

Impact of the early-ripening Champa rice – Are they *aus*?

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Abstract

Background The early-ripening rice races are important because they may escape droughts, avoid floods and reduce the growing period. Thus, they could be cultivated for at least two cropping seasons each year in sub-tropical or tropical areas. According to Song Dynasty history, many rice accessions were brought to China from the Champa Kingdom, and these lines were drought-resistant and non-photoperiod-sensitive. Here, we address the impact of Champa rice on rice production, and which subtype the Champa rice belong to.

Results We performed a phylogenetic analysis of rice landraces in China and Taiwan that had the word “Champa” in their names. We also cooperated with rice breeders in Vietnam, where the ancient Champa Kingdom was. Together with the publicly available genome sequencing data, we confirmed that many Taiwan landraces are also Champa rice. We also showed that these Champa rice played important roles in ancient and modern rice production. The most famous landrace is Dee Geo Woo Gen, one of the parental lines of IR8. This landrace had a loss-of-function *semi-dwarf 1* gene and thus is lodging-resistant. In addition, Champa rice is *indica* type but not *aus*.

Conclusions Champa rice is a group of *indica* rice. Many Champa rice accessions are early maturing and are resistant to biotic and abiotic stresses. Some are key accessions in the “green revolution” and have been very important in the modern breeding program.

Background

Rice (*Oryza sativa*) is one of the most important crops in the world. It is a short-day plant and was domesticated originally in a temperate zone, then brought to sub-tropical and tropical zones with warmer temperature and different photoperiod. One of the main reasons for the spread of rice cultivation to a wide range in Asia as well as the increase in production is the change in response to photoperiod in rice [1].

Flowering time, also known as heading date for rice, is an important trait for rice cultivation [2]. Flowering time is affected by photoperiod (day length) and also temperature [3]. Early maturing was one of the important traits in rice growing regions for hundreds or thousands of years. If humans could control the rice growth period, plants could escape/avoid stresses caused by seasonable typhoons, monsoons, drought, etc.

Another important trait for rice production is lodging resistance. The development of semi-dwarf varieties in both rice and wheat led to a sudden major increase in grain production to meet the huge increase in the world population during the 1960s. The key genetic resource for the semi-dwarf trait was Dee Geo Woo Gen (DGWG), a landrace from Taiwan.

According to the *History of Song Dynasty*, Champa rice was brought to China about 1000 years ago, when there was severe drought in the Yangtze and Hui river valley areas [4]. This Champa Kingdom was

located in what is now central Vietnam. A recent paper suggested that Champa rice belonged to the *aus* sub-population [5]. If indeed Champa rice is *aus*, there should be some *aus* rice accessions in the current Chinese collections. However, this statement is not true: some authors used a core collection representing the diversity of Chinese rice germplasm for genetic diversity and classification studies [6]. Using molecular markers, they identified 3 groups: temperate *japonica*, tropical *japonica* and *indica*, with no *aus* type. If there is no *aus* accession in the Chinese rice collection, the statement that “Champa rice was *aus*” might not be correct.

Another related question is Where are Champa rice currently? and Do these accessions play important roles in modern agriculture? Han people immigrated to Taiwan from southern China after the late Ming Dynasty (i.e., mid-17th century) and brought about 1000 *indica* rice accessions with them. Many of the landraces had the word “Champa (Chan)”, “Chien”, or “Gen” in their names. Chan, Chien, Gen are different dialects that belonged to Taiwanese, mandarin or Hakka but with the same meaning. An example is “Puh Chan”, “Tsaw Chan”, “Wu Chan”, “Wu Chien (also pronounced as Woo Gen)” [7, 8]. Many of these accessions were early maturing as well as resistant to several stresses such as drought, salt, and low fertility [8]. For instance, Wu Chien was a popular landrace in northern Taiwan during the Ching Dynasty, planted in February and harvested in June. In addition to early maturity, this accession had a white caryopsis, tasted delicious and was resistant to drought stress and thus was a popular landrace for the paddy field [9]. However, Pu Chan, another Champa rice had red caryopsis and tasted bad but had strong growth vigor and was resistant to drought as well as salt. Thus, it was mainly grown in upland fields and was used for making wine [9]. According to the older literature, the sib of Wu Chien (Woo Gen) (i.e., DGWG) appeared in history books in the 1860s [10].

