

Chapter 2

Genetic Diversity, Genetic Erosion, and Conservation of the Two Cultivated Rice Species (*Oryza sativa* and *Oryza glaberrima*) and Their Close Wild Relatives

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Abstract Rice cultivated gene pool includes two species. Asian rice, *Oryza sativa*, displays a very large phenotypic diversity resulting from a long history of domestication driven by human demographic expansion and sympatry with its wild relatives. African rice, *Oryza glaberrima*, represents a typical case of domestication bottleneck. Recent sympatry of the two species in Africa has given birth to new diversity. Current rice in situ genetic diversity results from the succession of a number of long-standing evolutionary events and the contemporary reversal of the trend of increasing diversity, referred to as genetic erosion. Since the early twentieth century, human demographic growth, agricultural modernisation and the advent of formal breeding systems, have affected the in situ diversity of cultivated rice species and their wild relatives. The evolutionary processes had produced a very large number of Landraces (LV) of which some 500,000 are conserved ex situ. The contemporary changes have resulted in the replacement of a large proportion of LV by a small number of Modern varieties (MV) in more than 70 % of rice-growing areas in Asia and Latin America, 38 % in Africa. The most important feature of rice in situ diversity emerging from our case studies in China, South and Southeast Asian countries, West Africa and Madagascar, is the diversity of situations. Aggregated data suggest massive absolute genetic erosion and sharp reduction of diversity indexes, particularly in irrigated ecosystems. Detailed surveys indicate smoother genetic erosion in rainfed ecosystems. However, the perspectives of rice in situ genetic diversity are gloomy even in rainfed ecosystems. The most realistic and promising option for the future is a dynamic management in the framework of the emerging concept of *ecological intensification*.

Keywords Rice • *Oryza sativa* • *Oryza glaberrima* • Genetic erosion • In situ diversity

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2.1 Introduction

Several types of events in the history of a crop lead to the diversity levels found at the present time. Such long-standing events include the domestication bottleneck (as only a subset of the diversity in the progenitor found its way into the domesticated species), directional selection (that affects key domestication genes, such as those regulating fruit size), dispersal bottlenecks (in which a small founder population experiences intense selection for agronomically desirable characteristics) and gradual increase of genetic diversity as a consequence of gene flow between the domesticated species and its wild relatives, or as a consequence of *de novo* generation of diversity through mutations and recombinations (van de Wouw et al. 2009).

A more contemporary event that has dramatically affected crop diversity found at the present time in farmers' fields, or in situ diversity, is the modernization of agriculture. It started in the middle of the nineteenth century in Europe and North America leading to the replacement of the large number of local varieties or landraces (LV) of major crops by a small number of modern varieties (MV). At present, in North America and northwestern Europe, LVs have become almost absent (Evenson 2003). In Asia and other developing countries, the phenomenon started in the beginning of the twentieth century and gained momentum in the 60s with the advent of the Green Revolution.

Taking place in the centers of genetic diversity of major food crops, the Green Revolution raised concerns about the survival of the genetic resources of those species (Harlan 1975). The perception of this threat gave birth to the concept of genetic erosion describing the process of loss of genetic diversity in agriculture (Pistorius 1997). It also gave impetus to national and international initiatives for collection and *ex situ* conservation of genetic resources on the one hand, for the *in situ* conservation of the LVs by farmers, on the other hand. Analyzing data from 27 crop species from five continents, to determine overall trends in crop varietal diversity on farm, Jarvis et al. (2008) found that for all crops, LVs dominated the planting area (from 80 to 100 % of the total crop area). The exception was rice, for which the range was from 7 to 100 % across the six sites.

About half of the world's population relies on rice as their staple food and rice cultivation provides livelihood for millions of people. Thanks to the extremely large morphological and physiological diversity of its ecotypes, rice is cultivated in a very broad range of environmental conditions in tropical, subtropical, and temperate regions around the world, in more than 100 countries and on every continent except Antarctica (Maclean et al. 2002). Rice cropping areas stretch from the latitude of 40° south, in Argentina, to 53° north in China; from the seaside to almost 3000 m of altitude in Nepal; from deepwater swamps (5–6 m deep) to strictly aerobic soils of steep slope in mountainous tropical areas; and from very acidic soils to the brackish waters of mangrove zones (Fig. 2.1). Likewise, its large diversity allows meeting a very broad range of grain quality requirements.

Being a major food crop, rice genetic diversity has undergone all of the above-mentioned impoverishment and enrichment events. Its large phenotypic diversity

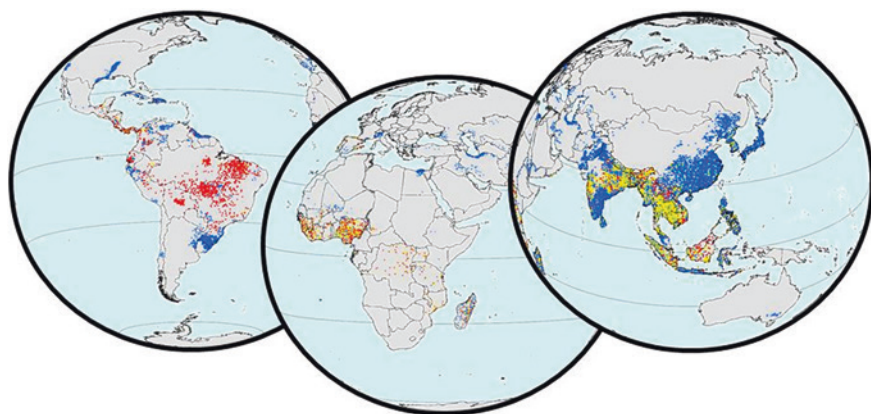


Fig. 2.1 Major rice growing areas and cropping ecosystems. Each *dot* represents 5000 ha of rice. *Blue* irrigated ecosystem; *Yellow* rainfed lowland ecosystem; *Red* rainfed upland ecosystem (After Rice Almanac; 2013)

results from a long history of domestication, driven by human demographic expansion, and by sympatry of the cultivated rice ecotypes with their wild relatives. Moreover, there are two species of cultivated rice, *Oryza sativa* L. or Asian rice, and *Oryza glaberrima* Steud or African rice, with distinct domestication histories. Last but not least, sympatry of these two species during the last five centuries in Africa has also given birth to a new original diversity.

This paper will provide a reminder of rice genetic diversity and of its early evolution, and present the post-Green Revolution evolution of rice in situ genetic diversity through a number of case studies. The extent of the effects of the modern breeding efforts on rice in situ diversity will be discussed. As wild species of *Oryza* have proved to be an important source of genes that add value to the cultivated rice genome, the gene pool considered includes the two cultivated rices and their close wild relatives.

2.2 Rice Gene Pool, Genetic Diversity, and Ex Situ Conservation

The genus *Oryza* is divided into four species complexes: the *O. sativa*, *O. officialis*, *O. ridelyi*, and *O. granulata* species complexes (Table 2.1). All members of the *Oryza* genus have a multiple of $n = 12$ chromosomes. While fertile offspring can be obtained rather easily from interspecific crosses within each complex, this is much more difficult in across-complexes crosses (Vaughan et al. 2003). The two cultivated rice species *O. sativa* and *O. glaberrima* belong to the *O. sativa* complex together with six closely related diploid wild species of the AA genome group: *O. nivara* and *O. rufipogon* present throughout Asia and Oceania; *O. barthii*

Table 2.1 Classification and distribution of species in the genus *Oryza*

Taxa	Genome	Distribution
<i>Sativa species complex</i>		
<i>O. sativa</i>	AA	Worldwide
<i>O. glaberrima</i>	AA	West Africa
<i>O. nivara</i>	AA	Tropical Asia
<i>O. rufipogon</i>	AA	Tropical Asia
<i>O. meridionalis</i>	AA	Tropical Asia to Northern Australia
<i>O. barthii</i>	AA	Africa
<i>O. longistaminata</i>	AA	Africa
<i>O. glumaepatula</i>	AA	South America
<i>Officinalis species complex</i>		
<i>O. minuta</i>	BBCC	Philippines, Papua New Guinea
<i>O. officinalis</i>	CC	Tropical Asia—Papua New Guinea
<i>O. rhizomatis</i>	CC	Sri Lanka
<i>O. malampuzhaensis</i>	CCDD	India
<i>O. punctata</i>	BB	Africa
<i>O. schweinfurthiana</i>	BBCC	Africa
<i>O. eichingeri</i>	CC	Africa, Sri Lanka
<i>O. alta</i>	CCDD	Central and South America
<i>O. grandiglumis</i>	CCDD	South America
<i>O. latifolia</i>	CCDD	Central and South America
<i>O. australiensis</i>	EE	Australia (<i>Australiensis</i> section)
<i>O. brachyantha</i>	FF	Africa (<i>Brachyantha</i> section)
<i>O. schlechteri</i>	HHKK	Indonesia and Papua New Guinea
<i>O. coarctata</i>	KKLL	South Asia to Myanmar (<i>Padia</i> section)
<i>Ridleyi species complex</i>		
<i>O. longiglumis</i>	HHJJ	Indonesia and Papua New Guinea
<i>O. ridleyi</i>	HHJJ	Southeast Asia—Papua New Guinea
<i>Meyeriana species complex (granulata species complex)</i>		
<i>O. granulata</i>	GG	South and Southeast Asia
<i>O. meyeriana</i>	GG	South and Southeast Asia
<i>O. neocaledonica</i>	GG	New Caledonia

endemic in West Africa; *O. longistaminata* found throughout Africa; *O. meridionalis* native to Australia and *O. glumaepatula* endemic in Central and South America. Divergence between *O. glaberrima* and *O. sativa* goes back to 0.6–0.7 million years (Zhu and Ge 2005; Ammiraju et al. 2008). The *O. officinalis* complex comprises five diploids BB, CC, and EE genomes, and six tetraploids with BBCC or CCDD genomes. The remaining species are more distantly related to the cultivated species, with genomes FF, GG, HHJJ, and HHKK.

The centers of species diversity and genomic diversity are the islands from Southeast Asia to the Pacific Ocean. Nine of the 24 wild relatives of rice occur in

Indonesia, and 7 of the 10 genome types are found in the Asian–Pacific islands. In addition, distinctive sets of species assemblages are associated with South Asia, Africa, and the Americas: each continent has its own set of wild species, and only one wild species (*O. eichingeri*) is found in more than one continent.

The geographic distribution of each cultivated species coincides with the ones of an annual autogamous and a perennial allogamous wild species of *O. sativa* complex: respectively, *O. nivara* and *O. rufipogon* for *O. sativa*; *O. barthii* and *O. longistaminata* for *O. glaberrima*. These wild species constitute the two ancestral pools that were directly subject to domestication and gave birth to the two cultivated species, though there is still debate over the relative contribution of the annual and perennial ancestors to domestication, especially in the case of *O. sativa*.

2.2.1 Asian Rice Gene Pool and Genetic Diversity

In Asia, *O. rufipogon* grows in perennial swamps across a broad geographic range spanning eastern India, Indochina, and portions of southern China. Men originally harvested it by continuous rationing. The domestication process started some 10,000 years ago by planting rice seeds outside those permanent wetlands, in seasonally wet terrain where selection for the annual growth habit that characterizes *O. sativa* took place. Out-planting away from wild stands would also have allowed selection toward non-shattering to be retained more easily with each successive monsoonal planting season (Allaby et al. 2008). Thus, the very process of radiation and migration on the part of humans was an essential part of the domestication process for rice right from the start.

