

Diversity in the *Oryza* genus

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The pan-tropical wild relatives of rice grow in a wide variety of habitats: forests, savanna, mountainsides, rivers and lakes. The completion of the sequencing of the rice nuclear and cytoplasmic genomes affords an opportunity to widen our understanding of the genomes of the genus *Oryza*. Research on the *Oryza* genus has begun to help to answer questions related to domestication, speciation, polyploidy and ecological adaptation that cannot be answered by studying rice alone. The wild relatives of rice have furnished genes for the hybrid rice revolution, and other genes from *Oryza* species with major impact on rice yields and sustainable rice production are likely to be found. Care is needed, however, when using wild relatives of rice in experiments and in interpreting the results of these experiments. Careful checking of species identity, maintenance of herbarium specimens and recording of genebank accession numbers of material used in experiments should be standard procedure when studying wild relatives of rice.

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Abbreviations

QTL quantitative trait loci
RAPD random amplified polymorphic DNA
RFLP restriction fragment length polymorphism

Introduction

The genus *Oryza* is small, including only about 23 species, but is remarkable in the diverse ecological adaptations of its species (Table 1). The *Oryza* genus has given rise to rice (*Oryza sativa* L.), a major source of nutrition for about two-thirds of mankind. Rice has been grown, perhaps uniquely, in sustainable high-output agroecosystems for thousands of years. In relation to genera containing other cereals, *Oryza* occupies a distinct phylogenetic position in a separate subfamily, the Ehrhartoideae [1].

The genus *Oryza* was named by Linnaeus in 1753. The haploid chromosome number of rice was determined by Kuwada in 1910, 46 years before the correct chromosome number of humans was known. It was not until the 1960s,

however, that the characters that define the *Oryza* genus were clarified [2,3]. The principle morphological characteristics of the genus include rudimentary sterile lemmas, bisexual spikelets, and narrow, linear, herbaceous leaves with scabrous margins.

The basic nomenclature of *Oryza* species has changed little since the 1960s (for review see [4•]). Tateoka [5] analyzed species across the whole genus on the basis of studies carried out in the world's main herbaria and in the field in Asia and Africa. His work clarified the basic groups of species within the genus, and he called these groups species complexes (Table 1). Since the 1960s, four new *Oryza* species have been described, *O. meridionalis*, *O. rhizomatis*, *O. indandamanica* and *O. neocaledonica*. These are all closely related to previously known species (Table 1).

Germplasm collection of wild *Oryza* species was initiated in the late 1950s (as compiled in [6•]). In the early 1970s, international efforts to collect landrace rice germplasm began in response to the spread of green revolution varieties [7]. Subsequently, these efforts broadened to collect more widely from the *Oryza* gene pool [8]. In this paper, we review and discuss issues related to wild *Oryza* genetic resources. We also highlight particular *Oryza* species that reveal the current focus of research involving wild relatives of rice from conservation, phylogenetic and breeding perspectives.

Issues

The domestication syndrome and its degeneration in the *O. sativa* complex (AA genome)

In AA genome *Oryza* species, it appears that natural selection and artificial selection (i.e. selection by humans) have different genetic consequences. Asian cultivated rice evolved from the wild species *O. rufipogon sensu lato* (an AA genome wild relative of rice that includes both annual and perennial ecotypes). The adaptation of *O. rufipogon*, particularly to different hydrological regimes, has resulted in distinct annual and perennial ecotypes. The genetic factors that are associated with these ecotypes are not clustered on chromosomes [9•]. However, the domestication of rice and the differentiation of the main varietal groups of *O. sativa*, *indica* and *japonica*, are associated with clustered genetic factors [9•,10]. It appears that the multi-factorial linkage of domestication traits is a common feature of cereals. Not all grasses have the same propensity for domestication, however, as is apparent from the difficulty of domesticating *Zizania* (North American wild rice), a close relative of *Oryza* [11]. A consequence of the lack of clustering of genetic factors that are associated with natural ecotypic differentiation within the AA genome of wild rice

Table 1

Oryza species: their chromosome number, DNA content, genome group and usual habitat.

