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The evolution of rice: molecular vignettes on its origins and spread

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Abstract The domesticated species *Oryza sativa* or Asian rice evolved starting approximately 9,000 years ago and from its centers of origin in China and India has subsequently spread throughout the Old World (and in historical times in the New World as well). This species is one of the key domesticated crop plants in the world and has emerged as a model for studying the origins and spread of domesticated taxa as well as in investigating the genetic basis for plant variation under domestication. Archaeological data has been critical in dissecting the origins and spread of rice throughout Asia, but molecular information has also provided a complementary approach to examining the evolutionary dynamics of this species. The evolutionary history of a species can leave its footprints within its genome. Moreover, genetic studies allow us to study the history of traits that do not leave an archaeological record—for example, grain stickiness or flowering time—which can provide insights into how crop species are adopted by different cultures. In this review, several molecular studies into the origin and spread of Asian rice are discussed and we explore the advances these genetic studies offer in our understanding of the evolution of domesticated species. We also discuss how archaeological data can provide critical insights that can help refine genetic models of the origin and spread of domesticated species.

Keywords Domestication · Genes · Japonica · Indica · Population genetics · Madagascar

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Rice and its demographic history

The domesticated species *Oryza sativa* or Asian rice is one of the key domesticated crop species in the world (Khush 1997) and has emerged as a model for studying the origins and spread of domesticated taxa as well as in investigating the genetic basis for plant variation under domestication (Ashikari and Matsuoka 2006). Molecular studies have suggested at least two separate domestication events of Asian rice leading to the establishment of two major variety groups (Londo et al. 2006) that originate from distinct gene pools in the wild ancestor *Oryza rufipogon* (Harushima et al. 2002; Li et al. 1997). Japonica varieties were initially domesticated in southern China, around the Yangtze Valley, which gave rise to the temperate and tropical varieties, both of which are the result of a northward and southward spread of rice, respectively (Londo et al. 2006; Khush 1997; Oka 1988; Garris et al. 2005). The indica varieties appear to have been initially domesticated in the foothills of the Himalayas in Eastern India and spread primarily to lowland environments throughout the Asian tropics and subtropics. From India, rice also traveled to Madagascar and East Africa and then to countries in West Africa (Khush 1997). The introduction of Asian rice into Africa also provided opportunities to hybridize with local African rice, *Oryza glaberrima*, which had originated independently from Asian rice 3,000 years ago (Semon et al. 2005).

Molecular data has provided clues on the demography of rice evolution, and one study in particular has used genome-wide markers and coalescent modeling from molecular population genetics to infer demographic parameters (Caicedo et al. 2007). This study utilized >100 gene fragments sequenced across the rice genome and phylogenetic analysis of the data confirms earlier studies on relationships between major rice variety groups (see Fig. 1). Of particular

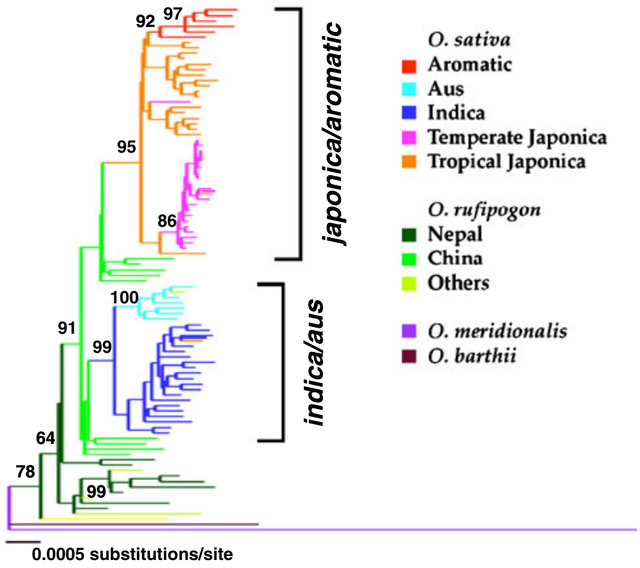

Fig. 1 Neighbor-joining phylogeny of domesticated Asian rice. This phylogeny is based on a genome-wide analysis of single nucleotide polymorphisms (SNPs; Caicedo et al. 2007). The different rice variety groups are color-coded as indicated, and the bootstrap replicates of key nodes greater than 50% are shown. The phylogeny shows a clear differentiation between japonica/aromatic and indica/aus clades, consistent with a separate origin for these two rice groups from *O. rufipogon*

significance is the finding that aromatic rice landraces, which are found in a geographically widespread region from Southeast Asia (jasmine rice) and South Asia (basmati rice), and whose grains superficially appear phenotypically similar to indica rice, actually originates as a close relative of the tropical japonica.

