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REVIEW

The Complex History of the Domestication of Rice

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INTRODUCTION

Rice is the world’s largest food crop, providing the caloric needs of millions of people daily. There are two distinct types of domesticated rice, Oryza sativa, or Asian rice and Oryza glaberrima, African rice, both of which have unique domestication histories. In order to examine the variation selected by humans over our long relationship with rice, we must first look at the ancestors of our modern cultivars. The genus Oryza contains 21 wild relatives of the domesticated rices (Vaughan et al., 2003). The genus is divided into four species complexes: the O. sativa, O. officinalis, O. rufipogon and O. granulata species complexes. All members of the Oryza genus have n = 12 chromosomes and while interspecific crossing is possible within each complex, it is difficult to recover fertile offspring from crosses across complexes (Vaughan et al., 2003). The O. sativa complex contains two domesticated species: O. sativa and O. glaberrima, and five or six wild species: O. rufipogon, O. nivara (also considered to be an ecotype of O. rufipogon), O. barthii, O. longistaminata, O. meridionalis and O. glumaepatula, all of which are diploids. Oryza sativa is distributed globally with a high concentration in Asia, while O. glaberrima is grown in West Africa. Oryza rufipogon can be found throughout Asia and Oceania. Oryza barthii and O. longistaminata are African species, O. barthii endemic in West Africa and O. longistaminata is found throughout Africa. Oryza meridionalis is native to Australia and O. glumaepatula is endemic in Central and South America. Given these distributions, it is easy to locate the ancestral pools from which modern rice were extracted. The African cultivars were domesticated from O. barthii (formally called O. brevigulata) and O. sativa was domesticated from O. rufipogon. There is still continuing debate over whether O. rufipogon, the perennial species, O. nivara, the annual species, or possibly both were the direct ancestors of O. sativa. For the purpose of this review we will reserve judgment and refer to both the annual and perennial forms as O. rufipogon.

Many phenotypic differences are obvious between O. sativa and its wild relatives (Xiao et al., 1998; Xiong et al., 1999; Bres-Parry et al., 2001; Cai and Morishima, 2002; Thomson et al., 2003; Uga et al., 2003; Li et al., 2006a) (Fig. 1). Wild rices typically display long awns and severe shattering for seed dispersal, whereas the domesticated type have short awns if any and reduced shattering to maximize the number of seeds that can be harvested.

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Dormancy levels are higher in the wild rices, allowing viable seeds to persist for years before germination, but these have been reduced in cultivars to give uniform germination. The pericarp and seed coat of wild grains contain a pigment giving them a red colour which modern Asian cultivars lack, but which many African cultivars retain. Seeds hulls are straw coloured in the domesticated but dark in the wilds. Mating habits differ, *O. rufipogon* and *O. barthii* are partially outcrossing, with estimates ranging from 10 to 50 %, while *O. sativa* and *O. glaberrima* are almost entirely inbreeding. Wild grains are consistently small while domesticated grains vary in size. The panicle structure has changed from an open panicle with few secondary branches bearing relatively few grains, to a densely packed panicle that can carry larger numbers of seeds than the wild ancestors.

These phenotypes are not perfectly partitioned between wild and cultivated plants. While we refer to domestication ‘events’ it is important to remember that domestication was a process that occurred over an extended period of time. Genetic loci that were selected from existing genetic variation in the wild species may appear fixed within domesticated rice, but will show variation within the wild rices. Although domestication traits are not favoured by natural selection, many of these traits are polygenic. A single allele promoting a more domesticated phenotype could be masked in the wild by a dominant allele at the same locus, or by alleles at other loci in the pathway, until a chance combination of different pre-existing wild alleles produces a plant with a domestication phenotype. This domesticated genotype would not survive long without artificial selection, but the parents contributing the variation leading to the domesticated phenotype can have wild phenotypes which would not be selected against. Positive mutations that occurred later in the domestication process may be absent from the wild gene pool or early landraces, but would be ubiquitous among more recently developed cultivars. On-going gene flow between domesticated and wild rice further complicates the picture. We consider domestication traits to be those that are favoured by humans, occur at significantly higher frequencies in domesticated compared with wild rices, and adversely affect a plant’s ability to survive and reproduce without human assistance. Genes influencing these traits and showing signs of ancient selection are considered domestication genes.

