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Phylogenetic Evolution of Rice: A Comprehensive Review of Domestication Events and Wild Progenitors

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Abstract This study reviews the phylogenetic process of rice, focusing on the domestication events and the key role of wild ancestors in rice domestication. The study suggests that *indica* and *japonica*, the major subspecies of Asian rice, may have been domesticated independently from different wild populations, although some domestication genes such as sh4 may have a single origin. Dynamic processes such as gene flow, gene introgression and hybridization between wild rice and cultivated rice significantly increased the genetic diversity of modern rice varieties. The domestication process of rice has multiple complexities and has been profoundly influenced by multiple gene exchanges between wild and cultivated populations. A thorough understanding of these domestication and evolutionary mechanisms is of great guiding significance for the breeding and conservation of rice varieties in the future. The purpose of this study is to provide theoretical basis and scientific reference for rice breeding and genetic improvement.

Keywords Rice domestication; Phylogenetic evolution; Wild progenitors; Genetic diversity; Introgression

1 Introduction

Rice (*Oryza sativa* L.) is now the mainstay of global food production-it supports the daily diet of more than half of the world's population (Zhu et al., 2007; Huang et al., 2012; Huang, 2024). Its presence is particularly felt in Asia: large paddy fields, seasonal rice planting and harvesting have long been integrated into the culture and history of this land (Wei and Huang, 2019). However, how rice became what it is today is no longer a simple agricultural issue. The evolutionary process, domestication path, and relationship with wild rice involved are still under debate today (Molina et al., 2011; Choi et al., 2017).

Interestingly, although it is generally believed that rice originated from wild rice (*Oryza rufipogon*), the research community does not completely agree on the specific location, time, or even number of times (Molina et al., 2011). Some studies have suggested that the two main subspecies of rice, *indica* (*O. sativa indica*) and *japonica* (*O. sativa japonica*), may not have been domesticated all at once, but rather experienced multiple independent domestication events (Huang et al., 2012; Choi et al., 2017). This view is also supported by some genomic data.

The decline in genetic diversity is a phenomenon that has been repeatedly mentioned in rice domestication - some scholars believe that this shows that rice has experienced a serious bottleneck effect (Zhu et al., 2007; Veltman et al., 2018). However, it is precisely these bottlenecks and selection pressures that have gradually allowed it to break away from the wild state and become the staple food we are familiar with. In recent years, with the help of various genomic analysis tools, researchers have gradually clarified the relationship and evolutionary context between rice and wild rice (Gao and Innan, 2008; Wambugu et al., 2015).

This study will not stop at a single event or conclusion, but will try to look at the history of rice domestication from multiple perspectives, including genetic background, population history, and phylogenetic information. We hope that by integrating existing research results, we can further understand how this key crop has gradually moved from the wild to the human table, and provide some useful clues for future breeding and food security.

2 Origin and Evolutionary History of Wild Rice

2.1 Classification and status of wild rice

Wild rice plays an important role in understanding the domestication history of rice. They belong to the genus *Oryza*, whose species have a complex genetic structure and show rich diversity. For example, *O. glumaepatula* and *O. longistaminata* are both species carrying AA genomes, but they form different branches within the genome (Wambugu et al., 2015; Moner et al., 2018). Species with AA genomes are most closely related to cultivated rice *Oryza sativa* and are therefore considered to be the main component of the rice gene pool.

In particular, *Oryza rufipogon* and *Oryza nivara* are often regarded as the direct wild ancestors of cultivated rice in Asia (Sang and Ge, 2007a; Molina et al., 2011; Huang et al., 2012). However, this taxonomic status also reflects the complex phylogenetic relationship between wild rice. Therefore, the formation process of *indica* and *japonica* rice may actually be closely related to the domestication of different wild rice species (Sang and Ge, 2007a; Vaughan et al., 2008; Singh et al., 2017).