The early spread of the Asian rice is tightly associated with the outflow of Neolithic lifestyles in the eastern Asian region, in a “spread, pause, adapt, spread, pause again” mode, in relation with environmental barriers and constraints (Bellwood 2011). The major steps are (i) 8000–6000 BC: pre-domestication of *japonica* rice in China, the Yangzi, Han, Huai, and lower Yellow River basins, (ii) 6000–3500 BC: gradual spread of Neolithic lifestyles through southern China, accompanied by an increasing predominance, especially after 4000 BC of fully domesticated (non-shattering) rice, (iii) 3500 BC: Neolithic settlement of Taiwan, presumably following developments in Fujian and/or Guangdong, (iv) 3000–2000 BC: Neolithic settlement of mainland Southeast Asia from Guangdong and Guangxi into northern Vietnam, and possibly down the Mekong river into southern Vietnam and Thailand, (v) 2000–1500 BC: Neolithic settlement of the Philippines and central Indonesia, via Taiwan, (vi) 500 BC establishment of wet rice cultivation in regions of high population growth such as Java and Bali.

Although domestication of the *indica* subspecies from annual forebears within a vast region south of the Himalayas Mountains (likely eastern India, Myanmar, and Thailand) takes place as early as 7000–4000 BC, it does not make an appearance in Southeast Asia until about 2000 years ago, contemporary with early contacts with India.

The domestication bottleneck was probably not very severe due (i) to large effective population sizes during the domestication process, as large quantities of grain were needed for subsistence and (ii) very likely multiple domestications. Directional selection then played a relatively important role. For instance, in glutinous rice the *waxy* locus shows a reduced nucleotide variation compared to other unlinked genes in the rice genome (Olsen and Purugganan 2002). Foundation effects are clearly visible when local or country level rice diversity is compared to global rice genetic diversity (Barry et al. 2007a; Radanielina et al. 2013a). Gene flow between *O. sativa* and its wild relatives have certainly played an important role in shaping the diversity of the cultivated rice LVs. Analyzing the DNA sequence variation in *O. sativa* and *O. rufipogon*, across 111 randomly chosen gene fragments, Caicedo et al. (2007) observed a genome-wide excess of high-frequency derived single nucleotide polymorphisms (SNPs) in *O. sativa* varieties. They concluded that the simple bottleneck model could not explain the derived SNP frequency spectrum in rice. Instead, a bottleneck model that incorporates selective sweeps, or a more complex demographic model that includes subdivision and gene flow, offers more plausible explanations for patterns of variation in domesticated rice varieties.

Later on, as *O. sativa* spread around the world, it has, especially the *indica* form, differentiated into a great number and diversity of LVs. *O. sativa* reached Madagascar (through India) and Europe (through Greece and Italy, and subsequently Spain) over 2000 years ago, and subsequently spread to other parts of Africa through Mozambique and to other countries of southern Europe. Secondary centers of distinctive *indica*-like diversity are particularly notable in Madagascar and Sri Lanka. More recent distinctive secondary centers of diversity are also apparent in Africa and the Americas. One of the most recent introductions, slightly over 100 years ago, is to Australia.

O. sativa displays a very large phenotypic diversity. This phenotypic diversity is associated with differentiation into two major genotypic groups, the *indica* and *japonica* types (Oka 1983). Given the low level of fertility of *indica* \times *japonica* hybrids, they are also referred to as subspecies. Surveying polymorphism at 15 isozyme loci in a sample of 1688 LV, Glaszmann (1987) distinguished, besides the two subspecies, some other minor groups such as *aus-boro* and *aromatic* (Fig. 2.2). The origins of these minor groups are still a matter of research and debate. The *indica-japonica* differentiation is also associated with ecological specialization (Khush 1997).

- The *indica* group, particularly diverse, is widespread across the tropical lowlands.
- The *japonica* group, less diverse, comprises two subgroups: the tropical subgroup cultivated in the upland ecosystems of tropical regions; and the temperate subgroup cultivated in the lowland ecosystem of countries such as Japan, Europe, and the USA.
- The *aus-boro* rice of the Bangladesh region.
- The *aromatic* rice from the Iran–Afghanistan–Pakistan–Nepal–North India region.

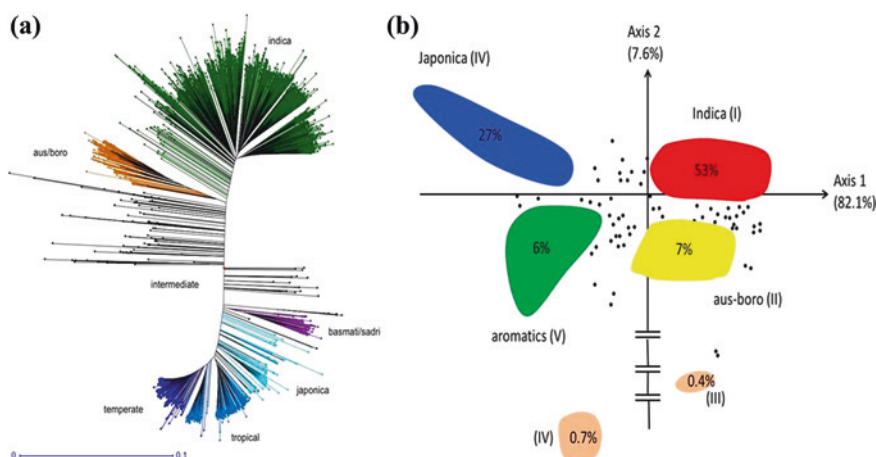


Fig. 2.2 Structuration of *O. sativa* genetic diversity. **a** Classification of 3000 rice accessions into five distinct varietal groups based on 5 sets of 200,000 random sets of SNP from the 18.9 million discovered SNP variants discovered (After 3000 rice genomes project, 2014). **b** Projection of 1688 Asian rice accessions on the first plane of a factor analysis of correspondences of isozyme variation at 15 loci. Sizes of the groups are indicated. *Isolated dots* represent 90 varieties with intermediate positions or unstable classification (After Glaszmann 1987)

Using genotypic data at 169 SSR loci in a sample of 232 accessions, Garriss et al. (2005) confirmed the above-mentioned classification and showed that 37.5 % of the variation was due to differences among groups with the remaining 62.5 % due to differences within groups. Differentiation between groups estimated with pairwise F_{ST} statistics was high between groups with values ranging from 0.20 to 0.42. The lowest F_{ST} were observed between *temperate* and *tropical japonica* (0.20) and between *aus* and *indica* (0.25). The five groups are not endowed with the same amount of intragroup diversity (Table 2.2). The *indica* group has the highest intragroup diversity, followed by the *tropical japonica* and *aus-boro* Garriss et al. (2005). Recently, Zhao et al. (2011) tagging the amount of intragroup genomic variation, by an array of 44,000 SNPs across 413 diverse accessions of *O. sativa* collected from 82 countries and measuring it by the pairwise SNP linkage disequilibrium (LD) among these SNPs, confirmed the particularly high diversity of the *indica* group (Table 2.2). On average, LD drops to almost background levels around 500 kb–1 Mb, reaching half of its initial value at about 100 kb in *indica*, 200 kb in *aus-boro* and *tropical japonica*, and 300 kb in *temperate japonica* (Zhao et al. 2011). The structuring of *O. sativa* in 5 groups (*indica*, *tropical japonica*, *temperate japonica*, *aus-boro*, and *aromatic*) was confirmed by the most recent and massive genotypic data produced in the framework of the 3000 rice genomes project (Fig. 2.2). The geographical distribution of the different genetic groups in major rice-growing areas of Asia is presented in Fig. 2.3.

This structuring of rice diversity into several groups with unequal intragroup diversity results from its autogamous reproduction system, its domestication

Table 2.2 Diversity parameters of the 5 major genetic groups within *O. sativa*

Study	Diversity parameters	<i>Aus</i>	<i>Indica</i>	<i>Aromatic</i>	<i>Japonica</i>		Adm
					Trop	Temp	
1	Sample size	57	87	14	96	96	62
	Private SNPs	822	1851	77	398	376	
	Polymorphic SNPs	23,270	30,449	12,059	24,813	14,688	
	MAF \geq 0.05	18,012	20,259	12,039	13,051	7775	
2	Sample size	21	79	19	41	48	24
	No. of alleles/locus	5.1	7.3	3.4	4.9	6.1	
	Gene diversity	0.54	0.55	0.39	0.39	0.47	
	Average PIC value	0.52	0.52	0.38	0.37	0.46	
3	Sample size	48	124	52	43	43	63
	Gene diversity	0.15	0.19	0.11	0.16	0.12	

1: Zhao et al. (2011); 2: Garris et al. (2005); 3: Ahmadi et al. (2013). *Adm* admixes. Private SNPs are unique to one specific group; Polymorphic SNPs are considered to be those that segregated in one specific group, irrespective of whether they also segregate in another group; *MAF* minor allele frequency

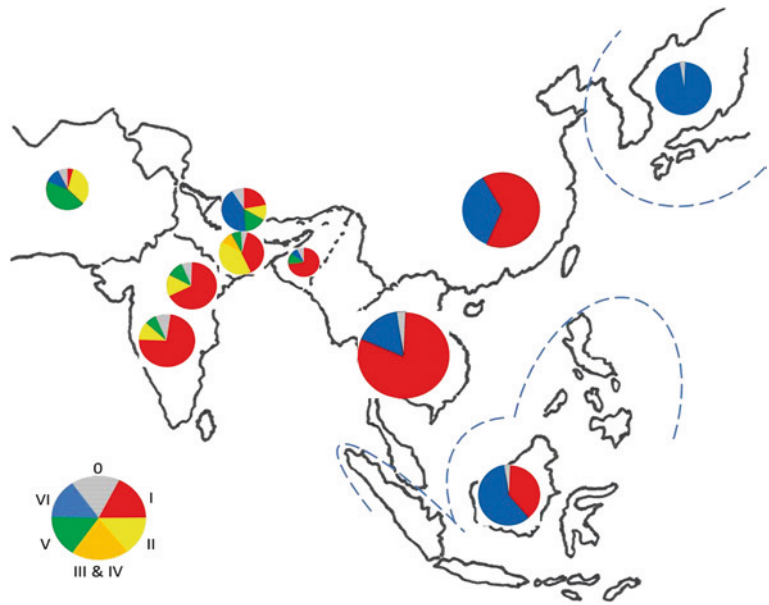


Fig. 2.3 Geographical distribution of the six varietal groups in major rice growing areas of Asia based on isozyme variation at 15 loci, in 1688 Asian landraces. I: *indica*; II: *aus*; III and IV: deepwater; V: *aromatic*; VI: *japonica*; 0: unclassified varieties (After Glaszmann 1987)

history, and the independent population histories of different groups. For example, the source of high level intragroup variation in the *indica* group relative to the others, with no evidence of a genetic bottleneck, could include mitigation of the domestication bottleneck by gene flow due to sympatric wild relatives or

a historically larger effective population size due to overland dispersal routes. Likewise the high level of intragroup diversity of *aus-boro* despite its small area of distribution argues for independent domestication.