In the present study, we performed whole-genome sequencing of several landraces collected from central Vietnam and several Taiwanese landraces with the word “Champ” in the name. We studied the phylogenetic relationship among these lines and the agronomic traits of these accessions. The Champa rice may have played important roles in old and modern rice production. In addition, we found that Champa rice is not *aus* but *indica*.

Materials And Methods

Plant Materials

In cooperation with the Vietnam National University of Agriculture, 3 Champa rice landraces were chosen: Rắn trắng, Nếp rẫy and Rắn đỏ. They were from Bình Thuận, a central Vietnam province. Rắn trắng is drought-tolerant and Nếp rẫy is flooding-tolerant. The names and collected locations of these accessions are in Table S1. In addition, we found 9 rice landraces in the Germplasm Center, Taiwan Agricultural Research Institute (TARI), that contained the term “Champa,” pronounced Chan in Chinese. They are DGWG, Wu Chien, Hei Chan, Pai Jih Tung Chan, Pai Ko Pu Chan, Ching Kuo Chan, Wu Chan, Hsin Chu Liu Chan and Lung Ya Chan. These 12 Champa rice accessions were used for sequencing and phylogenetic analysis.

Whole-genome Sequencing And Data Interpretation

Genomic DNA from rice plants was extracted from healthy leaves from a single-seed–descent plant by using the DNeasy Plant Mini Kit (Qiagen). After quality assessment, genomic DNA was randomly fragmented and size-fractionated. DNA fragments with the desired lengths were gel-purified. For whole-genome resequencing, paired-end libraries with 450- to 500-bp inserts were constructed and sequenced by using the HiSeq2000 system (Illumina). Adaptor sequences, low-quality bases and reads < 20-bp long were discarded. The trimmed paired reads were mapped against the Os-Nipponbare-Reference-IRGSP-1.0 [11, 12]. SAMtools [13] and VCFtools [14] were used to manipulate and transform the sequence alignment/map format (SAM) and variant call format (VCF) of the file. To detect single nucleotide polymorphisms (SNPs) and small indels, we used the command lines in the section “Variant Calling” in “Workflows” of the SAMtools manual without any restriction on depth or mapping quality. The information on SNPs and small indels was recorded in VCF files. The sequence data for all Champa-related landraces were deposited into the NCBI Sequence Read Archive. The accessions numbers are available in Table S2. Many other whole-genome sequencing data were from the 3K rice project [15] and were downloaded from the public database. They include 9 Taiwanese accessions, 4 from Bangladesh, 2 from Cambodia, 3 from India, 2 from Indonesia, 3 from Japan, 2 from Malaysia, 1 from Nepal, 1 from Pakistan, 2 from the Philippines, 2 from Thailand and 2 from Vietnam. The whole-genome sequencing data for *O. rufipogon*, an Asian wild rice, was used as an outgroup.

The VCF files were used to estimate heterozygosity with BCFtools v1.10.2 + htslib 1.10.2 (<https://samtools.github.io/bcftools/bcftools.html>). BCFtools stats was used to retrieve information about heterozygous and homozygous SNPs for each sample with read-depth > 5 and mapping quality > 20.

