Review

The evolving story of rice evolution☆

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Abstract

Recent research related to evolution in the primary gene pool of rice, which consists of *Oryza* species with the A-genome, provides new perspectives related to current and past eco-genetic setting of rice and its wild relatives and fresh insights into rice domestication. In Asia the traits of the rice domestication syndrome are many but due to the remarkable diversification of rice and introgression with wild rice, few traits are consistently different between wild and domesticated rice. Reduced shattering and reduced dormancy are the principal traits of domestication in rice. Using the principal criteria for distinguishing single and multiple origins of crops, recent key research results do not support a polyphyletic origin of domesticated rice in distinctly different geographic regions. While domestication is a long-term *process* and continues today, a single *event* during domestication, the selection of the non-shattering *sh4* allele, resulted in rice becoming a species dependent on humans for survival - domesticated. Here the apparent contradictions between a single origin of Asian rice and deep genetic divisions seen in rice germplasm are resolved based on a hypothesis of cycles of introgression, selection and diversification from non-shattering domesticated rice, importantly in the initial stages in its center of origin in the region of the Yangtze river valley, and subsequently beyond, as domesticated rice spread. The evolution of African rice differs from Asian rice mainly in the more restricted gene pool of wild rice from which it was domesticated, ecological diversification rather than eco-geographic diversification, and historic introgression from the Asian rice gene pool. The genetics of post-domestication evolution in Asian rice is well illustrated by changes at the waxy locus. For both Asian and African rice becoming domesticated was a single event, it was the subsequent evolution that led to their genetic complexity.

Contents

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1. Introduction

The sequencing of the whole genome of rice, more than once, has predictably resulted in a rapid surge in research on rice genetics and evolution. Cloning rice genes has concentrated on the most important domestication related genes. Two recent papers describe cloning different genes related to shattering in rice [1,2]. Two other papers have subsequently appeared related to evolution of shattering in rice [3,4]. Aside from molecular studies, new studies in other branches of plant science, such as archaeobotany, are furnishing information that are providing new perspectives on the evolution of rice.

It might be expected that recent rice research would resolve questions concerning the evolution of rice, but apparently conflicting results and their interpretations have yet to resolve some central questions. The objective of this paper is to discuss topics related to the evolution of rice that have recently provided new insights. We first discuss the primary gene pool of the cultivated rices before discussing research related to the domestication of rice in Asia and Africa.

2. Setting the scene—the primary gene pool of rice and its components

To understand the domestication of Asian and African rice it is necessary to understand the gene pools from which they came. That requires understanding these gene pools as they are found today and also how they might have been in the past.

The primary gene pool of a crop is considered to be equivalent to a biological species consisting of germplasm that can be crossed resulting in fertile hybrids [5]. There are many barriers to hybridisation in the A-genome *Oryza* (for review see [6]), but hybridisation does occur among these species when they grow together and flower at the same time. In Asia introgression between the various A-genome *Oryza* species is common [7,8]. In Africa introgression and hybrids between introduced *Oryza sativa* and wild and cultivated African species (also with the A-genome) have been reported [9,10]. Weedy forms between the Latin American A-genome wild species, *Oryza glumaepatula*, and rice (*O. sativa*) are commonly found in Venezuela (Dr. Zaida Lentini, CIAT, personal communication 2007). Artificial A-genome interspecific hybrids have nearly normal meiosis but have variable pollen and seed fertility [11,12].

Two cultivated rice species were domesticated from the A-genome of *Oryza* independently in Asia and Africa, but probably by a similar processes based on contemporary ways in which wild rice is harvested in these continents [13] (Figs. 1 and 2). The cultivated Asian rice (*O. sativa*) is now spread worldwide, and African rice (*Oryza glaberrima*) is now confined almost exclusively to West Africa. Recently a breeding program that has focussed on combining the best qualities of Asian and African rice has resulted in a series of varieties called NERICA (New Rice for Africa) rices that are spreading to many regions of Africa [14,15].

The taxonomy of the A-genome *Oryza* species has long been 'a matter of opinion', and the distinction of species has mainly been based on three criteria: geography, annual/perennial habit and cultivated or wild habitat (Table 1). These criteria do not provide reliable key morphological characters for distinguishing species. Introgression among A-genome *Oryza* species is widespread and only *Oryza longistaminata* can reliably and consistently be distinguished from other species by its well-developed rhizomes. However, the species names provided in Table 1 are at present the best summary of A-genome *Oryza* species diversity, the most commonly found names in the literature and most helpful categories for understanding the primary gene pool of rice.

Fig. 1. Plants of *O. nivara* twisted together to prevent shattered seeds dropping thus facilitating their harvest, Madhya Pradesh, India.

Fig. 2. Harvesting *O. rufipogon* in West Bengal, India.

Table 1
Geographic distribution, life cycle and cultivation status of A-genome *Oryza* species

Annual/perennial	Wild/cultivated	Latin America	Africa	Asia	Australia and New Guinea
Perennial	Wild	*O. glumaepatula* Steud.	*O. longistaminata* A. Chev. et Roehr.	*O. rufipogon* Griff.	
Annual	Wild		*O. barthii* A. Chev.	*O. nivara* Sharma et Shastry	*O. meridionalis* Ng
Annual	Cultivated		*O. glaberrima* Steud.	*O. sativa* L. (now worldwide)	

Many accessions in gene banks are not 'pure' representatives of these species especially the wild species and for a variety of reasons may be misidentified [16–18]. Many accessions of African cultivated rice, *O. glaberrima*, have genes introgressed from *O. sativa* [10]. In addition, geographic origin alone is insufficient to identify a 'species' because not only *O. sativa* but also other A-genome species have been introduced to new geographic regions. An accession of wild rice from Cuba is an Asian *Oryza rufipogon* based on various analyses [19,20]. *O. longistaminata* has been collected from Martinique, in the Caribbean [21].

Perennial A-genome wild *Oryza* have considerable intra-specific genetic variation. Three regional variants of *O. glumaepatula* can be distinguished (a) the Central American, Caribbean, and northern South American type (perennial), (b) the Amazonian type (perennial-intermediate) and (c) the central South American type (perennial) [22]. Five distinct groups of *O. longistaminata* are found based on ecology and self-incompatibility systems [23]. *O. rufipogon* has consider-able geographic variation with *O. rufipogon* from New Guinea being recognised as distinct and called 'Oceanian' type [6].

An understanding of the ecological setting of wild rice in Asia is critical when considering domestication of rice. One of the major questions regarding the evolution of rice is from which type of Asian wild rice did it evolved? Perennial *O. rufipogon* has many ecotypes and is widely distributed across Asia to Papua New Guinea and Australia (Fig. 3a). The principal ecotypes of *O. rufipogon* differ by the degree to which they produce seeds. Asian *O. rufipogon* tends to be poorly represented in germplasm collections because populations in many regions are primarily vegetative. This is especially the case in equatorial Asia (Sumatra and Kalimantan, Indonesia)

where year round rainfall results in lakes and rivers with a relatively stable water level. *O. rufipogon* growing in these conditions is mainly vegetative and seed production is low. The second main ecotype of *O. rufipogon* exhibits mixed mating, with both vegetative and seed reproduction, and copiously produces seeds. High seed producing ecotypes of *O. rufipogon* are found in areas where water levels rise and fall considerably between seasons, such as in southern Papua New Guinea. In these areas *O. rufipogon* grows where the soil retains residual moisture enabling populations to survive from season to season. Such ecotypes can also be found in continental Asia, but because of introgression from cultivated rice it is not possible to be sure which *O. rufipogon* are high seed producing as a result of introgression from cultivated rice. One type of high seed producing *O. rufipogon* from Thailand is considered to be an intermediate type between annual and perennial wild rice [24]. High seed producing wild ecotypes of perennial *O. rufipogon* do exist and would have been an attractive source of nutrition in the age of hunters and gatherers. Today in India such "wild" *O. rufipogon* is harvested (Fig. 2). Natural habitats of wild *O. rufipogon* are generally lakes or waterways surrounded by forest. Disturbance in these habitats is primarily the result of water flow.