2.2 Geographical distribution and habitat

Wild rice has a wide distribution range, covering multiple tropical and subtropical continents, especially Asia, Africa and Australia. Their wide distribution is partly due to multiple long-distance dispersals over the past million years (Wambugu et al., 2015). For example, the Yangtze River and Pearl River basins in Asia are generally considered to be the core areas of rice domestication (Molina et al., 2011; Huang et al., 2012), which also makes these places important gathering areas for wild rice. However, wild rice communities in northern Australia show signs of earlier genetic differentiation, belonging to the ancient lineage of the AA genome, showing significant geographical and genetic isolation (Moner et al., 2018). Geographical separation has led to independent evolutionary paths, thus increasing the overall genetic diversity of wild rice.

2.3 Genetic diversity of wild rice

The genetic diversity of wild rice is very rich, far exceeding that of modern cultivated rice, and this characteristic is extremely critical for rice domestication and breeding. Studies have found that the frequency of nucleotide variation in wild rice is high, while the genetic diversity of cultivated rice has decreased due to the genetic bottleneck experienced during the domestication process (Zhu et al., 2007; Huang et al., 2012).

In addition, there are a large number of different haplotypes in the wild rice population, and there is frequent gene flow between wild species and cultivated species (Figure 1) (Singh et al., 2017; Moner et al., 2018). This gene exchange and diversity provide genetic resource support for improving the stress resistance and adaptability of cultivated rice (Stein et al., 2018). From a phylogenetic perspective, complex gene introgression and selection processes have jointly shaped the genetic relationship between wild rice and cultivated rice (Sang and Ge, 2007a; Vaughan et al., 2008; Singh et al., 2017).

4 Genetic Basis of Rice Domestication

4.1 Key domestication genes

Several genes were particularly critical during the domestication of rice, especially in the early stages of cultivation. For example, a special version of the sh4 gene can significantly reduce grain shedding, which is important for maintaining yield. This non-threshing sh4 allele is now almost fixed in all cultivated rice, indicating that it has undergone strong artificial selection (Sang and Ge, 2007a; Zhang et al., 2009). However, the specific details of the selection of important genes such as qSH1 in different rice subspecies are not clear (Zhang et al., 2009). There is also the *qSW5* gene, which controls the width of the grain. The loss of the gene causes the grain to hold more starch, thereby increasing yield (Shomura et al., 2008). These genes all indicate that traits that improve harvest efficiency and yield are the focus of selection during the domestication process.

However, some exceptions cannot be ignored. For example, different variants of these genes also exist in some wild rice species, indicating that domestication is not simply "having" or "not having" these genes, but is achieved by selecting specific versions.

4.2 The role of quantitative trait loci (QTL) in domestication

QTL is actually a key genetic factor regulating various morphological and physiological traits of rice, and they play an important role in domestication. A large number of studies have found QTLs related to domestication, such as those that control grain abscission, seed dormancy and plant morphology (Cai and Morishima, 2002; Li et al., 2006). These QTLs often appear in clusters, especially in the comparison between wild and cultivated rice. The existence of these clusters suggests the correlation between traits and also reflects the coordinated adjustment of these traits by natural selection (Cai and Morishima, 2002). It is worth noting that some QTLs with particularly large effects, such as the one on chromosome 7, significantly affect yield and plant structure (Li et al., 2006). The concentrated distribution of these QTLs may be the genetic basis of the "domestication syndrome" and also explain the phenomenon of "linkage drag" in breeding. However, the effects of some QTLs are not always directly apparent. Sometimes they are affected by other genes and show complex genetic interactions.

