

Review Article

Wild rice: unlocking the future of rice breeding

Xiaoming Zheng^{1,2,3,*} , Youlin Peng⁴, Jiyue Qiao⁴, Robert Henry⁵  and Qian Qian^{1,2,4,*} ¹National Key Facility for Crop Gene Resources and Genetic Improvement, Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, Beijing, China²Sanya National Research Institute of Breeding in Hainan, Chinese Academy of Agricultural Sciences, Beijing, China³International Rice Research Institute, Metro Manila, Philippines⁴Yazhouwan National Laboratory, Sanya, China⁵University of Queensland, Brisbane, Queensland, Australia

Received 28 February 2024;

revised 16 July 2024;

accepted 17 July 2024.

*Correspondence (Tel 089837365566;

fax 089837365566; email [qianqian188@](mailto:qianqian188@hotmail.com)hotmail.com (QQ) and emailzhengxiaoming@caas.cn (XZ)

Summary

Germplasm resources serve as the foundations of advancements in breeding and are crucial for maintaining food security. Wild rice species of the genus *Oryza* include rich sources of genetic diversity and high adaptability, making them a substantial resource for rice breeding. The discovery of wild-type cytoplasmic male sterility resources enabled the achievement of the 'three lines' goal in hybrid rice, significantly increasing rice yields. The application of resistance alleles from wild rice enables rice production to withstand losses caused by stress. Reduced genetic diversity due to rice breeding poses a significant limitation to further advances and can be alleviated through a systematic use of wild genetic resources that integrate geographic, climatic and environmental data of the original habitat, along with extensive germplasm collection and identification using advanced methods. Leveraging technological advancements in plant genomics, the understanding of genetic mechanisms and the application of artificial intelligence and gene editing can further enhance the efficiency and accuracy of this process. These advancements facilitate rapid isolation and functional studies of genes, and precise genome manipulation. This review systematically summarizes the utilization of superior genes and germplasm resources derived from wild rice sources, while also exploring the collection, conservation, identification and utilization of further wild rice germplasm resources. A focus on genome sequencing and biotechnology developments is leading to new breeding and biotechnology opportunities. These new opportunities will not only promote the development of rice varieties that exhibit high yields, superior stress resistance and high quality but also expand the genetic diversity among rice cultivars.

Keywords: wild rice, germplasm resources, rice breeding, cultivated rice.

Introduction

The genus *Oryza* L., belonging to the subfamily *Oryzoideae* of the *Poaceae* Barnhart family, can be traced back ~15 million years in Asia. The genus *Oryza* may have first originated in the tropical and subtropical regions of Southeast Asia (Vaughan, 1989). The wetland environments in this area provided favourable conditions for the growth, reproduction and evolution of *Oryza* species. The *Oryza* have significant economic and ecological value, especially Asian and African rice, which are major global food crops. The genus *Oryza* comprises 24 species, encompassing 2 cultivated and 22 wild rice species (Figure 1a; Ge *et al.*, 1999; Wing *et al.*, 2018). The two cultivated rice species are Asian cultivated rice (*Oryza sativa* L.) and African cultivated rice (*Oryza glaberrima* Steud.; Figure 1a). In the past half-century, continuous efforts have been devoted to understanding the genomic composition and relationships among rice species. The 22 wild rice species can be categorized into 11 distinct chromosome groups based on chromosome karyotype analysis, encompassing six diploid types (AA, BB, CC, EE, FF and GG) and five allotetraploid types (BBCC, CCDD, HHJJ, HHKK and KKLL) (Figure 1a; Ge *et al.*, 1999; Lu

et al., 2009; Wing *et al.*, 2018; Zou *et al.*, 2008). The 22 wild rice species are primarily distributed across 77 countries and regions in Asia, Africa, Australia, the Americas and other tropical and subtropical areas (Wing *et al.*, 2018). Based on the degree of gene exchange with cultivated rice, rice genera gene sources have been categorized into three classes: primary gene sources (GP-1), secondary gene sources (GP-2) and tertiary gene sources (GP-3) (Figure 1b; Harlan and De Wei, 1971). According to Harlan and De Wet's definition of crop primary gene sources, Asian and African cultivated rice and their ancestors in cultivated rice from the primary gene pool, which includes two parts: *O. sativa*, and the current descendants of its ancestors *O. rufipogon* Griff. and *O. nivara* Sharma *et al.* Shastry; and *O. glaberrima* and its wild relative *O. barthii* A. Chev. The genetic resources of these primary gene sources will most easily provide transferable beneficial genes for the further improvement and improvement of cultivated rice varieties (Lu, 1998). The secondary gene sources include germplasm resources of AA genome species other than cultivated rice and its progenitor species, which are more closely related to cultivated rice but cannot produce normal fertile progeny through free hybridization. The tertiary gene sources

Please cite this article as: Zheng, X., Peng, Y., Qiao, J., Henry, R. and Qian, Q. (2024) Wild rice: unlocking the future of rice breeding. *Plant Biotechnol. J.*, <https://doi.org/10.1111/pbi.14443>.

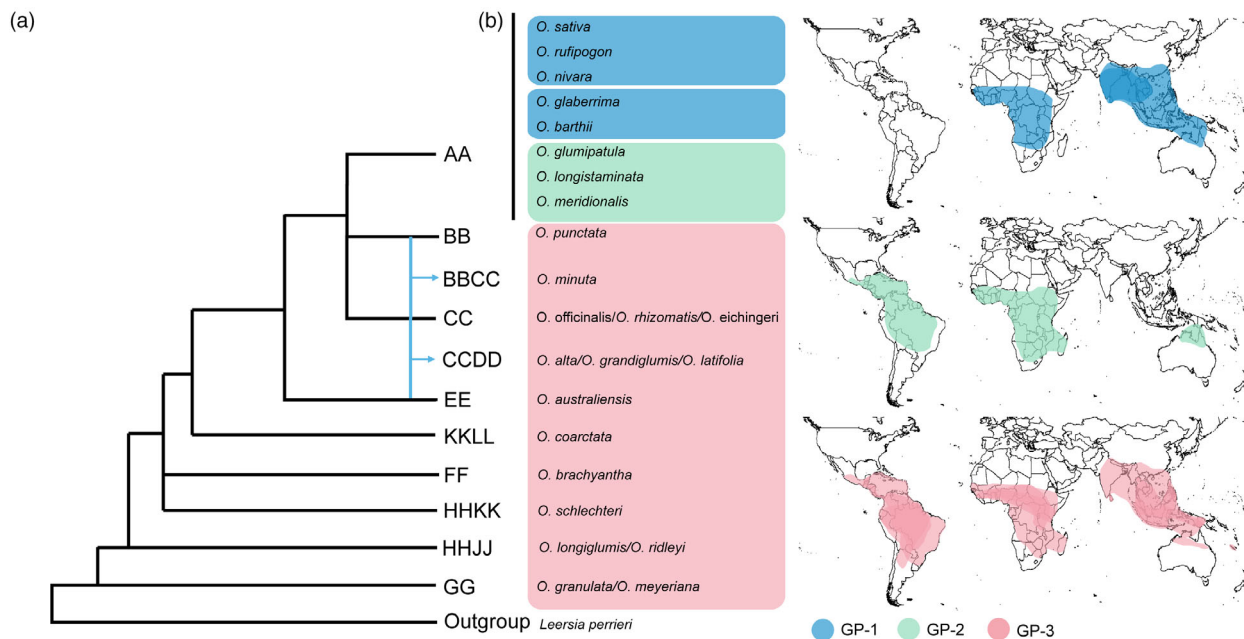


Figure 1 Phylogenetic relationships, classification and geographic distribution of species in the genus *Oryza*. (a) Phylogenetic relationships among the species of the genus *Oryza* (Lu, 1998). (b) Taxonomy and geographic distribution of species in the genus *Oryza*.

comprise species from outside the AA genome group within the genus *Oryza*, as well as other germplasm resources in the rice tribe that are distantly related to cultivated rice. These genes can only be transferred to cultivated rice using special biotechnological and genetic engineering methods, as natural gene exchange is mostly not feasible (Brar and Khush, 1997).

