Annals of Botany **100**: 951–957, 2007
doi:10.1093/aob/mcm128, available online at www.aob.oxfordjournals.org

OXFORD JOURNALS
OXFORD UNIVERSITY PRESS

REVIEW

The Complex History of the Domestication of Rice

MEGAN SWEENEY and SUSAN McCOUCH*

Department of Plant Breeding and Genetics, Cornell University, 161 Emerson Hall, Ithaca, NY 14850, USA

Received: 13 December 2006 Returned for revision: 1 February 2007 Accepted: 22 May 2007 Published electronically: 6 July 2007

• *Background* Rice has been found in archaeological sites dating to 8000 BC, although the date of rice domestication is a matter of continuing debate. Two species of domesticated rice, *Oryza sativa* (Asian) and *Oryza glaberrima* (African) are grown globally. Numerous traits separate wild and domesticated rices including changes in: pericarp colour, dormancy, shattering, panicle architecture, tiller number, mating type and number and size of seeds.
• *Scope* Genetic studies using diverse methodologies have uncovered a deep population structure within domesticated rice. Two main groups, the *indica* and *japonica* subspecies, have been identified with several subpopulations existing within each group. The antiquity of the divide has been estimated at more than 100 000 years ago. This date far precedes domestication, supporting independent domestications of *indica* and *japonica* from pre-differentiated pools of the wild ancestor. Crosses between subspecies display sterility and segregate for domestication traits, indicating that different populations are fixed for different networks of alleles conditioning these traits. Numerous domestication QTLs have been identified in crosses between the subspecies and in crosses between wild and domesticated accessions of rice. Many of the QTLs cluster in the same genomic regions, suggesting that a single gene with pleiotropic effects or that closely linked clusters of genes underlie these QTL. Recently, several domestication loci have been cloned from rice, including the gene controlling pericarp colour and two loci for shattering. The distribution and evolutionary history of these genes gives insight into the domestication process and the relationship between the subspecies.
• *Conclusions* The evolutionary history of rice is complex, but recent work has shed light on the genetics of the transition from wild (*O. rufipogon* and *O. nivara*) to domesticated (*O. sativa*) rice. The types of genes involved and the geographic and genetic distribution of alleles will allow scientists to better understand our ancestors and breed better rice for our descendents.

Key words: *Oryza sativa*, domestication, shattering, pericarp colour, QTL, subpopulation structure, subspecies.

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. officialis*, *O. ridelyi* 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. breviligulata*) 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-Patry *et al.*, 2001; Cai and Morishima, 2002; Thomson *et al.*, 2003; Uga *et al.*, 2003; Li *et al.*, 2006*a*) (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.

