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Deciphering the Saga of Evolution and Genomics of Cultivated Rice

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Abstract

Rice is one of the most important cereal crop which is being cultivated globally, the crop has come a long way and improved a lot in terms of production, productivity, insect-pest resistance, quality and abiotic stress tolerance aspect. Still there is a need for continuous improvement in order to tackle the major challenges ahead like- global changing climate scenario, increasing world population, always evolving pathotypes of insects and other pathogens and some other major bottlenecks. Rice genome was the first crop genome to be sequenced which helped the researchers in underpinning of the major as well as the minor QTLs governing the traits which are of relevance to crop breeders. Consequently, the developments in rice genomics has helped in enriching the research domain by working out synteny and collinearity of rice genomes with genomes of other cereals. This review paper bring into light various researches like- theories of single and multiple origins of cultivated rice, role of domestication and of introgression of genes and also origin and evolution of fragrance in rice. Domestication led to rapid genetic erosion and loss of variability so there is a need to study properly the evolution of rice and excavate more and more wild relatives. Such wild relatives can then be scouted to find numerous genes of interest, which we can transfer in our cultivated varieties today for an overall improvement of the rice cultivars that are being grown today and try to improve yield.

Keywords

Rice, Evolution, Genomics

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1. Introduction

1.1. The Saga of Rice Evolution

With the advent of era of genomics and a tremendous development of technological backup, the work of sequencing of the whole genome of rice was done and as a result expectedly there was an upsurge in research in the genetics, genomics and evolution of rice. Research mainly focused on domestication related traits and those are the genes that were mostly cloned rice genes [1, 2]. Recent papers emerged on such domestication related traits and focused on evolution of such traits and finally providing some insights regarding the evolution of rice [3, 4]. With more researches coming our way and additional support from the field of genomics it can be expected that we can put an end to the controversies revolving around the evolution of rice soon.

The objective of this review paper is to provide the reader an insight into the evolution of rice along with some genomics background.

1.2. Background

To facilitate more headway into rice research and in order to shape the future of the global increasing consumption demand, we need to understand the evolution of rice. In the genus of *Oryza*, there are two cultivated species and more

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than 20 wild species and the wild species having evolved in a wider range of environments over millions of years [5]. It was long ago proved that the species of rice has been domesticated from the A-genome of *Oryza* in two independent events in Asia and Africa, and in these two continents the contemporary ways of harvesting the crop for human-desirable traits has complemented their evolution into their modern day forms [6]. Asian rice i.e., *Oryza sativa* is now cultivated widely worldwide whereas in case of African rice viz., *Oryza glabberima* is mostly confined to Western Africa. Many studies revolving around the diversity of *O. rufipogon* (A-genome wild rice) in china have been conducted to elucidate the domestication of Asian rice [7]. *O. nivara / O. rufipogon* is considered to be the ancestor of wild rice and it evolved into cultivated Asian rice by repeated gene introgression, selection and eco-geographic diversification. Deciphering the evolution pathway through research is difficult as the wild rice populations in china are declining through habitat degradation and thus causing inter population genetic differentiation [8]. The annual wild rice ecotype, *O. nivara* is not described in chinese provinces but reported from Indian states. In China, the Yunnan Province is found to be a centre having the major traditional rice diversity which proves the role of eco-geographic diversity as well as diversity due to ethnic to have played a major role in rice domestication [9, 10].

Numerous archaebotanical surveys states the Chinese Yangtze river valley to be the area of rice domestication [11, 12]. Findings regarding cyclic and periodical changes in climatic conditions in the Yangtze river valley area, supports the probability of asian rice domestication and diversification in that area [13].

Rice domestication in Africa happened after the domestication of rice in Asia [14, 15]. Domestication of *O. glabberima* in African Niger river (now Mali), is well-supported by archaeo-botanical data and surveys conducted near the river [16]. Reseach conducted to pinpoint 3500 BC [17] as the correct time of domestication of African rice. Regarding the genectics of *O. glabberima,* knowledge is less in comparison to *O. sativa* [18]. *O. glabberima* is annual with fewer secondary panicles than *O. sativa,* having round and short ligule and reddish pericarp, although the comparison between the two cultivated species for domestication trait alleles has not yet been done. But, today a percentage of African rice is found to have introgression of genes from Asian cultivated counterparts [19]. *O. barthii*, the ancestor of African rice, probably had its ancestors in Asia which were introduced to Africa. Genetic diversity is less in african rice [20].