While the existence of these groups is not contested, debate about their origin(s) continues. Indeed, while the domestication of *O. sativa* goes back to an estimated 10,000 years (Higham and Lu 1998; Sweeney and McCouch 2007), the seniority of the *indica-japonica* differentiation within its wild ancestor *O. rufipogon* has been estimated at more than 100,000 years (Wang et al. 1992). Based on this early differentiation, it was often concluded that *O. sativa* had undergone two independent domestications from the divergent pools of *O. rufipogon* (Second 1982; Cheng et al. 2003). However, considering the domestication not as an event but as an evolutionary process promoted by interactions between plant and man, Oka (1988) suggested multiple and diffuse domestications of *O. sativa*, in a large area stretching from the Himalayan footsteps of India to China. The latest in-depth analysis of the domestication sweeps and genome-wide patterns based on genome sequences from 446 geographically diverse accessions of *O. rufipogon* and from 1083 cultivated *indica* and *japonica* varieties reveals that the *japonica* group was first domesticated from a specific population of *O. rufipogon* around the middle area of the Pearl River in southern China, and the *indica* group arose subsequently from crosses between *japonica* rice and local wild rice as the initial cultivars spread into South East and South Asia (Huang et al. 2012).

Whatever the early history of domestication of *O. sativa*, by the mid-twentieth century, selective pressure exerted by man and the new environments he colonized had given birth to hundreds of thousands of LVs, each adapted to the specific environmental conditions and cropping requirements of a small agricultural area. No direct statistics regarding the number of such *O. sativa* rice LVs are available neither at the level of individual countries nor at the global level. A rough estimate of the minimum number is provided by the number of accessions of *O. sativa* genetic resources being conserved in international and national genebanks around the world: over 500,000 in 2007 (IRRI 2010).

2.2.2 African Rice Gene Pool and Genetic Diversity

In Africa, *O. glaberrima* was domesticated independently from *O. barthii* (syn. *O. breviligulata*) in the inland delta of the upper Niger River, in what is today Mali, some 2000 or 3000 years ago. The species then spread to two secondary centers of diversification, one on the coast of Gambia, Casamance and Guinea Bissau, the other in the Guinean forest between Sierra Leone and western Ivory Coast (Portères 1970; Second 1982).

O. glaberrima represents a typical case of reduction of genetic diversity observed in crops compared to their wild progenitors because of dual bottlenecks imposed by domestication and breeding (Buckler et al. 2001; Zeder et al. 2006). Indeed, based on isozyme, RFLP, SSR and MITE markers, all previous studies

have found dramatic reduction in genetic diversity associated with the domestication of African rice and have revealed substantially lower genetic diversity in African than in Asian rice (Second 1982; Wang et al. 1992; Ishii et al. 2001).

The most recent analysis of diversity comparing SNP variation in of independent genes between *O. glaberrima* and *O. barthii* showed that both cultivated and wild African rice maintained extremely low levels of nucleotide diversity. Moreover, genetic loss in African rice is much more severe after domestication, with 76 % less diversity in the domesticated species than in its wild progenitor (Li et al. 2011). An obvious explanation for the low genetic diversity of *O. glaberrima* would be a severe genetic bottleneck during its domestication from small initial populations of *O. barthii*. The ecogeographical diversity seems so low that clustering analysis is unable to refine the domestication place and dispersion of *O. glaberrima* (Li et al. 2011). Therefore, the hypothesis developed by Portères (1970) remains today the most probable considering that African rice was first domesticated in the inland delta of the upper Niger River and subsequently spread in two secondary centers along Sahelian rivers and their tributaries.

Genome-wide LD investigated in 198 accessions of *O. glaberrima* using 93 SSR markers (Mande et al. 2005) detected very high levels of LD among distantly located loci, separated by more than 100 cM (~25,000 kb). Free recombination among loci at the population genetic level was shown (i) by a lack of decay in LD among markers on the same chromosome and (ii) by a strictly increasing composite likelihood function for the recombination parameter. This suggested that the elevation in LD was due not to physical linkage but to other factors, such as population structure. Structure analysis using the Bayesian clustering analysis approach confirmed this hypothesis, indicating that the sample of *O. glaberrima* in this study was subdivided into at least five cryptic subpopulations. Two of these subpopulations clustered with control samples of *O. sativa*, subspecies *indica* and *japonica*, indicating that some *O. glaberrima* accessions represent admixtures. The remaining three *O. glaberrima* subpopulations were significantly associated with specific combinations of phenotypic traits—possibly reflecting ecological adaptation to different growing environments and plant type described by Portères (1970): the floating, non-floating, and upland types (Mande et al. 2005).

Until the mid-fifteenth and early sixteenth centuries, *O. glaberrima* was the only rice species grown in West Africa. Some ethnical groups such as the Jola of south Senegal were growing wet rice and using intensive techniques, such as diking to retain rainwater and transplanting, at the time they first encountered Europeans (Linares 2002). Although it is not known with certainty when and where the first varieties of *O. sativa* were introduced into West Africa, the general consensus is that, beginning in the sixteenth century, the new species spread and was adopted by peoples living on the Upper Guinea Coast who had previous experience growing the local African species. Since then, *O. glaberrima* has undergone an extinction process. Given its lower productivity, its high degree of shattering and its red caryopses, not praised by the European merchants and colonizers, *O. glaberrima* was soon relegated to the rank of secondary species cultivated in marginal rice-growing ecosystems (deepwater, depleted upland areas) and/or for specific purposes, such as traditional ceremonies (Linares 2002).

2.2.3 *Ex Situ Conservation of Rice Genetic Resources*

According to a survey implemented by International Rice Research Institute (IRRI) in 2007, over 500,000 accessions of rice genetic resources are conserved in international and national gene banks around the world (IRRI 2010). The majority are only kept in a small number of gene banks (Fig. 2.4). The largest six gene banks are all in Asia, and together conserve around 70 % of total world holdings. In order of number of accessions, they are: IRRI, the National Bureau of Plant Genetic Resources (NBPGR) in India, the Institute of Crop Germplasm Resources (CAAS) in China, the China National Rice Research Institute (CNRRI), the National Institute of Agrobiological Sciences (NIAS) in Japan, and the Rural Development Administration (RDA) gene bank in the Republic of Korea. These gene banks hold well-organized long-term seed storage facilities.

The three largest collections outside Asia are: Africa Rice, the National Center for Genetic Resources Preservation (NCGRP) in the USA, and Brazil; but these collections are considerably smaller than the large Asian collections, and together they hold only 10 % of the global holdings. The remaining 20 % of global

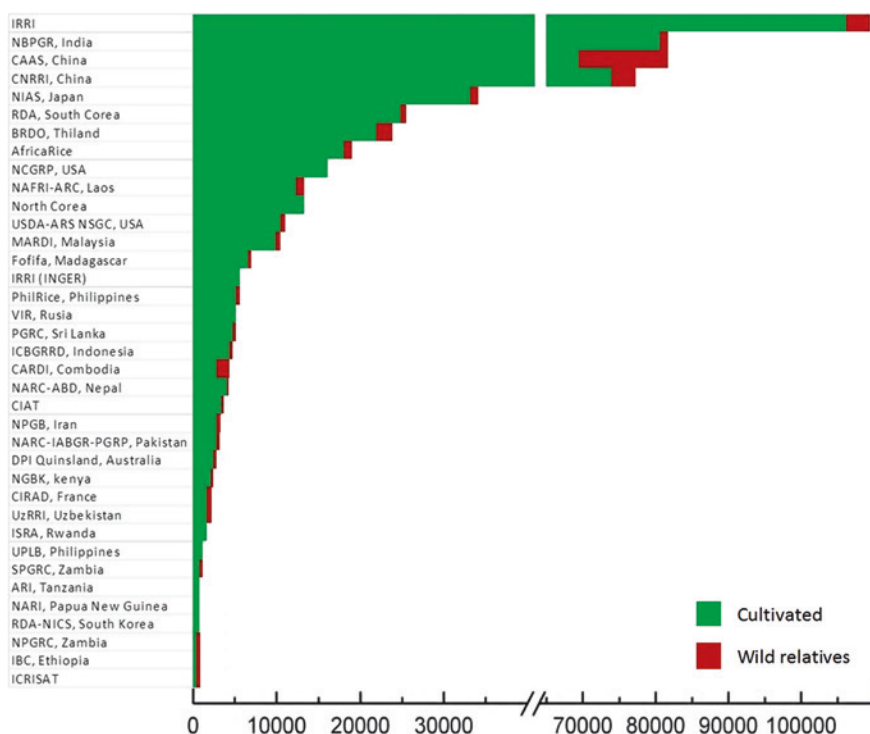


Fig. 2.4 Ex situ conservation of the rice gene pool. Numbers of cultivated or wild rice accessions held at the institutes indicated (as in May 2007). Total number of accessions: 575,029 (After IRRI 2010)

holdings are distributed across a large number of small national collections widely distributed through rice-growing regions of the world.

Accessions of wild rice are conserved *ex situ* in fewer gene banks, presumably because of the difficulties of their conservation and use. The largest collections of wild rice are at CAAS and CNRRI in China and at IRRI, with other significant collections at the Indonesian Center for Rice Research (ICRR), the Biotechnology Research and Development Office (BRDO) in Thailand, NBPGR India, and NIAS Japan.

In the early 2000s, IRRI took the initiative of developing a Global Conservation Strategy for Rice. After a large array of consultations, the strategy document was completed and distributed for review in April 2010 (IRRI 2010). The initiative was motivated by the need for rice scientists to have free access to the entire rice gene pool, including that of wild rice species, so that they could incorporate desirable genes into varieties that are evermore productive and/or tolerant to abiotic and biotic stresses. The objective is to establish an overarching strategy that will ensure the efficient and effective conservation of rice genetic resources globally and that will identify priority collections for support, upgrading, and/or capacity building. The strategy is intended to be an evolving program of assessment, prioritization, and action with respect to global rice genetic resources.

Key strategic targets are ensuring the global gene pool is securely conserved, ensuring the global gene pool can be effectively used and sharing and cross-referencing information to support joint actions and decisions. Recognizing that gene banks differ in mandate, targets and resources, sharing responsibilities emerges as a potentially important tool to improve efficiency and effectiveness (IRRI 2010).

2.3 In Situ Diversity and Genetic Erosion of Wild Rice Gene Pool

Agricultural modernization, the Green Revolution, and more generally human demographic and economic growth, have not only affected the *in situ* diversity of the two cultivated rice species but also that of their wild relatives. The habitats of wild species of *Oryza* have been increasingly suffering from the growth of human activities. No data are available about the recent evolution of the habitats of *O. glaberrima* wild relatives in Africa. We report here only on the case of *O. sativa* wild relatives.

Molecular surveys and screening of germplasm from different *Oryza* species has shown broad interpopulation diversity (Oka 1988; Second 1985). However, detailed inter- and intrapopulation genetic studies of *Oryza* species, other than those closely related to the cultivated rices, are lacking primarily because they are less common, populations are small and widely scattered and formerly were not useful to rice breeders. Here we will focus on the *O. rufipogon* case.

O. rufipogon is comprised, like *O. sativa*, of genetically identifiable subpopulations that show strong geographical and ecological differentiation (Banaticla-Hilario et al. 2013). It has a higher genetic diversity at the molecular level than *O. sativa*.

This contrasts with the variation pattern observed at the phenotypic level, in which *O. sativa* is more diverse than *O. rufipogon* (Morishima 2001). Comparison of the genetic diversity of *O. rufipogon* from nine countries in Asia (China, India, Thailand, Burma, Bangladesh, Cambodia, Indonesia, Malaysia, and Philippines), using RFLP markers (Sun et al. 2000), indicated that China's *O. rufipogon* had the largest genetic diversity which was followed by India. The average gene diversity of South Asian wild rice was higher than the one of Southeast Asia. Chinese *O. rufipogon* also had the highest degree of heterozygosity. *O. rufipogon* had 25 % more polymorphic loci and 40 % more alleles per loci than *O. sativa*.