Section	Complex	Species	Chromosome number (DNA content [pg/2C]) [*]	Genome group	Usual habitat
Oryza					
Oryza sativa complex					
		<i>Oryza sativa</i> L.	24 (0.91–0.93)	AA	Upland to deepwater; open
		<i>O. rufipogon sensu lato</i> [†] (syn: <i>O. nivara</i> for the annual form <i>O. rufipogon sensu stricto</i> for the perennial form)	24 (0.95)	AA	(Annual) Seasonally dry; open (Perennial) Seasonally deepwater and wet year round; open
		<i>O. glaberrima</i> Steud.	24 (0.87)	AA	Upland to deepwater; open
		<i>O. barthii</i> A. Chev.	24	AA	Seasonally dry; open
		<i>O. longistaminata</i> Chev. et Roehr.	24 (0.81)	AA	Seasonally dry to deepwater; open
		<i>O. meridionalis</i> Ng	24 (1.02)	AA	Seasonally dry; open
		<i>O. glumaepatula</i> Steud. [‡]	24 (0.99)	AA	Inundated areas that become seasonally dry; open
O. officinalis complex					
		<i>O. officinalis</i> Wall ex Watt	24 (1.45)	CC	Seasonally dry; open
		<i>O. minuta</i> JS Presl. ex CB Presl.	48 (2.33)	BBCC	Stream sides; semi shade
		<i>O. rhizomatis</i> Vaughan	24	CC	Seasonally dry; open
		<i>O. eichingeri</i> Peter [§]	24 (1.47)	CC	Stream sides, forest floor; semi shade
		<i>O. malapuzhaensis</i> Krishnaswamy and Chandrasakaran	48	BBCC	Seasonally dry forest pools; shade
		<i>O. punctata</i> Kotschy ex Steud.	24 (1.11), 48	BB, BBCC	(Diploid) seasonally dry; open (Tetraploid) forest floor; semi shade
		<i>O. latifolia</i> Desv. [#]	48 (2.32)	CCDD	Seasonally dry; open
		<i>O. alta</i> Swallen	48	CCDD	Seasonally inundated; open
		<i>O. grandiglumis</i> (Doell.) Prod.	48 (1.99)	CCDD	Seasonally inundated; open
		<i>O. australiensis</i> Domin	24 (1.96)	EE [¥]	Seasonally dry; open
Ridleyanae Tateoka					
		<i>O. schlechteri</i> Pilger	48	Unknown**	River banks; open
O. ridleyi complex					
		<i>O. ridleyi</i> Hook.	48 (1.31–1.93)	HHJJ	Seasonally inundated forest floor; shade
		<i>O. longiglumis</i> Jansen	48	HHJJ	Seasonally inundated forest floor; shade
Granulata Roschev.					
O. granulata complex[¶]					
		<i>O. granulata</i> Nees et Arn ex Watt	24	GG	Forest floor; shade
		<i>O. meyeriana</i> (Zoll. et Mor. ex Steud.) Baill.	24	GG	Forest floor; shade
Brachyantha B.R. Lu					
		<i>O. brachyantha</i> Chev. Et Roehr.	24 (0.72)	FF	Rock pools; open