2. Some Researches--That Are Setting of the Scene Towards the Ever-Evolving Scenario of Rice Evolution

2.1. Two Evolutionary History and Role of Domestication Genes

In evolutionary biology, the origin of indica and japonica, the two cultivated rice is a fascinating topic. With the advent of whole-genome sequencing, rice scientists have provided conclusive proof that there are two independent trajectory of evolution which the rice-genome embodies into it. The two cultivars has their own independent origin from wild rice-which is supported by gross genome-wide-pattern but it was further noted that genomic regions governing pivotal agronomic traits might have originated only once and then went on to disperse across other all cultivars through introgression and selection aided by humans [21].

2.2. Multiple or Single Origin of Cultivated Rice

Speaking about evolution, it is the characteristics change of a species as a result of the several generations of natural selection. So the theory says that all species are related and they gradually change over time. From shattering wild types to present-day evolved non-shattering type, it was found that *sh4* allele plays the key role in reducing the shattering in cultivated types. Moreover it was found that it was due to mutation of functional base pair and is common in most groups of rice [1, 2]. Another study, involving the locus *rc* (red pericarp, which is pre-dominant in wild rice), also supports the single domestication event. The *rc* locus affects the change from red pericarp to white pericarp in almost all kinds of domesticated rice. Moreover, no segregation is found in crosses of japonica and indica varieties and also, the recessive allele is common in all rice varieties giving rise to elite pericarp [22, 23]. So, these kind of studies mentioned above support the single domestication of rice and points towards domestication of rice being a local event [24] geographically.

On the contrary, for more than one or multiple domestication event, it was found that indica and japonica rice crosses produces progeny which segregates at numerous loci for wild alleles and there was reappearance of wild characteristics [14]. Phylo-geographic and haplotypes diversity analysis of genes in large number of wild and cultivated rice germplasms/accessions showed that wilds from south-east asia have association with Indica-like haplotypes whereas Chinese wild accession have japonica-type haplotypes [25] and diversity analysis amongst such haplotypes between

Indica and Japonica Varieties resulted into the formation of different nodal and discrete clusters [26].

2.3. Role of Introgression of Genes in Evolution

Some researchers have tried to decipher the role of Introgression of genes during the evolution of cultivated rice and they came up with the conclusion that although during evolution introgression has indeed occurred but for some key domestication alleles such introgression or gene transfer is not seen between some cultivated ecotypes. So, the model suggesting independent origin of japonica, indica and aus was proved consistent. Hence, it was conclusive that there was meagre contribution of inter-group of gene flow but those groups acquired the domestication alleles from standing variation in wild rice [27].

2.4. Origin and Evolution of Rice Fragrance

One of the most valuable trait of grain quality in rice is the fragrance present in rice grain. But, still it is unclear how the gene, *BADH2- fragrance causing gene*, originate or evolved. Researchers and scientists have found 8 putatively NF (non-functional) alleles of the BADH2 gene and further went on to prove that these alleles have separate/isolated geographic and genetic origins. Inspite of numerous origins of the fragrance-causing gene, one single allele *viz.,* badh2.1 is found which is the predominant allele in all fragrant rice varieties. Introgression of the, allele badh2.1 is shown to be from *Japonica* to *Indica* through Haplotype (group of genes within an organisms that was inherited together from a single parent) analysis and it was further established that the allele (badh2.1) has a single origin within the *Japonica* varietal group. [28]

3. The Genomics of Rice

3.1. Rice: A Cereal Genome Model

The initial interest among researchers to sequence the rice genome arose because of the small genome size of rice in comparison of its counterparts- maize and wheat. The small size of rice was presumed beforehand by some researches in molecular mapping involving RFLP markers.

