections under farmer circumstances.

Although IR64 has been effectively superseded by other types in the Philippines and Indonesia, the problem still exists in India, where the variety is still widely used. Replacement varieties must provide definite benefits, like increased yield or stress tolerance, in order to be successful. To ensure that farmers have a market for their products, the rice processing industry's assistance is also essential in easing the transition from old to new types.

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