The *Oryza* genus has given rise to Asian cultivated rice (*O. sativa*; Vaughan *et al.*, 2003), which serves as the staple food for over half of the global population and plays a crucial role in ensuring global food security. Its total production ranks third among crops in the world. Wild rice, the precursor of cultivated rice, has evolved significant genetic diversity and robust environmental adaptability through prolonged natural selection. It preserves genetic resources absent or lost in cultivated rice, including genes for high yield and resistance to bacterial leaf blight, rice blast, drought and cold stress. Wild rice serves as a valuable genetic resource for enhancing rice varieties (Yang *et al.*, 2023). Germplasm collection of wild rice began in the late 1950s (Morishima, 2002). In the early 1970s, in response to the spread of the Green Revolution varieties, international efforts to collect local rice germplasm resources began. Subsequently, these efforts expanded to more extensive collections in rice gene banks (Vaughan *et al.*, 2003). In China, Yuan Longping, the celebrated Chinese rice expert renowned as the 'Father of Hybrid Rice', successfully hybridized rice using a wild rice plant from Hainan, China, in 1973. This breakthrough marked the onset of the 'second green revolution' in rice production, boosting yields by 20% (Yuan, 1986). China was an early adopter of wild rice resources for rice hybrid breeding. In the 1930s, Mr. Ding Ying, a rice cultivation pioneer, created Zhongshan No. 1 by crossing cultivated rice with common wild rice. This variety exhibits strong resistance to pests, diseases, stress and wide adaptability while enhancing yields, setting a precedent for Chinese rice hybrid breeding (Li *et al.*, 2009). In 1970, Yuan Longping's team, led by Li Bihu, identified male-sterile strains in common wild rice for the

first time, enabling the successful implementation of 'three-line matching' in 1973 (Yuan, 1986). Since the 1970s discovery of cytoplasmic male sterile (CMS) resources in wild rice, China has selected numerous exceptional sterile lines. These resources have yielded various sterile lines like Wild abortive-type, Honglian-type, Gambiaka and Dissi-type, D-type, K-type, Boro II-type and Maxie-type, contributing significantly to hybrid rice development. These lines have found wide application in developing super-hybrid rice, leading to a substantial increase in rice yields. However, due to significant genetic differences between distant wild rice and cultivated varieties, issues related to reproductive isolation, poor embryo development and hybrid progeny instability may arise. Researchers have addressed these challenges by employing genetic transformation, embryo rescue, protoplast fusion, anther culture and gene-editing techniques to transfer beneficial genes from select wild rice resources. Here, we highlight the significance of wild rice as a valuable resource for rice breeding and emphasize the potential of genome sequencing and biotechnology for unravelling genetic diversity, discovering novel genes and enhancing rice varieties. By integrating these resources and technologies, we can diversify rice varieties, and improve their yield, resistance and quality to address food security and sustainable agricultural development challenges.

Use of biotic stress tolerance genes from wild rice

Wild rice has played a pivotal role in enhancing rice biotic stress tolerance genes for improved productivity and stability. Notably, several rice blast resistance genes, such as the new alleles of *Pirf2-1(t)* (Utami *et al.*, 2008), *Pi40(t)* (Jeung *et al.*, 2007), *Pi9* (Qu *et al.*, 2006) and *Pi54rh* (Das *et al.*, 2012), have been identified from wild rice varieties like *O. rufipogon*, *O. glumaepatula* Steud., *O. australiensis* Domin., *O. minuta* J.S. Presl. ex C.B. Presl. and *O. rhizomatis* Vaughan, respectively (Figure 2). Among these

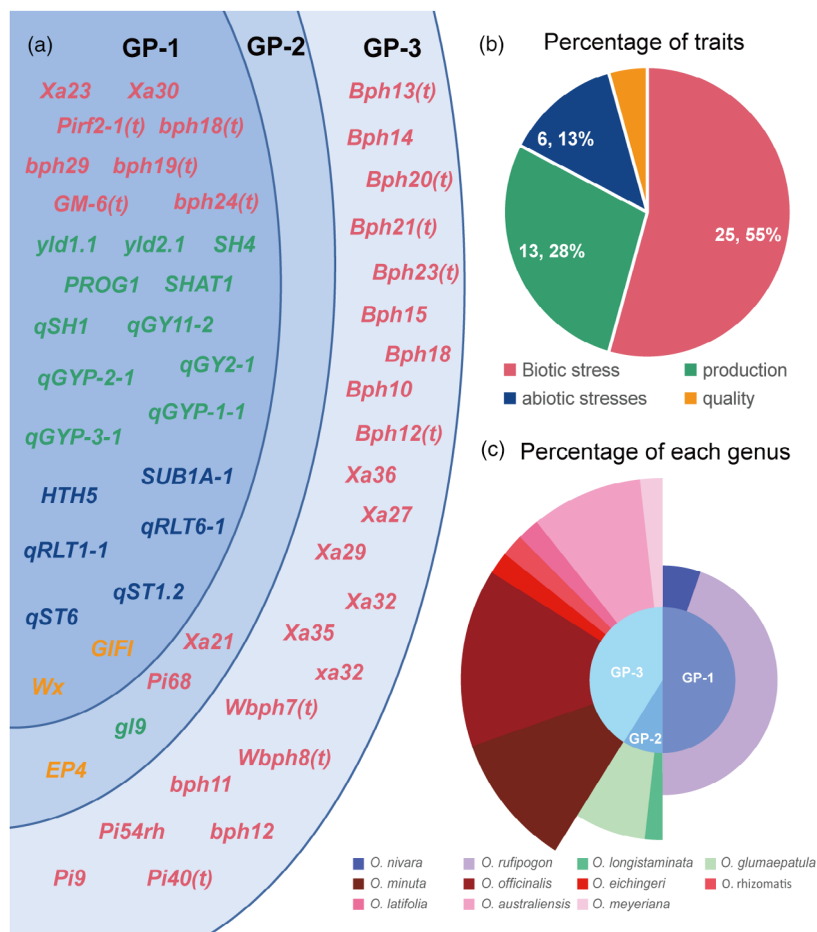


Figure 2 Genes of wild rice origin used in cultivated rice breeding. (a) Genes that have been cloned in wild rice. (b) Proportion of genes that have been applied in various traits cloned in wild rice. (c) Distribution of genes that have been cloned in wild rice among species of the genus *Oryza*.

genes, the new alleles of *Pi9* from *O. minuta* and *Pi54rh* from *O. rhizomatis* exhibit broad-spectrum resistance and are extensively utilized in breeding (Das *et al.*, 2012; Qu *et al.*, 2006). Furthermore, the new alleles of leaf blight resistance genes *Xa21*, *Xa23*, *Xa27* and *xa41(t)*, from wild rice (Figure 2; Chen *et al.*, 2020; Xing *et al.*, 2021; Yang *et al.*, 2022), have been cloned. *Xa21*, in particular, was the first gene cloned from wild rice with important functions and has gained widespread use in global rice breeding programmes to combat leaf blight (Figure 2; Yang *et al.*, 2022). Moreover, the grassy dwarf disease resistance gene *Gsv*, isolated from *Oryza nivara* (wild rice), was introduced into IR24 and other rice varieties, rendering all IR series varieties resistant to grassy dwarf disease (Li *et al.*, 2014). Additionally, at least 20 quantitative trait loci (QTLs)/genes (~40%) associated with rice planthopper resistance have been identified in wild rice varieties. For instance, the new alleles of *Bph14*, *Bph18* and *bph29* have been cloned from *O. officinalis* Wall ex Watt, *O. australiensis* and *O. rufipogon*, respectively (Figure 2, Table 1). The acquisition of resistance genes from wild rice, specifically for rice blast, leaf blight, grass clump dwarf disease and rice planthopper, has substantially bolstered rice's resistance to these pests and diseases, thereby reducing the use of pesticides, and ultimately promoting food safety.