The annual, inbreeding, *Oryza nivara*, has a more restricted distribution than the perennial, *O. rufipogon* (Fig. 3b). *O. nivara* is most common in the area of South and Southeast Asia with severe dry seasons. This is clearly seen in Sri Lanka where *O. nivara* is almost completely confined to the dry zone and *O. rufipogon* to the wet zone of the country. The natural habitat of *O. nivara* is uncommon but can be found in National Parks of Sri Lanka where it grows at the margins of seasonal pools in grassland. A characteristic of such habitats is that they are more
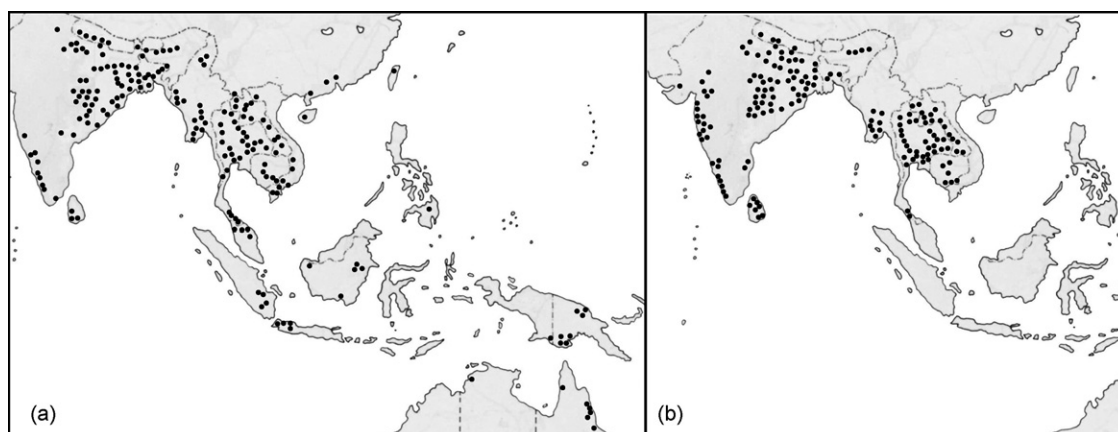

Fig. 3. (a) Distribution of *O. rufipogon* and (b) distribution of *O. nivara* (updated from [21]).

disturbed than habitats of perennial *O. rufipogon*, because these pools of water, in seasonally dry areas with few water sources, are frequented daily by a variety of animals. Thus, *O. nivara* is adapted to frequent grazing that requires rapid seed production for survival, and trampling that results in compacted soil in which seeds survive and germinate.

Introgression from cultivated rice to wild rice is a common occurrence where they are sympatric [6,7,25]. Due to floral structure perennial outcrossing wild rice is more likely to be a pollen receiver than annual inbreeding wild rice [7]. During cultivation of rice, selection pressure would have favoured high seed producing populations and hence inbreeding. Subsequently when rice was fully domesticated (non-shattering) it would have been sympatric with wild rice as it spread. Hybridisation and introgression would have occurred in a similar way to that recorded today. However, it is not known the degree of inbreeding in early domesticated rice. Compared to today higher outcrossing and introgression may have been a feature of early domesticated rice when there would have been few barriers to hybridisation among different types of wild, cultivated and newly domesticated rice. Introgression from wild rice of different genetic backgrounds into newly domesticated rice could readily have occurred enabling domesticated rice to adapt to new environments.

Most of the germplasm in gene banks of Asian wild rice was collected from human-disturbed or human-made habitats such as roadside ditches and irrigation channels. These are areas where introgression may have occurred between wild rice and rice. Consequently conclusions regarding the genetics of gene bank germplasm should be understood in this context. While high seed producing *O. rufipogon* and *O. nivara* are both adapted to disturbed habitats, they differ in the degree of disturbance and degree to which residual moisture occurs in the soil. Thus, the presence of annual *O. nivara* and perennial *O. rufipogon* in Asia are an adaptive response to habitat conditions with some genetic isolation due to differences in flowering time and also geographic variation reflecting isolation by distance. The differences in flowering time can result in local scale variation while geographic isolation is seen at the regional level and revealed by quantitative trait analysis [26]. Sequencing of particular genes [27] and multiple neutral genes [28] for polymorphisms does not reveal differences between *O. nivara* and *O. rufipogon*. This may reflect recent divergence and/or continual gene flow between these two ecotypes in mainland Asia.

Asian *O. sativa* has two major varietal groups or subspecies, japonica (keng) and indica (hsien), that have traditionally been recognised in the Chinese language [29]. Analyses of germplasm collections have revealed the main components of Asian rice diversity at the end of the 20th Century. Six groups of rice varieties were recognised using isozymes—indica, aus (early summer), ashwina (early deep water), rayada (long duration deep water), aromatic and japonica [30]. Subsequently the importance of the aus (indica aligned) and aromatic (japonica aligned) varieties has been confirmed using SSR markers. Differences were also recognised between temperate and tropical japonica varieties [31]. Within the tropical japonica varieties are a morphologically distinct group from Indonesia called bulu or javanica that have few tillers, long panicles and seeds with awns. The other two varietal groups recognised by isozyme analysis, ashwina and rayada, were selected for the environments of some villages in the Ganges river delta. Ashwina are early maturing deepwater varieties lacking strong photoperiod sensitivity while rayada are long duration, deepwater varieties lacking secondary dormancy. The unusual characteristics of these two small varietial groups may provide insights into rice domestication in the complex environments of deepwater areas. Rice diversity studies have relied on the germplasm collected for the past 40 years. The traditional lowland varieties of some areas were not or only poorly collected prior to the introduction of improved varieties from breeding programs, for example some parts of Myanmar. Thus, studies of rice genetic diversity represent a biased sampling of germplasm from a restricted time period in rice evolution and important germplasm for understanding rice evolution undoubtedly has been lost.

West African ecological diversification of *O. glaberrima* is similar to that of *O. sativa* in Asia but *O. glaberrima* has less genetic diversity. In *O. glaberrima* some distinct variations found using SSR markers are thought to be associated with ecological differentiation—floating, non-floating lowland and upland rice [10]. Sophisticated strategies for rice production have been developed within West African societies. Despite *O. glaberrima* having less diversity than *O. sativa*, the parallels are striking in the way African and Asian societies have selected rice and manipulated the environment to suit the crop. For example, the tidal wetlands rice cultivation practiced by the Diola of Senegal [32] is very similar to that described early in the 20th Century of 'kaipal' cultivation in Kerala, India [33]. People in both areas independently developed complex processes of diking, desalination, ridging and transplanting to cope with seasonal seawater intrusion. In East Asia land inundated with seawater was reclaimed for rice cultivation using somewhat different approaches such as the initial use of salt tolerant plants, like barnyard millet (*Echinochloa crus-galli*) to improve the land [34].