The estimates of nucleotide variation for both tropical japonica and indica, which is measured as nucleotide diversity π, are fairly low. The silent site $\pi=0.00157$ for topical japonica and slightly higher in indica at $\pi=0.00191$. These values are lower than the silent π of 0.00519 for the ancestral *O. rufipogon*, and this reduction in variation (almost universally observed in all domesticated crop species) has been attributed to the reduction in effective population size that characterizes the bottleneck of the crop species from the ancestor during the early period of domestication (Glemin and Bataillon 2009).

The pattern of single nucleotide polymorphism (SNP) variation was modeled using coalescent methods to infer key demographic parameters (Caicedo et al. 2007). The model was unrealistic in that it set the domestication bottleneck as beginning for both tropical indica and japonica at 12,000 years ago, with a subsequent 3,000-year bottleneck period. Current archaeological findings, however, suggests that this origin of domestication date is too early by possibly 25% (Fuller et al. 2009). Nevertheless, the results of the modeling are illuminating. The ancestral population size for *O. rufipogon* is found to be ~57,471 using the indica analysis and ~118,110 using the tropical japonica analysis. The difference in estimates may be due to differences in the founding population of each variety group (which is likely given that these two rice subspecies originated separately in different parts of the range), or differences in the actual timing of domestication between the two groups (which again is likely).

The model also infers a slightly more severe bottleneck for tropical japonica compared to indica (Caicedo et al. 2007). The effective population size of tropical japonica during the bottleneck is ~1,334, which indicates a bottleneck severity of 1.13%. This population has now expanded so that its current size is ~46,889. For indica, the bottleneck size is only slightly larger at ~1,413, but given that the estimate for the founding *O. rufipogon* population is also lower, the bottleneck severity for this variety group is less than that of tropical japonica at 2.46%. Its current estimated effective population size is 40,229. These numbers suggest that the impact of domestication was larger in tropical japonica compared to indica, which is reflected in the lower levels of variation in the former compared to the latter in current day landraces.

Migration history and the model of rice domestication

The inference of only a simple bottleneck as the demographic event in rice domestication, however, is called into question by certain features of the molecular data. One observation of SNPs in the rice data set is how much the frequency of polymorphisms deviates from predictions of the neutral theory. The site frequency spectrum examines the frequency of derived SNPs in a population sample and the neutral theory indicates that the number of SNPs should fall off at higher frequencies (Nielsen 2001). Indeed, this is the pattern observed in *O. rufipogon*, but both indica and, to an even larger extent tropical japonica, deviates from this prediction (Caicedo et al. 2007). Moreover, the simple bottleneck model described above also cannot account for this pattern; in order to explain this feature of the SNP frequency spectrum, we have to invoke more complex evolutionary models.

One model that was considered was population subdivision of the ancestral *O. rufipogon* population, followed by population bottlenecks in the domesticated lineage leading to tropical japonica and indica, and then gene flow between the domesticated lineages (see Fig. 2). This complex model was fit using a composite likelihood technique (Caicedo et al. 2007). The model is similar to the bottleneck model, but we assume migration between the subdivided ancestral *O. rufipogon* populations with rate M_R, and gene flow between the domesticated lineages and *O. rufipogon* at rate M_S.

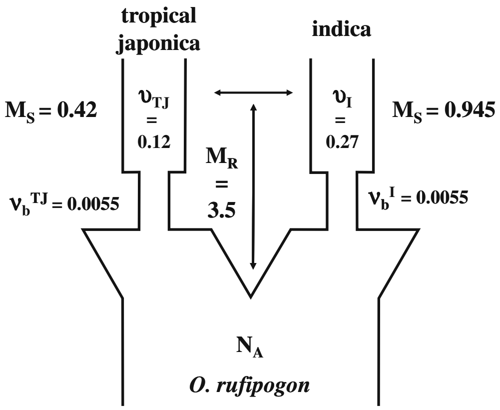

Fig. 2 Demographic model for the origin and evolution of Asian rice. The model depicts and ancestral *O. rufipogon* population of size N_A, and separate bottlenecks of size ν_b^I and ν_b^{TJ} during the origins of indica and tropical japonica rice, respectively. After the bottleneck period, the population sizes increase to ν^I and ν^{TJ} for the two rive variety groups. Migration into each variety group for the other is given by the migration parameter M_S, and between cultivated rice and wild rice as M_R. The parameters of this model was fit based on a genome-wide analysis of single nucleotide polymorphisms (Caicedo et al. 2007)