Natural hybridization between wild and cultivated rice occurs frequently and hybrid derivatives are found abundantly as weed types. Gene flow mainly comes from predominantly inbreeding cultivated races to *O. rufipogon* which exhibit an outcrossing rate ranging from 10 to 60 % (Oka 1988). Nowadays, truly wild populations without introgression of genes from cultivated rice in tropical rice-growing areas are very rarely found.

Following the worldwide effort of collection and ex situ conservation of LVs of *O. sativa*, undertaken after the spread of the improved varieties of the Green Revolution, a large number of accessions of wild relatives of the two cultivated rice species were collected during the 70s and 80s. Unfortunately, the momentum for protection of wild relatives of *O. sativa* did not last very long.

During the last 50 years, the habitats of wild species of *Oryza* have undergone rapid destruction due to the extension of rice-growing areas and/or urban development, resulting in local extinction of the wild species. For instance, in Taiwan, *O. rufipogon* was declared extinct in the wild due to urban development as early as the mid-70s (Kiang et al. 1979). In Thailand, a well-studied heterogeneous population of *O. rufipogon* in the northeast regions, showing genic divergence from other *O. rufipogon* populations of the country, was destroyed by the development of an army camp (Morishima 1986). The great flood of 1988 in Bangladesh destroyed many deepwater rice fields. This resulted in a shortage of rice straw for cattle. Populations of wild rice were consequently decimated as a shortage of forage intensified during the dry season. Along the cattle trading route from Tamil Nadu to Kerala in South India, grazing is extremely heavy; only the underwater parts of wild rices remain in many ponds (Vaughan and Chang 1992). In China, despite its abundant genetic diversity and relatively wide distribution, wild rice populations have declined so rapidly that they were listed as “rare and endangered plants” in the Chinese Red Data Book of Plant Species (Fu and Jin 1992).

While local extinctions due to destruction of habitats are easily recorded, a more insidious threat to rice wild relatives is the slower environmental changes and population fragmentation, leading to changes in populations' genetic structure.

In Thailand, a diachronic (1985–1994) analysis of the wild rice population in the central plain of the country, using isozyme variability at 17 loci, revealed severe decrease in gene diversity. Fragmentation of the population during the study period of 10 years has not only caused loss of genetic variability but has also forced the habitually outbreeding plants to inbreeding, thus accelerating genetic drift. Likewise, signs of introgression of the wild rice by cultivated rice, blurring

the intrinsic nature of wild rice, were detected. This acknowledgment of rapid genetic erosion has led the authors to call for action in the area of in situ conservation (Akimoto et al. 1999).

In China, gene flow from cultivated rice is considered as one of the most important threats that may alter the genetic structure of natural populations of *O. rufipogon* and eventually lead to its genetic erosion. Effective isolation measures are recommended in the regions where in situ conservation projects are carried out. And reintroduction is proposed as a complementary option to in situ conservation of remaining natural populations (Song et al. 2005). More recently, an extensive field investigation, of 201 natural populations or habitats of *O. rufipogon*, suggests that (i) the majority of the natural populations have been extinct, which has led to serious fragmentation of the population system as a whole; (ii) the surviving populations have become small in size and thus fragmented within the population as a result of the loss of subpopulations and (iii) extinction of wild rice germplasm seems closely related to the biodiversity related education of the rural population (Gao et al. 2012). The authors propose a strategy for in situ conservation that includes rules for selecting conservation sites, enhanced biodiversity education, creation of a positive incentive system for local communities and the involvement of local governments and academic institutions.

In India, the Indo-Gangetic plains are endowed with a great diversity of wild rices, still growing in their natural habitats. It is also one of the most intensively farmed zones of the world and is crucial for food security (Thakur and Pandey 2009). Analysis of diversity of 35 wild rice populations collected in 2011 from natural habitats of eastern Uttar Pradesh and Buxar district of Bihar, using 25 SSR markers and 14 phenotypic traits, clearly demarcated the wild rice accessions into two main groups representing *O. rufipogon* and *O. nivara* (Singh et al. 2013a, b). The widespread distribution of the two species in this region indicates that these species are still secure in the wild but there is great pressure on this habitat due to the developmental needs of the growing human population; risks for the loss of these populations include competition with weeds and land clearing for agriculture and developmental activities. Singh et al. (2013a, b) concluded that urgent action is needed for conservation of this gene pool; more extensive exploration, collection, and careful molecular analysis should be undertaken to ensure that this diverse resource remains available to support rice improvement.

In the Mekong Delta, because of new irrigation schemes dedicated to double or triple rice cropping with modern short duration varieties, the area for deepwater and floating rice has declined drastically. This has also affected *O. rufipogon*, which has been a weed in deepwater rice fields, and the potential for gene flow among the two species (Bui Chi Buu, pers. comm.).

Little information is available about the in situ maintenance of wild relatives of *O. sativa*, in other Asian countries. Vaughan and Chang (1992) advocated in situ conservation of wild *Oryza* species and suggested that priority should be given to *O. longistaminata* in Africa and to *O. rufipogon* in Asia as these species are genetically heterogeneous and difficult to conserve ex situ. They proposed a list of high priority sites in different Asian countries where several different *Oryza* species

occur together, or where unusually large stands of *O. rufipogon* are present, and ought to be protected. Likewise, noting that some wild rices were prized as healthy and/or auspicious food, they suggested a further enhancement of productivity of natural stands of wild rice by elimination of competition from other plant species, protection from grazing cattle, or the use of more effective harvesting techniques. A new global survey is needed to update information about the current in situ maintenance of rice wild relatives.

A positive fact somewhat balancing these negative trends is the introduction of genes and alleles from the wild relatives of *O. sativa* into improved rice varieties and the broad dissemination of these varieties. For instance, the IR64 variety cultivated in Asia over millions of hectares and extensively used in breeding programs worldwide bear an *O. rufipogon* introgression fragment representing approximately half of the short arm of rice chromosome 8 (Ballini et al. 2007).

2.4 In Situ Diversity and Genetic Erosion in Cultivated Rice

Crop genetic erosion is referring to a reversal of the trend of increasing diversity after the domestication and dispersal bottlenecks, as a consequence of scientific and formal breeding systems and modern agriculture where a relatively small number of breeders has replaced the multitude of farmers involved in the generation and maintenance of diversity.

Genetic erosion has been given at least three definitions: (i) absolute loss of a crop, variety, or allele (Peroni and Hanazaki 2002), (ii) reduction in richness of the total number of crops, varieties, or alleles (Hammer and Laghetti 2005) and (iii) reduction in evenness of the frequencies of varieties or alleles in a given place (Khlestkina et al. 2004), as it is evaluated by Shannon's index (Maughan et al. 1996) or Nei's gene diversity index (Nei 1973).

The first definition is really incomplete as it does not take into account what replaced the lost diversity. The evaluation of reduction in richness is a better indicator for genetic erosion, as it does recognize the dynamics in the system. However, richness might only poorly reflect increased levels of uniformity in agriculture and the level of richness found depends on the intensity of the investigation. The evenness parameter provides information on the risks of losing alleles or varieties due to skewed distributions of each diversity unit.

Whereas the concept of genetic erosion emerged in the 60s, as early as the beginning of the eleventh century, in some places, the need to intensify rice production in the face of population growth has resulted in the centralized selection of rice varieties to grow and the abandonment of existing varieties. For instance, in 1012, faced with an influx of migrants from the north and a real shortage of arable land, Zhao Heng, the Emperor of China ordered two annual rice crops using a short duration variety imported from Annam (Jeanguyot and Ahmadi 2002). Likewise, in Japan, increasing the application of commercial fertilizers (fishmeal, soybean cakes)

in the late 1800s and chemical fertilizers in the early 1900s led to an early interest in the development of varieties with shorter stems. One of the first such varieties was selected in 1877 and soon replaced several local varieties (Matsuo 1955).

The contemporary trend of replacement of a large number of rice LVs by a small number of MVs goes back to the early years of the twentieth century when national rice research organizations were established in major Asian rice-growing countries, such as China and India. It had its first acceleration in the 1950s with the FAO Asian rice breeding program; some of the products of this program, such as the Mahshuri variety, are still cultivated over millions of hectares. The replacement process reached its momentum with the spread of semidwarf inbred lines developed by the IRRI and of hybrid rice varieties developed in China.

The percentage of the rice-growing area covered by MVs in 1998 was estimated to almost 70 % in Asia and in Latin America. At the same time, the share of improved rice varieties was only 38 % in Africa (Evenson and Gollin 2003). This evolution has contributed to the reduction of diversity in two ways: a foundation bottleneck due to the utilization of a limited number of LVs for the development of new varieties, and a reduced diversity due to directional selection for genes involved in dwarfing and/or response to fertilizers.

While several authors have analyzed the impact of the Green Revolution on rice in terms of areas covered by MVs, yield increase, etc. (e.g., Pinstup-Andersen and Hazell 1985), no direct quantitative assessment of its impact is available in term of genetic erosion at the global level. Furthermore survey methodologies and diversity indicators used in the few studies undertaken at the individual country or at subcountry levels are too heterogeneous for any form of formal meta-analysis. Therefore, we will rely on a small number of case studies to draw a general picture of rice genetic erosion during the last 40 years and the current state of in situ diversity.

2.4.1 Rice In Situ Genetic Diversity in China

China used to possess a remarkably rich biodiversity of *O. sativa*. This richness is illustrated by the large number of rice LVs collected and preserved in the national rice genebanks: since the beginning of the twentieth century, the majority of Chinese rice germplasm has been collected through several survey and collection campaigns. Some 76,646 accessions have been catalogued and 67,444 preserved, including 48,420 LVs, 4335 improved inbred lines and 5584 wild rice accessions (Ying 2000). About 93 % of rice LVs have been collected in a vast region in the south of the Qinling Mountains and Huaihe River, while about 6 % come from areas north of the Huaihe River in eastern China and less than 1 % from northern China (Cao et al. 1995). The LVs included both *indica* and *japonica* accessions and were classified into 50 “varieties” and 962 forms (Yu 1996).

China was also the country which first developed and popularized semidwarf inbred rice varieties in the 1960s and later hybrid rice varieties in the 1970s. In 2008, hybrid rice occupied about 63.2 % of the total rice production area, or 18.6 out of 29.4 Mha. In 2003 and 2004, in the most intensive rice-growing areas, such as the southern provinces of Hunan, Jiangxi and Sichuan, the adoption rates of hybrid rice, reached 75–91 % of the total rice acreage (Li et al. 2009). Moreover, the majority of hybrid combinations are derived from a small number of male-sterile and restorer lines and some of the hybrids have been grown on very large areas for a very long time. In 1984, only 42 hybrid varieties were available. Between 1984 and 2003, 14 hybrid combinations and four inbred lines were each planted on an area larger than 650,000 ha. In 1990, the most popular hybrid, Shanyou 63, was planted on more than 6.2 Mha (Cheng et al. 2007).

However, the average planting area and the share of planting area of large-scale extended varieties has decreased from 9.3 Mha (41.4 %) in 1986–1990 to 7.53 Mha (34.3 %) in 1991–1995, to 3.99 Mha (16.9 %) in 1996–2000 to 1.23 Mha (5.7 %) in 2001–2003. Likewise, the number of varieties with growing areas larger than 75,000 ha increased from 296 in 1986–1990 to 485 in 2001–2003. The main factor contributing to the increase of the number of varieties was hybrid rice. The number of hybrid varieties increased remarkably from 42 to 233 in 18 years, while the number of inbred varieties remained almost unchanged (Yang et al. 2006). Whatever this recent evolution, it is allowed to speculate that the spread of the improved rice varieties (inbred or hybrid) in southern China, home to 93 % of the registered LVs, has certainly provoked major genetic erosion, in terms of absolute diversity, and also of richness and evenness of in situ diversity.