* For correspondence. E-mail srm4@cornell.edu

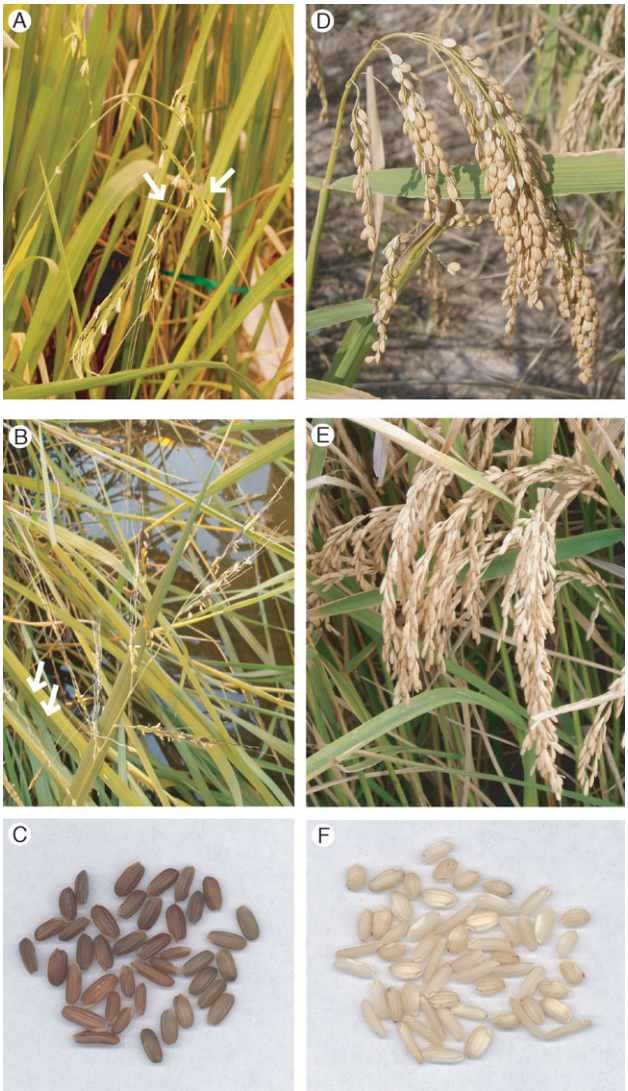

FIG. 1. Wild and domesticated rice phenotypes. (A) Immature panicle from *O. rufipogon* showing open panicle structure; arrows indicate extruded stigmas. (B) Mature panicle from *O. rufipogon* showing dark hulls and long awns; arrows indicate positions of seeds that have shattered. (C, F) Dehulled seed from *O. rufipogon* (C) and *O. sativa* (F). (D, E) Grain-bearing *O. sativa* ssp. *japonica* (D) and ssp. *indica* (E) panicles with straw-coloured hulls with a closed panicle structure.

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 Nigera. 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 NERICAs (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). Glazmann'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 then 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-Patry *et al.*, 2001; Cai and Morishima, 2002; Thomson *et al.*, 2003; Uga *et al.*, 2003; Li *et al.*, 2006*a*). 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.*, 2006*a*). 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.*, 2006*a*). 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.*, 2006*b*). QTL analysis of the F_2 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 domestications 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 subspecies, 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 rices 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.

ACKNOWLEDGEMENTS

We thank Lisa Polewczak for the photographs of rice plants and Lois Swales for administrative help. Funding to pay the Open Access publication charges for this article was provided by the OECD.

LITERATURE CITED

Blench R. 2006. *Archaeology, languages, and the African past*. Lanham: Alta Mira Press, 217–219.

Bres-Patry C, Lorieux M, Clement G, Bangraz M, Ghesquiere A. 2001. Heredity and genetic mapping of domestication-related traits in a *temperate japonica* weedy rice. *Theoretical and Applied Genetics* **102**: 118–126.

Cai W, Morishima H. 2002. QTL clusters reflect character associations in wild and cultivated rice. *Theoretical and Applied Genetics* **104**: 1217–1228.

Cao ZH, Ding JL, Hu ZY, Knicker H, Kogel-Knabner I, Yang LZ, *et al*. 2006. Ancient paddy soils from the Neolithic age in China's Yangtze river delta. *Naturwissenschaften* **93**: 232–236.

Chang KC. 1986. *The archaeology of ancient China.* New Haven, CT: Yale University Press.

Chang TT. 1976. Origin, evolution, cultivation, dissemination, and diversification of Asian and African rices. *Euphytica* **25**: 425–441.

Cheng CY, Motohashi R, Tsuchimoto S, Fukuta Y, Ohtsubo H, Ohtsubo E. 2003. Polyphyletic origin of cultivated rice based on the interspersion pattern of SINEs. *Molecular Biology and Evolution* **20**: 67–75.

Crawford G. 2005. The origins of rice agriculture: recent progress in East Asia. *Antiquity* **46**: 309–317.

Dresch J. 1949. La riziculture en Afique occidentale. *Annales de Geographie* **58**: 294–312.

Engle LM, Chang TT, Ramirez DA. 1969. The cytogenetics of sterility in F1 hybrids of *indica* × *indica* and *indica* × *japonica* varieties of rice (*Orzya sativa* L.). *Philippine Agricultural Scientist* **53**: 289–307.

Fuller DQ. 2006. Agricultural origins and frontiers in South Asia: a working synthesis. *Journal of World Prehistory* **20**: 1–86.

Fuller DQ. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. *Annals of Botany* **100**:

Fuller DQ, Harvey E, Qin L. 2007. Presumed domestication? Evidence for wild rice cultivation and domestication in the 5th millennium BC of the lower Yangtze region. *Antiquity* (in press).

Garris AJ, Tai TH, Coburn J, Kresovich S, McCouch S. 2005. Genetic structure and diversity in *Oryza sativa* L. *Genetics* **169**: 1631–1638.

Glaszmann JC. 1987. Isozymes and classification of Asian rice varieties. *Theoretical and Applied Genetics* **74**: 21–30.

Goff SA, Ricke D, Lan TH, Presting G, Wang R, Dunn M, *et al*. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). *Science* **296**: 92–100.

Gridley HE, Jones MP, Wopereis-Pura M. 2002. *Development of new rice for Africa (NERICA) and participatory varietal selection*. Bouaké, Côte d'Ivoire: West Africa Rice Development Association (WARDA), 1–6.