^{*}Data for diploid species from [71] and tetraploid species from [72]. [†]Many workers have considered that the annual and perennial wild relatives of *O. sativa* should be considered separate species. However, crop complexes consisting of perennial and annual wild relatives together with the cultigen have generally been given sub-specific ranking [11]. Research results suggest that for rice and its relatives, the evolution of annual forms from perennial forms is a local phenomenon, morphologically intermediate types are abundant and no major crossing barriers exist between rice and its close relatives [12]. [‡]We refer to the Latin American AA genome as *O. glumaepatula* because this name is widely used in the literature despite the fact that the taxonomy and nomenclature of this species is in a state of flux. No key characters have been found to distinguish this species from perennial *O. rufipogon* [52]. [§]There have recently been several reports of tetraploid *O. eichingeri*. However, all correctly identified germplasm of *O. eichingeri* that has had chromosome numbers checked by collectors has been diploid ([73]; DA Vaughan unpublished data). [#]A diploid population of *O. latifolia* from Paraguay has been reported but attempts to confirm this have failed. This report is thus discounted. [¶]Two other species have recently been named within this complex: *Oryza indandamanica* Ellis is restricted to Rutland Island, the Andamans, India, whereas *Oryza neocaledonica* Morat is from the Pouembout region of New Caledonia. The former is a diminutive variant of *O. granulata* and the latter was distinguished primarily on the basis of microscopic epidermal characters. Both species probably warrant sub-specific status only, but further studies of these two taxa are needed. [¥]Recently, it has been suggested that the EE genome is the same as the DD genome [24]. However, this has been shown not to be the case [21*,39]. ^{**}It has been suggested on the basis of molecular studies of part of the genome that *O. schlechteri* has the HHKK genome [24]. However, recent data indicate that this may not be correct [39]. Here, *O. schlechteri* is tentatively placed in section Ridleyanae. Further information is necessary to determine the sectional status of this species.

is that these genotypes have a high level of genetic diversity even at a local level [12].

Weedy rice is an increasing problem, particularly in areas where rice is sown by broadcasting [13]. Weedy rice has

spikelets that shatter very easily, leaving a seed bank in the soil that infests subsequent rice crops. It appears that weedy rice commonly evolves through the degeneration of domesticated rice, as weedy types of rice can occur where wild rice is not present [14]. The degeneration of

traits associated with domestication involves clusters of genes or quantitative trait loci (QTL) [15^{*}]. The clustering of the genes/QTL that are associated with weedy rice traits helps to explain the emergence of weedy rice within a few seasons and reflects aspects of the domestication syndrome in reverse.

Speciation associated with polyploidy in the *Oryza officinalis* complex

Nine of the 23 species of *Oryza* are allotetraploid (Table 1). The CC genome is one of the genomes for six of these allotetraploid species. This genome is considered to be closest to the AA genome, the genome of the two cultivated rice species [16–18]. However, the AA genome is only known in diploid species. Among the CC genome tetraploid species, polyploid events leading to stable species have occurred at least four times. On three occasions these events have resulted in BBCC genome species and probably on one occasion the CCDD genome species (see below).

Among the BBCC tetraploid species *O. minuta* and *O. malampuzhaensis* have cytoplasm from the diploid BB genome species *O. punctata*. The tetraploid form of *O. punctata* (BBCC) has cytoplasm from a CC genome species [19,20]. On the basis of distinct morphology [21^{*}], current distribution [22] and molecular analyses [23^{*}], it seems logical to conclude that *O. minuta* and *O. malampuzhaensis* arose from different polyploid events.

The CCDD genome species of Latin America, *O. latifolia*, *O. grandiglumis* and *O. alta*, have generated much research interest because no diploid DD genome species is known. Consequently, researchers have tried to determine whether the DD genome is a modification of a genome in a currently known diploid species. Among the most frequently proposed candidates for the origin of the DD genome are the CC genome [17] and the EE genome [24]. However, current data support the original cytological observations that suggest that the DD genome is distinct [21^{*}]. The DD genome originated either in an extinct species or in an extant one that has yet to be discovered. The diploid DD genome species may be undiscovered because specific germplasm collecting for *Oryza* species has yet to be undertaken in large parts of Latin America, including coastal Ecuador and Venezuela.

The CCDD genome species of Latin America are very closely related and appear to have diversified in relation to different ecological conditions. The key characteristics that distinguish these species are not clear. For example, a population in the Amazon appears to be a mixture of *O. grandiglumis* and *O. alta* [6^{*}]. Such field observations suggest that the CCDD genome species are in fact one complex species with different ecotypes, and this hypothesis is supported by molecular and cross-compatibility data [25,26].