The Yunnan province is hosting a significant share of Chinese rice diversity with more than 6000 LVs registered. This abundant genetic diversity of LVs originated from a combination of socioeconomic (large number of ethnic groups), environmental (altitudes of 400–2406 m) and cropping system (upland and irrigated lowland) diversity. Surveying four villages in two regions of the Yunnan province with the most genetically diverse rice LVs, Sun et al. (2012) did not detect major absolute genetic erosion between 1980 and 2007. Conversely, Zhu et al. (2003) surveying a total of 44 townships, in the framework of developing a conservation strategy through crop diversity management, had noticed the almost disappearance of LVs among the varieties cultivated by farmers. This contradictory information coming out of the two case studies in the same province is very likely due to differences in target ecosystems and cropping systems, upland rice in the first case and lowland rice in the second case.

Thus the available data lead to the conclusion that while rice in situ diversity has been maintained in some marginal areas and cropping systems, the mainstream rice-growing areas and cropping systems have undergone a very drastic reduction of diversity. In order to have a more precise idea of the change in in situ diversity a comparison of genetic diversity of a representative panel of MVs currently grown with one in the representative panel of 48,000 Chinese rice LVs is needed (Gao 2003).

2.5 Rice In Situ Genetic Diversity in South Asia (Bangladesh, India and Nepal)

2.5.1 Bangladesh

Bangladesh is famous for extensive rice biodiversity, allowing rice cultivation over three different cropping seasons (*aus*, *aman*, and *boro*) as well as in specific agro-ecological conditions. It is reported that the IRRI genebank contains more than 8000 traditional rice varieties collected from Bangladesh. Formal rice research there dates back to 1935. Cultivation of MVs really started in the 1950s under an FAO project, and then intensified at the beginning of the 1970s with IR8 developed by IRRI. In 1981, the area grown with MVs rice was about 22 % of the total rice-growing area. Between 1973 and 2005, the Bangladesh Rice Research Institute (BRRI) has released 57 improved rice varieties, while a few additional ones had been released by other institutions (Hossain et al. 2013).

The total number of LVs as well as the area planted with LVs in Bangladesh is declining over time (Hossain et al. 2012). However, several LVs are still popular among farmers/consumers due to their special traits. They are maintained in small areas as special purpose rice (such as *kalizira* for *polao*), for superior grain quality that fetches a high price in the market (such as *Katari bhog*) or for tolerance to extreme environmental stresses (such as *Mota dhan* in the coastal areas). Hossain and Jaim (2009) reported that farmers in Bangladesh still cultivate more than 1000 LVs.

In order to provide precise information on the diffusion of MVs and the disappearance of LVs, a nationwide farm survey was undertaken in 2005, using a multistage random sampling for selection of villages and a purposive sampling of the households. A total of 14,400 farmers distributed in 1800 villages from 600 blocks from the six regions of the country, representative for diversity in farm size, farmer's age, education, etc., were interviewed (Hossain et al. 2013).

The survey found that 515 rice varieties were cultivated during the *aman* (monsoon) season of 2004, 261 varieties in *boro* (dry season) season of 2005 and 295 in the *aus* (pre-monsoon) season of 2005. The top ten varieties for the *aman* season all belonged to improved types, covered 1.1–26.5 % of the total *aman* crop area and accounted for over two-thirds of this area. In *boro* season, the top ten varieties were again improved ones and the top two together covered about 60 % of the rice-growing total area. In *aus* season, eight of the ten top varieties were improved types but their individual share of the total cropping area was much smaller, varying from 2.0 to 9.0 %. Regarding regional variability, in favorable areas with irrigation facilities and homogeneous terrain, only a few varieties occupy the landscape. In diverse ecosystems with large variations in microecology, farmers are growing a much larger number of varieties. The survey also revealed that 572 LVs for the *aman* season and 426 LVs for the *boro* season were extinct (not cultivated any more) or on their way toward extinction (not cultivated over a significant area). The main reason given for dropping these formerly popular

varieties is their low yield, as reported by more than 70 % of the farmers. The other reasons are a longer growing duration, lodging because of heights and weak stems, pest incidence, etc. (Hossain et al. 2013).

Thus, in Bangladesh, rice in situ diversity has undergone both absolute genetic erosion and change in the evenness of utilization of existing diversity to the benefit of the MVs. The fact that almost all MVs are progenies of crosses involving Bangladeshi LVs somewhat balances this skewed evenness. However, an improved offspring contains only a small share of the diversity of its parent landrace as, similar to other places, each Bangladeshi landrace holds a high level of genetic variation, whereas the MVs are monomorphic (Choudhury et al. 2013).

2.5.2 India

India is home to some of the most singular compartments of *O. sativa* rice genetic diversity such as the *aus* and *Basmati* groups, and almost all major rice-growing ecosystems: irrigated (50 % of the rice-growing area and 65 % of production), rainfed lowland (LLE) (32 and 27 %), rainfed upland (ULE) (13.5 and 6 %), and deepwater rice (4.5 and 2 %). The Indian National Bureau of Plant Genetic Resources is maintaining some 80,000 rice accessions (IRRI 2010).

India was also one of the countries that hosted the earliest (1950–54) international effort in developing improved rice varieties. Launched simultaneously in India and Southeast Asian countries by FAO, and based on inter-subspecies crosses (*indica* × *japonica* and the reverse) the project led to varieties such as Mahshuri and ADT-27, which are still grown on millions of hectares. Since then, a total of 946 rice MVs were officially released all over India and as soon as 1980, the area cultivated with MVs was estimated to 18.5 Mha, 47 % of the country rice-growing area (Pinstrup-Andersen and Hazell 1985).

No data about the current state of rice in situ diversity countrywide or even about the current share of MVs countrywide are currently available. However, recent surveys undertaken in northeastern and eastern India (Assam, Orissa, Jharkhand, and West Bengal) on the adoption of MVs, also provide some insight into the state of current in situ diversity in the country.

2.5.2.1 In Orissa

The survey was conducted, in 2008, in 6529 households representing all 30 districts of the state (Hossain et al. 2012). It revealed that farmers were cultivating a large number (723) of varieties, most of them LVs, under rainfed conditions in the rainy season. Comparatively, the number (29) of varieties grown under the irrigated conditions of the dry season was much smaller, and all were MVs. However, even during the wet season, four of the five top varieties, covering about 54 % of the rice-growing area, were of improved type. Varietal diversity was also important

at the household level. The largest number of rice varieties grown by a single farmer was 14. However, about 30 % of the farmers cultivated only one variety while 33 % cultivated two varieties, 21 % cultivated three varieties and 16 % more than three varieties. The existence of a large number of LVs is directly related to the diversity of agroecological conditions in the Orissa state where rice is grown in the pre-monsoon season (mostly direct-seeded in the uplands), in the monsoon season (transplanted in LLEs) and in the summer dry season (mostly in the irrigated lowlands). These three seasons account for 17, 76 and 7 %, respectively, of the total rice area (Hossain et al. 2012).

2.5.2.2 In Jharkhand

The survey was conducted in 2007 in 3219 households representing 20 out of 24 districts of the state (Hossain et al. 2012). It showed wide variations in diversity and concentration of rice varieties grown in the highland, medium land, and lowland ecosystems. A total of 145 varieties were identified and the highest number was found in medium land (71), followed by lowland (55) and highland (19). Among these varieties, 70, 84 and 75 %, respectively, were LVs. In the highlands, a landrace grown by 65 % of farmers covered about 69 % of the rice-growing area. In the medium land, four MVs covered 87 % of the rice-growing areas with almost equal shares, and three LVs covered an additional 8 % of the medium-land areas. Finally, in the lowlands, an improved variety grown by 58 % of farmers covered 55 % of the total rice-growing area. It was followed by three LVs with shares of 3–5 %.

2.5.2.3 In Assam

The survey was carried out in 2008, in 200 households from four villages, representative of the two districts with a high prevalence of submergence stress and a high proportion of rainfed rice area (Pandey et al. 2012). In 2008, the state produced 5.39 Mt of rice on an area of 2.46 Mha, 70 % of the total cultivated areas (www.indiastat.com). It is grown in three seasons: a wet season (65 % of the total rice area) in July to December and in the two dry seasons (12 %) from January to May and November to May (23 %).

The extent of adoption of MVs in terms both of the proportion of households (97 %) and of area (61 %) was fairly high. However, almost all those households were also growing LVs and the average proportion of area dedicated to LVs was 39 %. The highest proportions of MVs were observed in LLEs which are the least prone to drought or flood stress. The total number of MVs was about 15. The number of LVs was not inventoried. Among the MVs, the share of area was 45 and 55 % for old MVs (released before 1990) and new MVs, respectively. One old MV and one new MV covered each 30 and 37 % of the MV grown areas, respectively.

2.5.2.4 In West Bengal

The survey was carried out in 2008 in 300 households from two villages in each of the four representative rainfed districts of the state (Pandey et al. 2012). West Bengal rice production accounted for 16 % of India's 131 Mt production in 2009. Rice-growing areas include irrigated lowlands as well as drought and salinity prone LLEs and uplands. On average, rice is grown on at least 84 % of the cultivated areas during the wet season and on 64 % during the dry season. In 2009, the average yield was 3.9 t/ha, among the highest in the country.

MVs dominate regardless of season: 92 and 100 % of farmers were growing only MVs during the wet and dry seasons respectively. None were growing LVs during the dry season, 7 % were growing both MVs and LVs in the wet season. Strong correlations were observed between the rice cropping season and the generation of MVs grown. Old-generation MVs (released before 1990) are grown mainly during the wet season (77 % of the total MV grown areas), while new-generation MVs dominate during the dry season (99 % of the total MV grown areas). Whereas ICAR statistics have reported the release of some 47 rice varieties for West Bengal since 1960, the survey showed that around 20 MVs were grown during the wet season and only nine MVs during the dry season. Among the MVs, a rather new variety, released in 1994, occupies 43 % of the total MV area of the sample farmers, and an old MV, released before 1990, was grown on 39 % of the area.

These very valuable surveys show highly contrasted situations of rice in situ diversity in India. While in Orissa and Jharkhand, LVs still have an important share of the rice-growing area, it is not anymore the case in Assam and in West Bengal. The data also show a large variability among varieties as regards the share of farmers who are growing them and the area they cover. This uneven utilization of varieties is not directly related to the spread of MVs. Some LVs are also very popular and are grown by a large share of farmers, while some others have very specific usages and are grown by a much smaller number of farmers.

2.5.3 Nepal

In Nepal, rice is grown on 1.5 Mha, from low elevation areas (50 m) to high mountain valleys and mountain slopes (2830 m), the highest altitude of rice-growing locations in the world. Rice is mainly cultivated during the wet monsoon season in LLE and upland ecosystems. It is also grown during the spring season as an irrigated crop. According to national statistics (Singh 2009), from 1961 to 2008, rice production grew at 1.7 % per annum, but yield increased only by 20 kg/year. While in 1981, the area grown with MVs was about 26 % of the total rice-growing area (Pinstrup-Andersen and Hazell 1985), in 2008 this share was of 88 %.