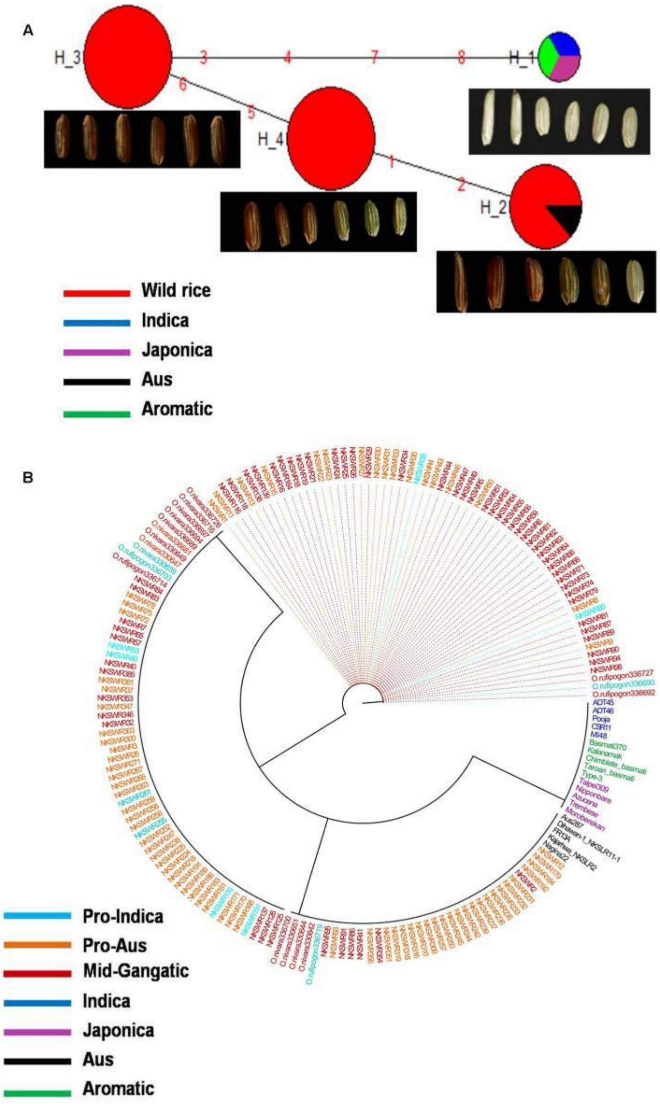

Figure 1 (A) A haplotype network of *Rc* gene along with its pericarp color, in total four haplotypes were formed, *Rc*-H3 was the ancestral haplotype of wild rice; (B) Haplotype based phylogenetic tree of *Rc* gene was constructed using 179 diverse rice genotypes and were separated into four major distinct groups (Adopted from Singh et al., 2017)

Image caption: (A) The size of each circle is proportional to haplotype (allele) frequency. To determine the origin and dispersal of these mutations in *Rc* gene we examined in total 179 diverse rice genotypes. Color-coding represents different population groups (Red-Wild rice, Blue-*Indica*, Black-Aus, Green-Aromatic, and Magenta-*Japonica*); (B) Color-coding represents different varietal groups (Cyan-Pro-*Indica*, Orange-Pro-Aus, Red-Mid-Gangetic, Blue-*Indica*, Black-Aus, Green-Aromatic, and Magenta-*Japonica*) (Adopted from Singh et al., 2017)

4.3 Comparative genomics of wild rice and cultivated rice

Whole genome sequencing allows us to see the full picture of the genetic differences between wild rice and cultivated rice. Although the traditional view is that *indica* rice and *japonica* rice have different origins, studies have found that the two actually share some low genetic diversity regions, which may have been formed by a single selection event and subsequent gene introgression (He et al., 2011). These low-diversity regions are often rich in domestication candidate genes, indicating their important role in the domestication process. In addition, gene regions related to key agronomic traits such as grain size and weight also show signs of selective elimination and positive selection (Kumar et al., 2020). This not only reveals the direction of genetic change, but also reflects the driving force of evolution. Through Bayesian phylogenetic analysis combined with population model support, existing evidence shows that both *indica* and *japonica* rice originated from the same wild rice species O. rufipogon, which provides a unified perspective for the overall understanding of rice domestication (Molina et al., 2011). Of course, this model is also constantly being challenged and improved by new data. After all, genetic evolution is never a single-line process.