In contrast to many other crops, Asian and African rice is primarily grown where it evolved and, hence, where its wild relatives occur. In Asia, introgression from wild rice to cultivated rice is more likely to occur in indica varieties than japonica varieties because of where these two varietal groups are grown. Tropical japonica varieties in mainland Asia are generally grown in highland where wild rice does not grow and in insular Asia, particularly Java, where A-genome wild rice is rarely in proximity to rice fields. Indica varieties are mainly lowland varieties that on mainland Asia often grow sympatric with wild rice.

Finally, a major and increasingly important component of the primary gene pool of rice is weedy rice. Weedy rice grows in rice fields and is adapted to the rice cropping system. Due to its genetic similarity to rice it is difficult to eliminate from rice fields without careful attention to land preparation. As discussed above introgression between components of the primary gene pool can result in weedy rice derived from

hybridisation events. In addition, weedy rice can be derived from natural selection for shattering in rice growing environments due to cultural practices. Direct seeding, particularly where land preparation is inadequate, can quickly result in shattering and unwanted non-shattering off types because rice plants are scattered, rather than in transplanted rows, making weeding difficult. A full discussion of this topic can be found in six chapters of [35].

3. Before domestication—the A-genome *Oryza* gene pool evolution

Oryza is an ancient genus allied to the bamboos [36]. Based on phytolith evidence the ancestors of *Oryza* were present 65 million years ago (Mya) [37]. Molecular clock data suggests that diversification of the genus *Oryza* occurred 8–14 Mya [38] and diversification within the A-genome over the past 2 Mya [18,39].

Given the current pan-tropical distribution of A-genome *Oryza* many scientists have tried to elucidate the evolutionary relationships within and between these species. Some scientists consider *O. longistaminata* is the most diverged of all the A-genome *Oryza* species [40]. *O. longistaminata* is a rhizomatous, perennial, self-incompatible species found in much of sub-Saharan Africa. Many molecular studies using RAPD [41], RFLP [17,19], MITE-AFLP [42], and intron sequences of four nuclear genes [18] point to *Oryza meridionalis* as the most diverged of the A-genome *Oryza* species. This inbreeding, annual species, found in habitats similar to *O. nivara* in mainland Asia, is distributed across northern Australia and has been found in Irian Jaya, Indonesia.

If *O. meridionalis* is closest to the ancestral type of the A-genome, *Oryza* germplasm collections are missing an outcrossing, perennial species linked to the ancestor of A-genome *Oryza*, since all *Oryza* closely related to A-genome species are perennial. Comprehensive surveys of *Oryza* in northern Australia and New Guinea are lacking, so it is possible there is a perennial type similar to *O. meridionalis*. A perennial *O. rufipogon* ecotype was found in the Sepik River of northern Papua New Guinea and it has some genome regions characteristic of *O. meridionalis* ([19], Hai Fei Zhou et al. Institute of Botany, Chinese Academy of Sciences, unpublished data). We still have incomplete knowledge about the A-genome *Oryza* from Australia and New Guinea, so further collecting and analysis of germplasm from that region should be a priority.

Given that *O. meridionalis* and *O. longistaminata* are the most diverged of the A-genome *Oryza* species, the question arises how were these species, confined to different continents, were dispersed? The Gondwanaland hypothesis for the distribution of *Oryza* [43,44] is no longer tenable based on what is now known about the time grasses and *Oryza* arose and when continental drift occurred. A hypothesis proposing that animals, including birds and humans, are the major factor in disseminating *Oryza* species was put forth [45]. In addition to *Oryza*, species in the genus *Sorghum*, *Gossypium* and *Vigna*, among others, are also found in Africa and Australia. Further understanding of the relationships between *O. meridionalis* and *O. longistaminata*, that have differences in life cycle, breeding and morphological characteristics, are needed to gain a better understanding the origins of the A-genome.

4. Domestication

4.1. The domestication syndrome

Among crops Asian rice varietal diversity is remarkable. This is a reflection of its early domestication and subsequent spread to one of the worlds most geographically diverse regions around Yunnan province, China, introgression from wild rice, and selection for a broad range of ecological conditions and taste preferences by many ethnic groups [46,47]. In addition, the selection associated with domestication resulted in a greater degree of inbreeding and reduced recombination. Thus, both beneficial and deleterious mutations, accumulated in diverse lines [48]. A consequence of the high level of rice diversity is that there are few domestication related traits that are consistently associated with cultivated rice, except for two.

These two traits were key to the domestication of rice—degree of spikelet shattering and loss of strong secondary dormancy. In rice, shattering and dormancy are complex traits with many QTLs for each trait in many linkage groups of the rice genome [47]. Both traits vary considerably depending on the variety or varietal group. Ease of shattering differs among different types of rice. Japonica varieties do not have an abscission layer at the spikelet (seed) base, indica varieties have a partial abscission layer while wild and weedy rice have a complete abscission layer. Differences in the ease of shattering is reflected in cultural practices associated with traditional methods of threshing.

Table 2
Extreme range for three characters in rice

Category	Species name	Panicle length		Grain length		Grain width	
		Longest (cm)	Shortest (cm)	Longest (mm)	Shortest (mm)	Widest (mm)	Narrowest (mm)
Cultivated	*O. sativa*	43	10	14.4	3.5	4.9	1.4
	O. glaberrima	32	14	10.5	6.1	3.6	2.2
Wild	*O. barthii*	40	9	12.3	7.7	3.5	2.2
	O. nivara	35	9	10.5	5.2	3.4	1.5
	O. rufipogon	40	12	11	4.8	3.2	1.1

Based on data from the T.T. Chang Genetic Resources Center, IRRI, rice collection, June 2007.

Dormancy is a complex trait consisting of seed and hull dormancy with QTL for dormancy found on most of the chromosomes of rice [49]. Secondary dormancy remains an important characteristic in indica varieties, where seeds retain viability during hot, humid conditions between planting seasons. The most detailed studies of dormancy have been conducted with an accession of wild-like weedy rice from Thailand (accession SS18-2) that exhibits hull-imposed dormancy [50–55]. One dormancy related QTL in this accession on chromosome 7, explaining about 13% of the phenotypic variance, is closely linked (or pleiotropic) to the gene for red grain and some other domestication related QTL [50–53]. But the most important dormancy related QTL in this Thai accession was located on chromosome 12 explaining about 50% of the phenotypic variance [51,53]. This chromosome 12 QTL may be the most important to study in relation to rice domestication not only because of its large effect but also unlike some other dormancy QTL it is largely independent of loci for interrelated characteristics such as red pericarp, hull colour and awn length [51]. If this major dormancy QTL on chromosome 12 is widespread in the rice genepool, when it is cloned [51], it may be as informative as the shattering QTL *sh4* has been regarding rice domestication.