Use of abiotic stress tolerance genes from wild rice

Wild rice genes that confer adaptation and tolerance to abiotic stresses, including high temperature, salinity, drought and low temperature, have been harnessed in rice breeding. *HTH5*, derived from the high-temperature-tolerant allele of common wild rice (*O. rufipogon*), increased *japonica* rice's setting rate by 30% at 38°C under high-temperature stress (Cao *et al.*, 2022). *O. rufipogon* offers valuable genetic resources for mitigating high-temperature-induced rice sterility. Soil salinization poses a serious threat to the rice industry (Ganie *et al.*, 2019). Studies demonstrate that wild rice genes notably enhance salt tolerance in cultivated rice (Quan *et al.*, 2018). A study of a backcross recombinant inbred line (RIL) population of *indica* rice 9311 with *O. longistaminata* A. Chev. et Roehr. identified 27 QTLs related to salt tolerance were identified, with 18 originating from *O. longistaminata* (Yuan *et al.*, 2022). The study by Prusty *et al.* demonstrated that wild species such as *O. alta*, *O. latifolia*, *O. coarctata*, *O. rhizomatis*, *O. eichingeri*, *O. minuta* and *O. grandiglumis* employ tissue tolerance mechanisms to manage salt stress (Prusty *et al.*, 2018). Drought is one of the major threats to agricultural production, and wild rice germplasm hosts numerous drought-tolerant genetic resources. Alleles from

Table 1 Useful genes that have been cloned in wild rice

ID	Gene	GP	Traits	Reference
1	<i>Xa23</i>	GP-1	Biotic stress	(Wang <i>et al.</i> , 2015a)
2	<i>Xa30</i>	GP-1	Biotic stress	(Cheema <i>et al.</i> , 2008)
3	<i>Pirf2-1(t)</i>	GP-1	Biotic stress	(Utami <i>et al.</i> , 2008)
4	<i>bph18(t)</i>	GP-1	Biotic stress	(Jena <i>et al.</i> , 2006)
5	<i>bph29</i>	GP-1	Biotic stress	(Wang <i>et al.</i> , 2015b)
6	<i>bph19(t)</i>	GP-1	Biotic stress	(Chen <i>et al.</i> , 2006)
7	<i>Gm-6(t)</i>	GP-1	Biotic stress	(Katiyar <i>et al.</i> , 2001)
8	<i>bph24(t)</i>	GP-1	Biotic stress	(Wang <i>et al.</i> , 2021)
9	<i>ylf1.1</i>	GP-1	Production	(Song <i>et al.</i> , 2005)
10	<i>ylf2.1</i>	GP-1	Production	(Swamy <i>et al.</i> , 2014)
11	<i>SH4</i>	GP-1	Production	(Li <i>et al.</i> , 2006)
12	<i>PROG1</i>	GP-1	Production	(Jin <i>et al.</i> , 2008, Tan <i>et al.</i> , 2008)
13	<i>SHAT1</i>	GP-1	Production	(Zhou <i>et al.</i> , 2012)
14	<i>qSH1</i>	GP-1	Production	(Konishi <i>et al.</i> , 2006)
15	<i>qGY11-2</i>	GP-1	Production	(Li <i>et al.</i> , 2002)
16	<i>qGYP-2-1</i>	GP-1	Production	(Chen, 2010)
17	<i>qGY2-1</i>	GP-1	Production	(He <i>et al.</i> , 2006)
18	<i>qGYP-1-1</i>	GP-1	Production	(Jing <i>et al.</i> , 2010)
19	<i>qGYP-3-1</i>	GP-1	Production	(Jing <i>et al.</i> , 2010)
20	<i>HTH5</i>	GP-1	Abiotic stresses	(Cao <i>et al.</i> , 2022)
21	<i>SUB1A-1</i>	GP-1	Abiotic stresses	(Lin <i>et al.</i> , 2023)
22	<i>qRLT1-1</i>	GP-1	Abiotic stresses	(Liu <i>et al.</i> , 2003)
23	<i>qRLT6-1</i>	GP-1	Abiotic stresses	(Liu <i>et al.</i> , 2003)
24	<i>qST1.2</i>	GP-1	Abiotic stresses	(Quan <i>et al.</i> , 2017)
25	<i>qST6</i>	GP-1	Abiotic stresses	(Quan <i>et al.</i> , 2017)
26	<i>Wx</i>	GP-1	Quality	(Yamanaka <i>et al.</i> , 2004)
27	<i>GIF1</i>	GP-1	Quality	(Wang <i>et al.</i> , 2008)
28	<i>Xa21</i>	GP-2	Biotic stress	(Song <i>et al.</i> , 1995)
29	<i>Pi68(t)</i>	GP-2	Biotic stress	(Devi <i>et al.</i> , 2020)
30	<i>gl9</i>	GP-2	Production	(Lin <i>et al.</i> , 2023a,b)
31	<i>EP4</i>	GP-2	Quality	(Zhang <i>et al.</i> , 2015)
32	<i>Bph13(t)</i>	GP-3	Biotic stress	(Jena and Kim, 2010)
33	<i>Bph14</i>	GP-3	Biotic stress	(Hu <i>et al.</i> , 2017)
34	<i>Bph20(t)</i>	GP-3	Biotic stress	(Rahman <i>et al.</i> , 2009)
35	<i>Bph21(t)</i>	GP-3	Biotic stress	(Rahman <i>et al.</i> , 2009)
36	<i>Bph23(t)</i>	GP-3	Biotic stress	(Hou <i>et al.</i> , 2011)
37	<i>Bph15</i>	GP-3	Biotic stress	(Yang <i>et al.</i> , 2004)
38	<i>Bph18</i>	GP-3	Biotic stress	(Ji <i>et al.</i> , 2016)
39	<i>Bph10</i>	GP-3	Biotic stress	(Jena <i>et al.</i> , 2006)
40	<i>Bph12(t)</i>	GP-3	Biotic stress	(Yang <i>et al.</i> , 2002)
41	<i>Xa36</i>	GP-3	Biotic stress	(Miao <i>et al.</i> , 2010)
42	<i>Xa27</i>	GP-3	Biotic stress	(Gu <i>et al.</i> , 2004)
43	<i>Xa29</i>	GP-3	Biotic stress	(Tan <i>et al.</i> , 2004a,b)
44	<i>Xa32</i>	GP-3	Biotic stress	(Zheng <i>et al.</i> , 2009)
45	<i>Xa35</i>	GP-3	Biotic stress	(Guo <i>et al.</i> , 2010)
46	<i>xa32</i>	GP-3	Biotic stress	(Zhang <i>et al.</i> , 2009)
47	<i>Wbph7(t)</i>	GP-3	Biotic stress	(Tan <i>et al.</i> , 2004a)
48	<i>Wbph8(t)</i>	GP-3	Biotic stress	(Tan <i>et al.</i> , 2004b)
49	<i>bph11</i>	GP-3	Biotic stress	(Hirabayashi <i>et al.</i> , 1999)
50	<i>bph12</i>	GP-3	Biotic stress	(Hirabayashi <i>et al.</i> , 1999)
51	<i>Pi54rh</i>	GP-3	Biotic stress	(Das <i>et al.</i> , 2012)
52	<i>Pi40(t)</i>	GP-3	Biotic stress	(Jeung <i>et al.</i> , 2007)
53	<i>Pi9</i>	GP-3	Biotic stress	(Qu <i>et al.</i> , 2006)

Dongxiang wild rice (*O. rufipogon*) can enhance drought tolerance in hybridized rice, with 11 QTLs linked to drought tolerance (Zhou, 2005). Notably, the drought tolerance gene *DROT1* likely

originated in wild rice (Sun *et al.*, 2022). Wild rice, primarily found in warm, humid tropical or subtropical regions, has evolved to become resilient to cold environments in northern regions. Dongxiang wild rice, the northernmost known wild rice, exhibits robust cold tolerance and harbours abundant cold-tolerant genes. Although the genetic features of Dongxiang wild rice resemble those of wild rice, limited research methods and experimental approaches constrain their exploration. Nevertheless, these robust cold-tolerant genes are crucial for improving cold resistance. The genetic resources within wild rice germplasm are invaluable for enhancing the stress tolerance of cultivated rice. Nonetheless, there is a scarcity of studies and practical applications for leveraging these resources to augment rice's resistance to abiotic stressors such as high temperature, salinity, drought and cold. To address challenges such as soil salinization, drought, high temperature and cold and thereby contribute to food security, it is imperative to thoroughly explore and breed stress tolerance genes within wild rice germplasm resources.