Allotetraploid species that have the CC genome do not always have CC-genome components that might be expected from studies of diploid CC-genome species. For example, some CC-genome genes do not appear in CCDD genome species [27], and some repetitive DNA probes that are specific for the CC genome and that are detected in the diploid species *O. officinalis* are not detected in the BBCC and CCDD species [28]. The CC and BB genomes (but not the AA genome) have been repeatedly involved in polyploid events, leading to widely distributed species. Why this is so and the genetic consequences of such polyploid events in *Oryza* require further investigation.

Population genetic structure

Population studies have focused primarily on the close relatives of Asian rice, which have the AA genome. An impressive amount of information has now been assembled on the population genetic structure of these species in selected regions (for review see [29]). For AA genome species, experiments are biased towards accessions that produce seeds when conserved *ex situ*. In several regions in Australasia where there is little annual fluctuation in water level, such as northern Sumatra and northern Papua New Guinea, vast stands of *O. rufipogon* with strong perenniality produce few seeds. Similarly in Africa, many populations of rhizomatous *O. longistamminata* produce few seeds. When these African populations are conserved *ex situ*, they generally need to be maintained in a vegetative state.

Across much of mainland Asia, common *O. rufipogon sensu lato* and cultivated rice either are or were sympatric, and gene flow between them is possible. Thus, the results of studies using wild rice must be interpreted carefully as the wild populations may contain genes from the cultigen [30]. Truly wild *O. rufipogon* occurring in habitats not shaped by man is probably rare in mainland Asia. Analyses of *O. rufipogon* using restriction fragment length polymorphisms (RFLPs) and random amplified polymorphic DNAs (RAPDs) have shown that Chinese populations of *O. rufipogon* have a wider genetic diversity than those from other regions [31,32^{*}]. It has been suggested that gene flow from cultivated rice to natural populations of wild perennial rice is a factor that may explain the high genetic diversity of Chinese *O. rufipogon* populations [31]. True wild rice, growing far from rice cultivation, may be found in parts of Australia, Indonesia, South America and Papua New Guinea.

Recently, more information has become available on the population structure of a broad array of *Oryza* species. *O. officinalis* (CC genome) and *O. granulata* (GG genome) have a high level of genetic differentiation between populations [33,34,35^{*},36]. *O. officinalis* appears to have an intermediate level of intra-population diversity, however, with outcrossing estimated at a surprisingly high level of 33% [35^{*}]. Analysis of the balance between vegetative and sexual (seed) reproduction in *O. rufipogon*

(AA genome) has revealed the importance of local disturbance and soil moisture in the genetic make up of populations [37*]. The genetic and ecological information gradually being accumulated on a range of ecotypes and species in the genus *Oryza* can help to determine the location and numbers and sizes of population for appropriate *in situ* and *ex situ* conservation of these species.

Molecular markers, taxonomy and misidentified germplasm

Molecular methods have been proposed as tools for identifying *Oryza* genomes (e.g. dot blot and genome-specific ribosomal DNA [rDNA] probes [38], and restriction sites of PCR-amplified alcohol dehydrogenase [*Adh*] genes [39]) and for validating the identification of wild *Oryza* species (e.g. RAPDs [40]). However, the results obtained using molecular markers do not always concur with those generated by other methods, such as assessment of morphological characters [41]. The foundations of basic nomenclature rely on observable differences among taxa (which allow the construction of taxonomic keys) and the principle of priority, the historic sequence of valid names determines which name is correct. Thus, there exists an International Code for Botanical Nomenclature (ICBN). In addition, although molecular markers may be a useful adjunct for identification, they cannot always be used and are far from inexpensive in terms of equipment, chemicals and personnel costs.

The scientific literature reveals various difficulties associated with using wild *Oryza* species, particularly regarding identification. During an experiment, it may be clear that germplasm is misidentified whereas in other cases misidentification may be less obvious. For species that can be readily identified on the basis of their morphology, this should not pose a problem. However, morphological distinction among species that are cross compatible is often not clear. This is the case, for example, among Asian, Australian and Latin American AA genome species and can adversely affect the interpretation of experimental results. Using a RAPD analysis, Martin *et al.* [40] reported that 16 out of the 93 AA genome accessions analyzed had an identity that appeared to be different from that provided by the genebank. Despite bagging panicles, it is impossible to rule out hybridization among cross-compatible germplasm during regeneration in a genebank. This has important implications when choosing germplasm for use in comparative studies. Experimental documentation should always include (seed and herbarium) voucher specimens of the wild *Oryza* germplasm used in published experiments. Careful genetic monitoring and identification of germplasm in genebanks by trained staff is important, particularly as the number of regeneration cycles increases.