A survey conducted in 2008 in 300 households in the districts with a high prevalence of drought prone LLEs across different regions of the country

(Pandey et al. 2012) revealed that on average, MVs covered 86 % of the total rice area. Important variations existed among sites in terms of both proportion of area covered by MVs, number of farmers growing them, and season: an average of 99 % of farmers and 98 % of the area in flat low elevation sites, 47 % of farmers and 71 % of the area in hill sites. MVs are predominant in lowlands, more limited in unbounded uplands. In all cases, the proportion of farmers growing MVs (91 %) is higher than the proportion of area under MVs (86 %) indicating that farmers also grow some LVs on some portions of their farms. Most of the MVs belonged to older generations (released in the early 1970s and 1980s). It accounted for approximately 60 % of the total MVs area.

The average percentage of farmers growing only LVs was 9 % (1–23 % according to sites) and the average percentage of the area was 14 % (2–29 %). The average percentage of farmers growing MVs and LVs was 26 % (6–43 % according to sites).

These data suggest major evolutions of rice in situ diversity in the country. But it does not necessarily imply absolute genetic erosion. Indeed, a survey of the uptake of three modern rice varieties by farmers in high-altitude villages in the Kaski district of Nepal (Steele et al. 2009) found that although seven LVs had been dropped in favor of the MVs, the allelic diversity of the remaining LVs cultivated over up to 40 % of the rice area, compensates the loss. Using a model, the authors found that the partial replacement of LVs increased genetic diversity if the MVs were adopted on up to 65 % of the area. Only above these levels did overall diversity decline.

2.6 Rice In Situ Genetic Diversity in Southeast Asia (Cambodia, Laos, Thailand, and Vietnam)

In some Southeast Asian countries, farmers are living in relatively homogeneous rice-growing environments, where controlled irrigation and good access to fertilizer inputs are the norm. There, they have realized tremendous production gains, thanks to the introduction of high-yielding rice MVs developed by national and international rice breeding programs. As soon as 1980, the area grown with MVs reached 60 % of the total rice-growing area in Indonesia, 55 % in Malaysia, and 78 % in the Philippines. This is not the case for some other countries. Irrigation covers only 12 % of Cambodia's rice land, 23 % in Laos, and less than 30 % of Thailand. In 1980, the area share grown with MVs in Thailand only reached 9 %.

2.6.1 Cambodia

In Cambodia, rice is grown over more than 2.5 Mha, mainly in LLE ecosystems (84 %). In the mid-70s, while the country was achieving its greatest ever rice crop,

under the effect of the Green Revolution, the Red Revolution dramatically disturbed rice production and the maintenance of the national rice genetic resources with more than 500 accessions. A new rice collect campaign was undertaken in the 20 provinces of the country from 1989 to 1996. It harvested more than 6000 samples. From these samples a total of 2557 distinct LVs accessions were identified and stored in genebanks in Cambodia for short- and medium-term storage and a duplicated set at the IRRI genebank for long-term storage (Smolders 2002). The largest share (88 %) of those LVs was collected in LLE ecosystems, followed by the ULE (10.6 %) and deepwater/floating (1.2 %) ecosystems. Only 0.2 % of samples came from the irrigated/recession ecosystem. A very large phenotypic diversity was observed among those LVs for spikelet and caryopsis color, for aroma, amylose contents—including 8 % glutinous varieties—duration and photoperiod sensitivity.

Thus, rice in situ diversity was still high in Cambodia at the end of the 1990s. According to more recent reports (Ouk and Sakhan 2010), despite the country's ambition to become a “rice basket” and a major exporter of milled rice, almost 80 % of the rice-growing area is still cultivated with LVs. An unusual threat to rice in situ diversity is the emergence of invasive weedy rice, especially in the area with a high prevalence of the wild species *O. rufipogon*.

2.6.2 Laos

In Laos, rice is the single most important crop accounting for more than 80 % of the cropped area. In 1998–1999, the rice harvested area was estimated at 717,000 ha, the LLEs accounting for 67 % of the area and 71 % of the production, and the ULEs for 21 % of the area and 12 % of the production. Dry season irrigated rice only accounted for 12 % of the area and 17 % of the production.

A 5-year systematic collect program of rice varieties implemented between 1995 and 2000 led to the collection of 13,192 accessions of cultivated rice, and 237 accessions of six wild rice species. The number of accessions collected from the northern region mainly cultivating upland varieties was much higher (44.8 % of the total) than in the central (35.1 %) and southern (20.1 %) provinces. Unfortunately, this strikingly high density of Lao rice in situ diversity, with an average of one accession every 54 ha, conceals a rapidly changing environment. MVs are rapidly replacing the LVs, particularly in the favorable LLE environment. While in 1993, less than 10 % of the whole LLE area was grown with improved cultivars, in 2002, they covered more than 50 % of the rainfed area in the central provinces of Khammouane, Saravane, Borikhamxay, Champassak, and Savannakhet and Vientiane. Some farmers no longer grow LVs. In Savannakhet, the area planted to MVs is as high as 80 %. Only MVs are grown in the dry season irrigated environment throughout the country (Appa Rao et al. 2002).

2.6.3 Thailand

Thailand is one of the ten top rice producing countries with 11 Mha and it is one of the three top rice exporters. More than 80 % of the rice-growing area is under rain-fed conditions. Less than 20 % of the area can be irrigated for rice cropping in the dry season. Thailand is home to one of the most famous aromatic rices, Kaw Dawk Mali. The ex situ collection of rice germplasm at the National Rice Genebank, which began in 1937, holds 24,000 entries (Rerkasem and Rerkasem 2002).

While in 1980, the share of MVs grown rice area was of 9 %, it had reached more than 75 % in 1996. However, important regional variability existed on the one hand, and some of the MVs, especially the aromatic ones, are in fact, pure lines extracted from LVs. LVs were still grown over some 20 % of the country's cultivated rice land in 1997 (OAE 1998).

A survey of rice germplasm grown in Thailand's main rice ecosystems (upland, irrigated, deepwater, and acid sulfate soil) was conducted, in 2002, through interviews of 75–80 % of the farmers in villages representative of these ecosystems (Rerkasem and Schaal 2002). There were 14–18 named varieties found to be grown in each village. The average number of varieties grown by a farmer ranged from 1.5 in irrigated lowland villages to three in shifting cultivation upland rice villages. Each village reported the loss of 10–14 named varieties during the last 15–20 years. In villages representative of the irrigated lowland ecosystem, the two top varieties were of MV type. The most popular one was cultivated by 75 % of the farmers and covered 55 % of the land. The second important variety (aromatic glutinous MVs) was grown by 34 % of the farmers on 18 % of the land. The remaining 27 % of the land were cultivated with the 13 other varieties, each grown by only a few farmers. The villages representative of the LLE and upland ecosystems were much more conservative with their rice germplasm. But similar to the irrigated ecosystem, all the LVs were not evenly used.

A common feature of the rice germplasm is the variation within seed lots and the practice of seed selection by individual farmers giving rise to differences between seed lots within the same varieties. Analysis of the genetic structure of 33 subpopulations of the same local rice variety collected from 33 farms in 13 villages in Chiang Mai and Mae Hong Son provinces in northern Thailand, using Microsatellite markers, revealed a high level of intra subpopulations variation despite predominant inbreeding in the crop. It also showed slight but significant genetic differentiation among villages. The data suggested that rice LVs are a dynamic genetic system that responds to evolutionary forces, imposed both by nature and by humans (Pusadeea et al. 2009).

2.6.4 Vietnam

Vietnam is also one of the ten top rice producing countries, with 7.3 Mha of rice-growing area and 35.6 Mt of rice production in 2007, and one of the three top rice exporters. There are three major areas: the southern Mekong River delta (60 % of

the total rice area), with a warm and humid climate throughout the year; the northern Red River delta (32 %) with tropical monsoons and cold winters; and the highlands in the North hosting the upland rice cropping systems (8 %). No precise data are available about the number of Vietnamese LVs rice accessions conserved ex situ, as several independent collections exist: the National Plant Resource Centre maintains over 3000 rice accessions in the National Genebank; the Cuu Long Rice Research Institute has a collection of over 1200 LVs; the Vietnam Agricultural Science Institute maintains some 6500 rice accessions (VAAS 2006). These numbers probably do not reflect the Vietnamese overall wealth of rice genetic diversity.

The utilization of improved rice varieties in the country goes back to 1950 at least, with the development of short duration varieties allowing double rice cropping in the mountain areas of North Vietnam. By the mid-1970s the share of MVs had already reached 35 %. Starting with the release of IR8 both in the northern and southern delta rice-growing areas, a total of 89 IRRI breeding lines have been released as varieties in Vietnam. IRRI varieties now cover 70 % of the rice-growing areas in Vietnam (<http://irri.org/our-work/locations/vietnam>, Jun 28, 2014).

Data about the current state of rice in situ diversity in the country are somewhat contradictory. A survey carried out in 2001, in the Red River delta and in the Mekong River delta showed that the number of LVs, though still remaining considerably high, was much lower than that of MVs. The area planted to rice LVs was also very small, accounting for less than 4 % in irrigated rice lands, up to 21 % in the marginal rainfed environments such as upland, coastal sandy and flood-prone areas, which represent some 2 Mha. According to another study looking at the structural change of rice varieties cultivated in three sites of the Mekong River delta (Nguyen 2005), the general trend showed an increase in the total number of varieties at the community level, mainly due to the increase in the number of MVs. The number of LVs decreased in the areas where it was higher before 1980. The reduction of the number of LVs and the lower evenness of the share in total rice area both contributed to the decrease in the diversity index. It was also noted that most LVs were grown by few households and over small areas. However, although the MVs were used with increased frequency, some LVs were maintained as common varieties with a large distribution. The study also indicated that 100 % of LV seed used by farmers was supplied by informal systems. Finally, a recent effort in collecting rice LVs yielded around 1000 accessions in the Mekong River delta only. After elimination of the duplicates, 812 have been conserved and evaluated by Can Tho University, among which 517 were reintroduced for cultivation and evaluation by farmers under various growth conditions (VAAS 2006).

2.7 Rice In Situ Diversity in West Africa and Madagascar

West Africa is not only home to the African species of cultivated rice *O. glaberrima*, but has also hosted the Asian species of rice *O. sativa* for more than five centuries; as a consequence, the sympatry of the two species has also given birth to a new original diversity.

In the 1970s, fears of the negative effects of the Green Revolution led national and international institutions to undertake collect campaigns in different African countries and in Madagascar. Several thousands of accessions, including wild species were thus collected. Today, the Africa Rice genebank is maintaining some 16,000 accessions including 1500 *O. glaberrima*.

During the last 50 years (1960–2010), a total of 708 rice MVs have been officially released in Africa, among which some 260 have been widely cultivated in one or more countries (Sanni et al. 2013). However, the Green Revolution has not affected rice cropping systems anywhere as intensely as in Asia. In 1998, MVs covered only 38 % of the rice-growing area in Africa (Evenson and Gollin 2003). More recent analyses consider that, to some degree, a rice revolution has already begun in Africa and practices that have proved successful in Asia could also be applied in Africa. But for many reasons, Africa's rice revolution has been, and will continue to be, characterized by a mosaic of successes, situated where the conditions are right for new technologies to take hold (Larson et al. 2010).

Here we will provide insight into rice in situ diversity in Africa through two country case studies and a special focus on *O. glaberrima*.