The use of genes for yield and quality from wild rice

The breeding of high-yielding rice has always been the primary goal pursued in rice breeding. The yield of rice is controlled by three key components: the number of effective panicles, the number of grains per panicle and grain weight (Xing and Zhang, 2010). Notably, multiple genes have been identified in the regulation of yield, plant architecture (e.g. *PROG1*, Tan *et al.*, 2008) and grain shattering (e.g. *SH4*, *qSH1*, *SHAT1* and *gl9*; Li *et al.*, 2006; Lin *et al.*, 2022) during rice improvement and domestication. *O. rufipogon*, the ancestor of *O. sativa* (Wang *et al.*, 2018), possesses numerous yield-regulating QTLs. The discovery and isolation of the *PROG1* (*PROG7* locus in African cultivated rice) from wild rice holds great significance in exploring the molecular basis of rice evolution and plant architecture regulation (Figure 2; Tan *et al.*, 2008). The *PROG1* gene mutation (*prog1*) during rice evolution was pivotal in the transition from the prostrate growth of wild rice to the erect growth of cultivated rice, significantly improving plant structure, grain count and overall yield. Genes associated with shattering properties like *SH4*, *qSH1* and *SHAT1* directly impact grain yield (Li *et al.*, 2006; Zhang *et al.*, 2009; Zhou *et al.*, 2012; Figure 2). In Dongxiang wild rice (*O. rufipogon*), two high-yield QTLs, *qGY2-1* and *qGY11-2*, located on chromosomes 2 and 11, respectively, increased the yield of Gui Chao 2 by 25.9% and 23.2% per plant, respectively (Li *et al.*, 2002). The *qSTGL8.0* was identified from the extremely large stigma trait in *O. longistaminata*, which increased out-crossing rate and hybrid seed production (Prahallada *et al.*, 2021). Additionally, the *gl9* from *O. glumaepatula* contributed to slender rice kernels, reduced chalkiness and increased thousand-kernel grain weight (Figure 2; Lin *et al.*, 2022). The process of rice evolution and domestication emphasizes yield enhancement. To meet the needs of a hungry world, grain morphology has been optimized and thousand-grain weight increased (Doebly *et al.*, 2006).

During the long domestication process of wild rice, humans gave priority to the yield of rice, but with the improvement of people's living standards and the changing of consumption habits, the demand for high-quality rice is increasing. Quality traits encompass protein, starch, amino acids and microelements. Wild rice is rich in minerals, vitamins, proteins, starch, dietary fibre and antioxidant phytochemicals, while also being low in fat

(Surendiran *et al.*, 2014). Currently, new alleles of *Wx* and *GIF1* related to rice quality have been identified from wild rice (Figure 2; Wang *et al.*, 2008). The *Wx* gene, located on chromosome 6, regulates amylose content and encodes granular starch synthetase. *GIF1*, which encodes a cell wall transformation enzyme and is located on chromosome 4, controls amylose content and grain filling (Wang *et al.*, 2008). Although the discovery of these genes has bolstered efforts to enhance modern rice quality (Surendiran *et al.*, 2014; Wang *et al.*, 2008), research on quality improvement genes in wild rice is limited. Wild rice garners global attention due to its antioxidant properties and potential health benefits. Compared to cultivated rice, wild rice offers higher protein content, lower fat content and abundant dietary fibre and essential amino acids, which are associated with chronic disease prevention (Chu *et al.*, 2019). Therefore, exploring antioxidants in wild rice and developing related food products may contribute to the prevention of cardiovascular diseases, cancer, autoimmune disorders and inflammatory diseases.

Genome sequencing of wild rice germplasm resources is pivotal for understanding genetic diversity, genome structure and functional genes. By performing whole-genome resequencing on 50 samples of both wild and cultivated rice samples, researchers uncovered that *O. sativa* ssp. *indica* is closely related to *O. nivara*, whereas *O. sativa* ssp. *japonica* is related to *O. rufipogon*, particularly Dongxiang wild rice in the Yangtze River Basin (Hou *et al.*, 2011; Huang *et al.*, 2012). By analysing 446 wild rice samples with varying geographical distribution and 1083 cultivated rice genomes, a detailed genetic variation map was created. This study offers profound insights into rice genome variation. Furthermore, the resequencing of 20 cultivated rice and 94 wild rice samples from Africa indicated that *O. glaberrima* closely resembles a wild rice population (OB-V) along the Niger River, which is a potential centre of rice domestication in Africa (Wang *et al.*, 2014). Comparative genomic analysis of 13 different rice species within the *Oryza* genus uncovered the emergence of new genetic elements, such as transposons and various genes, driving rapid species diversification without significant chromosomal changes. This discovery elucidates the underlying phylogenetic mechanisms within the *Oryza* genus which have evolved over time (Stein *et al.*, 2018). Analysis of domesticated rice has shown that only two functional distinct chloroplast genomes are present (Moner *et al.*, 2020), suggesting two maternal domestications in *O. sativa*, and indicating that the domestication of other chloroplast genotypes could potentially introduce new genetic variation. In conclusion, these findings provide a crucial theoretical foundation for studying rice domestication and evolutionary patterns, assessing genetic diversity in germplasm resources and accurately mining genes associated with complex traits.

With the gradual improvement in germplasm collection, we anticipate discovering additional genes that impact rice grain yield and quality. The in-depth examination of wild rice genomes and molecular mechanisms, coupled with modern genetic and gene editing techniques, enhances our comprehension of wild rice domestication and its relevance to grain yield and quality traits. This will provide a robust scientific foundation for rice breeding and future genetic enhancements.

Prospects for the utilization of wild rice germplasm resources

The wild species related to cultivated rice have rich genetic diversity and strong environmental adaptability through

long-term natural selection and provide the germplasm resources such as resistance to white leaf blight, blast, drought and cold, needed for the genetic improvement of cultivated rice and are a valuable gene pool for the improvement of cultivated rice. However, the utilization of desirable wild rice genes remains limited, emphasizing the need for further comprehensive exploration and utilization.

Enhancing germplasm resource utilization by expanding scientific collections of wild rice

Despite the existence of a wide range of wild rice germplasm collections, some populations remain uncollected. For example, within China's collected wild rice germplasm, varieties from other countries account for <10%, significantly below the global average of 45%. Additionally, the distribution and proportion of wild rice accessions from different regions are uneven (Wang *et al.*, 2011a,b; Zhang and Yang, 2003). Studies have found that wild rice populations in different countries across South Asia, Southeast Asia and Northern Australia, may represent distinct gene pools (Cai *et al.*, 2004; Sun and Yang, 2009; Zheng and Ge, 2010). Expanding international wild rice collections in the many countries with wild rice genetic resources, while also refining the collection methods and enhancing habitat-related geographical, climatic and environmental data, is strategically vital. This effort holds immense significance for enriching and enhancing wild rice genetic resources.

Enhancing phenotypic identification of wild rice to increase the utilization of genetic resource

Conventional morphological traits primarily focus on characteristic parts (e.g. auricles, ligules, leaf sheaths, internodes, awns and underground stems), colour, plant shape, tillering capacity, grain fallibility and spike branching (Fan *et al.*, 2023). While identifying phenotypes in wild rice is more straightforward at various levels, including physiological, tissue, cellular and molecular, there is limited research on evaluating the tolerance of specific wild rice varieties to biotic and abiotic stresses. To address the inefficiencies in material phenotyping, we established a multi-level phenomics identification platform using not only visible light and near-infrared imaging methods but also drones and robots as imaging carriers. Our platform integrates and analyses phenome data through computer vision and artificial intelligence, facilitating high-throughput, large-scale phenotype identification (Zheng *et al.*, 2023). We utilized the phenome analysis platform to monitor the growth, development, adaptation to adversity, yield composition, quality formation, resistance to pests and diseases, nutrient utilization efficiency and dynamic changes in root system structure in diverse wild rice germplasm resources. This study aims to elucidate phenotypic diversity and environmental adaptability in wild rice germplasm resources, laying a strong foundation for breeding efforts by incorporating environmental factors such as geography, climate and soil data.