Domestication of many crops is associated with an increase in size of the organs that are consumed. Thus, cultivated sorghum has much larger seed size than wild sorghum [56]. However, rice has not always been selected for larger seed size (Table 2). Most rice varieties have a seed size little different from wild rice. The International Rice Research Institute rice collection of cultivated rice has accessions up to 30% longer and shorter than wild rice. In the case of African rice, *Oryza barthii* accessions have the longest and shortest seeds. They exceed those of the longest and shortest seeds of the cultigen, *O. glaberrima* by 15 and 20%, respectively (Table 2). Thus, seed size is not a reliable character to distinguish wild and domesticated rice. Other traits have been more important during domestication such as number of seeds per panicle and synchronous maturity. The number of panicles per plant is highly variable among rice varieties. Some varietal groups, particularly tropical japonica from Indonesia (bulu types), have one or very few productive tillers. Culm (stem) length is highly variable, with the culms of domesticated deepwater rice being able to grow to a length of 5 or 6 m [57].

Only three traits, culm length, panicle length and spikelet shattering, were consistently recorded in six studies that investigated QTLs for domestication related traits [49,57–62]. Secondary branching of panicles, spikelets per panicle and heading date were recorded in five of these studies.

Thus, studies of the domestication syndrome in rice have identified important QTL's for domestication—but these QTL's are related to the parents of hybrid populations. After domestication subsequent diversification has resulted in domestication related traits varying greatly from varietal group to varietal group and within varietal groups. Further understanding of the domestication syndrome in rice will require more crosses designed to dissect specific traits associated with domestication in different varietal groups.

4.2. Single or multiple origins of Asian rice

The pendulum has swung in the last 30 years from the view that rice was domesticated once [6,43,63] to being domesticated two or more times [18,64–67]. In Box 1 we list recent research that appears to support single or dual/multiple origins of domesticated rice. The list numerically favours dual/multiple origins. Here we discuss this issue with reference to the criteria to distinguish single from dual/multiple origins of crops elaborated

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Box 1. Evidence supporting single and multiple events leading to domesticated rice

Single domestication

1. The *sh4* allele that is most important in reducing shattering in rice, accounting for about 70% of the loss in shattering. This loss of shattering results from a functional base pair mutation that is the same in the various groups of rice [2,4].
2. The red pericarp locus, *rc*, that affects change from red pericarp, ubiquitous in wild rice, to white pericarp common in all types of domesticated rice, does not show segregation in crosses between japonica and indica varieties. This recessive allele leading to white pericarp is common in nearly all rice varieties (97.9%) [70,71].
3. The bottleneck of domestication is strong in rice [28,65,69]. While a severe genetic bottleneck does not rule out multiple domestication one explanation for this surprising result is that domestication of rice was a geographically local event [28] that would support a single domestication event.

Dual or multiple domestication

1. Crosses between indica and japonica rice result in progeny that segregate for wild alleles at several loci and wild characteristics reappear [99].
2. Indica, japonica, aromatic and aus varieties of cultivated rice tend to form monophyletic groups and contain unique alleles suggesting they are derived from unrelated wild populations [18,31].
3. Comparison of cytoplasmic diversity in wild and cultivated rice suggests multiple lines of evolution [110].
4. Genotyping and gene sequencing of cultivated and wild rice has suggested that indica and japonica accessions are related to different accessions of wild rice [17,63,66,67,72,111].
5. Genomic divergence between indica and japonica predates domestication and has been estimated to have occurred 0.4–0.2 Mya [18,39,112].
6. Phylogeographic analysis of three genes in a broad set of wild and cultivated rice accessions revealed indica-like halotypes associated with wild rice from South and Southeast Asia and japonica-like haloptypes associated with wild accessions from China [65].
7. Haplotypes diversity analysis of genes reveals distinct nodal clusters of haplotypes associated primarily with indica and japonica varieties [84,105].

by Zohary [68]. He considered that in general domestication of the same species twice is uncommon, at least in the Middle East. He suggested three tests to discriminate single from multiple origins under domestication [68]:

- Presence or absence of patterns indicative of founder effects in the cultivated gene pools, compared to the amount of variation in the wild progenitor.
- Uniformity or lack of uniformity (within a crop) in genes governing principal domestication traits.
- Species diversity.

4.2.1. Founder effects

In rice the domestication bottleneck has been studied based on (a) nucleotide diversity data for 10 unlinked nuclear loci [28]; (b) haplotype diversity of one chloroplast and two nuclear genes [65]; (c) genome-wide patterns of nucleotide polymorphism [69]. These provide somewhat different pictures of the rice domestication bottleneck. The gene-based studies suggest a strong domestication bottleneck while the genome-wide study suggested differences in patterns of diversity between wild and cultivated rice as a result of both a genetic bottleneck and selective sweeps after domestication. However, it is clear a small fraction of the rich genetic diversity of wild rice that must have existed across Asia 10,000 years ago, was involved in domestication. This suggests rice is a product of a single or very few introductions into cultivation.

4.2.2. Domestication traits

The most important domestication trait in rice is the loss of shattering because that results in rice being dependent on humans for survival—a domesticate. The main shattering allele on chromosome 4 is *sh4* (synonymous with the gene *SHA1* in reference [4]), as it accounts for about 70% of the phenotypic variance for shattering [2]. Zohary [68] states '... if in *all* cultivars of a crop, a given domestication trait is found to be governed by the *same* major gene (or *same* combination of genes), this uniformity suggests a single origin' (italics by Zohary). The non-shattering allele of *sh4* results from the same base pair change in both indica and japonica cultivars from different parts of Asia [4] conforming to that requirement.

Another domestication related trait, but not a trait that is critical for domestication, is the change from red pericarp (in wild rice) to white pericarp (in most cultivated rices). All white pericarp indica (169 accessions) and japonica (186 accessions) analysed are the result of the same 14 bp deletion [70,71]. Sweeney et al. [71] state that 'the presence of this deletion in 97.9% of white-grained rice varieties found throughout the world today suggests either *that the gene was dispersed during the early phases of domestication and is common by descent in modern varieties* or that very strong, positive selection for the allele led to its introgression and maintenance in already established gene pools' (italics are ours). The first reason in the previous sentence seems the simplest and most logical explanation. Sweeney et al. [71] support independent origin of indica and japonica and suggest "early agriculturalists ... moved (the *rc* mutation) around the Himalayan mountain range that is found between the

proposed centers of indica and japonica domestication ..., and, having traversed this substantial geographic barrier, was rapidly introgressed into all major subpopulations of rice despite an emerging fertility barrier". It seems more reasonable that the *rc* mutation, that is thought to have originated in a japonica type haplotype [71], arose in the Yangtze river valley and was rapidly introgressed into rice of various genetic backgrounds growing in close proximity.

If there had been independent domestication of indica and japonica rice we would expect the most important domestication traits to be the result of different mutations. As the above examples do not reveal different mutations for the two main groups of rice this suggests a single origin of rice followed by diversification.

4.2.3. Species diversity

Zohary [68] further suggests that if there are different wild progenitors that could be domesticated it is possible to determine how many of these wild species were cultivated and then domesticated. While there is strong evidence to support some differentiation of indica and japonica genomes long before rice domestication [18,39] there is no information regarding whether these proto-indica and proto-japonica genomes evolved in geographical isolation. Several studies have suggested that indica cultivars are derived from *O. nivara* and japonica cultivars from *O. rufipogon* [67,72,73]. However, *O. nivara* and *O. rufipogon* are a genetic continuum and not 'good' taxonomic species. In addition, both these wild species can be sympatric and gene flow is possible between them. Research has shown that there is a lack of clear geographic differences in the A-genome wild rice with japonica-like and indica-like haplotypes based on the analysis of ten unlinked loci in nearly complete linkage disequilibria [74,75]. Thus, it is not possible to draw a firm conclusion on the importance of 'species' diversity in relation to the origin of rice.