2.7.1 Rice In Situ Genetic Diversity in Guinea

Guinea is a center of diversification of the cultivated species *O. glaberrima* (Portères 1950), and an important reservoir of rice genetic diversity in West Africa. It has been proposed as an area for the in situ conservation of African rice varieties (Bezançon 1995). Currently, rice is cultivated on an area of 800,000 ha. Slash-and-burn cropping of upland rice accounts for 65 % of the rice-growing area, LLE for 19 % and 'mangrove' rice cultivation for 16 %. For several decades, efforts to disseminate improved rice varieties have been undertaken in the country (Dalton and Guei 2003). This was particularly the case for the NERICA varieties during the last 15 years (Jones et al. 1997).

The organization of rice genetic diversity in the country was analyzed using SSR markers genotyping of 170 accessions collected in farmers' fields in the Maritime Guinea region (Barry et al. 2007a). Similarly to what has been observed in Asia, the organization was tightly linked with the rice-growing ecosystems, with *indica* varieties grown in the lowlands and tropical *japonica* in the uplands. The two major ecotypes of *O. glaberrima* ("floating" and "upright") were also present. Moreover, an original genetic compartment was detected, highlighting the occurrence of *glaberrima* \times *sativa* hybridization. Allelic diversity was found to be comparable to that noted worldwide for *indica* and *japonica* groups of *O. sativa*, but not as large for *O. glaberrima*.

Recent changes in rice in situ diversity was analyzed on the basis of a survey of 1679 farms located in 79 villages of the four regions of the country in 2001 (Barry et al. 2009). Varietal diversity was high, especially in forest Guinea and lower Guinea with 33 known varieties and 21 cultivated varieties per village, on

average. LVs accounted for 72–88 % of the total number of varieties present in each village. The number of varieties per village had increased during the last 5 years (1996–2001) by 10–30 %, according to the region, for the LVs and by 40–80 % for the MVs, particularly the newly promoted NERICA MVs. The evenness index calculated at the village level was generally much lower than one, indicating a high variability in the number of farmers cultivating each of the varieties present in the villages. A very small share of varieties present in the village could be considered as major varieties, used by more than 50 % of farms. There were also considerable differences between and within regions in the number of major varieties. Most of the major varieties belonged to the LV category. Depending on the region, MVs accounted for only 10–30 % of the major varieties in the villages, while NERICA represented only 5 % of the major varieties.

The temporal evolution of rice genetic diversity was further monitored through a diachronic comparison approach using samples collected in six villages in 1982 and in 2003. The names and number of varieties inventoried and the polymorphism of microsatellite markers were used as diversity indicators (Barry et al. 2008). The number of varieties appeared not to be comparable between the two dates, due to differences in the collection methods. The varietal composition had evolved very substantially between the two collection dates. Many long duration varieties present in 1982 had been abandoned and several MVs had been introduced. The mean number of alleles per locus and per accession was significantly higher in accessions collected in 2003. Pairwise comparisons of the mean number of alleles per locus in 1982–2003 homonymous accession pairs indicated higher intra-accession diversity for the 2003 collections (Fig. 2.5). Genetic differentiation, measured with the F_{ST} values, was very high and significant for more than 80 % of these pairs of accessions. The overall genetic differentiation between accessions from the two collection dates was also significant. Furthermore significant changes were observed for allelic composition. However, alleles specific of each collection date had a much lower frequency, compared to alleles common to the two collection dates.

Finally, partitioning rice genetic diversity between farms, varieties, and within-variety diversity were analyzed using the genotype at 10 SSR loci of 1200 individual plants belonging to 45 accessions collected in eight farms (Barry et al. 2007b). It revealed an even share of molecular variance between and within accessions, while the farm effect was almost nil. Local varieties had a multiline genetic structure. The number of multilocus genotypes was proportional to the utilization rate of the variety in the village. The F_{ST} values between different accessions of each variety were significant which indicated low genetic consistency in the variety names. This varietal structure could mainly be explained by the migration phenomenon and the high varietal turnover. Compared to allelic diversity, multilocus genotypic diversity seemed to be the most suitable indicator of the quantitative distribution of diversity at different management scales (accession, farm, and village). The within- and between-farm F_{ST} values were in the same order of magnitude. The within-farm diversity was not farm-specific but quantitatively high, i.e., up to 50 % of the total genotypic diversity of a given village. Given the relative

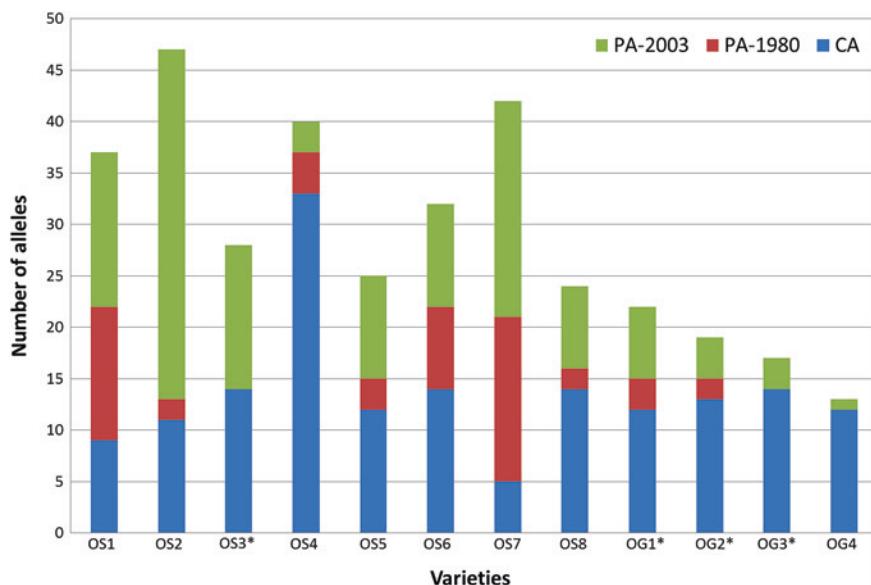


Fig. 2.5 Allelic composition over 10 SSR loci of homonymous rice varieties collected in 1979 and in 2003 in six villages of Maritime Guinea. *OS* *O. sativa* variety; *OG* *O. glaberrima* variety. Variety number followed by an *asterisk* indicate nonsignificant F_{ST} between the two collections dates. CA Allele common to 1979 and 2003; PA private allele. The PA had a frequency of at most 20 %, whereas more than 80 % of CA had a high frequency of over 20 % (After Barry et al. 2008)

importance of the within-variety diversity, the in situ approach stands out as the most effective solution. As farms do not host specific diversity the in situ approach could be implemented by working with a small number of farms.

It was concluded that the rice in situ diversity pattern was typical of the subsistence farming system with a high share of LVs. Over the last 30 years, genetic diversity had been maintained or even enhanced. The recent dissemination of NERICA varieties had not caused any form of genetic erosion. These short-duration varieties were mainly used as a complement to the long-duration LVs and thus enhanced varietal diversity. Given the relative importance of the within-variety diversity, Barry et al. (2007b) advocated for the in situ conservation of rice genetic resources in Guinea.

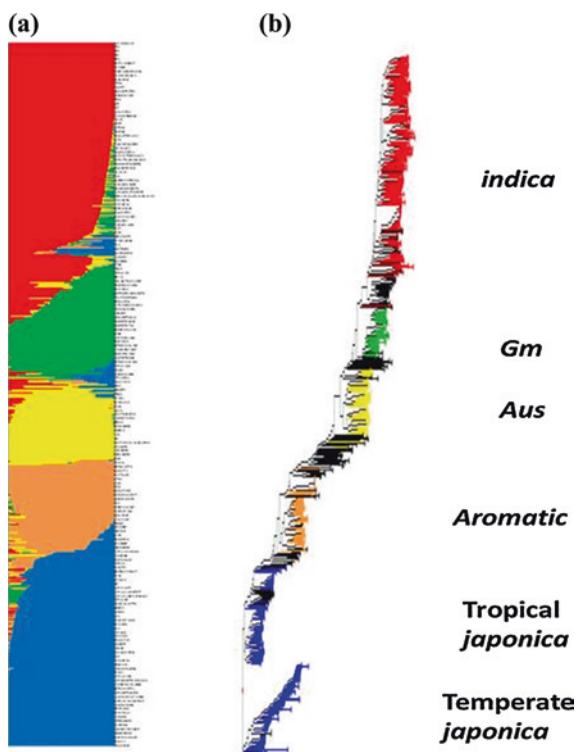
2.7.2 Rice In Situ Genetic Diversity in the Island of Madagascar

Madagascar is producing some 3.6 Mt of rice over 1.3 Mha of irrigated lowlands (20 %), LLEs (59 %), ULE (10 %) and swidden uplands (SUE). The national genebank maintains more than 5000 rice LVs. All major rice genetic

groups are present in the country including the aromatic groups. The highlands of Madagascar have been identified as a key site of rice genetic diversity. Using morphophysiological and isozymic data, Ahmadi et al. (1991) have identified, in addition to the well-known *indica* and *japonica* subspecies of *O. sativa*, an atypical group specific to Madagascar and preferentially present in the central highlands of the country. Comparing diversity patterns in 1105 SNP loci—including LD, introgression patterns and haplotypes—between a panel of 147 Malagasy rice varieties, and a reference panel of 370 Asian rice, we recently confirmed the existence of the Malagasy-specific group (*Gm*). Pattern of diversity of *Gm* group positioned it half-way from *indica* and *aus* groups (Fig. 2.6).

The *Gm* group most probably arose from founder effect coming from intermediary forms of rice originating from either India or Sri Lanka that did not belong to the five major *O. sativa* groups. It then underwent human selection for cold tolerance. Madagascar also hosted cold tolerant tropical *japonica* varieties, with very long grain. Migration bottleneck has resulted in 30–40 % reduction of diversity among the *indica* and *japonica* groups in Madagascar. The Malagasy panel also showed much fewer *indica* × *japonica* recombinations compared to the Asian panel, suggesting that the two groups had undergone much less recombinations when migration to the Island occurred (Ahmadi et al. 2013).

Fig. 2.6 Structuring of rice genetic diversity in Madagascar. **a** Population structure in the Asian (373 accessions) and Malagasy (147 accessions) panels estimated from 1105 genome-wide SNPs. **b** Distance-based neighbor-joining tree of the same panels. *Gm* group specific to Madagascar



To define conservation strategies, a multidisciplinary analysis was performed focusing on rice genetic diversity and factors shaping its distribution in the Vakinankaratra region of Madagascar. Individual and collective surveys, and collection and characterization of samples of cultivated rice varieties in 1050 farms located in 32 villages were realized (Radanielina et al. 2013a). A total of 349 rice accessions were collected, 306 grown in the lowland ecosystem and 43 in the upland ecosystem. Among these accessions, several collected in different villages had the same name. The 306 lowland accessions comprised 149 distinct names and the 43 upland accessions, 19 distinct names. Among the lowland accessions, 77 % were of LV type, while all upland accessions were of MV type. The proportion of MVs was higher in low altitude villages. The proportion of farmers using MVs was 48 % in villages below 1250 m altitude, 18 in villages between 1250 and 1500 m, 11 % between 1500–1750 m, and only 6 % above 1750 m.

The average numbers of rice varieties used per village (10.9) and per farm (2.2) were comparable with other traditional agrosystems, nevertheless great regional variability was observed. The determinants of this variability were the altitude, the village production system, the type of rice cultivation system, and the farm economic wealth. An important disparity in the frequency of the use of varieties was observed with large proportions of “minor” varieties used by less than 10 % of farms (Fig. 2.7).