Incongruous results

There have been attempts to explain evolution in the genus *Oryza* on the basis of the analysis of different

classes of major DNA sequences [42,43]. Sometimes the results of these analyses agree with what might be expected from other branches of biosystematics. Other times, however, the results are incongruous. Phylogenetic interpretation of the transposable element group *Tourist* in *Oryza* provides two examples. Among the *Tourist* elements, the *Tourist-olo9* (*O. longistamminata*-9) class has only been found in the AA (*O. sativa* complex) and FF (*O. brachyantha*) genomes of *Oryza*, and this has been interpreted to suggest that these two genomes are closely related [44]. However, many taxonomic and other molecular studies suggest otherwise [4*,45,46]. *O. brachyantha* is a distinct *Oryza* species within its own section that seems to be closely related to the genus *Leersia*.

Analysis of the *Tourist* element in the 5'-flanking region of the *CatA* (Catalase A) orthologue gave rise to the suggestion that the AA genome species diverged from the ancestor of *O. longistamminata* (AA genome) before the divergence of the ancestors of the other *Oryza* genomes [47]. This interpretation fits the data from the analysis of the *Tourist* element but is contrary to all previous interpretations of *Oryza* evolution.

These examples show that the phylogenetic interpretation of the results from analyses of parts of the genome must be interpreted in the light of all other data. We do not yet understand the array of factors that influences rates of evolutionary change (convergence and divergence) in different parts of the genome, and there does not seem to be a single 'molecular clock' with which to gauge the rate of evolution [48]. Particular parts of the genome may be evolving at different rates in closely related species, as suggested for the rDNA spacer in *Oryza* [27].

Species-focused research

The wild relatives of rice were initially used in breeding because of the need for new traits in the cultivated rice gene pool [49]. However, the ability to introduce QTL from wild *Oryza* germplasm in wide crosses that could potentially improve quantitative traits, such as yield [50], and the desire to broaden the genetic base of rice cultivars [51] have recently resulted in the development of wide-hybridization programs in many countries. In the following sections, we describe two species for which there have been new collections and analyses of their genetic resources, *O. glumaepatula* and *O. eichingeri*, and discuss how these species are used within breeding programs.

Oryza glumaepatula (synonym Latin American *O. rufipogon*, AA genome)

AA-genome wild rice is found in various parts of Latin America from 23°N in Cuba to 23°S in Brazil. This taxa is now generally known as *O. glumaepatula*, although this name was first used to describe a cultivated rice from Suriname. No clear morphological characteristic distinguishes *O. glumaepatula* from AA-genome wild rice from

Asia and Australia [52]. However, there are sterility barriers between accessions of this species and AA-genome accessions from Asia [53,54]. Although it is clear that there is an indigenous AA-genome wild rice in Latin America, the possibility that AA-genome wild rice from Asia and/or Africa was also historically introduced into Latin America cannot be discounted. The ecological and genetic complexity of *O. glumaepatula* revealed by recent studies may support this.

Most of the *O. glumaepatula* germplasm in the international *Oryza* species collections results from collecting missions in the early 1960s in the Caribbean and South America and in the 1990s in Brazil [6•] and Costa Rica [55]. The materials from these collecting missions have been the basis of ecological and diversity studies [56,57] and of genetic studies [51,58–60,61•].