Strengthening wild rice germplasm conservation for future genetic breeding stock of cultivated rice

The endangerment of wild rice germplasm resources stems from human production activities and the invasion of alien species. This results in a reduced genetic diversity of wild rice. Additionally, insufficient regulation and funding have degraded wild rice during *in situ* and *ex situ* conservation (Yang *et al.*, 2023; Zhang and Yang, 2003). To safeguard wild rice germplasm, we must

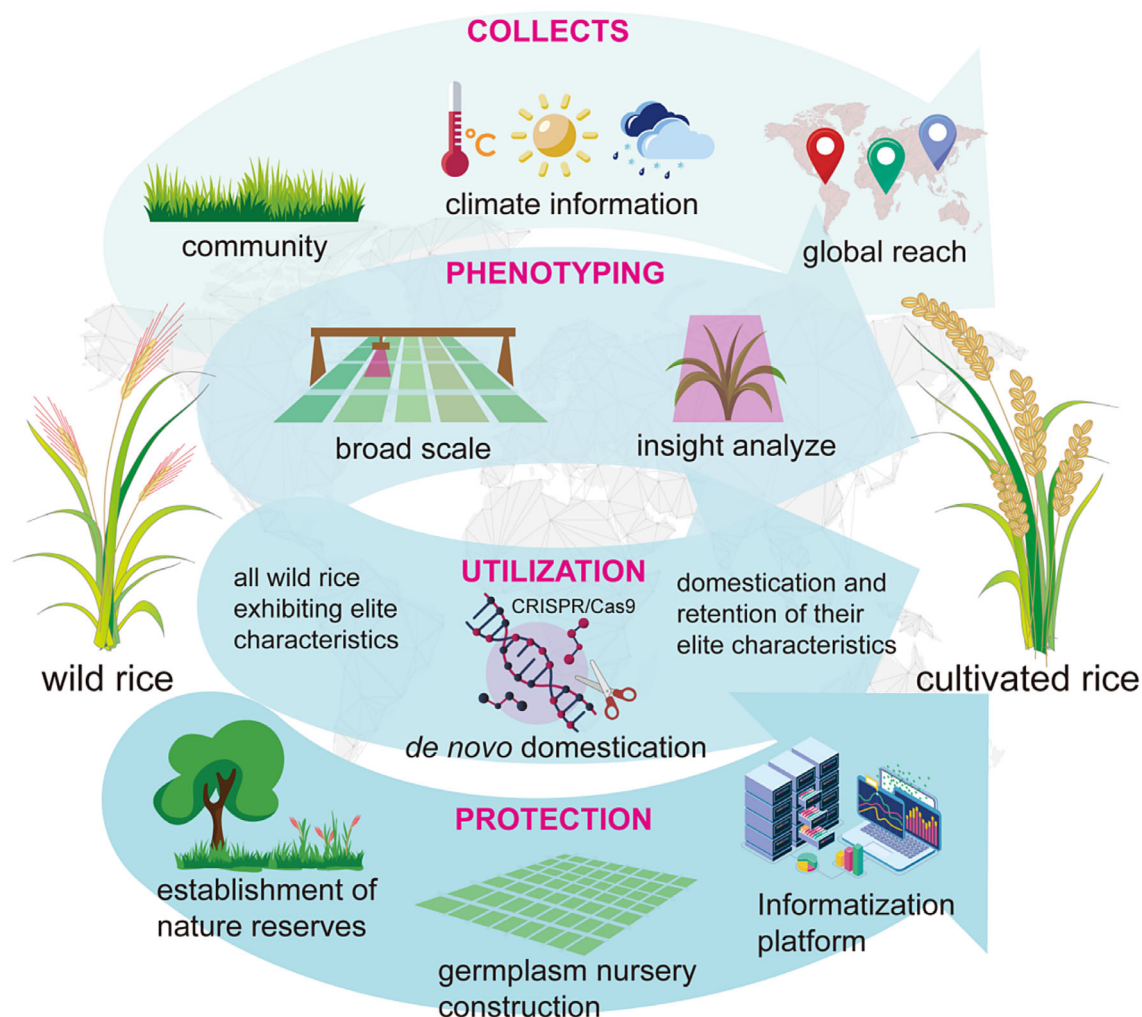


Figure 3 Infographic showing the workflow to optimize the collection, identification, conservation and utilization of wild rice and to promote the genetic improvement of cultivated rice.

enhance *in situ* conservation and improve monitoring and early warning methods. These sites offer a secure environment for wild rice growth and reproduction. Simultaneously, bolstering biodiversity protection in these sites maintains a healthy ecological balance for wild rice in its natural habitat. *In situ* conservation, we need to tailor environmental conditions to the different rice species' habitats, renew seed stems and potting soil regularly and perform routine leaf-cutting and stubble treatments (Fan *et al.*, 2009). Expanding the scope of *ex situ* conservation, beyond the existing site, is crucial. Currently, only a few samples of wild rice species are in *ex situ* conservation, which limits the genetic diversity of wild rice. To address this, we can establish protected areas across various regions to cover more wild rice species. A combined *in situ* and *ex situ* conservation system will protect more wild rice germplasm resources, increase genetic diversity and offer more options for future genetic breeding of cultivated rice. The protection of wild rice germplasm resources is essential for food security, ecological preservation and sustainable development. Therefore, strengthening conservation awareness and active participation in wild rice protection is crucial. This not only holds significant value but also signifies our respect for nature and our responsibility for humanity's future.

Strengthening the application of wild rice breeding to fully tap its potential breeding value

Wild rice serves as a strategic reserve resource and seed 'chip' with attributes including disease and pest resistance, as well as tolerance to salt, drought, cold, barren conditions and other unique traits. For example, perennial rice varieties can be developed by using the characteristic of rhizome from *O. longistaminata*, which saves a lot of labour and input costs (Zhang *et al.*, 2023). However, species within the *Oryza* genus, found in GP2 and GP3, cannot produce fertile offspring when crossed freely with cultivated rice (Harlan and De Wei, 1971). Overcoming interspecific reproductive barriers in wild rice is vital for harnessing its rich genetic resources. To address this challenge, gene editing and the development of gene-linked molecular markers in wild rice represent pivotal advancements enabling future applications. Utilizing gene editing to disable interspecific reproductive isolation genes can enhance trait improvement in both cultivated and wild rice through hybridization. Moreover, the genetic enhancement of semi-wild rice with lower domestication, involving knocking out genes linked to long awns, seed drop facilitation, light sensitivity, culm susceptibility, plant shape

irregularities and low yield, is achievable (Hao, 2020). Accelerating wild rice breeding is feasible by identifying molecular markers closely associated with quality traits within the population (Grover and Sharma, 2016). DNA markers are essential tools for genetic analysis and breeding. Recent efforts in the development of genome-wide InDel marker sets have opened new avenues for harnessing the genetic diversity present in AA- and BB-genome wild species (Hechanova *et al.*, 2021; Malabanan-Bauan *et al.*, 2023). The newly developed InDel markers may be useful for the identification of valuable genetic factors from the AA and BB-genome wild rice species and also for transferring the identified genes/QTLs into elite variety backgrounds.

Conclusion

Biodiversity, as the repository of genetic diversity, plays a crucial role in rice production all over the world. Wild rice, a vital source for rice germplasm innovation and enhancement, offers abundant genetic resources. Sanya, Hainan Province, hosts the world's largest wild rice germplasm resource nursery (National Resource Nursery) which houses 21 wild rice species and 13 000 germplasm copies. Supported by platforms like the Global Transit Base for Plant and Animal Germplasm Resources, the National Resource Nursery has promoted the International Wild Rice Alliance and advanced the global system for protecting, researching and utilizing wild rice relatives and local rice varieties. Collaborative germplasm resource investigations, an extensive all-around, wide-ranging and multi-level international exchange platform, and resource introduction and exchange have been facilitated through major international cooperation projects like the International Conference on Wild Rice. The goal is to enhance the safe preservation and efficient utilization of germplasm resources. The future holds a continued emphasis on conserving and utilizing wild rice germplasm resources to identify valuable wild rice genes for contemporary and future rice cultivation. This endeavour aims to establish a world-class national crop germplasm resource bank, fostering new rice varieties and contributing essential genetic resources to modernized rice breeding. Our approach to conserving wild rice germplasm resources emphasizes simultaneous conservation and utilization. By studying wild rice, we can identify high-quality genotypes for rice cultivation while respecting and safeguarding these resources to prevent misuse and over-exploitation.

To advance the transition from traditional breeding to the highly efficient, precise and targeted Molecularly Designed Intelligent Breeding 5.0, we must intensify wild rice genomics research and tap into its exceptional gene reservoir. When combined with modern molecular marker-assisted selection methods, we can enhance rice breeding and production more effectively (Figure 3).