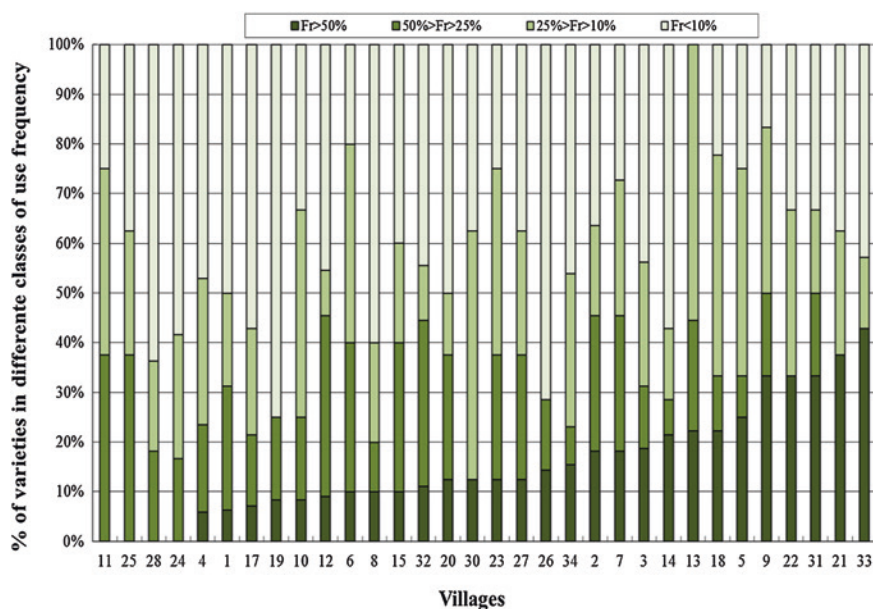


Fig. 2.7 Relative importance of four categories of varieties according to the proportion of farms (Fr) that use them, in 33 villages of Vakinankaratra region of Madagascar. The number of varieties per village ranged from 6 to 19 with an average of 10.9 (After Radanielina et al. 2013b)

Partitioning of the molecular variance between intervals of altitude, villages and farms revealed that, within-village variance represented more than 75 % of the total, and within-farm variance, 70 % of within-village variance. Genetic diversity at the individual field level, or within-variety diversity, was also high in fields cropped with LVs. However, the within-variety diversity at the level of an individual farm represented a rather small fraction of the total diversity of the variety estimated by sampling several villages (Radanielina 2013a).

It was concluded that, given the hierarchical distribution of molecular variance, a small number of samples per scale (altitude interval, village and farm) could allow to capture most of the genetic diversity observed. However, within-variety diversity was also important making ex situ conservation strategies impractical and costly.

2.7.3 *In Situ Diversity of the African Cultivated Rice Species O. Glaberrima*

O. glaberrima was the only cultivated rice in West Africa until the fifteenth century. No direct statistics regarding the current share of rice-growing areas or the number of *O. glaberrima* varieties still cultivated are available. A rough estimate of the minimum number of such varieties in the mid-1970s is provided by the number of *O. glaberrima* accessions conserved in international genebanks: some 2000, probably with several duplicates.

Recent germplasm collection campaigns conducted in different West African countries inventoried the presence of significant numbers of *O. glaberrima* accessions. In Niger, the germplasm collection conducted in 2008 in 51 villages covering the diversity of rice-growing ecosystems of the country yielded 241 non-redundant accessions, among which 25 % belonged to *O. glaberrima* species (Sow 2011). In Burkina Faso, a survey covering almost all rice-growing districts in the country led to the identification of 320 LVs accessions, among which 15 % belonged to *O. glaberrima* species (Kam 2011). In Guinea, our germplasm collection conducted in 2011, in 35 villages distributed over three natural regions of the country out of four, yielded 496 accessions, among which 19 % belonged to *O. glaberrima*. A similar collection campaign conducted in the same villages of Guinea in 1980 had yielded 250 accessions, among which 23 % belonged to *O. glaberrima* (our unpublished data).

However, our recent (2012 and 2013) detailed, village-level analyses of *O. glaberrima* in situ diversity in three West African countries (Burkina Faso, Guinea and Senegal), based on a diachronic approach, did not confirm the reassuring pictures drawn by those large-scale collection campaigns.

In the Cascades region of Burkina Faso, a detailed survey at the level of three villages, cropping rice mainly in the LLE ecosystem, led to an inventory of more than 20 known *O. glaberrima* varieties, only three of which were still cultivated. In each village, less than 10 % of the farmers were growing *O. glaberrima* varieties on less than 50 % of their rice-growing area.

In Guinea, the situation was more contrasted. The survey was conducted in three villages representative of the LLE and ULE and SUE rice cultivation system of Maritime Guinea. A total of 22, 19 and 24 varieties were inventoried in the LLE, ULE and SUE village, respectively. The LLE village had only *O. sativa* varieties while the ULE village had five *O. glaberrima* varieties and the SUE village 10 *O. glaberrima* varieties. Compared to the inventory of rice varieties collected in the same village between 1979 and 1982, the LLE village had lost its unique *O. glaberrima* varieties but had gained 13 *O. sativa* varieties. The ULE village had lost five *O. glaberrima* varieties but had gained eight *O. sativa* varieties. In the SUE village, while the *O. glaberrima* varieties had been present for generations, all *O. sativa* varieties had been introduced progressively since 1980. The LLE village had two major varieties (cultivated by more than 50 % of the farmers), both *O. sativa* LVs. The ULE and SUE village had only one major variety, respectively, an *O. sativa* LV and an *O. glaberrima* LV. In general, *O. glaberrima* was perceived as the most “*economical rice*” because of its higher yield in the most unfertile soils and its excellent swelling after cooking. It was also considered as the rice of the poorest, because of its poor grain appearance.

In Senegal, a free-listing survey conducted in 12 villages of the Casamance region led to an inventory of 281 known rice varieties among which 205 were still cultivated. And among these last accessions, only four belonged to the *O. glaberrima* species. The number of varieties present in each village varied from 12 to 44 and the number of varieties per farm from three to six. Comparatively, a collection campaign conducted in the same village in 1975 had yielded some 60 *O. glaberrima* accessions.

The contrasted pictures drawn by the large-scale collection campaigns and the more detailed survey at the individual village level is probably due to the fact that the collection campaigns were specifically oriented toward *O. glaberrima* varieties and did not evaluate other parameters like the proportion of farmers growing *O. glaberrima* or the area grown with *O. glaberrima* varieties. Our village-level survey suggests that even in the most remote and marginal areas the use of *O. glaberrima* varieties is declining sharply. The most optimistic estimates of the current share of area cultivated with *O. glaberrima* varieties in Africa would be less than 0.1 %.

2.8 Conclusions

The report on the process of “development of the global conservation strategy for rice” (IRRI 2010) indicates the existence of more than 500,000 accessions of rice genetic resources conserved in international and national genebanks around the world. A very large proportion of these accessions were collected during the 1970s in order to protect local LVs against one of the drawbacks of the Green Revolution leading to the rapid replacement of the multitude of LVs by a small number of MVs, particularly in the favorable irrigated rice ecosystems of Asia.

Whereas reports on the impact of the Green Revolution, inventorying areas cropped with MVs, indirectly provide some insight into the evolution of rice in situ genetic diversity, no direct quantitative estimate of the global genetic erosion is available, whatever the term of genetic erosion is considered.

The most important feature of rice in situ diversity emerging from our case studies is the diversity of situations. Almost all aggregated data suggest massive absolute genetic erosion and a reduced evenness in the utilization of the existing genetic diversity, particularly in irrigated ecosystems. In this relatively homogeneous rice-growing environment, the absence of major abiotic stresses, the controlled irrigation and the good access to fertilizer inputs has facilitated the deployment of a small number of MVs with large adaptability, nicknamed mega-varieties, over several million hectares each. Detailed surveys indicate that in Asia the pace of replacement of LVs by MVs was smoother in rainfed rice ecosystems compared to the irrigated ecosystem. This lesser penetration of MVs in the rainfed lowland and upland ecosystems is due to their much poorer performances under the adverse and spatiotemporally variable abiotic constraints (drought, submergence, salinity, iron toxicity, ...) and the often limited access farmers have to fertilizer and other resources in these ecosystems. In Africa, while the extinction of *O. glaberrima* is accelerating, no significant genetic erosion is observed among the *O. sativa* LV in the rainfed ecosystems. So far, in both Asia and Africa, the spread of MVs in the rainfed ecosystems is not synonymous to absolute genetic erosion as they do not completely replace the LVs. The partial replacement of LVs by MVs may even lead to increased genetic diversity.

However, the relative sparseness of rice in situ diversity in the rainfed ecosystems may not last very long. The prospects are gloomy. Indeed, yield increase through the utilization of improved varieties in all rice-growing ecosystems constitutes the central pillar in the strategy of the international rice research community for taking up the challenge of the increasing demand for rice while the rice growing area is not extensible. The strategy relies on the development of a new generation of MVs endowed with multiple tolerances to abiotic stresses encountered in the rainfed ecosystems. The new submergence tolerant varieties endowed with the submergence tolerance gene *Sub1* provide a flavor of this evolution. A small number (4–5) of these varieties are spreading at an unprecedented pace in India, Bangladesh and Nepal, and are expected to cover more than 5 Mha by 2014 in these three countries (Singh et al. 2013a, b). Similar breakthroughs are expected for salinity and drought tolerance in the near future, in both Asia and Africa. As the rainfed lowland ecosystems coincide with major centers of rice genetic diversity, especially in west and south Asia, where genetic diversity is much higher and the genetic structure is more complex (all genetic groups are encountered there, together with many unclassifiable varieties), the spread of the new generation of MVs will almost certainly lead to sharp genetic erosion, similar to the one observed in the irrigated ecosystem during the Green Revolution.

Since the preoccupation of increasing rice productivity will almost certainly prevail over the maintenance of rice in situ diversity, new options need to be considered. One of these options is the establishment of protected areas in a small

number of sites where representatives of different rice genetic groups are sympatric of their wild relatives. It assumes incentive mechanisms for rice farmers in the area. It also assumes the revival of the momentum for preservation of in situ genetic diversity among the scientific community which has declined sharply during the last decade. Another complementary and promising direction is the valorization of genetic diversity in the framework of the emerging concept of *ecological intensification* (Griffon 2007). It assumes a more detailed understanding of biological interactions involved in improving the performances (primary production and its stability) of deployment of genetic diversity at the landscape level (varietal mosaic) and/or at the individual plot level [varietal mixture or monospecific stands endowed with a functional diversity (Kiær et al. 2009)] to help select the best possible complementary components. Which traits are to be diversified, and how to go about it without adversely impacting the homogeneity desirable for other traits? Similarly, the concept of *evolutionary plant breeding* has emerged recently. It envisages the deployment of varietal stands that are capable of adapting to changes in environmental conditions (Döring et al. 2011). Given the rapid development of precision and high throughput breeding methods, on the one hand, and the spreading of information sharing tools, on the other hand, it should be possible to move in a near future from the Green Revolution model of widely deploying a small number of improved varieties toward the new model of *ecological intensification* or *evergreen revolution* with a larger (and more diverse) number of improved varieties and a more precisely targeted deployment.

Genetic erosion is affecting not only the cultivated rice species *O. sativa* and *O. glaberrima*, but also their wild relatives. In situ conservation of these species is all the more necessary as ex situ conservation is very difficult. This indispensable conservation requires more awareness about their importance and the establishment of protected areas.

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Genetic Diversity and Erosion in Plants

Case Histories

Ahuja, M.R.; Jain, S.M. (Eds.)

2016, VIII, 438 p. 72 illus., 11 illus. in color., Hardcover

ISBN: 978-3-319-25953-6