**DOMESTICATION OF O. GLABERRIMA**

Linguistic evidence supports an African origin of *O. glaberrima*, as rice words in several west African language families (malo, maro, mano, etc.) predate the Portuguese-derived words associated with Asian rice (Blench, 2006; Porteres, 1970). Archaeologists have found ceramic impressions of rice grains dating from 1800 BC to 800 BC in Ganjigana located in north-east Nigeria. These go back to 1800 BC and continue through to 800 BC. At the neighbouring site of Kursakata, scientist have uncovered abundant charred grains of rice dating from 1200 BC through to AD 0 (Klee et al., 2000). However, there is no evidence that the grains from either of these sites are domesticated and not wild rices. The oldest documented domesticated *O. glaberrima* dates between 300 BC and 200 BC and comes from Jenne-Jeno, Mali on the Inland Niger Delta (McIntosh, 1995). Molecular data beginning with isozyme studies and confirmed by simple sequence repeat (SSR) and single nucleotide polymorphism (SNP) data, unequivocally demonstrate the uniqueness of African rice and its close genetic relationship to *O. barthii* (Second, 1982; Semon et al., 2005). The centre of diversity for *O. glaberrima* is thought to be the upper Niger River Delta. Porteres (1970) hypothesized that *O. glaberrima* was first cultivated in the floodwaters using floating rice cultivars. Rice culture then spread to the brackish waters using non-floating cultivars and subsequently further
selections were used to plant upland fields watered only by rainfall. Asian rice was introduced into O. glaberrima’s range after the initial domestication and the two species are now sown side by side in West Africa (Dresch, 1949). Recently, breeders have crossed O. sativa and O. glaberrima, combining the stress-tolerance traits of O. glaberrima with the yield potential of O. sativa (Jones et al., 1997; Gridley et al., 2002). Known as NERICA (NEw RICE for Africa) these varieties have become popular among West African farmers. The remainder of this review will focus on O. sativa, about which much more is known.

**ARCHAEOLOGICAL EVIDENCE OF O. SATIVA DOMESTICATION**

The oldest archaeological evidence of rice use by humans has been found in the middle and lower Yangzi River Valley region of China. Phytoliths, silicon microfossils of plant cell structures, from rice have been found at the Xianrendong and Diotonghuan sites and dated to 11,000–12,000 BC (Zhao, 1998). Scientists have uncovered other sites in this region, including Shangshan, and Bashidang with significant quantities of rice remains, some dating back to 8000 BC (Higham and Lu, 1998; Pei, 1998; Jiang and Liu, 2006; Fuller, 2007). There is much debate over whether or not the rice discovered at these sites represents domesticated, cultivated rice, cultivated wild rices or if they are wild rices, which had been foraged from nature. As improvements continue to be made in ancient DNA amplification techniques and more rice domestication genes are cloned, it may soon be possible to answer these questions directly. However, at present we must infer from indirect evidence.

A few bone ‘spades’ were recovered at Kuahuqiao in the lower Yangzi (6000–5400 BC), although the design indicates they would not have been used for heavy tillage (Zhejiang Provincial Institute of Cultural Relics and Archaeology, 2004; discussed in Fuller et al., 2007). However the nearby Hemudu site (5000–4000 BC) contains many bone scapulas which would be useful as spades or hoes and are thought to have been used in rice cultivation (Chang, 1986; Fuller et al., 2007). Rice grains sieved from the oldest known paddy fields in the lower Yangzi River Valley date to 4000 BC (Cao et al., 2006), giving clear-cut evidence for rice cultivation at this point in time.