The analysis found a very large value of migration between the ancestral subdivided *O. rufipogon* population with the model showing maximum likelihood at $M_R>7$. This fits with the finding of little population differentiation within *O. rufipogon*, so the ancestral population structure was considered negligible as a factor and the modeling went forward considering only one ancestral population structure. The bottleneck severity of both tropical japonica and indica is set to be equivalent at 0.55%. The ratio of effective population size of tropical japonica to *O. rufipogon* is 0.12, and indica to *O. rufipogon* at 0.27. The start of domestication was also set at ~12,000 years ago. In this model, we find that there is greater migration into indica (migration rate=0.945) compared to tropical japonica (migration rate=0.42). It should be noted, however, that this rate is based on population size, and thus accounts for discrepancy in rates.

Exploring the details of the model suggests several constraints that must be met: a very strong bottleneck, high rates of migration between domesticated lineages as well as *O. rufipogon*, and lower current effective population sizes for the domesticated groups. There are restrictions on correlations between parameters (Caicedo et al. 2007). Nevertheless, this model fits the observed site frequency spectrum moderately to fairly well (P=0.72 for indica, P=0.22 for tropical japonica).

It should be noted that other complex models fit the data as well, including the presence of multiple selective sweeps in the genome of tropical japonica and indica. Moreover, it is clear that some of the parameters in these demographic models, whether a simple bottleneck model or the more complex one incorporating population subdivision and migration, need to be re-evaluated using more realistic parameters of timing and rate of domestication. In this regards, archaeological findings will be invaluable in developing models that are constrained by historical reality (Fuller et al. 2009). One clear area where archaeology can be of critical use in genetic modeling is providing dates for the domestication process. Geneticists generally model domestication as occurring fairly rapidly (Innan and Kim 2004; Caicedo et al. 2007), but this assumption is being challenged by archaeological data. Excavations in the Lower Yangtze Valley, for example, indicates that the non-shattering trait in rice (and hence domestication) increase fairly slowly, with fixation occurring over a period of ~3,500-4,000 years (Fuller et al. 2009). The slow process of domestication is echoed by studies in Near East founder crops (e.g., Tanno and Willcox 2006), and together these results suggest a more protracted model for the evolution of crop species (Allaby in press; Purugganan and Fuller 2009; Purugganan and Fuller, submitted). Future modeling of genetic data needs to incorporate these new archaeological findings to better reflect the dynamics of domestication.

The origin and spread of domestication traits

Crop plants differ from their ancestral wild species in a large number of physiological and morphological traits. This divergence is the result of two distinct evolutionary phases—(1) an initial domestication process that leads to the immediate divergence of a crop from a wild ancestral species as the result of human cultivation or tending (Purugganan and Fuller 2009) and a crop diversification or improvement phase, in which continued divergence occurs within the already domesticated species that leads to further differentiation within and between species (Yamasaki et al. 2005).

The study of the genetic basis of both domestication and diversification or improvement traits has been a major research area, and there have been efforts to identify genes that control these traits (Doebley et al. 2006; Purugganan and Fuller 2009; Yamasaki et al. 2005). Of particular interest are domestication genes, since they represent the first genes that were the targets of selection associated with the rise of human agriculture and the evolution of cultivated species by early farmers from wild taxa that were the food targets of hunter-gathers. Mapping of quantitative trait loci (QTL) associated with domestication has been a key approach in identifying domestication genes and several have led to the isolation of domestication genes (Doebley et al. 2006), including the *tb1* locus that accompanies shoot architecture evolution in twb.maize (Clark et al. 2004), the *sh4* and *qSH1* loci that leads to loss of shattering in rice (Li et al. 2006; Konishi et al. 2006).