A further critical consideration is that if rice was domesticated once with rapid dispersal of the key domestication gene within an area of diverse wild rice we would not expect indica and japonica groups of varieties have a different time span after domestication. Indeed recent modelling of the bottleneck of domestication based on genome-wide patterns of nucleotide polymorphism in rice has suggested that equal timing of domestication has occurred for indica and tropical japonica [69].

Based on the above comments rice appears to be the result of a single domestication event despite many studies – using present day germplasm – that point to dual or multiple domestication of rice. The discrepancy can be explained by post-domestication introgression, selection and diversification that are reflected in the current rice germplasm.

Below the scientific basis to support a hypothesis that can resolve the seemingly contradictory results regarding how rice was domesticated is presented.

4.3. The domestication of Asian rice

4.3.1. Diversity of wild and cultivated rice in China

There have been many studies of the diversity of populations of A-genome wild rice, *O. rufipogon*, in China [25,76–81].

Chinese wild rice populations are declining due to habitat destruction and degradation, resulting in a high level of genetic differentiation among populations [81]. Wild rice in China includes populations with diverse population structures from perennial, essentially clonally, propagated populations to mainly seed propagated populations [80]. Wild rice at different locations within a particular site has different characteristics [80]. The usual type of wild rice in China is mixed mating with the ability to ratoon and also produce seeds [26,76]. The ecotype of annual wild rice, *O. nivara*, originally described from India has not been reported in China (Fig. 3b).

Wild rice in China consists of representatives of both indica-like and japonica-like wild rice based on RFLP analysis [19]. Wild rice from Guangxi, where wild rice in China is most diverse, had allozyme types characteristic of both indica and japonica rice [81]. The presence of japonica-like wild rice in Guangxi is significant since this is an area where most rice production is indica type hence allozyme pattern in wild rice might not be a simple reflection of introgression from sympatric cultivated rice. Two groups of wild rice were found in China using SSR markers that were differentiated based on geography: one group consisted of populations of wild rice from Hainan Island, and the other group from provinces to the north [81]. Chinese wild rice had a higher percentage of polymorphic loci, more alleles, greater number of genotypes and greater heterozygosity than wild rice from other regions in a comparison of genetic diversity using RFLP variation of wild rice from South Asia, Southeast Asia and China [82]. China is at the northern edge of A-genome wild rice diversity but it has a very high level of genetic diversity.

The Yunnan province, China, is historically a major center of traditional rice diversity [83], reflecting the effects of ecogeographic variation and ethnic diversity [47]. There is no evidence to suggest that rice originated where it is traditionally most diverse and genetic diversity of wild rice in Yunnan is not as diverse as in other parts of China [76].

The allelic diversification related to apiculus pigmentation shows phenotypic divergence in cultivated rice but not wild rice. Phenotypic divergence is due to the *C* locus having multiple alleles [84]. The main group of haplotypes for the *C* locus for anthocyanin pigmentation at the apiculus is common in most japonica and indica varieties. Two wild rice samples from China included in the study were also in this group of haplotypes. Cultivated Chinese rice also includes accessions belonging to a second haplotype group similar to one other cultivated accession from Laos, and both 'nivara' and 'rufipogon' like wild rice from Bangladesh, India and Thailand. This indicates a high level of allelic variation in Chinese cultivated rice.

The presumed neutral nuclear pseudogene *p-VATPase* had a haplotype diversity that reportedly reflected the geographic pattern of the rice germplasm analysed [65]. However, cultivated rice accessions from China (9 accessions) and India (13 accessions) had exactly the same array of haplotypes. The other two genes analysed also had highly similar haplotype diversity between Chinese and Indian cultivated rice [65].

As with wild rice, cultivated rice in China is highly diverse. Chinese rice varieties span from indica to temperate japonica from south to north and from indica to tropical japonica cultivation in some parts of southern and southwestern provinces where tropical japonica rice is grown by some ethnic groups and at higher altitude.

4.3.2. An eco-genetic hypothesis for the domestication of Asian rice

There is sufficient archaeobotanical evidence to state that rice was domesticated in the region of the Yangtze River valley of China [85,86]. There is currently insufficient archaeobotanical evidence to determine if rice was separately domesticated elsewhere [63]. The paleo-climate and paleo-ecology of China is critical to understanding rice domestication. Prior to the period when wild rice was cultivated and subsequently domesticated, there were short and long cyclic periods of warmer and cooler, wetter and dryer climates. Some of these changes were a response to global climatic changes [87] others reflected regional or local phenomena such as weather patterns emanating from China's Gobi desert region contributed pulsations of arid and humid conditions [88]. Vegetation shifts across China over the last 10,000 years have been mapped and reveal advancing and retreating patterns of warm temperate and subtropical forests in the Yangtze River region [89]. These periodic changes in climatic conditions and advancing retreating plant migrations probably contributed to the complex genetic mosaic of locally adapted wild rice in China.

After the Younger Dryas (13,000–11,500 BP) climates warmed and wild rice would have migrated north (Fig. 4). However, beginning about 8000 BP the climate of China cooled and monsoon rainfall declined. This mid-Holocene climate change in China would have had an impact on wild rice populations that likely declined and becoming locally extinct and it has been suggested that this may have promoted a faster rate of domestication [90] as other food sources such as nuts were also in decline (Fig. 4).

Studies of vegetation history at Lake Daihan, west of Beijing, have suggested that warm, humid weather patterns between 3950–3500 BP and 1700–1350 BP [91]. At these times, after rice was domesticated, wild rice migrated as far as the Yellow River and this is recorded in historic literature [92]. Wild rice stands were vast with wild rice being harvested in various parts of China, with a record dated to 1100 BP for Hebei (Hopei) province near Beijing that states "wild rice ripened in an area of more than (13,333 ha), much to the benefit of the poor in local and neighbouring counties" [92]. Thus, high seed producing wild rice ecotypes existed and were harvested in China long after rice itself was domesticated. However, since domesticated rice was also being grown in the same area at this time, opportunities for introgression would have been abundant. Now wild rice in China is restricted to southern and southwestern provinces (Fig. 5). Present wild rice populations in China have introgressed with cultivated rice, are rare, widely scattered and declining in both size and number [77,81]. Therefore, contemporary Chinese wild rice germplasm provides a poor reflection of what wild rice genetic diversity might have been like in the past. In order to imagine wild rice in the past in China, contemporary studies of adjacent areas of
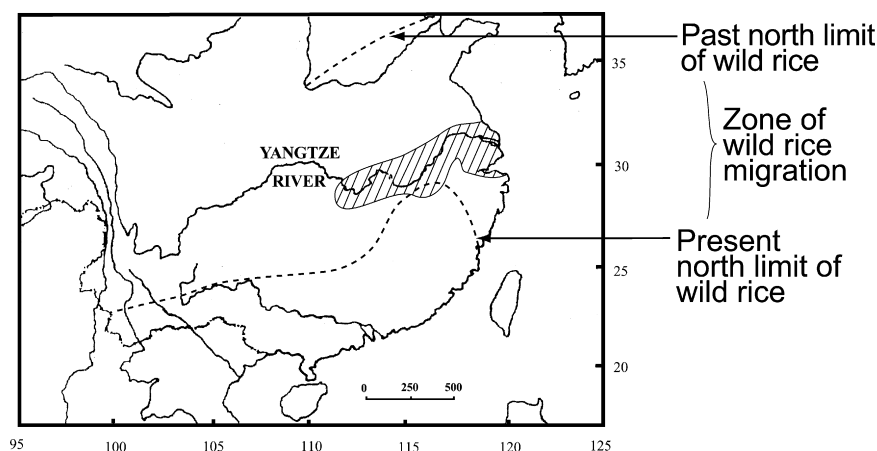
Fig. 4. Northern limit of past and present wild rice distribution in China.