3.1.1. The Genome of Rice

The genome decoding project of rice is one of the best example of multinational collaboration [29]. This project seemed like many countries running with their respective flags and planting them on each of the chromosomes of rice just like how new territories are captured by early explorers. In 2000, Arabidopsis genome had been sequenced and next was rice. Rice has nearly four times the genome size of Arabidopsis. Chromosome 1, 6, 7 and 8 was sequenced by Japan, Taiwan choose Chromosome no. 5, 3 and 10 by US etc. International Rice Genome Sequencing Project (IRGSP) attracted numerous researchers to be a part of the project. In this collaborative project many meetings were held for proper planning and execution and to successfully shape the rice genome Project. Rice was a clone-by-clone and sanger-sequenced genome. In this method clones of BAC were selected inn sequence, assembled exclusively and then woven together, that led to the formation of pseudo-chromosomes. Rice genome was one of the last crop to have followed the aforementioned techniques. Another striking feature of this project is the sequencing of the gaps in the highly repetitive regions in the genome, a first of its kind and has been the 1st sequenced complex eukaryotic centromere present on 8th chromosome [30]. How was it Possible? Cytogenetic analysis conducted has showed us the diminutive nature of the 8th chromosome and because of the smaller size of about 64kbp of satellite repeats which is even less than the centromeres of Arabidopsis. So, we can infer that rice had been the crop of choice to researchers when it comes to study of structure and function of centromeres. Cytogenetic analysis seems to be important before choosing and particular chromosome and the United States might not have chosen chromosome 9 if they had cytogenetic descriptors of that particular chromosome considering its complexity. Sequencing complexity includes- one arm being highly heterochromatic and prevalence of repetitive DNA sequences. Rice genome draft was made available in public domain following a hierarchical shotgun sequencing method by Monsanto Co. in 2000 and Syngenta in 2002 [31]. The humongous task of annotation took place after it got published in IRGSP in 2006, and since then it has been one of the rare plant genomes having conflicting annotations [32, 33]. But, eventually researchers resolved such conflicts and came up with universal single annotation [34].

3.1.2. Synteny: Between Rice and Other Cereals

Accountable genetic synteny was revealed when rice model cereal genome was compared to other cereals. Sorghum and Maize had reported preserved synteny in several early works [35]. As research advanced on conserved marker order between several grasses over long timeframe of evolution, it revealed conserved synteny and helped in developing a concentric circle genomes [36]. But, when genomic regions which are orthologous, are sequenced- then gene content, size and repeat structure revealed considerable variation. After the completion of sequencing of rice genome when several cereals *viz.,* sorghum, maize and rice, extensive size variation is revealed alongwith inflation in maize. Moreover low copy sequences among the three species are conserved [37]. Comparisons among genomes have also showed that while some genes are absent in rice but present in other cereals and vice-versa. Support to the above statement can be found in Rice-Barley comparison involving a disease resistance locus which reported that six more genes are found in barley which was not there in orthologous region of rice [36]. So, with the emergence of more and more data on genomics of all cereals it would be possible to pinpoint the genetics of various traits in these crops.

3.2. Contribution of Rice-Genomics to Crop Improvement

In many ways the development in the field of rice genomics have contributed to crop improvement. The number of molecular markers in the crop has seen a dramatic increase. The order of such markers was elucidated through physical mapping and such underpinning of markers in close proximity of annotated genes helped in prediction of marker-gene-trait associations. Cost of DNA sequence reduced and this has allowed researchers to sequence more and more accessions of rice and to put light in several variations in their nucleotide when compared to the reference genome [38]. Subsequently, sequence based analysis of wild and cultivated rice was carried out and it helped plant breeders to have a clear-cut idea of genetic variation and led to proper, effective utilization of such variations [39]. Moreover, better understanding of molecular basis of some nutrient- use relating traits have given new avenue to plant engineers to develop ‘Green Super Rice’ – which requires less inputs and thus can help in ensuring global food security in coming decades [40].

4. Concluding Remarks

So the review, instead of being written from evolution to genomics can also be turned completely upside down and be written as genomics to evolution. I am concluding this as because the advent and development of the genomics era had brought numerous high-throughput technologies which were exploited to get a crystal clear picture about how rice originated or evolved.

Study of evolution of crop plants has turned out to be of utmost important now to rectify our sins that we have committed during the domestication of our crops. Domestication had led to narrowing gene pool and genetic erosion making our crops more vulnerable to evolving pathogens and climate as a whole. Now again we are looking backwards to deduce the evolutionary pathway properly and find more and more wild relatives in the process. In doing so we can enrich ourselves with invaluable genes which can help us tackle the adversities of unforeseeable future. In a nutshell, we can conclude with these remarks that the past two decades there have been a rapid surge in genomic and sequencing data helping us to do mining of useful alleles and QTLs and also solve the evolutionary dilemmas involving several close relatives. Looking onwards and upwards from here rice breeders can carry on their effort and there is a lot to achieve in terms of overall development of the crop.

Abbreviations

BAC- Bacterial Artificial chromosome; QTL- Quantitative Trait Loci; BADH- betaine aldehyde dehydrogenase; BP- Base Pair; i.e.,- that is; viz.,- namely

Competing Interests

The author declares that he has no competing interest.

Author’s Contribution

Written by D. Roy.

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