As more genes associated with domestication are identified, it becomes possible to compare archaeological and genetic data and address issues on the origin and spread of domestication traits. At least two genes for non-shattering in rice, for example, has been isolated—including the *sh4* (Li et al. 2006) and *qSH1* (Konishi et al. 2006) genes. The *qSH1* non-shattering allele appears to be of relatively limited distribution in cultivated rice (Konishi et al. 2006), while the *sh4* non-shattering allele has a single origin but is found and fixed in both japonica and indica (Li et al. 2006; Zhang et al. 2009). Molecular population genetic analysis indicates that the amount and pattern of genetic diversity at the *sh4* gene is consistent with recent positive selection, as would be expected for a key domestication gene (Zhang et al. 2009). One puzzling issue is that this analysis suggests that the non-shattering allele was fixed in a very short period (~100 years) [Zhang et al. 2009], which differs for the archaeological record that indicates a more protracted period of fixation for the non-shattering phenotype (Fuller et al. 2009; Purugganan and Fuller, submitted). As pointed out earlier, this may require a reassessment of the genetic models used in exploring the dynamics of the domestication process.

Another issue is whether domestication proceeds by mutation and selection in similar or different genes in different evolutionary lineages. Comparative molecular genetic analysis of domestication genes or QTLs allow us

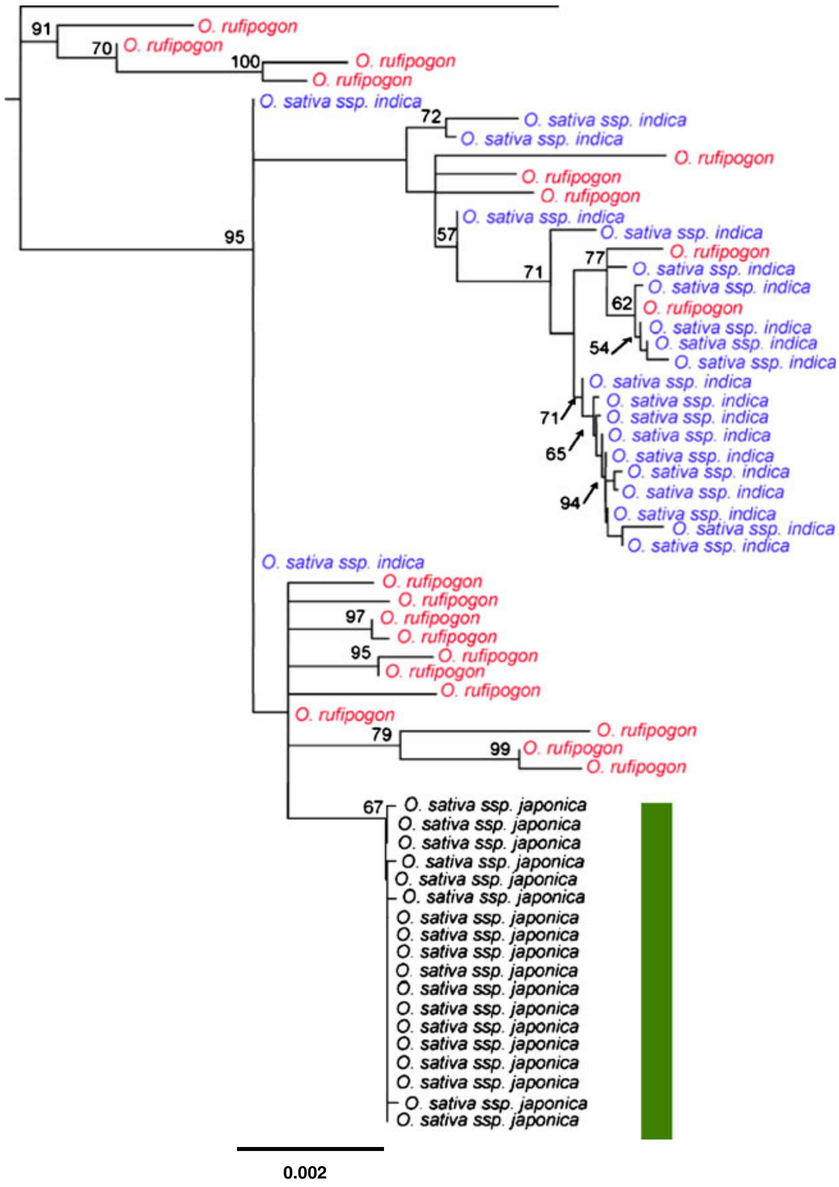

Fig. 3 Neighbor-joining phylogeny of domestication QTL at the proximal arm of chromosome 3. The phylogeny was based on SNPs across a region that spans the seed shattering QTL sh3.1 (Thomson et al. 2003). The indica accessions are indicated in *purple*, while the *green bar* shows the tropical japonica accessions. The tropical japonica landraces all show little molecular variation in the region, consistent with positive selection at this QTL in this variety group