Genetic changes causing the shift from wild to domesticated rice are harder to pinpoint.Mutations leading to a reduction in the degree of grain shattering are a perquisite for domestication. Communities that foraged wild, shattering rice seeds would likely gather them before maturity since most of the mature grains quickly fall to the ground. Immature rice grains have a smaller width than fully mature seeds, because rice grains reach their full length early in seed development, and subsequent grain filling increases the width of the seeds. A survey of diverse modern rices has shown that mature modern cultivated grains rarely have a width <2 mm, although some mature wild grains do (Fuller et al., 2007). Therefore, if width of the assemblage of ancient grains from a site falls below 2 mm it is unlikely that they represent mature domesticated grains. Whether harvested as immature grains from a highly shattering plant or as mature grains from a non-shattering plant with thin O. rufipogon-type seeds cannot be determined by this method. What can be documented is that seeds with measurements similar to mature, modern O. sativa do not appear until 4500 BC at Chengtoushan in the Middle Yangzte and approx. 4000 BC in the Lower Yangzte area (Fuller et al., 2007). These seeds are certainly domesticated. Before this time the genetic changes conditioning a lack of shattering and/or the mutations leading to thicker grains had not been selected. While these mutations are genetically independent, they result in the same grain width phenotype.

Rice moved north to the Yellow River basin in Central China beginning in 3000–2000 BC (Crawford, 2005). South of the Yangzi River, work in Taiwan and Vietnam date the earliest rice finds there to roughly the same time period, 2500–2000 BC (Higham and Lu, 1998). Archaeological work in India uncovered the Neolithic site Lahuradewa in the Ganges Valley containing evidence of rice consumption dating to 7000–5000 BC (discussed in Fuller, 2006). Archaeological studies have not yet been able to determine whether this dispersal primarily consisted of a transfer of cultivation technology that was applied to local wild rices, or if the domesticated varieties travelled with the paddy technology. For the moment we turn to other lines of evidence to address the question of how many times rice was domesticated.

**POPULATION STRUCTURE IN ASIAN RICE**

As early as the Chinese Han dynasty in China (approx. AD 100) there are have records of two different types of rice called Hsien and Keng (Matsuo et al., 1997). Today these groups are commonly referred to the indica and japonica subspecies respectively. The distinctness of these groups has been confirmed by many different approaches over the course of rice research. There are distinguishing morphological features, including leaf colour, seed size and apiculus hair length, but the variation for these traits precludes using them to definitively classify varieties into subspecies (Kato et al., 1928; Oka, 1988). Researchers have also observed that progeny derived from crosses between these groups exhibited sterility (Kato et al., 1928). A third group or subpopulation was identified based on morphology and was referred to as javanica (Matsuo, 1952). This group is now known as the tropical japonica subpopulation (Glaszmann, 1987; Garris et al., 2005). Genetic analysis by Morishima and Oka (1970, 1988), in addition to Engle’s cytological studies (Engle, 1969), corroborated the distinctness of the three rice groups previously established by morphology.

Modern molecular methods have confirmed the ancient observations about divisions within O. sativa and added new levels of clarity to questions concerning the origins of rice. Isozymes were used to clearly differentiate the indica and japonica groups within O. sativa, and suggested further division within these two groups (Second, 1982; Glaszmann, 1987). Glaszmann’s landmark study using 15
polymorphic loci on nearly 1700 diverse *O. sativa* varieties identified six different groupings or subpopulations, *indica*, *japonica*, *aus*, *aromatic*, *rayada* and *ashina*. This level of differentiation was not confirmed by the RFLP studies which distinguish only the *indica* and *japonica* subspecies (Wang and Tanksley, 1989). A recent study using SSR markers examined 169 nuclear loci in 234 diverse accessions of rice (Garris *et al.*, 2005). This work identified five major subpopulations: *aus* and *indica*, grouping within the traditional *indica* subspecies while the *temperate japonica*, *tropical japonica* and *aromatic* subpopulations grouped within the *japonica* subspecies. These groupings corresponded well with Glazmann's original classification, and support the idea that *O. sativa* contains many genetically distinct groups. The data from nuclear and chloroplast SSRs, as well as the isozymes, demonstrated that the *aromatic* subpopulation (associated with Basmati and other types of high quality rice) was much more closely related genetically to the *japonica* subpopulations than to *indica* or *aus*. This is contrary to traditional classification, which had placed the *aromatic* group within the *indica* subspecies based on the long-thin grains for which the basmatic *aromatics* are known.