The combination of field observations and studies of genetic diversity has revealed characteristics of Brazilian *O. glumaepatula* that are related to life-history traits [56,57]. The gene flow and intra-population genetic diversity of Amazonian *O. glumaepatula*, unlike those of the related wild AA-genome species of Asia, appear to reflect seed flow rather than pollen flow. *O. glumaepatula* is predominantly an inbreeding species and a prolific seed producer (possibly with an essentially annual life cycle). These traits reflect the habitat of *O. glumaepatula*, which can be dry in one season followed by flooding of 10–20 m in the next season. The greatest genetic diversity is generally found downstream of high ground, probably because the culms tend to detach just above the node in rising water causing plants to float down stream ([56]; Figure 1). In other parts of Latin America, *O. glumaepatula* is subject to different ecological conditions and has different characteristics, implying that certain traits are being selected; for example,

Figure 1



O. glumaepatula detached from its roots and floating downstream in the Rio Negro, Amazon Basin, Brazil.

O. glumaepatula in the Paraguay river system has much lower inter- and intra-population genetic diversity than Amazonian *O. glumaepatula* [57].

AA-genome *Oryza* germplasm exhibits remarkable eco-geographic differentiation worldwide, both regionally and locally. Thus, this wild germplasm can be expected to have significant adaptive gene differences among accessions.

Detailed morphological, biochemical and molecular analyses suggest that *O. glumaepatula* consists of at least two main groups: one group centered on the Amazon basin and the other in the Pantanal of Brazil and Caribbean regions. Studies of variations in mitochondrial, chloroplast and nuclear DNA suggest that *O. glumaepatula* has multiple origins [62,63]. Various accessions of *O. glumaepatula* are more similar either to the African annual AA-genome wild rice, *O. barthii*, or to the African perennial AA-genome wild rice, *O. longistaminata*. Dally and Second [19] found two accessions of Latin American AA-genome wild rice that have a chloroplast plastotype that is related to that of the Asian AA-genome species.

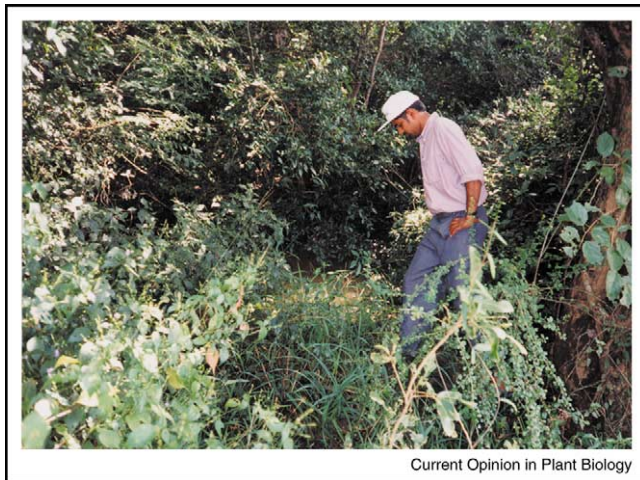
Several studies have tried to make practical use of genetic variation within *O. glumaepatula*. Reciprocal introgression lines between *O. glumaepatula* and *O. sativa* have been developed [58]. These introgression lines have been developed so that most parts of the *O. glumaepatula* genome are represented in lines with both *O. sativa* cytoplasm and *O. glumaepatula* cytoplasm. These lines are leading to the identification of novel genes, such as *Rhw* for restoration of hybrid weakness from *O. glumaepatula* cytoplasm [60] and *S22* for pollen semi-sterility/hybrid sterility from *O. glumaepatula* [59].

Microsatellite markers have been developed from an *O. glumaepatula* genomic library and used, with other molecular markers from rice, to map an interspecific cross between *O. glumaepatula* and *O. sativa* [51]. The main focus of the interspecific cross was to broaden the genetic base of Brazilian rice cultivars and to identify useful traits from *O. glumaepatula* in the genetic background of rice. Potentially useful QTL have been found that are associated with tiller and panicle numbers [61•].