to test determine whether the same or distinct genes (or alleles) underlie domestication in these distinct domesticated lineages drawn from the same progenitor wild species gene pool. As we have discussed above, domestication may be a complex process that includes gene flow among independent domesticated lineages. As noted above, the sh4 non-shattering allele has spread in both japonica and indica, possibly from hybridization between these two variety groups (Zhang et al 2009). The *Rc* domestication gene, which leads to white pericarp in rice, is another example of possible gene flow leading to the spread of domestication traits; the white pericarp allele appears to have originated from tropical japonica and spread to indica by hybridization (Sweeney et al. 2007). We also find other genes, such as the *prog1* gene for erect growth, appear to be identical in japonica and indica (Tan et al. 2008), which may also suggest either parallel evolution or introgressive hybridization between these lineages.

We have recently analyzed three QTL regions on rice chromosome 3 (Xie et al., in preparation) that were identified in a large-scale QTL mapping study between tropical japonica and *O. rufipogon* (Thomson et al. 2003). We find that the levels and patterns of polymorphism in these three domestication QTL regions are consistent with the possibility of recent positive selection. Patterns of polymorphism, however, indicate that selective sweeps are found in tropical japonica and not indica suggesting distinct genetic architectures of domestication for these distinct evolutionary lineages of Asian rice (see Fig. 3). This is at variance with the results from *Rc* (Sweeney et al. 2007) and *prog1* (Tan et al. 2008), as well as other domestication QTL regions we have studied (unpublished results). This suggests that while some genes may spread between tropical japonica and indica, other domestication alleles are found only in the former and not the latter.

The origin and spread of diversification traits: linking selection, environment, and cultural preference

Other genes associated with post-domestication crop diversification have spread (or facilitated the species' spread) have also been studied. One of the best-studied has been the rice waxy gene, which encodes an amylose biosynthetic enzyme and mutations of which lead to increase amylopectin content in grain starch and sticky rice (Olsen and Purugganan 2002; Olsen et al. 2006). Glutinuous rice arises from a mutation in the first intron splice donor site in this gene, and phylogeographic studies indicate that this likely originated in peninsular Southeast Asia (see Fig. 4), possibly in the mountainous regions that comprise what is referred to as the "glutinous rice zone" (Golomb 1976). Moreover, it has been shown that this mutation spread northwards across East Asia and south and west to island Southeast Asia as glutinous rice (see Fig. 4), and is also now prevalent in temperate japonica that is utilized in Northeast Asia (Olsen et al. 2006). It is in these regions that sticky rice is culturally prized and has thus been selected in the last few thousand years.

Another selected diversification trait that is favored by local cultures, primarily in South and Southeast Asia, is fragrance in rice, which results from the production of 2-acetyl-1-pyrroline (Buttery et al. 1982). Fragrant or aromatic rice is the result of the *fgr* gene in chromosome 8, which has been shown to encode the betaine aldehyde dehydrogenase gene *BADH2* (Chen et al. 2008). Evolutionary analysis of this gene indicates that mutations that reduce the activity of BADH2 lead to rice fragrance; furthermore, multiple non-functional alleles of this gene have been identified in rice cultivars (Kovach et al. 2009). Although numerous alleles of this gene have been identified, one in particular—the badh2.1 allele—is found at highest frequency among fragrant rice varieties. This mutant allele appears to have