5 Phylogenetic Relationships and Hybridization Events

5.1 Phylogenetic trees and rice evolution

Phylogenetic relationships are key to understanding the evolution and domestication history of rice. Asian rice is mainly divided into *indica* and *japonica*, and these two subspecies are actually domesticated from different wild populations of *Oryza rufipogo*n (Sang and Ge, 2007a; 2007b; Huang et al., 2012). Here, genomic analysis revealed significant genetic differences between them (Molina et al., 2011; Choi et al., 2017). However, this is not a simple branching relationship. The study also used a complete set of chloroplast genome sequences to reveal the phylogenetic details of AA genome rice species and highlighted the geographical differentiation of wild rice populations (Wambugu et al., 2015). In fact, these results make it clearer that the evolution of rice is not as linear as we imagined, but rather a combination of multiple lineages and regional variations.

5.2 Hybridization between wild rice and cultivated rice

Hybridization is common and important in the evolution of rice. Gene flow between cultivated and wild rice continues, and this gene introgression enriches the genetic background of modern rice (Sang and Ge, 2007a; 2007b; Moner et al., 2018). Interestingly, there was also gene introgression between early independently domesticated varieties, which helped to fix key domestication genes, which is the so-called combination model. The "snowball model" proposed by other studies emphasizes the continued role of gene introgression from local wild populations in ancestral domesticated populations (Sang and Ge, 2007a; 2007b). Moreover, similar continuous hybridization events have been observed in wild rice in Australia, which is very similar to the gene flow during the initial domestication of rice (Moner et al., 2018). This shows that gene exchange has always existed from ancient times to the present, and it is not so simple.

5.3 Impact on genetic diversity

Rice domestication has a profound impact on genetic diversity, but the situation is not that simple. In general, domestication reduces genetic diversity, mainly due to selection pressure and population bottlenecks. For example, the nucleotide diversity of *indica* and *japonica* rice only retains about 10% to 20% of wild species (Zhu et al., 2007). However, despite the overall reduction in diversity, hybridization and gene introgression events can alleviate this problem and even promote the recovery of genetic diversity. The alleles of early domesticated *japonica* rice were transferred to populations such as proto-indica and proto-aus through gene introgression, which is critical for maintaining the genetic variation of these populations (Choi et al., 2017). Therefore, the genetic structure of rice is not static, but is constantly affected by gene exchange, showing dynamic diversity.

6 Wild ancestors and Modern Varieties

6.1 Contribution of wild ancestors to modern rice

The formation of modern rice varieties is inseparable from their wild ancestors, such as *Oryza rufipogon* and *Oryza nivara*. In fact, there is a lot of genetic diversity in the genome structure of cultivated rice, which is mainly passed down from these wild rice species (Sang and Ge, 2007a; Huang et al., 2012; Singh et al., 2017). However, the process of rice domestication is not just a simple selection. Important traits such as reducing grain shedding are controlled by the sh4 gene, which is clearly pointed out in the study (Sang and Ge, 2007a; 2007b). *Indica* and *japonica* rice seem to be very different, but in fact, the genetic differences are largely derived from their respective wild ancestors. Especially for *indica* rice, when it spread to South Asia and Southeast Asia, it also hybridized with local wild rice, which also affected its evolutionary trajectory (Huang et al., 2012; Choi et al., 2017). However, not all wild rice participated in domestication, and the specific participating populations need to be further subdivided.

6.2 Application in modern breeding programs

Modern breeding work is increasingly dependent on these wild rice species. In fact, using the beneficial genes carried by wild rice is an effective means to improve the disease resistance, drought tolerance and yield of cultivated rice (Yang et al., 2012; Singh et al., 2017; Stein et al., 2018). Speaking of which, wild rice populations from Australia are particularly valued because of their unique genetic background, and are even considered to have an important impact on global rice food security (Moner et al., 2018). Of course, such utilization is not always smooth. For example, when transferring domestication genes from *japonica* rice to *indica* rice, there were also problems with gene compatibility. However, this work is generally of great significance to modern variety improvement (Molina et al., 2011; Yang et al., 2012). In fact, this hybridization and gene transfer has always been one of the important methods of rice improvement.