Higham C, Lu TL-D. 1998. The origins and dispersal of rice cultivation. *Antiquity* **72**: 867–877.

Jain S, Jain R, McCouch S. 2004. Genetic analysis of Indian aromatic and quality rice (*Oryza sativa* L.) germplasm using panels of fluorescently-labeled microsatellite markers. *Theoretical and Applied Genetics* **109**: 965–977.

Jiang L, Liu L. 2006. New evidence for the origins of sedentism and rice domestication in the lower Yangzi river, China. *Antiquity* **80**: 355–361.

Jones MP, Dingkuhn M, Aluko/snm GK, Semon M. 1997. Interspecific *Oryza sativa* L. × *O. glaberrima* Steud. progenies in upland rice improvement. **94**: 237–246.

Kato S, Kosaka H, Hara S. 1928. On the affinity of rice varieties as shown by the fertility of rice plants. *Central Agricultural Institute of Kyushu Imperial University* **2**: 241–276.

Klee M, Zach B, Neumann K. 2000. Four thousand years of plant exploitation in the Chad Basin of northeast Nigeria. I. The archaeobotany of Kursakata. *Vegetation History and Archaeobotany* **9**: 223–237.

Konishi S, Izawa T, Lin SY, Ebana K, Fukuta Y, Sasaki T, Yano M. 2006. An SNP caused loss of seed shattering during rice domestication. *Science* **312**: 1392–1396.

Li C, Zhou A, Sang T. 2006a. Genetic analysis of rice domestication syndrome with the wild annual species, *Oryza nivara. New Phytologist* **170**: 185–194.

Li C, Zhou A, Sang T. 2006b. Rice domestication by reducing shattering. *Science* **311**: 1936–1939.

Lin SY, Sasaki T, Yano M. 1998. Mapping quantitative trait loci controlling seed dormancy and heading date in rice, *Oryza sativa* L., using backcross inbred lines. *Theoretical and Applied Genetics* **96**: 997–1003.

Londo JP, Chiang Y, Hung K, Chiang T, Schaal BA. 2006. Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. *Proceedings of the National Academy of Sciences of the USA* **103**: 9578–9583.

Longbiao G, Zhu L, Xu Y, Zeng D, Wu P, Qian Q. 2004. QTL analysis of seed dormancy in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics* **140**: 155–162.

Ma J, Bennetzen JL. 2004. Rapid recent growth and divergence of rice nuclear genomes. *Proceedings of the National Academy of Sciences of the USA* **101**: 12404–12410.

McIntosh SK. 1995. *Excavations at Jenne-Jeno, Hambarketolo, and Kaniana (Inland Niger Delta, Mali): the 1981 Season*. Berkeley, CA: University of California Press.

McCouch SR, Sweeney M, Li J, Jiang H, Thomson M, Septiningsih E, *et al*. 2006. Through the genetic bottleneck: *O. rufipogon* as a source of trait-enhancing alleles for *O. sativa*. *Euphytica* **154**: 317–339.

Matsuo T. 1952. Genecological studies on cultivated rice. *Bulletin of the National Institute for Agricultural Science, Japan* **D3**: 1–111.

Matsuo T, Futsuhara Y, Kikuchi F, Yamaguchi H. 1997. *Science of the rice plant.* Tokyo: Food and Agriculture Policy Research Center.

Miura K, Lin S, Yano M, Nagamine T. 2002. Mapping quantitative trait loci controlling seed longevity in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics* **104**: 981–986.

Moncada MP, Martinez CP, Tohme J, Guimaraes E, Chatel M, Borrero J, *et al*. 2001. Quantitative trait loci for yield and yield components in an *Oryza sativa* × *Oryza rufipogon* BC_2F_2 population evaluated in an upland environment. *Theoretical and Applied Genetics* **102**: 41–52.

Morishima H, Oka HI. 1970. A survey of genetic variations in the populations of wild *oryza* species and their cultivated relatives. *Japan Journal of Genetics* **45**: 371–385.

Oka HI. 1988. Indica-japonica differentiation of rice cultivars. In: *Origin of cultivated rice*. Tokyo/Amsterdam: Japan Science Society Press/ Elsevier, 141–179.

Pei A. 1998. Notes on new advancements and revelations in the agriculture archaeology of early rice domestication in the Dongting Lake region. *Antiquity* **72**: 878–885.