Acknowledgements

The authors would like to express sincere gratitude to Shaojie Zheng, Xueqiang Wang and Cheng Cheng for helping in revising this article.

Funding information

This article was supported by grants from the National Key Research and Development Program of China (2021YFD1200101), National Natural Science Foundation of China (32188102, 32350710198), the Project of Sanya Yazhou Bay Science and Technology City

(SCKJ-JYRC-2023-47, SKJC-2023-02-001) and Hainan Province Science and Technology Special Fund (ZDYF2022XDNY260).

Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Q.Q. conceived the manuscript; X.M.Z., Y.L.P. and J.Y.Q. drafted the manuscript; and X.M.Z., Y.L.P., J.Y.Q. and R. H. revised the manuscript. The authors read and approved the final manuscript.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

References

- Brar, S.D. and Khush, G.S. (1997) Alien introgression in rice. *Plant Mol. Biol.* **35**, 35–47.
- Cai, H.W., Wang, X.K. and Morishima, H. (2004) Comparison of population genetic structures of common wild rice (*Oryza rufipogon* Griff.), as revealed by analyses of quantitative traits, allozymes, and RFLPs. *Heredity* **92**, 409–417.
- Cao, Z., Tang, H., Cai, Y., Zeng, B., Zhao, J., Tang, X., Lu, M. *et al.* (2022) Natural variation of *HTH5* from wild rice, *Oryza rufipogon* Griff., is involved in conferring high-temperature tolerance at the heading stage. *Plant Biotechnol. J.* **20**, 1591–1605.
- Cheema, K.K., Grewal, N.K., Vikal, Y., Sharma, R., Lore, J.S., Das, A., Bhatia, D. *et al.* (2008) A novel bacterial blight resistance gene from *Oryza nivara* mapped to 38 kb region on chromosome 4L and transferred to *Oryza sativa* L. *Genet. Res. (Camb)* **90**, 397–407.
- Chen, J.W., Wang, L., Pang, X.F. and Pan, Q.H. (2006) Genetic analysis and fine mapping of a rice brown planthopper (*Nilaparvata lugens* Stål) resistance gene *bph19(t)*. *Mol. Gen. Genomics* **275**, 321–329.
- Chen, L., Zhang, P., Liu, F., Wang, G., Ye, S., Zhu, Z., Fu, Y. *et al.* (2010) QTL analysis of yield-related traits using an advanced backcross population derived from common wild rice (*Oryza rufipogon* L.). *Molec. Plant Breed.* **51**, 692–704.
- Chen, S., Wang, C.Y., Yang, J.Y., Chen, B., Wang, W.J., Su, J., Feng, A.Q. *et al.* (2020) Identification of the novel bacterial blight resistance gene *Xa46(t)* by mapping and expression analysis of the rice mutant H120. *Sci. Rep.* **10**, 12642.
- Chu, M.J., Du, Y.M., Liu, X.M., Yan, N., Wang, F.Z. and Zhang, Z.F. (2019) Extraction of proanthocyanidins from Chinese wild rice (*Zizania latifolia*) and analyses of structural composition and potential bioactivities of different fractions. *Molecules* **24**, 1681.
- Das, A., Soubam, D., Singh, P.K., Thakur, S., Singh, N.K. and Sharma, T.R. (2012) A novel blast resistance gene, *Pi54rh* cloned from wild species of rice, *Oryza rhizomatis* confers broad spectrum resistance to *Magnaporthe oryzae*. *Funct. Integr. Genomics* **12**, 215–228.
- Devi, S. *et al.* (2020) Identification and characterization of a large effect QTL from *Oryza glumaepatula* revealed *Pi68(t)* as putative candidate gene for rice blast resistance. *Rice* **13**, 17.
- Doebley, J.F., Gaut, B.S. and Smith, B.D. (2006) The molecular genetics of crop domestication. *Cell* **127**, 1309–1321.
- Fan, W.Y., Liu, Z.R., Yun, Y., Tang, Q.J., Zhou, S.Z., Xiao, X.R., Zheng, X.M. *et al.* (2023) Collection and preliminary identification of germplasm resources resistant to bacterial blight of wild rice from Hainan province. *J. Plant Genetic Res.* **24**, 117–125.
- Fan, Z.L., Pan, D.J., Li, C., Chen, J.Y., Chen, Y. and Liu, W. (2009) Collecting and conserving method of wild rice germplasm resources. *Guangdong Agric. Sci.* **07**, 12–14.