Asia today, with lower human population density than China, might provide a suitable comparison. The wild rice diversity on the Vientiane Plain of Laos has been studied in depth [8,93,94]. Annual and perennial wild rice, including high seed producing populations of *O. rufipogon*, can be found scattered across the Vientiane Plain [94]. *O. rufipogon* and *O. nivara* are usually found at separate locations several kilometres apart and are generally reproductively isolated by both distance and flowering time. Such an environment with high level of village-to-

village wild rice diversity would likely have existed along the Yangtze River in the past.

The Yangtze River valley has a myriad of lakes where wild rice must have grown in the past. The extent of these lakes and the degree to which the water level rose and fell annually would have determined the types of ecotypes of wild rice that evolved there. These populations of wild rice were the material for the domestication of rice. Post-Han dynasty records for wild rice in Jiangxi province on the Yangtze River dated at 1300 BP state "In early spring . . . (autumn?) . . . wild rice ripened in an area of 1400 ha and perennial rices ripen in an area of (12,000 ha)" [92, p. 67]. This clearly indicates two distinctly recognisable types of wild rice in the Yangtze valley in the past.

Therefore, the Yangtze River valley seems to have had various ecotypes of *O. rufipogon* that evolved in a similar way to the complexity of wild rice that can currently be found in the river plains of the Brahmaputra, Ganges, Irrawady, Chao Pray and Mekong river valleys. Today both *O. rufipogon* and *O. nivara* grows in these river valleys of South and Southeast Asia, but not in the valleys of the fast flowing Salween and Red rivers. When temperatures warmed in China after the Younger Dryas the wild rice of the Yangtze River valley might have been similar to that we find in areas with similar climates today, with annual and perennial ecotypes of wild rice in different areas. This may explain the high degree of residual genetic diversity found today in Chinese wild rice (discussed above).

Hunters and gatherers would have been familiar with wild rice as a source of nutritious seeds, and probably developed methods similar to those used today to gather different ecotypes of wild rice. Annual *O. nivara* is still harvested by tying plants with leaves into bundles so that the grain falls into the centre of the bundle not the ground, and the bundles are then harvested (Fig. 1). Perennial *O. rufipogon*, a taller plant, is harvested by beating the panicles over a basket (Fig. 2). In deep water, where *O. rufipogon* grows, boats may have been used for harvesting, as practiced by Native Americans to harvest *Zizania* (American wild rice). Early rice harvesters and cultivators made boats [95], but we are not aware of wild rice being harvested by boat today in Asia or Africa.
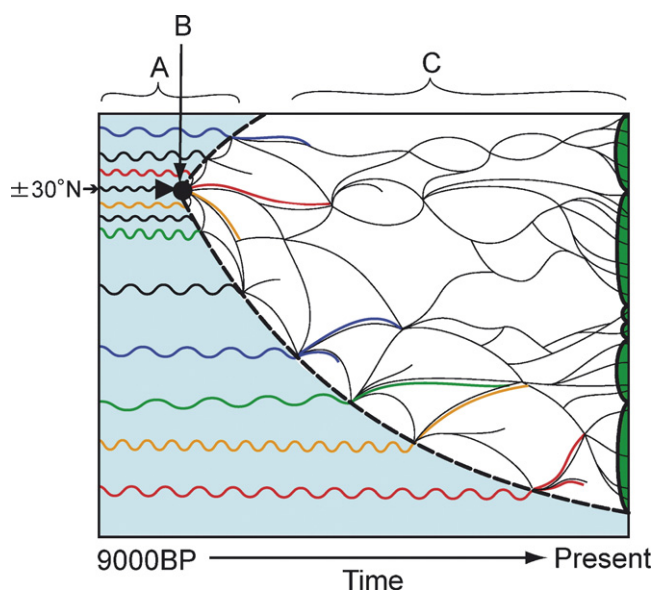

Fig. 5. How a single domestication event led to Asian rice evolving into highly diverse varietal groups with deep genetic divisions. (A) Wild rice gene pool with populations distributed across Asia (shaded light blue). The wavy line with arrow represents the population from which domesticated rice first evolved. Other wavy lines represent populations with significant variation that introgressed into domesticated rice. (B) Finding of a non-shattering mutant. Dashed line emanating from (B) represents the porous boundary to gene flow between the wild and domesticated rice gene pools. (C) Introgression at the wild/domestication boundary resulted in diverging lines of domesticated rice that in turn sometimes introgressed with one another, some lines becoming extinct, leading to the present day genetic diversity of domesticated Asian rice indicated by green. The more complex pattern of lines within domesticated rice compared to wild rice represents movement due to transport by humans.

A scenario can be envisaged where some groups went out fishing on lakes and harvested tall deepwater wild rice by one method. While others, perhaps women and children, stayed close to settlements where forests had been opened, harvested short stature, annual wild rice from the more disturbed pools and lake margins by a different method. The Mesolithic people in the lower Yangtze manipulated and responded to their environment with a level of sophistication [96]. Between 8000 and 7000 BP there is evidence to suggest wetland management that encouraged growth of wild grasses (including wild rice) and reeds (*Typha*) [96]. There is also evidence that early forms of domesticated rice were present in the same areas at about 7000 BP [86].

The Yangtze River valley (about 31°N) is now the dividing line between japonica and indica rice cultivation in China [97]. As the climate cooled between 7000 and 5000 BP some types of rice would have adapted to cooler temperatures while others adapted to warmer temperatures, as they were taken to southern latitudes.

This scenario means indica-like and japonica-like wild rice could have been gathered and subsequently cultivated in parallel in the same region. The Yangtze River valley would have provided natural zones of hybridisation and diversity that were exploited during the process of rice domestication. The key discovery of the mutation at the *sh4* locus giving non-shattering spikelets that resulted in domesticated rice could then have quickly spread throughout this region where different types of wild rice were gathered/cultivated. As discussed earlier introgression may have been even more prevalent when rice was first domesticated than today because both inbreeding reproductive system and barriers to hybridisation would not have been well-developed. Gradual human migration with domesticated rice would have been accompanied by introgression with wild rice in areas to which rice was spread leading to distinct regional allelic profiles in rice. The successive cycles of selection and introgression would have filtered the best allelic combinations that would have further spread. Our hypothesis combines the elements of both models for domestication of rice presented by Sang and Ge [98]. Their models envisage either a single origin of domesticated rice (the snowball model—for a tropical crop!) or the multiple origins of domesticated rice (combination model). While the important non-shattering allele was found in one population (snowball model) the concurrent and sympatric cultivation of different types of wild rice some more japonica-like and some more indica-like would have enabled this non-shattering allele to rapidly spread over a restricted region while enabling the multiple types of rice in an area to retain there other main characteristics. After the gradual spread of the non-shattering allele resulting in the domestication of diverse wild rice ecotypes subsequent gene flow would have enabled, over time, other key domestication alleles to be introgressed from one type of rice to another (combination model). This would help to explain why the mutation that resulted in the main non-shattering allele is common to indica and japonica rice varieties today [2,4]. In addition, domestication of rice in a single region would account for the domestication genetic bottleneck for rice [28,65,69].