The *F*_st values provide a quantitative estimate of the degree of differentiation between subpopulations (Remington *et al.*, 2001). The *F*_st values calculated in the Garris study are much higher than those typically found for maize or other crops with a single domestication event (Garris *et al.*, 2005). The genetic divergence between the *indica* and *japonica* groupings have led many to conclude that these subspecies may represent independent domestications from divergent pools of *O. rufipogon* that had differentiated over thousands of years of geographical isolation. As more data about the genetic distinctiveness of the *aromatic* and *aus* groups is gathered it has been proposed that these subpopulations may have also been independently domesticated from unique subpopulations of *O. rufipogon* (McCouch *et al.*, 2006). Specifically, the fact that these groups contain unique alleles not found in other subpopulations of *O. sativa* argues against them having been selected from within these subpopulations (Jain *et al.*, 2004; Garris *et al.*, 2005). In contrast, the close genetic relationship between the *temperate* and *tropical japonica* subpopulations (shared alleles, though at different frequencies) suggests that these groups are selections from a single genetic pool that have been adapted to different climatic conditions (Garris *et al.*, 2005). Whether there are two or more than two domestication events in *O. sativa*, independent domestications of the two major subspecies are supported by several lines of evidence.

Genotyping of domesticated rice and wild relatives using isozymes and RFLPs demonstrated that *indica* and *japonica* accessions were more closely related to different accessions of *O. rufipogon* than to each other (Second, 1982; Wang *et al.*, 1992). A recent study confirmed this result using sequence haplotype analysis at three genetic loci (Londo *et al.*, 2006). With the complete genomic sequence from both ‘Nipponbare’ (*japonica*) and ‘9311’ (*indica*), three groups estimated that the *indica* and *japonica* subgroups diverged between 200 000 and 400 000 years ago (0.2–0.4 mya) based on intronic sequence from four genes and patterns of retrotransposon insertion (Ma and Bennetzen, 2004; Vitte *et al.*, 2004; Zhu and Ge, 2005). These dates significantly predate the earliest archaeological evidence for rice consumption by humans. Taken together, the data suggests that the *O. rufipogon* ancestor must have contained at least two, possibly four, differentiated subgroups from which different subpopulations were independently domesticated (Chang, 1976; Second, 1982; Wang *et al.*, 1992; Cheng *et al.*, 2003; Garris *et al.*, 2005). More research is needed to fully understand the domestication history of the different rice subpopulations. Understanding this population structure is important because these gene pools represent valuable reservoirs of genetic variation and their effective use by both breeders and geneticists requires a deeper understanding of the relationships between them.

In an effort to identify the geographical locations of different domestication events, Londo *et al.* (2006) examined the geographical distribution of the sequence haplotypes at three genetic loci using a large collection of wild and domesticated rices (Londo *et al.*, 2006). Looking at the sequence of the atpB-rbcL, p-VATPase and SAM genes, they compared *indica* and *japonica* haplotypes with haplotypes from a geographically diverse panel of *O. rufipogon*. While conclusions drawn from a sample of three genes cannot be considered definitive, the data show an association between *japonica*-like haplotypes and wild accessions from China and *indica*-like haplotypes and wild accessions collected across the Himalayan Mountains in Thailand, India and neighbouring countries. Interestingly, some domesticated *japonicas* do not share a haplotype with any *O. rufipogon* accessions, suggesting either that the wild population that was ancestral to these *japonicas* was not sampled in this survey, or that it is now extinct. This work suggests the subspecies separation was enforced by significant geographical barriers in addition to the genetic sterility barriers.