6.3 Protection of wild rice genetic resources

Protecting wild rice genetic resources is the basis for maintaining continuous rice improvement. With more and more artificial selection, the genetic diversity of cultivated rice is decreasing, which makes the protection of wild rice populations more important (Sang and Ge, 2007b; Moner et al., 2018). At present, the collection and sequencing of wild rice genomes is in progress, which not only helps to understand their evolutionary history, but also provides valuable resources for breeding (Yang et al., 2012; Stein et al., 2018). However, wild rice populations are not static. For example, in wild rice in Australia, genes have been introgressing new mutations, which reminds us to continue to monitor these resources to ensure better use in the future (Moner et al., 2018). Conservation work is not only about preservation, but also about paving the way for future germplasm innovation.

7 Domestication Bottleneck and Genetic Variation

7.1 Loss of genetic diversity during domestication

After domestication, the genetic diversity of rice has decreased significantly, as can be seen from multiple studies. For example, compared with its wild ancestors *Oryza rufipogon* and *Oryza nivara*, the nucleotide diversity of cultivated rice (*Oryza sativa*) is only 10% to 20% of that of wild rice (Zhu et al., 2007). This reduction indicates that the domestication process has experienced a serious genetic bottleneck. African rice (*Oryza glaberrima*) has encountered a similar situation, with its genetic diversity only retaining about 30% of that of its wild ancestor *O. barthii* (Li et al., 2011; Nabholz et al., 2014). However, there are exceptions. Although the overall diversity of some rice varieties has decreased, they still perform well in certain regions. In general, the sharp decline in genetic diversity has a negative impact on the adaptability and stress resistance of rice.

7.2 Genetic variation in local varieties and improved varieties

Although overall genetic diversity has decreased due to domestication, there is still a lot of genetic variation in local varieties and modern improved varieties of rice. Local varieties are mostly the result of long-term selection by farmers, and thus retain more genetic diversity. For example, local varieties show rich differences in grain shape, size and aroma, and these variations provide a basis for the preservation of genetic diversity (Ray et al., 2013). Studies in South Korea have shown that the nucleotide diversity of local varieties is even higher than that of weedy rice (Tong et al., 2017), which shows that traditional varieties are still an important source of genetic resources (Figure 2). This type of diversity is very important for breeding and improvement, and can inject more potential into modern varieties.