***Oryza eichingeri* (CC genome)**

The diploid CC-genome species, *O. eichingeri*, belongs to a group of species that show morphological and genetic differentiation in relation to habitat and geographic origin. *O. eichingeri* is particularly interesting because it has a remarkably disjunct distribution in West and East Africa and in Sri Lanka. This may be one reason why this species exhibits a surprising degree of intraspecific variation at the genome level [17,19]. *O. eichingeri* usually grows in shade or semi-shaded forest environments (Figure 2). This species is believed to be the genome donor to the

Figure 2



O. eichingeri growing in a shallow shaded pool at the edge of a forest in the northern central plain of Sri Lanka.

tetraploid form of *O. punctata* of Africa and is genetically the closest of the CC-genome species to the tetraploid *Oryza* species of Latin America (*O. latifolia*, *O. alta* and *O. grandiglumis*) [23*].

Germplasm collections for *O. eichingeri* were undertaken in Africa in the 1960s [6*] and 1990s [55], and this species has also been found in and collected from various parts of Sri Lanka (DA Vaughan, unpublished data). *O. eichingeri* has a similar morphology and is found in similar habitats in Africa and Sri Lanka. This species has been used in recent diversity studies [23*,64] and cytological studies [21*], and in rice improvement [65].

O. eichingeri has been used in a rice breeding program as a source of resistance to brown planthopper [65]. Wide hybridization and introgression of alien genes can give insights into genome interaction and the creation of novel variation. However, the rate of success for intergenomic crosses is very low [66]. In crosses between *O. sativa* and two accessions of *O. eichingeri*, the rate of success was just 0.36% and 1.65% [65]. Embryo rescue was necessary to produce F₁ plants and the F₁ plants were almost always sterile. Subsequent to the original cross, monosomic alien addition lines (MAALs), backcross euploid plants, and a triploid plant were generated. It was possible to identify the chromosomal constitution of these plants by fluorescent *in situ* hybridization (FISH) and genomic *in situ* hybridization (GISH) [18]. The analysis of introgression in 67 euploid plants by RFLP revealed six RFLP markers that could detect small introgressed segments from *O. eichingeri* in between 28 and 42 plants. The fact that the same six markers could be used in so many of the backcross progeny suggests there may be 'hot spots' for high meiotic recombination [67**].

One intriguing result of wide crosses in the genus *Oryza* has been the discovery of novel variation [67**,68]. Several explanations have been suggested for this novel variation, including inter-genomic translocation and the activation of some transposable elements [49,67**].

Repeated studies of inter-genomic introgression in *Oryza* have shown that the size of introgressed segments is very small [49,67**,68]. This has caused some to suggest that the mechanism of alien-gene introgression in *Oryza* is not conventional [49].

Conclusions and future directions

The sequencing of the rice nuclear (in 2001–2002), chloroplast (in 1989) and mitochondrial (in 2002) genomes of rice has now been completed. The next decade will see the sequencing of other *Oryza* genomes. The recent approval of funding for the construction of a bacterial artificial chromosome (BAC) library for the genomes of *Oryza* is progress in this direction [69]. An early genome map using the CC-genome species *O. officinalis* initiated the study of comparative genomics in the genus *Oryza* [70]. During the coming years, studies of the different *Oryza* genomes will open the door to rapid advances in *Oryza* research and will answer some of the complex questions related to the genus *Oryza*. Among these questions are those related to the genetic and ecological characteristics of *Oryza* species that are not present in rice, such as polyploidy and rhizome formation.

Standard accessions for each taxa are needed, in the same way that the Kasalath and Nipponbare varieties have been used as standards for rice genome studies, to ensure that our growing understanding of the genus *Oryza* is placed on a firm foundation. The study of well-characterized standard accessions in many laboratories and from different perspectives would be valuable, and the International Rice Research Cooperative may take a lead in determining the appropriate accessions.

Much basic research, particularly in the area of overcoming cross-compatibility barriers, must be undertaken to lay the foundation for the use of *Oryza* genomes in routine rice improvement. Rice improvement programs that incorporate germplasm from wild relatives of rice in pre-breeding may lead to important breakthroughs. Genes from the common wild rice (*O. rufipogon*) have already provided cytoplasmic male sterility, triggering the hybrid rice 'green revolution'. Other *Oryza* genes may lead to new directions in rice improvement.

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