Phylogenetic Analysis

To reveal the position of the Champa rice accessions relative to other Asian rice, we used phylogenetic analysis with next-generation sequencing data. Table S2 lists the names, types, origins and sequence information for these lines. The clean reads were mapped to the Nipponbare reference genome (IRGSP v1.0) by using BWA v0.7.13-r1126 mem with default parameters [12, 16]. The mapped results were merged, and data with low mapping quality ($q < 20$) were removed as BAM files by using Samtools v1.3 [13, 17]. Picard v2.1.1 MarkDuplicates was used to identify and remove duplicate reads in the same DNA fragments (<http://picard.sourceforge.net>). The Genome Analysis Toolkit v3.5-0-g36282e4 RealignerTargetCreator was used to identify regions around indels, then the Genome Analysis Toolkit IndelRealigner was used for local realignment [18]. Samtools and Bcftools were used for variant calling including SNPs and indels with filter by depth and mapping quality. Genetic distance with the p-distances model was calculated, and a neighbor-joining tree was constructed with 1,000 bootstraps by using PHYLIP v3.695 (<http://evolution.genetics.washington.edu/>) [19]. MEGA v7 [20] was used to display the phylogenetic tree.

Results And Discussion

History of Champa rice

According to the *History of Song Dynasty*, there was a severe drought in Yangtze and Hui river valley areas and in the eastern and western Zhejiang paddy rice area in 1012 [4]. The emperor Zhenzong (a.d. 992–1022) heard that Champa rice was drought-resistant, early maturing, and non-photoperiod-sensitive [21]. He sent governors to Fujian Province and brought 30,000 bushels of Champa seeds and distributed them to farmers in the drought area. This Champa Kingdom was located in what is now central Vietnam. According to the history, as compared with Chinese rice, this Champa rice had longer panicles, no awn, less difference in grain size, could grow well in marginal land, and was drought-resistant and not sensitive to photoperiod [21, 22]. Therefore, Champa rice, with many good traits, came from Vietnam to Fujian (southern China) first and later to the Yangtze region (central China) during the early Song Dynasty in the 11th century. Barker explored the origin and spread of Champa rice and asked his colleague Susan McCouch at Cornell University about it. She mentioned she found a Champa rice in her collection and the DNA test indicated it was *aus* rice [5].

About 1000 rice landraces were brought from southern China to Taiwan by the Han people during late Ming to early Ching dynasty, around 400 years ago. They were propagated and maintained first by local farmers and then by rice breeders during the Japanese colonial time. All these accessions were *indica* and are now stored in the Germplasm Center, TARI. DGWG, one of the parental lines of IR8, was one of the accessions. These accessions were old landraces in China hundreds of years ago, but most, including DGWG, are not present in the current Chinese germplasm. We found 9 accessions that contained the term “Champa” in the TARI collection, as listed in the Materials section. Thus, many Champa rice accessions were used in the current study, including 3 from central Vietnam.

Most of the Champa rice genome has high heterozygosity

Rice is a selfing plant, and the genome of most modern varieties has high homozygosity. The homozygous and heterozygous SNPs of the Champa rice accessions used in the current study were calculated from the genome sequencing data, as indicated in the Methods section. Table 1 lists the 2 types of SNPs of Champa rice accessions and 2 modern varieties, Koshihikari and IR64, for comparison. The homozygous SNP numbers of all Champa accessions ranged from 2.1 to 2.5 million, as expected. However, the heterozygous SNPs, ranging from 0.6 to 1 M, were quite high in number as compared with the modern variety IR64: 445,517. Thus, similar to other landraces, the genome of Champa rice accessions still has high heterozygosity.

Table 1
Heterozygosity of Champa rice accessions.