**QTLs between wild and domesticated**

Many researches have made crosses between *O. rufipogon* and *O. sativa* cultivars looking for genes controlling domestication traits (Xiao *et al.*, 1998; Xiong *et al.*, 1999; Bres-Paty *et al.*, 2001; Cai and Morishima, 2002; Thomson *et al.*, 2003; Uga *et al.*, 2003; Li *et al.*, 2006a). These studies have shown that domestication traits are influenced by many different loci. Several researchers have noted that QTLs for domestication traits tend to cluster within certain regions of the rice genome. The centromere region of chromosome 7 is the site of QTLs for seed colour, panicle structure, dormancy and shattering, among others (Xiong *et al.*, 1999; Li *et al.*, 2006a). Other clusters for domestication traits have been reported on rice chromosomes 3, 4, 6, 8, 9, 11 and 12 (Cai and Morishima, 2002; Li *et al.*, 2006a). This positional convergence may represent clusters of domestication loci, or possibly major domestication genes with pleiotrophic effects on many traits.

Based on the previously presented evidence of independent domestications for *indica* and *japonica* we would expect that different suites of genes and corresponding mutations influencing domestication traits would have
been selected within the different subspecies or subpopulations. Therefore, when crosses are made between the two subspecies, the offspring should segregate for wild alleles at several loci and wild characteristics should re-appear among sub-specific populations. This has, in fact, been observed. Most notably for traits like dormancy and shattering, intra-specific crosses between parents with low dormancy and shattering give rise to progeny that have higher levels of dormancy and shattering than either parent (Lin et al., 1998; Miura et al., 2002; Longbiao et al., 2004; Konishi et al., 2006). However, levels of dormancy and shattering in these crosses are not as high as wild accessions, suggesting either that indica and japonica share some domestication alleles or that independent mutations within the same domestication loci occurred in each subspecies which fail to compliment when crossed. Another confirmation that different domestication genes were under selection in different subpopulations comes from QTL studies. Populations derived from crosses between a single wild accession and diverse cultivars often identity different QTLs for domestication traits (Xiao et al., 1998; Moncada et al., 2001; Septiningsih et al., 2003; Thomson et al., 2003; McCouch et al., 2006; Xie et al., 2006).

**Domestication genes that have been cloned**

The large number of resources currently available to rice researches, not the least of which is genome sequence from representatives of both japonica (Nipponbare) and indica (93-11) cultivars (Goff et al., 2002; Yu et al., 2002), has resulted in an increase in the pace of gene cloning in rice. Recently several groups have reported the cloning of genes influencing traits associated with the domestication syndrome.

Two of these papers report the cloning of genes affecting shattering. The first of these papers looked at a cross between the wild species *O. nivara* and an indica cultivar (Li et al., 2006b). QTL analysis of the F2 progeny from this cross identified three genomic regions affecting shattering. One of these regions, sh4, explained 69% of the observed variation, and mapped to the same position where other large-effect shattering QTLs had been mapped in previous studies. The effect of the locus was so great that a single allele caused all mature grain on the panicle to drop when the panicle was simply tapped, while the absence of this allele required shaking to induce shattering. Fine mapping identified the gene underlying this QTL as a Myb transcription factor and association and transformation studies pinpointed the functional nucleotide polymorphism (FNP) to a single base pair within the DNA binding domain of this gene. The non-shattering allele was also found in several non-shattering accessions of *O. nivara*. These accessions most likely represent outcrosses with domesticated plants that transferred the non-shattering allele back into the wild germplasm, as the non-shattering wild plants which were selected and further modified by human selections would have faced strong negative selective pressures in the wild.