Porteres R. 1970. Primary cradles of agriculture in the African continent. In: Fage JD, Olivier RA, eds. *Papers in African prehistory*. Cambridge: Cambridge University Press, 43–58.

Remington DL, Thornsberry JM, Matsuoka Y, Wilson LM, Whitt SR, Doebley J, *et al*. 2001. Structure of linkage disequilibrium and phenotypic associations in the maize genome *Proceedings of the National Academy of Sciences of the USA* **98**: 11479–11484.

Second G. 1982. Origin of the genic diversity of cultivated rice (*Oryza* spp.): study of the polymorphism scored at 40 isozyme loci. *Japanese Journal of Genetics* **57**: 25–57.

Semon M, Nielsen R, Jones M, McCouch SR. 2005. The population structure of African cultivated rice O*ryza glaberrima* (Steud.): evidence for elevated levels of LD caused by admixture with *O. sativa* and ecological adaptation. *Genetics* **169**: 1639–1647.

Septiningsih EM, Trijatmiko KR, Moeljopawiro S, McCouch SR. 2003. Identification of quantitative trait loci for grain quality in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. *Theoretical and Applied Genetics* **107**: 1433.

Sweeney MT, Thomson MJ, Pfeil BE, McCouch S. 2006. Caught red-handed: *Rc* encodes a basic helix-loop-helix protein conditioning red pericarp in rice. *The Plant Cell* **18**: 283–294.

Thomson MJ, Tai TH, McClung AM, Lai X-H, Hinga ME, Lobos KB, *et al*. 2003. Mapping quantitative trait loci for yield, yield components and morphological traits in an advanced backcross population between *Oryza rufipogon* and the *Oryza sativa* cultivar Jefferson. *Theoretical and Applied Genetics* **107**: 479–493.

Uga Y, Fukuta Y, Cai HW, Iwata H, Ohsawa R, Morishima H, *et al*. 2003. Mapping QTLs influencing rice floral morphology using recombinant inbred lines derived from a cross between *Oryza sativa* L. and *Oryza rufipogon* Griff. *Theoretical and Applied Genetics* **107**: 218–226.

Vaughan DA, Morishima H, Kadowaki K. 2003. Diversity in the *Oryza* genus. *Current Opinion in Plant Molecular Biology* **6**: 139–146.

Vitte C, Ishii T, Lamy F, Brar D, Panaud O. 2004. Genomic paleontology provides evidence for two distinct origins of Asian rice (*Oryza sativa* L.). *Molecular Genetics and Genomics* **272**: 504–511.

Wang Z, Second G, Tanksley S. 1992. Polymorphism and phylogenetic relationship among species in the genus *Oryza* as determined by analysis of nuclear RFLPs. *Theoretical and Applied Genetics* **83**: 565–581.

Wang ZY, Tanksley SD. 1989. Restriction fragment length polymorphism in *Oryza sativa* L. *Genome* **32**: 1113–1118.

Xiao J, Li J, Grandilloa S, Ahn SN, Yuan L, Tanksley SD, *et al*. 1998. Identification of trait-improving quantitative trait loci alleles from a wild rice relative, *Oryza rufipogon*. *Genetics* **150**: 899–909.

Xie X, Song MH, Jin F, Ahn SN, Suh JP, Hwang HG, *et al*. 2006. Fine mapping of a grain weight quantitative trait locus on rice chromosome 8 using near-isogenic lines derived from a cross between *Oryza sativa* and *Oryza rufipogon*. *Theoretical and Applied Genetics* **113**: 885–894.

Xiong LZ, Liu KD, Dai XK, Xu CG, Zhang Q. 1999. Identification of genetic factors controlling domestication-related traits of rice using an F2 population of a cross between *Oryza sativa* and *O. rufipogon*. *Theoretical and Applied Genetics* **98**: 243–251.

Yu J, Hu S, Wang J, Wong GK, Li S, Liu B, *et al*. 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). *Science* **296**: 79–92.

Zhao Z. 1998. The middle Yangtze region in China is one place where rice was domesticated: phytolith evidence from Teh Diaotonghuan Cave, northern Jiangxi. *Antiquity* **72**: 885–897.

Zhejiang Provincial Institute of Cultural Relics and Archaeology. 2004. *Kuahuqiao*. Beijing: Cultural Relics Publishing House [in Chinese with English summary].

Zhu Q, Ge S. 2005. Phylogenetic relationships among A-genome species of the genus *Oryza* revealed by intron sequences of four nuclear genes. *New Phytologist* **167**: 249–265.