Accessions	Homo SNPs	Hetero SNPs	Accessions	Homo SNPs	Hetero SNPs
Koshihikari	116,648	95,041	HsinChuLiuChan	2,259,093	683,763
IR64	2,120,758	446,517	LungYaChan	2,324,790	723,491
HeiChan	2,111,886	584,125	Rần trắng	2,470,139	646,492
PaiJihTungChan	2,224,496	700,637	Nếp rẫy	2,442,619	588,552
PaiKoPuChan	2,247,859	707,499	Rần đỏ	2,543,887	738,536
ChingKuoChan	2,207,227	696,877	Dee-Geo-Woo-Gen	2,476,224	1,087,516
WuChan	2,214,929	636,558	ChiayiWuKo	2,324,487	603,287
SNP, single nucleotide polymorphisms; homo, homozygous; hetero, heterozygous					

Some Champa rice accessions are resistant to biotic and abiotic stresses

The agronomic traits of about 3500 rice accessions in the TARI germplasm center were screened by rice breeders in the early 1960s [23]. All these accessions were grown in paddy fields for phenotyping. In addition to the yield components, flowering behavior, resistance to abiotic and biotic stresses etc. were also recorded. From the TARI monograph, Pai Ko Pu Chan, Wu Chan, Hsin Chu Liu Chan, and Lung Ya Chan are drought-resistant and Ching Kuo Chan, Wu Chan, Hsin Chu Liu Chan, Lung Ya Chan and DGWG are resistant to rice blast. According to the record of Vietnam Plant Resource Center, Rần trắng is drought-resistant and Nếp rẫy is flooding-resistant. Thus, many of these Champa rice accessions are resistant to biotic and abiotic stresses.

Some Champa rice accessions are not sensitive to photoperiod and have the loss-of-function *hd1* gene

Several recent reviews provided detailed information on the regulation of rice flowering (e.g., [24]; [25]; [26]). A few key genes have been suggested to affect flowering time, including *Heading date 1 (Hd1)*, which encodes a B-box zinc-finger protein and is the ortholog of Arabidopsis *CONSTANS (CO)* [27]. The functional Hd1 protein is required for suppressing flowering under long-day conditions and promoting flowering under short-day conditions. Takahashi and Shimamoto [2] suggested that *Hd1* was a possible target of selection to generate different flowering-time response in different regions. Using about 60 diverse rice accessions, Kim et al. [28] also concluded that accessions from tropical or sub-tropical regions preferentially have the non-functional alleles of *hd1*. In our previous analysis of data mining on the genome sequencing information in the public domain, we classified 10 loss-of-function haplotypes [29]. Rice plants with any of these 10 alleles did not respond to photoperiod and might have at least 2 growing seasons each year in sub-tropical and tropical regions. The whole-genome sequencing data for the Champa rice accessions from Vietnam and Taiwan revealed that several indeed had the loss-of-

function *hd1*: DGWG, Hsin Chu Liu Chan, Wu Chien and Wu Chan contained type 7 *hd1* and Lung Ya Chan type 13 *hd1* (Table 2).

Table 2
Types of loss-of-function *hd1* genes in the Champa rice accessions

Accession	Haplotype	Accession	Haplotype
Dee Geo Woo Gen	Type 7	Hei Chan	--
Taichung Native 1	Type 7	Pai Jih Tung Chan	--
Wu Chan	Type 7	Pai Ko Pu Chan	--
Hsin Chu Liu Chan	Type 7	Ching Kuo Chan	--
Taichung Woo Gen2	Type 7	Rắn trắng	--
Lung Ya Chan	Type 13	Nếp rẫy	--
		Rắn đỏ	--

Also, according to the TARI monograph [23], DGWG, Pai Ko Pu Chan, Ching Kuo Chan, Wu Chan, Hsin Chu Liu Chan and Lung Ya Chan could grow twice a year in a paddy field and thus were not sensitive to photoperiod (i.e., they belonged to the early-flowering type).