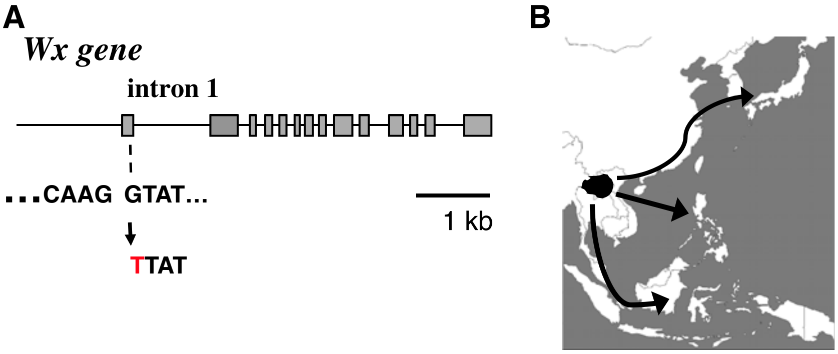

Fig. 4 The origin and spread of the *Waxy* (*Wx*) mutation that leads to sticky rice. **a** The structure of the rice *Wx* gene, with boxes as exons. The G-to-T mutation at the intron 1 splice donor site leading to glutinous rice is shown by the *arrow*. **b** A model of the origin and spread of the *Wx* splice donor mutation based on its geographic distribution and that of its ancestral haplotype (Olsen and Purugganan 2002; Olsen et al. 2006). The *blackened region* in Laos/Thailand is the likely geographic origin of the mutation, based on both molecular and cultural evidence. The mutation subsequently spread to northeast Asia and the rest of Southeast Asia associated with cultural preference for glutinous rice in festival foods and desserts as well as sticky temperate japonica in Korea and Japan

originated from japonica rice and subsequently spread into indica by hybridization (Kovach et al. 2009).

Another gene is possibly associated with spread of rice to temperate regions. The *Ghd7* gene encodes a CCT-domain containing protein that regulates heading date and yield potential in rice (Xue et al. 2008). Expression of this gene under long days delays heading and increases plant height and panicle size. The natural allele *Ghd7-1* appears to be associated with cultivars found in areas with hot summers and long growing seasons. The *Ghd7-2* differs from this allele by four amino acids and show reduced function of this gene, are found in temperate japonica varieties in Japan and Northern China. A non-functional *Ghd7-0* allele is found in early rice varieties that grow in two-crop systems in China, while the non-functional *Ghd7-0a* is found in varieties in northeastern China that has cool summers and a short growing season. These results suggest multiple mutations that may have been selected for early heading in rice grown in cooler climates, although a formal test for selection at this gene has yet to be undertaken using molecular population genetic techniques.

Founder events, isolated populations, and a diversion to genetic mapping

As domesticated species spread from the centers of origin, they colonize and are established in new habitats and cultures. Such spread may involve only a limited set of cultivars, and thus create population bottlenecks associated with founder events that are manifested by the reduced amount of genetic diversity in these newly established populations. Understanding the migration history of domesticated species allows us to examine the spread of agriculture as well as the continuing co-evolution of humans and their domestic species.

Founder events as a result of domesticated species introductions, and in some cases subsequent isolation, also have a practical side, since they provide an opportunity to develop new mapping populations to identify genes underlying organismal variation and adaptation (Varilo and Peltonen 2004). Current strategies in candidate gene association and linkage disequilibrium mapping have relied on isolated populations, which have several clear advantages over species-wide mapping populations (Varilo and Peltonen 2004; Peltonen et al. 2000; Jorde et al. 2000). By definition, these populations arise from a limited set of founder individuals leading to a more uniform genetic background.

Isolated rice populations: the case of Madagascar

The island of Madagascar off the coast of East Africa, which was settled by humans only 2,000 years ago, was one of the last major Old World areas of introduction of rice after its domestication as a cultivated species and before extensive historical global trade in this crop. Asian rice was introduced in Madagascar from India, the Malay peninsula, and Indonesia (Ahmadi et al. 1988; 1991; Rabary et al. 1989), possibly at the height of trade traffic in the Indian Ocean ~800 to 1,400 years ago. Studies of domestication traits characteristic of the two independently domesticated Asian rice subspecies, indica and tropical japonica, suggest two major waves of migrations into Madagascar (Koji 1997).

The introduction of cultivated ice and rice farming to the offshore African island of Madagascar has been traced to the expansion of Austronesian-speaking people from Southeast Asia, between 400 and 1000 A.D. (Vaughan et al. 2004). Cultural practices of these peoples, possibly Malays or Javanese, are found primarily on the east coast of Madagascar. Tropical japonica varieties of rice may have been introduced by migrating people from the Malay archipelago in the fifth and sixth century, possibly from Indonesia (Khush 1997; Dewar and Wright 1993). Indica varieties were then subsequently introduced to Madagascar from the Indian subcontinent, the timing of which is not well understood and resulted in hybridization with tropical japonica varieties previously brought to Madagascar by the Malay (Vaughan et al. 2004).

Morphological and early genetic studies have found indica and tropical japonica, with some temperate japonica landraces, in Madagascar as a result of these island introductions. Population genetic studies using allozyme markers indicate lower diversity of Madagascar rice landraces than those found in other Asian regions (Ahmadi et al. 1991). This suggests a genetic bottleneck associated with founder effects of island introduction, whereby minor alleles present in Asian rice are lost in the Madagascar varieties. At the same time, other alleles less frequent in Asia appeared at a much higher frequency in Madagascar, possibly due to genetic drift or selection on the island (Ahmadi et al. 1991). The differentiation of indica and japonica variety groups is also observed, but there is evidence of hybridization and recombination between landraces from these two groups in the island. A unique rice group specific to the island and found in the high plateau region at altitudes of 1,000-1,500 m has been described (Ahmadi et al. 1991), and morphological data suggests it is intermediate between indica and tropical japonica for most traits.