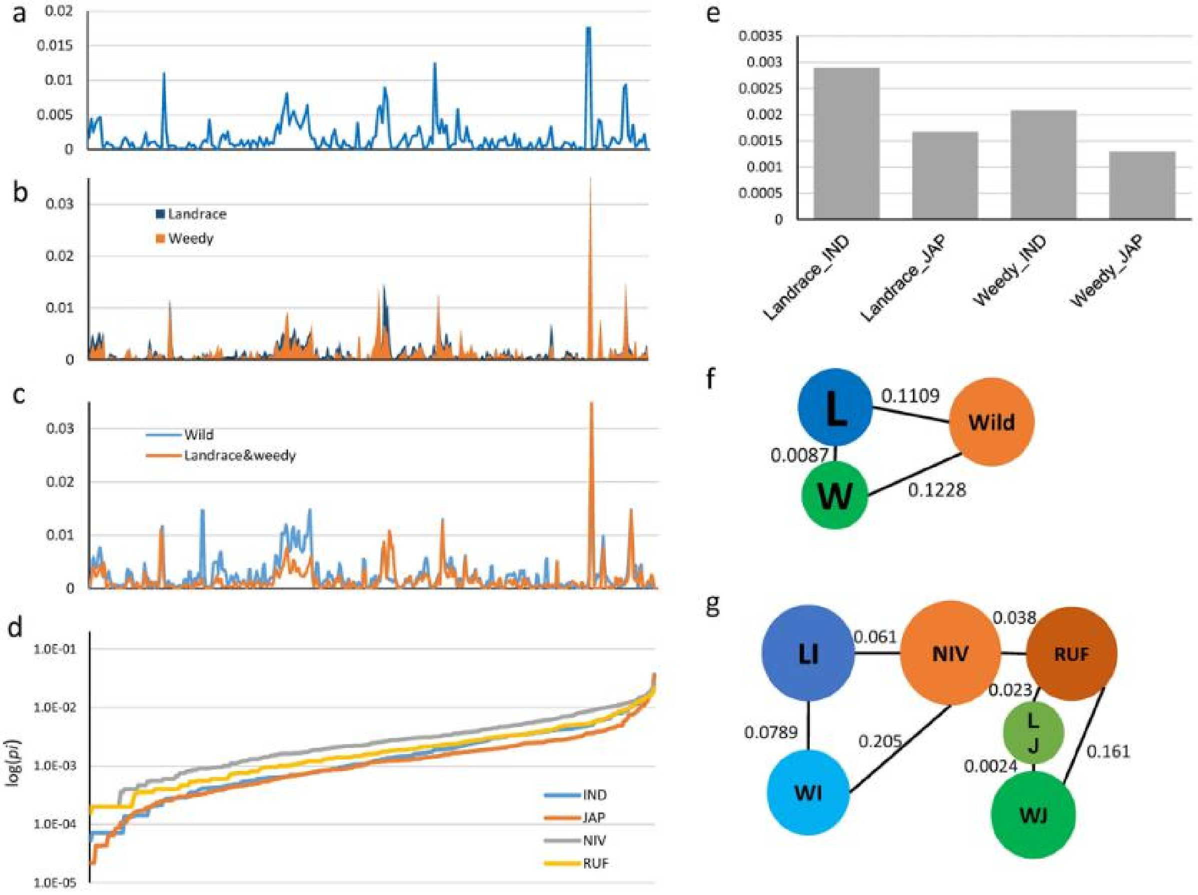

Figure 2 Mitochondrial genome nucleotide diversity (*pi*) and genetic distance (*Fst*) (Adopted from Tong et al., 2017)

Image caption: (a-c) *pi* of the whole collection; landrace and weedy rice; wild and the others (landrace and weedy rice). (d) The *pi* of *indica*, *japonica*, *O. nivara* and *O. rufipogon*. Values are sorted by ascending. (e) The average *pi* of *indica* and *japonica* in landrace or weedy rice. (f, g) The *Fst* between different groups. The circles indicated different groups and the circle size indicated the *pi* value. The *Fst* value between each two groups were represented by the distance between them. L: landrace rice, W: weedy rice, Wild: wild rice. LI: *landrace_indica*, WI: *weedy_indica*, LJ: *landrace_japonica*, WJ: *weedy_japonica*, NIV: *O. nivara*, RUF: *O. rufipogon* (Adopted from Tong et al., 2017)

7.3 Strategies for reintroducing genetic variation

Scientists have proposed several strategies to compensate for the loss of genetic diversity caused by domestication. For example, wild relatives with rich genetic diversity, such as O. rufipogon and O. nivara, are used as a source of new genes (Zhu et al., 2007). In addition, variation and emerging mutations in weedy rice are also seen as potentially valuable resources (Qiu et al., 2017). Modern methods such as genome-wide association studies (GWAS) help locate and introduce gene regions associated with desirable traits, promoting the introduction of genes from traditional and wild varieties into modern varieties (McNally et al., 2009). The goal of these practices is to enhance rice stress resistance and yield, and to tap the potential of wild and traditional genetic resources。

8 Case Study: Evolution and Domestication of Cultivated Rice

8.1 Historical background of domestication of cultivated rice

As one of the world's major food crops, the domestication history of cultivated rice (*Oryza sativa*) has always been a focus of debate among researchers. In fact, cultivated rice is not the result of a single domestication. Studies have shown that its origin is closely related to its wild ancestor *Oryza rufipogon*, but this process may have undergone multiple independent domestications. For example, the two main rice species, *indica* rice and *japonica* rice, were domesticated from different wild populations. It is generally believed that *indica* rice was formed in the area south of the Himalayas, such as eastern India, Myanmar, Thailand, etc., while the origin of *japonica* rice was locked in southern China (Huang et al., 2012). However, it is worth noting that this process was not smooth sailing. A serious genetic bottleneck occurred during the domestication process, resulting in the genetic diversity of cultivated rice being far less than that of its wild ancestor (Zhu et al., 2007; Gao and Innan, 2008).