Curiously, the non-shattering allele was present in all the *O. sativa* varieties surveyed, including members of indica, tropical and temperate *japonica* subpopulations. If in fact the domestimations of the indica and japonica subspecies were completely independent, we might expect mutations at the same locus, but would not expect to see the same functional polymorphisms at domestication loci. It is highly unlikely that the same SNP would independently arise in both subpopulations, and the likelihood decreases dramatically when we consider the fact that all *O. sativa* varieties surveyed shared not only the functional SNP but five other SNPs within the gene that differed among wild haplotypes. Independent mutations occurring in different genetic backgrounds would be expected to carry different signature haplotypes across the target region. The fact that both the FNP and the corresponding haplotypes were identical in both indica and japonica cultivars at the sh4 locus provides strong evidence for the conclusion that the allele arose once and then crossed the geographic and genetic barriers that divide the two subspecies. Why the allele for non-shattering and not the non-shattering plants themselves was dispersed is an interesting puzzle, suggesting that early farmers were selecting for the non-shattering trait in combination with additional traits not found in the original non-shattering plants. Cloning other domestication genes and tracing their evolutionary history and patterns of distribution will allow us to determine whether introgression across subspecies is a common occurrence in the domestication of rice, or an isolated case for sh4. It is possible that one subspecies was domesticated and subsequently was crossed to local wild rices as it was carried to new locations. Heavy natural and artificial selective pressures combined with loss of progeny due to intra-specific sterility barriers between the indica and japonica genomes would give rise to plants that resembled the locally adapted wild species but that contained a few valuable introgressions harbouring domestication genes from the new introductions. Alternatively, domestication events in the subspecies may have been truly independent and when the early domesticates were grown in close proximity, they crossed. Beneficial alleles with a clear advantage were thus transferred and would have been the targets of selection by early agriculturalists.

Despite a fixed sh4 allele within *O. sativa* there is significant variation between and within subpopulations for degree of shattering. Traditionally, indicas have been reported to have higher shattering levels than japonicas and, as mentioned above, crosses between indica and japonica display transgressive segregation for shattering (Konishi et al., 2006). This suggests that shattering alleles at loci other than sh4 are differentially fixed within each of the two populations. The second group to clone a shattering gene worked with a cross between the *aus* variety, Kasalath, and the temperate *japonica* variety, Nipponbare (Konishi et al., 2006). The mapped QTL, called qSH1 again explained 69% of the variation between these two domesticated groups. Fine mapping pinpointed the FNP to an SNP 12 kb upstream of a BEL1-type homeobox gene and the function of this promoter polymorphism was confirmed using transformation. In situ hybridization
demonstrated that this change in the promoter region eliminated the expression of the homeobox gene at the provisional abscission layer without changing expression of the gene elsewhere. Within the isoline carrying the Nipponbare qSH1 allele in a Kasalath background, the lack of qSH1 gene expression in this tissue results in the complete lack of an abscission layer. Screening the varieties within temperate japonica showed an association between this allele and levels of shattering but also demonstrated that selection for the qSH1 allele was not as intense nor as expansive as selection for the sh4 allele, as qSH1 is not fixed, even within the temperate japonica subpopulation, let alone the whole of O. sativa.

A third domestication gene that was recently cloned is the Rc gene which confers a red pericarp (Sweeney et al., 2006). Red pericarp colour is ubiquitous in wild populations where it confers resistance to various biotic stresses. Early landraces are red; however, modern cultivars are almost universally white. While red-grained varieties are still preferred in some places due to traditional or medicinal reasons, white rice has been under strong selection for thousands of years. Unlike shattering, which is clearly a polygenic trait, only one locus, Rc, has been reported to affect a change from red pericarp to white. This locus was positionally cloned from a cross between O. rufipogon and the tropical japonica variety, Jefferson. Using a combination of fine mapping and sequence analysis of multiple alleles, Sweeney et al. (2006) identified Rc as a bHLH transcription factor. The gene’s function is impaired in the Jefferson cultivar by a 14-bp frame-shift deletion that truncates the protein before the bHLH domain. While association studies examining the prevalence of this mutation among white rice varieties throughout O. sativa have yet to be reported, the fact that this trait does not segregate in crosses between white indicas and white japonicas suggests two possible scenarios. Either the recessive allele leading to white pericarp is common within O. sativa, as was the case with sh4, or independent mutations within the Rc gene occurred in the different subpopulations and these different mutations fail to complement when crossed.

By tracing the origin of the alleles of domestication genes and the paths they travelled to achieve their current distribution, we gain fresh insights into the history of human interactions, a history that was not recorded but is written in the genomes of the plants we selected and upon which we have come to depend.

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