We have recently completed an analysis of molecular variation in Madagascar landraces (Molina et al., in preparation). The differentiation of Madagascar rice into indica varieties and tropical japonica varieties observed in a population structure analysis using SNP data combined with their sampling localities suggests that these two variety groups are geographically structured on the island. We also observe evidence of hybridization and recombination between indica and tropical japonica variety groups on the island, which does indicate a history of gene flow between these two major variety groups. Our results suggest that the contact between indica and japonica varieties occurred via separate introductions in Madagascar and has led to novel hybrid landraces there. The finding of reduced diversity for Madagascar rice, coupled with evidence of limited hybridization and recombination, also provides an opportunity to use these populations to identify genes underlying plant variation and adaptation.

Summary

Archaeological data is a key element in documenting the origins and spread of rice from its centers of origin throughout much of Asia. Molecular techniques, however, provide an independent approach to examining the evolutionary dynamics of this species. The history of a species can leave imprints on its genes, and by studying molecular variation among populations of domesticated species, we are able to explore its demographic history. Moreover, genetic studies allow us to trace the evolution of specific traits that do not leave an archaeological record—traits such as grain stickiness or flowering time—and this provide clues as to the pressures that may have led to adoption of a crop species by different cultures. Nevertheless, molecular models of crop origins and diversification have to be constrained by new findings from archaeology, which will hopefully provide more realistic models of how domesticated species evolve.

In this perspectives review, we discussed selected topics on the evolution of rice and the use of molecular data in the evolutionary study of domestication. This review is not meant to be comprehensive and draws largely from our own research studies, but hopefully provides an opportunity to reflect on the synergisms that can be obtained when exploring the origins of domesticated species and agriculture from the viewpoints of archaeological and molecular genetics.

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References

Ahmadi N, Becquer T, Larroque C, Arnaud M (1988) Genetic variability of rice in Madagascar. Agron Trop 43:209–221

Ahmadi N, Glaszmann JC, Rabary E (1991) Traditional highland rices originating from intersubspecific recombination in Madagascar. In: Rice genetics II. IRRI Press, Manila, pp 67–79

Allaby R (2010) Integrating the processes in the evolutionary system of domestication. J Exp Bot (in press)

Ashikari M, Matsuoka M (2006) Identification, isolation and pyramiding of quantitative trait loci for rice breeding. Trends Plant Sci 11:344–350

Buttery RG, Lilng LC, Juliano BO (1982) 2-Acety-1-pyrroline: An important aroma component of cooked rice. Chem Ind 958–959

Caicedo AL, Williamson SH, Hernandez RD, Boyko A, Fledel-Alon A, McCouch SR, Bustamante CD, Purugganan MD (2007) Genome-wide patterns of nucleotide polymorphism in domesticated rice. PLoS Genetics 3:1745–1756

Chen S, Yang Y, Shi W, Ji Q, He F, Zhang Z, Cheng Z, Liu X, Xu M (2008) Badh2, encoding betaine aldehyde dehydrogenase, inhibits the biosynthesis of 2-acetyl-1-pyrroline, a major component in rice fragrance. Plant Cell 20:1850–1861

Clark R, Linton E, Messing J, Doebley JF (2004) Pattern of diversity in the genomic region near the maize domestication gene *tb1*. Proc Natl Acad Sci USA 101:700–707

Dewar RE, Wright HE (1993) The culture history of Madagascar. J World Prehist 7:417–466

Doebley JF, Gaut BS, Smith BD (2006) The molecular genetics of crop domestication. Cell 12:1309–1321

Fuller D, Qing L, Zheng Y, Zhao Z, Chen X, Hosoya LA, Sun GP (2009) The domestication process and domestication rate in rice: spikelet bases from the Lower Yangtze. Science 323:1607–1610

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

Glemin S, Bataillon T (2009) A comparative view of the evolution of grasses under domestication. New Phytol 183:273–290

Golomb L (1976) The origin, spread and persistence of glutinous rice as a staple crop in mainland Southeast Asia. J Southeast Asian Stud 7:1–15