- Ganie, S.A., Molla, K.A., Henry, R.J., Bhat, K.V. and Mondal, T.K. (2019) Advances in understanding salt tolerance in rice. *Theor. Appl. Genet.* **132**, 851–870.
- Ge, S., Sang, T., Lu, B.R. and Hong, D.Y. (1999) Phylogeny of rice genomes with emphasis on origins of allotetraploid species. *Proc. Natl. Acad. Sci. USA* **96**, 14400–14405.
- Grover, A. and Sharma, P.C. (2016) Development and use of molecular markers: past and present. *Crit. Rev. Biotechnol.* **36**, 290–302.
- Gu, K., Tian, D., Yang, F., Wu, L., Sreekala, C., Wang, D., Wang, G.L. et al. (2004) High-resolution genetic mapping of *Xa27(t)*, a new bacterial blight resistance gene in rice, *Oryza sativa* L. *Theor. Appl. Genet.* **108**, 800–807.
- Guo, S.B. et al. (2010) Identification and mapping of a novel bacterial blight resistance gene *Xa35(t)* originated from *Oryza minuta*. *Sci. Agric. Sin.* **43**, 2611–2618.
- Hao, Y. (2020) *De Novo Domestication of a Salt-Tolerant Weedy Rice by Genome Editing*. Master Thesis. South China Agricultural University.
- Harlan, J.R. and Wei, J.M. (1971) Toward a national classification of cultivated plants. *Taxon* **20**, 509–517.
- He, G., Luo, X., Tian, F., Li, K., Zhu, Z., Su, W., Qian, X. et al. (2006) Haplotype variation in structure and expression of a gene cluster associated with a quantitative trait locus for improved yield in rice. *Genome Res.* **16**, 618–626.
- Hechanova, S.L., Bhattarai, K., Simon, E.V., Clave, G., Karunaratne, P., Ahn, E.K., Li, C.P. et al. (2021) Development of a genome-wide InDel marker set for allele discrimination between rice (*Oryza sativa*) and the other seven AA-genome *Oryza* species. *Sci. Rep.* **11**, 8962.
- Hirabayashi, H. et al. (1999) RFLP analysis of a new gene for resistance to brown planthopper derived from *O. officinalis* on rice chromosome 4. *Breed. Sci.* **48**, 48.
- Hou, L.-Y. et al. (2011) Genetic analysis and preliminary mapping of two recessive resistance genes to brown Planthopper, *Nilaparvata lugens* Stål in rice. *Rice Sci.* **18**, 238–242.
- Hu, L., Wu, Y., Wu, D., Rao, W., Guo, J., Ma, Y., Wang, Z. et al. (2017) The coiled-coil and nucleotide binding domains of BROWN PLANTHOPPER RESISTANCE14 function in signaling and resistance against Planthopper in rice. *Plant Cell* **29**, 3157–3185.
- Huang, X., Kurata, N., Wei, X., Wang, Z.X., Wang, A., Zhao, Q., Zhao, Y. et al. (2012) A map of rice genome variation reveals the origin of cultivated rice. *Nature* **490**, 497–501.
- Jena, K.K., Jeung, J.U., Lee, J.H., Choi, H.C. and Brar, D.S. (2006) High-resolution mapping of a new brown planthopper (BPH) resistance gene, *Bph18(t)*, and marker-assisted selection for BPH resistance in rice (*Oryza sativa* L.). *Theor. Appl. Genet.* **112**, 288–297.
- Jena, K.K. and Kim, S.-M. (2010) Current status of brown planthopper (BPH) resistance and genetics. *Rice* **3**, 161–171.
- Jeung, J.U., Kim, B.R., Cho, Y.C., Han, S.S., Moon, H.P., Lee, Y.T. and Jena, K.K. (2007) A novel gene, *Pi40(t)*, linked to the DNA markers derived from NBS-LRR motifs confers broad spectrum of blast resistance in rice. *Theor. Appl. Genet.* **115**, 1163–1177.
- Ji, H., Kim, S.R., Kim, Y.H., Suh, J.P., Park, H.M., Sreenivasulu, N., Misra, G. et al. (2016) Map-based cloning and characterization of the *BPH18* gene from wild rice conferring resistance to brown planthopper (BPH) insect pest. *Sci. Rep.* **6**, 34376.
- Jin, J., Huang, W., Gao, J.P., Yang, J., Shi, M., Zhu, M.Z., Luo, D. et al. (2008) Genetic control of rice plant architecture under domestication. *Nat. Genet.* **40**, 1365–1369.
- Jing, Z., Qu, Y., Yu, C., Pan, D., Fan, Z., Chen, J. and Li, C. (2010) QTL analysis of yield-related traits using an advanced backcross population derived from common wild rice (*Oryza rufipogon* L.). *Molecular Plant Breeding* **1**, 1–10.
- Katiyar, S.K., Tan, Y., Huang, B., Chandel, G., Xu, Y., Zhang, Y., Xie, Z. et al. (2001) Molecular mapping of gene *Gm-6(t)* which confers resistance against four biotypes of Asian rice gall midge in China. *Theor. Appl. Genet.* **103**, 953–961.
- Konishi, S., Izawa, T., Lin, S.Y., Ebana, K., Fukuta, Y., Sasaki, T. and Yano, M. (2006) An SNP caused loss of seed shattering during rice domestication. *Science* **312**, 1392–1396.
- Li, C.B., Zhou, A.L. and Sang, T. (2006) Rice domestication by reducing shattering. *Science* **311**, 1936–1939.
- Li, D.J., Sun, C.Q., Fu, Y.C., Li, C., Zhu, Z.F., Liang, C., Cai, H.W. et al. (2002) Identification and mapping of genes for improving yield from Chinese common wild rice (*O. rufipogon* Griff.) using advanced backcross QTL analysis. *Chin. Sci. Bull.* **47**, 1533–1537.
- Li, J.Q., Yan, G.X.Q. and Lu, Y.G. (2009) The reviews and enlightenments on the breeding and popularization of rice variety Yasten no. 1 and its derived ones. *J. Plant Genetic Resources* **10**, 317–323.
- Li, L.Y., Ying, D.S. and Zhang, R.L. (2014) Research and application progress of valuable genes of wild rice. *Chinese J. Tropical Agric.* **34**, 34–41.
- Lin, C.C., Lee, W.J., Zeng, C.Y., Chou, M.Y., Lin, T.J., Lin, C.S., Ho, M.C. et al. (2023) SUB1A-1 anchors a regulatory cascade for epigenetic and transcriptional controls of submergence tolerance in rice. *PNAS Nexus* **2**, pgad229.
- Lin, S.J., Liu, Z.P., Zhang, K., Yang, W.F., Zhan, P.L., Tan, Q.Y., Gou, Y.J. et al. (2023) *GL9* from *Oryza glumaepatula* controls grain size and chalkiness in rice. *Crop J.* **11**, 198–207.
- Liu, F. et al. (2003) Identification and mapping of quantitative trait loci controlling cold-tolerance of Chinese common wild rice (*O. rufipogon* Griff.) at booting to flowering stages. *Chin. Sci. Bull.* **48**, 2068–2071.
- Lu, B.R. (1998) Diversity of rice genetic resources and its utilization and conservation. *Chinese Biodiversity* **6**, 63–72.
- Lu, F., Ammiraju, J.S., Sanyal, A., Zhang, S., Song, R., Chen, J., Li, G. et al. (2009) Comparative sequence analysis of *MONOCULM1*-orthologous regions in 14 *Oryza* genomes. *Proc. Natl. Acad. Sci. USA* **106**, 2071–2076.
- Miao, L.L. et al. (2010) Molecular mapping of a new gene for resistance to rice bacterial blight. *Sci. Agric. Sin.* **43**, 3051–3058 (in Chinese with English abstract).
- Moner, A., Furtado, A. and Henry, R.J. (2020) Two divergent chloroplast genome sequence clades captured in the domesticated rice gene pool may have significance for rice production. *BMC Plant Biol.* **20**, 472.
- Morishima, H. (2002) *Reports of the study-tours for investigation of wild and cultivated rice species. Parts I and II.*
- Prahalada, G.D., Marathi, B., Vinarao, R., Kim, S.R., Diocton, R., IV, Ramos, J. and Jena, K.K. (2021) QTL mapping of a novel genomic region associated with high out-crossing rate derived from *Oryza longistaminata* and development of new CMS lines in rice, *O. sativa* L. *Rice* **14**, 80.
- Prusty, M.R., Kim, S.R., Vinarao, R., Entila, F., Egdane, J., Diaz, M.G.Q. and Jena, K.K. (2018) Newly identified wild rice accessions conferring high salt tolerance might use a tissue tolerance mechanism in leaf. *Front. Plant Sci.* **9**, 417.
- Qu, S., Liu, G.F., Zhou, B., Bellizzi, M., Zeng, L.R., Dai, L.Y., Han, B. et al. (2006) The broad-spectrum blast resistance gene *Pi9* encodes a nucleotide-binding site-leucine-rich repeat protein and is a member of a multigene family in rice. *Gen* **172**, 1901–1914.
- Quan, R. et al. (2017) Improvement of salt tolerance using wild rice genes. *Front. Plant Sci.* **8**, 2269.
- Quan, R.D., Wang, J., Hui, J., Bai, H.B., Lyu, X.L., Zhu, Y.X., Zhang, H.W. et al. (2018) Improvement of salt tolerance using wild rice genes. *Front. Plant Sci.* **8**, 2269.
- Rahman, M.L., Jiang, W., Chu, S.H., Qiao, Y., Ham, T.H., Woo, M.O., Lee, J. et al. (2009) High-resolution mapping of two rice brown planthopper resistance genes, *Bph20(t)* and *Bph21(t)*, originating from *Oryza minuta*. *Theor. Appl. Genet.* **119**, 1237–1246.
- Song, B.K., Nadarajah, K., Romanov, M.N. and Ratnam, W. (2005) Cross-species bacterial artificial chromosome (BAC) library screening via overgo-based hybridization and BAC-contig mapping of a yield enhancement quantitative trait locus (QTL) *yl1.1* in the Malaysian wild rice *Oryza rufipogon*. *Cell. Mol. Biol. Lett.* **10**, 425–437.
- Song, W.Y., Wang, G.L., Chen, L.L., Kim, H.S., Pi, L.Y., Holsten, T., Gardner, J. et al. (1995) A receptor kinase-like protein encoded by the rice disease resistance gene, *Xa21*. *Science* **270**, 1804–1806.
- Stein, J.C., Yu, Y., Copetti, D., Zwickl, D.J., Zhang, L., Zhang, C., Chougule, K. et al. (2018) Genomes of 13 domesticated and wild rice relatives highlight genetic conservation, turnover and innovation across the genus *Oryza*. *Nat. Genet.* **50**, 285–296.
- Sun, X.M., Xiong, H.Y., Jiang, C.H., Zhang, D.M., Yang, Z.L., Huang, Y.P., Zhu, W.B. et al. (2022) Natural variation of *DROT1* confers drought adaptation in upland rice. *Nat. Commun.* **13**, 4265.