8.2 Genetic insights into cultivated rice subspecies

When we look at *indica* and *japonica* rice, we find that they are genetically distinct, which has led to different views on whether they were domesticated independently or have a common origin. The latest multi-locus and population model analyses reveal that although the two are genetically different, there is actually gene flow between them, indicating that the evolutionary history of the two subspecies is quite complex, and they even partially share the same ancestral population (Gao and Innan, 2008; Molina et al., 2011). Whole-genome studies have also found a number of selection pressures and gene introgression events that have affected the genetic composition of modern rice varieties (Zhao et al., 2010; Choi and Purugganan, 2018; Stein et al., 2018). In particular, artificial breeding and cultural exchanges have played a significant role in shaping these genetic characteristics (Huang et al., 2012; Veltman et al., 2018).

8.3 Impact of modern breeding

It is of great significance to apply the genetic understanding of domestication and evolution of cultivated rice to modern breeding. By understanding the genetic diversity and population structure of rice, we can better locate important genetic regions and improve key traits such as yield, disease resistance and stress tolerance (Zhao et al., 2010; Stein et al., 2018). For example, the release of whole genome assemblies and new haplotypes, such as the genome of the “IR 8 miracle rice”, has become a valuable tool for breeding improvement (Stein et al., 2018). In addition, understanding the phenomena of gene introgression and hybridization not only helps us to utilize the genetic resources of wild relatives, but also broadens the genetic base of cultivated rice and makes it more adaptable to changing environmental conditions (Garris et al., 2005; Choi and Purugganan, 2018).

9 Challenges and Future Directions

9.1 Complex genetic history

The genetic background of rice is actually very complex, which is related to the independent domestication of *indica* and *japonica* rice from different wild ancestors. What's more troublesome is that there has been gene introgression between the two subspecies and their wild relatives, which makes the genetic relationship more confusing (Sang and Ge, 2007a; Zou et al., 2008; Stein et al., 2018). The rapid species differentiation within the genus Oryza has brought a large number of genetic changes and new genetic elements over millions of years, which undoubtedly makes the reconstruction of phylogeny very difficult (Zou et al., 2008; Stein et al., 2018). However, these rapid differentiations have also led to contradictions in genetic lineages, increasing the difficulty of understanding the evolutionary relationships of the genus Oryza (Zou et al., 2008). Therefore, it is difficult to clarify the entire evolutionary process by relying solely on traditional methods.

9.2 Technical limitations in genomic research

Although genomic technology is advancing, phylogenetic research on rice still faces many technical difficulties. In particular, genomes rich in highly repetitive sequences and structural variations are particularly difficult to assemble and annotate (Li et al., 2014; Stein et al., 2018). Short-read sequencing technology often cannot assemble a complete genome, resulting in the masking of some phylogenetic signals. Although long-read sequencing technology has improved, such as in the genome assembly of the "IR 8 miracle rice", its high cost and technical barriers limit its popularity (Stein et al., 2018). In addition, to accurately compare and compare diverse rice materials, it is necessary to rely on advanced bioinformatics tools and huge computing resources, which is a practical obstacle for many research teams (Li et al., 2014).

9.3 Socioeconomic and cultural impacts

The domestication and cultivation of rice are inseparable from the socioeconomic and cultural background, which directly affects the research direction and the promotion of new technologies. As the staple food of more than half of the world's population, especially in Asia, rice plays an important role in food security and economic stability (Wambugu et al., 2015; Wei and Huang, 2019). However, traditional agricultural practices and local preferences for certain rice varieties sometimes limit the acceptance and promotion of genetically improved varieties. Not to mention that many small farmers have low socioeconomic status and limited access to advanced agricultural technologies and resources, which has slowed down the progress of rice breeding and research to a certain extent (Li et al., 2014).

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Conflict of Interest Disclosure

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

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