Thus, deep genetic divisions that exist among rice cultivars today can be explained by a single domestication event in a geographic region of high wild rice diversity and subsequent diversification. The initial domesticated founder populations that spread from a core region would have undergone cycles of introgression (where wild rice occurred) and selection for genes enabling rice to adapt to the new environments as it spread (Fig. 5). Thus, all the evidence for dual and multiple domestication presented in Box 1 can be explained by this hypothesis. The interpretation that rice has been domesticated more than once is a consequence of analysing present day germplasm that has undergone several thousand years of rapid evolution under human influence and impacted by the components of the primary gene pool of rice.

Can this hypothesis be checked? It seems that accumulated data on the diversity among varieties for key rice domestication related genes—shattering and dormancy will be most important. If a new mutation is found resulting in a new allele that causes non-shattering via *sh4*, clearly single domestication hypothesis for Asian rice will be untenable. Therefore, a search for such an allele should be made. It is also likely that new techniques to analyse increasing numbers of archaeological remains of rice at the molecular level will help in the reconstruction of ancient wild, cultivated and domesticated rice genetic diversity.

4.4. Evolution of rice in Africa

While there are perennial (*O. longistaminata*) and annual (*O. barthii*) A-genome wild species in Africa, they do not have the same close genetic relationship that is found between perennial and annual wild rice of Asia [18]. However, *O. longistaminata* and *O. barthii* can commonly be found growing in the same area. As discussed above, perennial *O. longistaminata* diverged early in the evolution of the A-genome. Phylogenetic studies suggest the annual *O. barthii* evolved from an ancestor of Asian wild rice not *O. longistaminata* [18,45].

The domestication of rice in Africa occurred later than in Asia but unequivocally prior to the introduction of Asian rice [99,100]. The best evidence from archaeobotanical data for the domestication of *O. glaberrima* comes from the site of Dia, in the middle Niger Delta, and Mali [101]. Abundant grains were recovered from all levels at this site, the earliest occupation of which was dated at between 2800 and 2500 BP. Based on dimensions of grain and their lack of change in size over time they were all presumed to be from domesticated plants. The accelerator-based mass spectrometry C-14 dating of these rice grains suggests that the time previously proposed for the domestication of African rice of about 3500 BP [102] might be close to the correct time.

Knowledge of the genetics of *O. glaberrima* is far less than *O. sativa* although it is thought that the two rice species have similar genetic architecture for many traits [6]. *O. glaberrima* differs from Asian rice by its more strictly annual habit, few secondary panicle branches, short rounded ligule and red pericarp. The domestication trait alleles in African rice have not yet been compared to those of Asian rice.
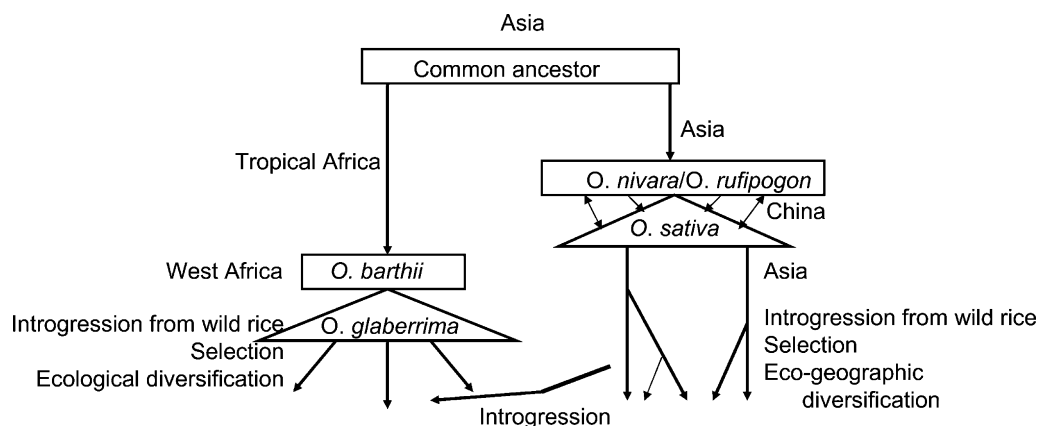
Fig. 6. Scheme for the evolution of the cultivated rices. African rice has a restricted geographic distribution compared to Asian rice hence does not exhibit the geographic variation that Asian rice.

O. glaberrima is the product of a double evolutionary bottleneck. The first associated with the divergence from Asian *Oryza*, perhaps ancestors of *O. barthii* were introduced to Africa from Asia. The second was due to domestication. This helps to explain in part the lack of genetic diversity in *O. glaberrima* compared to *O. sativa* [43]. Although genetic diversity of *O. glaberrima* is less than Asian rice, genetic subgroups were detected in a large-scale SSR analysis of *O. glaberrima* germplasm that was thought to reflect the ecological specialization of *O. glaberrima* in deepwater, saline affected and upland habitats [10]. The domestication process for African rice probably was similar to Asian rice, as the

methods used today to harvest wild rice are very similar in both continents (cf. Figs. 1 and 2 with figures on page iv in reference [6]). However, the introduction of Asian rice in historic times to Africa added a new dynamics to African rice culture. Today, a proportion of African rice has introgressed genes from *O. sativa* [10]. An illustration of a simple evolutionary model for the domestication of Asian and African rice is presented (Fig. 6).