- Sun, X.P. and Yang, Q.W. (2009) Comparative study on genetic diversity of common wild rice in China and three Southeast Asian countries (Vietnam, Laos and Cambodia). *Acta Agronomica Sinica* **35**, 679–684.
- Surendiran, G., Alsaif, M., Kapourchali, F.R. and Moghadasian, M.H. (2014) Nutritional constituents and health benefits of wild rice (*Zizania* spp.). *Nutr. Rev.* **72**, 227–236.
- Swamy, B.P. et al. (2014) Mapping and introgression of QTL for yield and related traits in two backcross populations derived from *Oryza sativa* cv. Swarna and two accessions of *O. nivara*. *J. Genet.* **93**, 643–654.
- Tan, G.X., Ren, X., Weng, Q.M., Shi, Z.Y., Zhu, L.L. and He, G.C. (2004) Mapping of a new resistance gene to bacterial blight in rice line introgressed from *Oryza officinalis*. *Acta Genet. Sin.* **31**, 724–729 (in Chinese with English abstract).
- Tan, G.X., Weng, Q.M., Ren, X., Huang, Z., Zhu, L.L. and He, G.C. (2004) Two whitebacked planthopper resistance genes in rice share the same loci with those for brown planthopper resistance. *Heredity* **92**, 212–217.
- Tan, L.B., Li, X.R., Liu, F.X., Sun, X.Y., Li, C.G., Zhu, Z.F., Fu, Y.C. et al. (2008) Control of a key transition from prostrate to erect growth in rice domestication. *Nat. Genet.* **40**, 1360–1364.
- Utami, D.D., Moeljopawiro, S., Aswidinnoor, H. and Hanarida, I. (2008) Blast resistance genes in wild rice *Oryza rufipogon* and rice cultivar IR64. *Indones. J. Agric.* **2**, 71–76.
- Vaughan, D.A. (1989) *The Genus Oryza L.: Current Status of Taxonomy*. Manila: International Rice Research Institute.
- Vaughan, D.A., Morishima, H. and Kadowaki, K. (2003) Diversity in the *Oryza* genus. *Curr. Opin. Plant Biol.* **6**, 139–146.
- Wang, C., Zhang, X., Fan, Y., Gao, Y., Zhu, Q., Zheng, C., Qin, T. et al. (2015a) XA23 is an executor R protein and confers broad-spectrum disease resistance in rice. *Mol. Plant* **8**, 290–302.
- Wang, E., Wang, J.J., Zhu, X.D., Hao, W., Wang, L.Y., Li, Q., Zhang, L.X. et al. (2008) Control of rice grain-filling and yield by a gene with a potential signature of domestication. *Nat. Genet.* **40**, 1370–1374.
- Wang, M.H., Yu, Y., Haberer, G., Marri, P.R., Fan, C., Goicoechea, J.L., Zuccolo, A. et al. (2014) The genome sequence of African rice (*Oryza glaberrima*) and evidence for independent domestication. *Nat. Genet.* **46**, 982–988.
- Wang, S.M., Li, L.H., Li, Y., Lu, X.X., Yang, Q.W., Cao, Y.S., Zhang, Z.W. et al. (2011a) Report on the state of plant genetic resources for food and agriculture in China. *J. Plant Genet. Res.* **12**, 1–12.
- Wang, S.M., Li, L.H., Li, Y., Lu, X.X., Yang, Q.W., Cao, Y.S., Zhang, Z.W. et al. (2011b) Report on the state of plant genetic resources for food and agriculture in China (II). *J. Plant Genet. Res.* **12**, 167–177.
- Wang, W., Mauleon, R., Hu, Z., Chebotarov, D., Tai, S., Wu, Z., Li, M. et al. (2018) Genomic variation in 3,010 diverse accessions of Asian cultivated rice. *Nature* **557**, 43–49.
- Wang, X., Guo, X., Ma, X., Luo, L., Fang, Y., Zhao, N., Han, Y. et al. (2021) Development of new rice (*Oryza sativa* L.) breeding lines through marker-assisted introgression and pyramiding of brown planthopper, blast, bacterial leaf blight resistance, and aroma genes. *Agronomy* **11**, 2525.
- Wang, Y., Cao, L., Zhang, Y., Cao, C., Liu, F., Huang, F., Qiu, Y. et al. (2015b) Map-based cloning and characterization of *BPH29*, a B3 domain-containing recessive gene conferring brown planthopper resistance in rice. *J. Exp. Bot.* **66**, 6035–6045.
- Wing, R.A., Purugganan, M.D. and Zhang, Q.F. (2018) The rice genome revolution: from an ancient grain to Green Super Rice. *Nat. Rev. Genet.* **19**, 505–517.
- Xing, J., Zhang, D.Y., Yin, F.Y., Zhong, Q.F., Wang, B., Xiao, S.Q. and Ke, X. (2021) Identification and fine-mapping of a new bacterial blight resistance gene, *Xa47(t)*, in G252, an introgression line of Yuanjiang common wild rice (*Oryza rufipogon*). *Plant Dis.* **105**, 4106–4112.
- Xing, Y.Z. and Zhang, Q.F. (2010) Genetic and molecular bases of rice yield. *Annu. Rev. Plant Biol.* **61**, 421–442.
- Yamanaka, S., Nakamura, I., Watanabe, K.N. and Sato, Y.-I. (2004) Identification of SNPs in the *waxy* gene among glutinous rice cultivars and their evolutionary significance during the domestication process of rice. *Theor. Appl. Genet.* **108**, 1200–1204.
- Yang, H., Ren, X., Weng, Q., Zhu, L. and He, G. (2002) Molecular mapping and genetic analysis of a rice brown planthopper (*Nilaparvata lugens* Stal) resistance gene. *Heredity* **136**, 39–43.
- Yang, H., You, A., Yang, Z., Zhang, F., He, R., Zhu, L. and He, G. (2004) High-resolution genetic mapping at the Bph15 locus for brown planthopper resistance in rice (*Oryza sativa* L.). *Theor. Appl. Genet.* **110**, 182–191.
- Yang, X.H., Zhou, J.F. and Feng, L. (2023) Utilization and protection of wild rice germplasm resources in China. *China Rice* **29**, 1–8.
- Yang, Y., Zhou, Y.H., Sun, J., Liang, W.F., Chen, X.Y., Wang, X.M., Zhou, J. et al. (2022) Research progress on cloning and function of *Xa* genes against rice bacterial blight. *Front. Plant Sci.* **13**, 847199.
- Yuan, L., Zhang, L.C., Wei, X., Wang, R.H., Li, N.N., Chen, G.L., Fan, F.F. et al. (2022) Quantitative trait locus mapping of salt tolerance in wild rice *Oryza longistaminata*. *Int. J. Mol. Sci.* **23**, 2379.
- Yuan, L.P. (1986) Hybrid rice in China. *Chin. J. Rice Sci.* **1**, 8–18.
- Zhang, L.B., Zhu, Q., Wu, Z.Q., Ross-Ibarra, J., Gaut, B.S., Ge, S. and Sang, T. (2009) Selection on grain shattering genes and rates of rice domestication. *New Phytol.* **184**, 708–720.
- Zhang, S., Huang, G., Zhang, Y., Lv, X., Wan, K., Liang, J., Feng, Y. et al. (2023) Sustained productivity and agronomic potential of perennial rice. *Nat. Sustain.* **6**, 28–38.
- Zhang, W.X. and Yang, Q.W. (2003) Collection, identification and conservation of wild rice in China. *Journal of Plant Genetic Resources* **4**, 369–373.
- Zhang, Y., Zhou, J., Yang, Y., Li, J., Xu, P., Deng, X., Deng, W. et al. (2015) A novel gene responsible for erect panicle from *Oryza glumaepatula*. *Euphytica* **205**, 739–745.
- Zheng, C.-K., Wang, C.-L., Yu, Y.-J., Liang, Y.-T. and Zhao, K.-J. (2009) Identification and molecular mapping of *Xa32(t)*, a novel resistance gene for bacterial blight (*Xanthomonas oryzae* pv. *oryzae*) in rice. *Acta Agron. Sin.* **35**, 1173–1180.
- Zheng, X., Wei, F., Cheng, C. and Qian, Q. (2023) A historical review of hybrid rice breeding. *J. Integr. Plant Biol.* **16**, 532–545.
- Zheng, X.M. and Ge, S. (2010) Ecological divergence in the presence of gene flow in two closely related *Oryza* species (*Oryza rufipogon* and *O. nivara*). *Mol. Ecol.* **19**, 2439–2454.
- Zhou, S.X. (2005) *Development of Drought Tolerance Introgression Lines of Common Wild Rice (O. rufipogon Griff.) from Dongxiang in Jiangxi Province and QTL Mapping of Drought Tolerance*. Beijing: China Agricultural University.
- Zhou, Y., Lu, D.F., Li, C.Y., Luo, J.H., Zhu, B.F., Zhu, J.J., Shanguan, Y.Y. et al. (2012) Genetic control of seed shattering in rice by the APETALA2 transcription factor *shattering abortion1*. *Plant Cell* **24**, 1034–1048.
- Zou, X.H., Zhang, F.M., Zhang, J.G., Zang, L.L., Tang, L., Wang, J., Sang, T. et al. (2008) Analysis of 142 genes resolves the rapid diversification of the rice genus. *Genome Biol.* **9**, R49.