Harushima Y, Nakagahra M, Yano M, Sasaki T, Kurata N (2002) Diverse variation of reproductive barriers in three intraspecific rice crosses. Genetics 160:313–322

Innan H, Kim Y (2004) Pattern of polymorphism after strong artificial selection in a domestication event. Proc Natl Acad Sci USA 101:10667–10672

Jorde LB, Watkins WS, Kere J, Nyman D, Eriksson AW (2000) Gene mapping in isolated populations: new roles for old friends? Hum Hered 50:57–65

Khush GS (1997) Origin, dispersal, cultivation and variation of rice. Plant Mol Biol 35:25–34

Koji T (1997) Malayan cultivated rice and its expansion. Agricultural Archaeology 1:73-78

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

Kovach M, Calingacion F, Fitzgerald M, McCouch SR (2009) The origin and evolution of fragrance in rice (*Oryza sativa* L.). Proc Natl Acad Sci USA 106:14444–14449

Li ZK, Pinson SRM, Paterson AH, Park WD, Stansel JW (1997) Genetics of hybrid sterility and hybrid breakdown in an intersubspecific rice (*Oryza sativa* L) population. Genetics 145:1139–1148

Li CB, Zhou AL, Sang T (2006) Genetic analysis of rice domestication syndrome with the wild annual species *Oryza nivara*. New Phytol 170:185–193

Londo JP, Chiang YC, Hung KH, Chiang TY, Schaal BA (2006) Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. Proc Natl Acad Sci USA 103:9578–9583

Nielsen R (2001) Statistical tests of selective neutrality in the age of genomics. Heredity 86:641–647

Oka H (1988) Origin of cultivated rice. Elsevier Science, Tokyo

Olsen KM, Purugganan MD (2002) Molecular evidence on the origin and evolution of glutinous rice. Genetics 162:941–950

Olsen KM, Caicedo AL, Polato N, McClung A, McCouch SR, Purugganan MD (2006) Selection under domestication: evidence for a sweep in the rice *waxy* genomic region. Genetics 173:975–983

Peltonen L, Palotie A, Lange K (2000) Use of population isolates for mapping complex traits. Nat Rev Genet 1:182–190

Purugganan MD, Fuller DQ (2009) The nature of selection during plant domestication. Nature 457:843–848

Rabary E, Noyer JL, Benyayer P, Arnaud M, Glaszmann JC (1989) Variabilité génétique du riz (*Oryza sativa* L.) à Madagascar: origine de types nouveaux. L´Agrononomie Tropicale 44:305–312

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

Sweeney M, Thomson MJ, Cho YG, Park YJ, Williamson S, Bustamante CD, McCouch SR (2007) Global dissemination of a single mutation conferring white pericarp in rice. PloS Genetics 3:e133

Tan L, Li X, Liu F, Sun X, Li C, Zhu Z, Fu Y, Cai H, Wang X, Xie D, Sun C (2008) Control of a key transition from prostrate to erect growth in rice domestication. Nature Genet 40:1360–1364

Tanno K, Willcox G (2006) How fast was wild wheat domesticated? Science 311:1886

Thomson MJ, Tai TH, McClung AM, Lai XH, Hinga ME, Lobos KB, Xu Y, Martinez CP, McCouch SR (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. Theor Appl Genet 107:479–493

Varilo T, Peltonen L (2004) Founder events and mapping: isolates and their potential use in complex gene mapping efforts. Curr Opin Genet Dev 14:316–323

Vaughan DA, Miyazaki S, Miyashita K (2004) The rice genepool and human migrations. In: Wener D (ed) Biological resources and migration. Springer, Berlin, pp 1–14

Xue W, Xing Y, Weng X, Zhao Y, Tang W, Wang L, Zhou H, Yu S, Xu C, Li X, Zhang Q (2008) Natural variation in Ghd7 is an important regulator of heading date and yield potential in rice. Nature Genet 40:761–767

Yamasaki M, Tenaillon MI, Bi IV, Schroeder SG, Sanchez-Villeda H, Doebley JF, Gaut BS, McMullen MD (2005) A large-scale screen for artificial selection in maize identifies candidate agronomic loci for domestication and crop improvement. Plant Cell 17: 2859–2872

Zhang LB, Zhu Q, Wu ZQ, Ross-Ibarra J, Gaut BS, Ge S, Sang T (2009) Selection on grain shattering genes and rates of rice domestication. New Phytol 184:708–720