5. Post-domestication—the waxy locus

Some cultures of Asia have selected glutinous forms of cereals even for cereals not native to Asia such as maize [103].
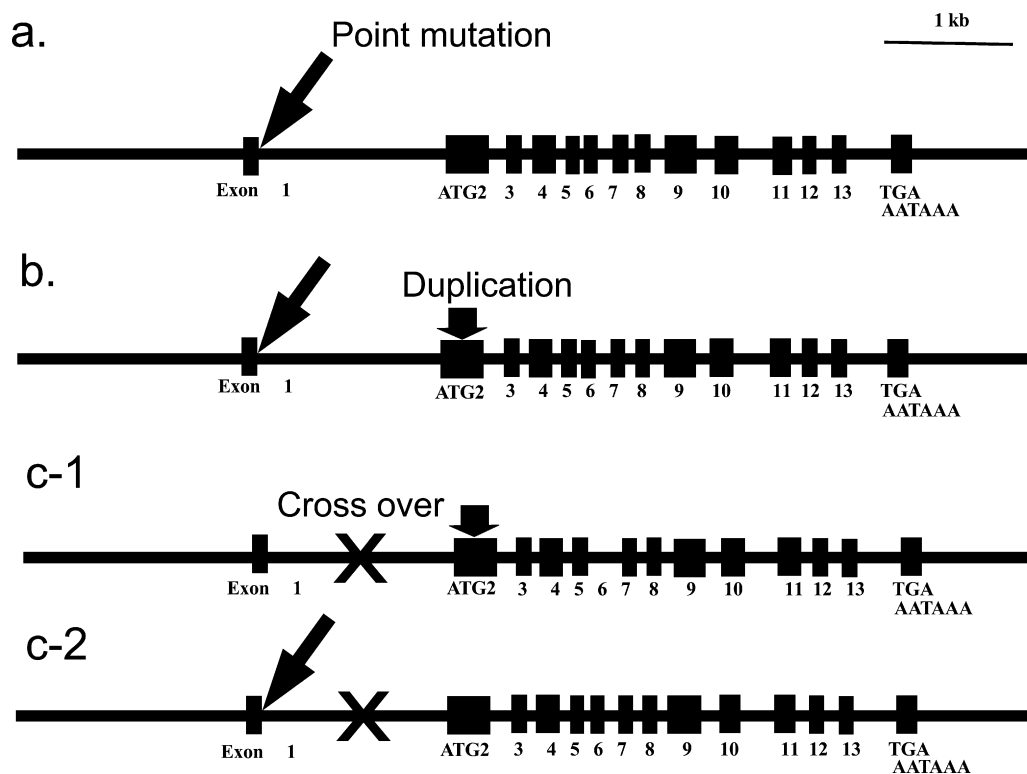

Fig. 7. Evolution at the waxy locus (structure of waxy locus based on [106]): (a) point mutation leading to low amylose; (b) duplication event resulting in glutinous rice; (c) crossover between glutinous and non-glutinous rice at the waxy locus between exons 1 and 2 resulting in progeny of glutinous rice without the point mutation at the first intron junction (c-1) and non-glutinous without the second exon duplication (c-2).

Wild rice does not have glutinous seeds. The mutation that resulted in glutinous rice was selected after domestication. The waxy locus is one of the most intensively studied regions of the rice genome because it is associated with the taste and texture of rice. This locus provides much information regarding how an important mutation spreads in a crop gene pool. It also provides information related to the impact of human selection at a genome level.

The alleles Wx_a (normal high amylose rice) and Wx_b (low amylose rice) differ by a single base pair mutation (G to T) at the 5′ junction of the first intron [104], and it was considered that this mutation was required for glutinous rice [105]. However, at the same time six indica and five tropical japonica varieties out of 353 glutinous varieties analysed did not have this mutation [72]. Using many tropical japonica varieties of germplasm from the glutinous rice zone of Asia, a 23 bp duplication in the 2nd exon of the waxy gene was found that is characteristic of tropical glutinous rice [106] (Fig. 7). Based on varieties screened to date, it is usually the 23 bp duplication that is the cause of the glutinous trait in rice ([107], but for a rare exception see reference [108]).

The evolution of glutinous rice seems to have occurred in several stages (Fig. 7). The first stage was the point mutation at the 5′ junction of the first intron that resulted in the waxy gene being less effective and producing low amylose rice, the Wx_b allele. This type of low amylose rice became common in temperate japonica varieties. Subsequently, the 23 bp duplication 1146 bp down stream from the low amylose associated point mutation occurred resulting in waxy rice with no amylose production. Some time later a recombination event(s) must have occurred between the point mutation and the 23 bp duplication that can explain why some waxy rices (about 3%) do not have the mutation at the 5′ junction of the first intron but do have the 23 bp duplication (S. Yamanaka, National Institute of Agrobiological Sciences, Japan, 2007, personal communication).

The genomic region around the waxy locus has shed light on the strong impact of selection on important traits. Clear evidence of a selective sweep, reduced variation among nucleotides neighboring a mutation as a result of strong selection was reported for the waxy locus [109]. The selective sweep showed reduced nucleotide variation in a 250 kb region around this locus. A comparison of the inferred selection coefficient of this region was made with gene regions in maize. While the selection coefficient was of the same order of magnitude in a similarly crop diversifying gene region in maize (Y1 related to endosperm colour), it was of a much higher order of magnitude than that for a principal maize domestication related gene tb1 (teosinte branched 1). The selective sweep at the waxy locus reveals the strong impact of human selection on crop gene evolution. As a result of the 10,000–8000 years that rice has been cultivated and selected by humans, rice cultivars express genes adapted to the needs of humans in finely organised arrays.

6. Conclusions

Results of genetic studies into the evolution of rice are biased by the small fraction of the historical rice diversity that now exists and is available for use from gene banks. Gene bank germplasm represents a secondary genetic 'footprint' of past Oryza variation in both time and space. Recent research suggests that Australian A-genome germplasm is important for understanding the evolution of Oryza A-genome diversity. There has been insufficient germplasm collection and analysis of Australian Oryza genetic resources. Current day rice germplasm has deep genetic divisions, not only indica and japonica varieties but also other varietal groups such as aus and aromatic varieties. While wild rice had some attributes associated with indica and japonica rice prior to domestication the genetic diversity in rice today largely reflects post-domestication events. The deep genetic divisions in rice result from selection within domesticated rice and continual introgression from wild rice. The single mutation in domesticated rice for the major non-shattering gene and the severe genetic bottleneck associated with rice domestication supports the view that Asian rice results from a single domestication event, at least for the major varietal groups. Initial domestication of rice would, however, have occurred in an area with a high level of wild rice diversity. We hypothesise that a rapid early spread of the main non-shattering gene of domestication in rice, and possibly other domestication traits, into wild rice representing different adaptive syndromes and subsequent introgression as domesticated rice was spread to new areas, can explain the deep divisions and diversity that we see today in the global rice germplasm collection. A dual domestication of indica and japonica rice in totally different geographic regions is not congruent with current data on rice domestication and key domestication related traits. African rice evolved from a common ancestor with Asian rice that had already diverged from the perennial African rice species O. longistaminata. While there are parallels between the evolution of Asian and African rice, African rice evolved from a more restricted wild gene pool and its evolution in historic times has been influenced by introduced Asian rice.

Post-domestication human influence on the rice genome is well illustrated by studies of the waxy locus that affects taste and texture of rice. Human selection has a major impact on genomic regions where important crop divergence genes are found and can result in useful mutations spreading widely in the crop gene pool.

Despite so much interest and research on the evolution of rice, it is surprising how much is still not known. Among areas of priority research is further understanding of dormancy, that is a complex trait consisting of kernal and hull components. Another important area of rice evolution research concerns de-domestication and how to prevent the occurrence and spread of weedy rice. Insights into reversal of some aspects domestication exhibited by various types of weedy rice might be valuable for understanding domestication itself. Thus, studies of all the QTL associated with both shattering and dormancy should be a priority. In addition, the imbalance in our understanding of domestication in Asian rice compared to African rice needs addressing given the array of useful genes for adaptation to West African environments in O. glaberrima. The current momentum to understanding rice evolution will continue as

new technologies are applied to study rice at all levels from molecule to whole plant. These new data from rice research will require synthesis with data from a broad range of disciplines to obtain a more precise understanding of rice evolution.

In conclusion we believe the event that resulted in the origin of the domesticated rice in Asia and Africa was simple, it was subsequent processes of domestication that makes the story appear complex.

Acknowledgements

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