Champa rice are *indica* instead of *aus*

To compare the relationship of Champa rice and other types, we used phylogenetic analysis of the Champa rice accessions along with some traditional accessions of *japonica*, *indica* and *aus* in Asia. A total of 52 accessions were used, and their types and collection locations are in Table S2. In total, 6 *Aus*, 5 *japonica* and 41 *indica* accessions, along with one wild rice, *O. rufipogon*, were used for analysis. All have > 10X sequencing redundancy. Those with the word Chan or Chien in the name from Taiwan (highlighted in green) were in the same clade as other Taiwan *indica* landraces (Fig. 1). Because DGWG, Woo Gen and the 7 newly sequenced Chan rice accessions clustered together, once again it was demonstrated that DGWG and Woo Gen were Champa rice. Together they were very close to the 3 accessions from central Vietnam (highlighted in blue). They were clustered with *indica* landraces collected from southeastern Asia but were quite far away from the *aus* accessions (highlighted in red). Thus, Champa rice was *indica* rather than *aus*. Together with absence of *aus* in the rice germplasm collection in China National Rice Research Institute [6], we suggest that Champa rice was *indica* type.

The impact of Champa rice

Many *indica* rice accessions were introduced to the Yangtze River region in China about 1000 years ago according to the *History of Song Dynasty*. Some points can be summarized: 1) Champa rice was already present in Southern China before the early Sung Dynasty, 2) many of the Champa rice accessions were resistant to biotic and abiotic stresses, and 3) perhaps there was no photoperiod-insensitive accession in

Central China before Champa rice was introduced. Champa rice was cultivated in the Yangtze River area and southern China since then.

The sequence analysis and phenotype screening confirmed again that Champa rice accessions had several good agronomic traits: they were early ripening and thus could grow at least twice a year in subtropical and tropical regions and were resistant to biotic and abiotic stresses such as blast, drought and salt. Before the semi-dwarf varieties were available, the Champa rice accessions were very popular for rice production in Taiwan. In the early 20th century, many Champa rice landraces were subjected to pure line selection in Taiwan. Examples are Kaoshiung Ching Kuo Chan No. 1 and Kaoshiung Pai Ko Pu Chan [10]. After WWII, cross breeding was also used in the breeding program. The most famous variety was Taichung Native No. 1 (TN1), with the parental lines DGWG and Tsai Yuan Chon. This is the first semi-dwarf modern variety in the world and is lodging-resistant. TN1 was released at 1957 and very quickly became the leading variety in Taiwan. When the International Rice Research Institute (IRRI) was established at 1960, rice breeders brought DGWG to the IRRI and it was subjected to a breeding program. The famous miracle rice IR8 (DGWG x Pita) was released at 1966 and quickly became the hallmark rice variety for the “green revolution”. DGWG has been in the pedigree of at least 80% of the world’s modern *indica* rice varieties. Thus, Champa rice has played important roles in ancient and modern rice production.

Conclusion

Many Champa rice accessions are early-maturing and are resistant to biotic and abiotic stresses. They were introduced into China about 1000 years ago when there was drought stress in the rice production area. Champa rice has been very important in rice production in Taiwan. DGWG, the most famous Champa rice, was one of the parental lines of the “green revolution” variety and has been used in breeding programs, not just in Taiwan but worldwide, for decades.

List Of Abbreviations

DGWG: Dee Geo Woo Gen; Hd1: Heading date 1; SAM: sequence alignment/map format;TARI: Taiwan Agricultural Research Institute; VCF: variant call format.

Declarations

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Authors’ contributions

CCW and YICH are responsible for the experimental design. DNA sample extraction was prepared by LTH, HTQ and NQT. YCT and DHW are responsible for the agronomic traits analysis. CCW is responsible for

the bioinformatics analysis. YICH wrote the manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

All DNA sequence data are available in the public domain, as listed in Table S2.

Competing interests

The authors declare that they have no competing interests.

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Figures

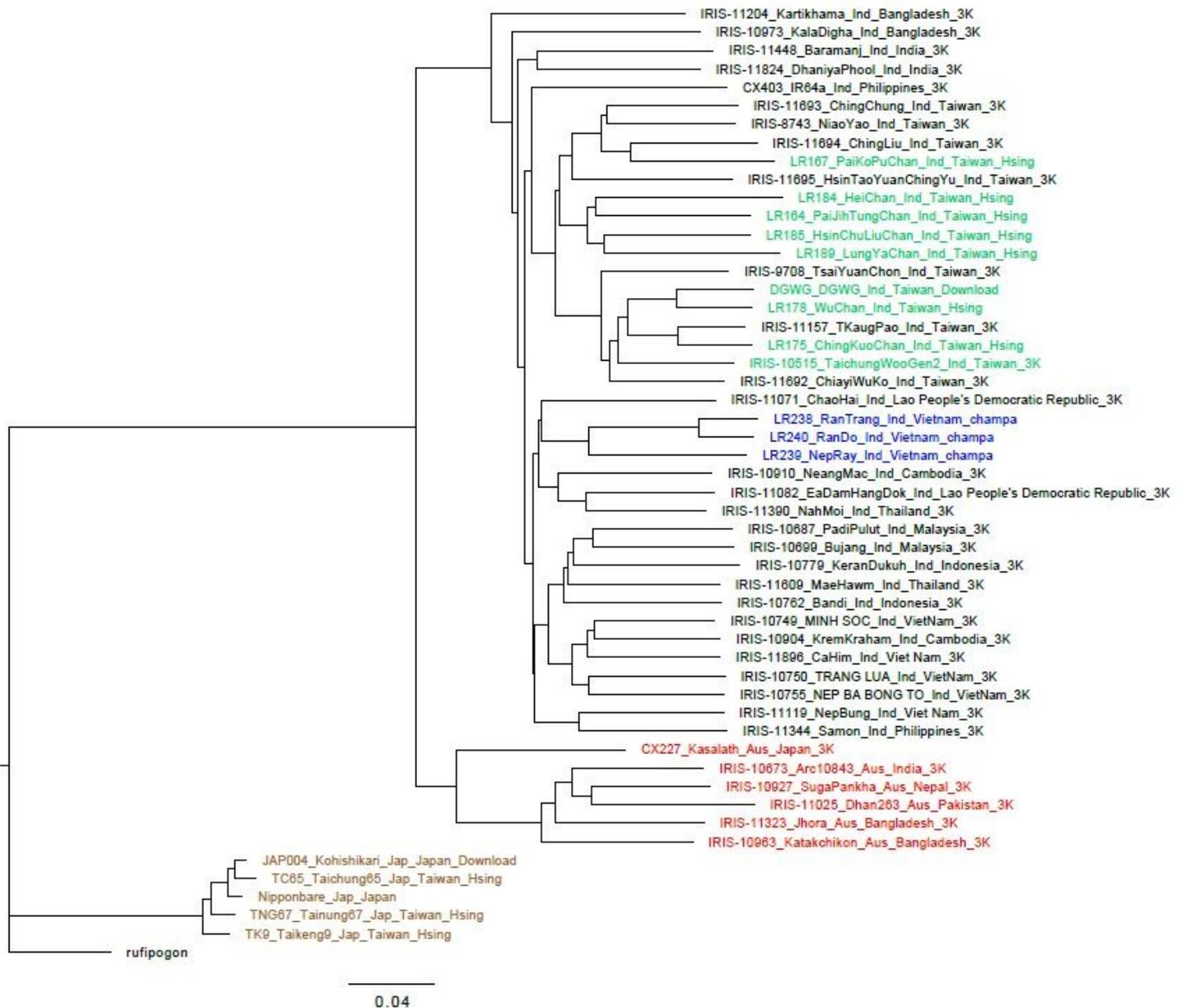


Figure 1

Phylogenetic analysis of Champa rice. Neighbor-joining phylogenetic tree based on all single nucleotide polymorphisms of the 52 accessions in Table S2. Red: aus, blue: Champa rice from Vietnam; green: Taiwan landraces with “Champa” (Chan or Chien) in name; black: indica rice; brown, japonica rice.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [TableS1.pdf](#)
- [ChampaTableS2.xlsx](#)