



PRELIMINARY STUDIES ON TAXONOMY AND BIOSYSTEMATICS OF THE AA GENOME ORYZA SPECIES (POACEAE)

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Abstract

The genus *Oryza* L. (*Oryzeae*) includes 22 wild species and two cultivated species—*O. sativa* L. (Asian rice) and *O. glaberrima* Steud. (African rice). Asian rice is an economically important crop; it is the staple food for half of the world's population. Eight taxa, including the cultivated ones, are classified in the *O. sativa* complex on the basis of their morphological similarity and their common AA genome. Wild species in this complex are the most accessible and valuable genetic resources for rice breeding. Because of considerable variation in the morphology and habitat preferences of these rice species, taxonomy in this complex has long been a problem in terms of species delimitation and nomenclature. This paper summarizes recent biosystematic studies of the AA genome *Oryza* species through interspecific hybridization and meiotic analysis of F_1 hybrids and their parental species. It concludes that most of the AA genome species in the *O. sativa* complex, such as *O. rufipogon*, *O. barthii*, *O. glumaepatula*, *O. meridionalis*, and *O. longistaminata*, are distinct species with prominent reproductive barriers between them, although differentiation of the AA genome is limited between different species in the complex. A hypothetical biosystematic relationship of the AA genome *Oryza* species is proposed.

Key words: Poaceae, *Oryza*, wild rice, taxonomy, biosystematics, meiotic pairing, differentiation.

INTRODUCTION

The genus *Oryza* L. is classified in the tribe *Oryzeae*, which contains 12 genera (Table 1), and includes 22 species widely distributed throughout the tropics. Great diversity in morphology and habitats has been observed for the various *Oryza* species. Following the taxonomic treatment of Vaughan (1989), species in this genus are classified in four complexes, with some species not yet placed in any (Table 2). Six basic genomes, AA, BB, CC, EE, FF, and GG, as well as three genomic combinations, BBCC, CCDD, and HHJJ, have been designated respectively in diploid and tetraploid *Oryza* species, although the origin of DD, HH, and JJ is still unknown. This reflects remarkable genetic variation in the genus. Because of considerable morphological variability, the frequent occurrence of intermediate types between some species, and the wide distri-

bution of *Oryza* species, the taxonomy has long been a problem, particularly in the *O. sativa* complex, in terms of species delimitation and nomenclature.

There are two cultivated rice species that originated independently from different wild ancestral species in Asia and Africa. The Asian cultivated rice (*Oryza sativa* L.) is an economically important world cereal crop and is the staple food for about half of the world's population. This species probably originated across a broad area extending over the foothills of the Himalayas and its adjacent mountain regions in Asia, and is now grown worldwide. The African cultivated rice (*O. glaberrima* Steud.) was domesticated in West Africa and is still cultivated in some farming systems today. Rapid expansion of human populations and decreases in agricultural land require much higher rice production than that which is now achieved. Wild relatives of rice,

Table 1. Genera, number of species, distribution, and chromosome number in the tribe Oryzeae (adapted from Vaughan 1989).

Genus	No. of species	Distribution	2n
<i>Chikusiochloa</i>	3	China, Japan (t) °	24
<i>Hygroryza</i>	1	Asia (t + T)	24
<i>Leersia</i>	17	worldwide (t + T)	48, 60, 96
<i>Luziola</i>	11	North and South America (t + T)	24
<i>Maltebrunia</i>	5	tropical and southern Africa (T)	Unknown
<i>Oryza</i>	24	pan-tropics (T)	24, 48
<i>Porteresia</i>		South Asia (T)	48
<i>Prospytochloa</i>		southern Africa (t)	Unknown
<i>Potamophila</i>		Australia (t + T)	24
<i>Rhynchoryza</i>		South America (t)	24
<i>Zizania</i>	3	Europe, Asia, N. America (t + T)	30, 34
<i>Zizaniopsis</i>	5	North and South America (t + T)	24

° T = tropical area, t = temperate area.

particularly those having the AA genome, are extremely valuable genetic resources that serve to broaden the genetic background of cultivated rice because the two cultivated rice species also have the same genome. They are therefore the most accessible genetic resources in the rice gene pool.

Eight *Oryza* species, including the two cultigens, have the AA genome and are classified in the *O. sativa* complex (Table 2). These are *O. rufipogon*, *O. nivara*, and *O. sativa*, which are native to Asia, although the Asian cultivated rice is now grown worldwide; *O. longistaminata*, *O. barthii*, and *O. glaberrima*, which are endemic to Africa; and *O. meridionalis* and *O. glumaepatula*, which are only found in Australia and Latin America, respectively (Fig. 1). Although geographically and genetically isolated,

species in this complex from different continents have been reported to have considerable morphological similarities and intermediate types are also found between species occurring sympatrically. This has led to considerable taxonomic and nomenclature changes in the wild species in this complex.

NOMENCLATURE AND TAXONOMIC CHANGES IN AA GENOME ORYZA SPECIES

The two cultivated rice species have been given a large number of names and undergone considerable nomenclature revision (see Sampath 1962; Harlan and de Wet 1971; Vaughan 1989 for a review), but *Oryza sativa* L. and *O. glaberrima* Steud. have become well accepted and widely adopted names.

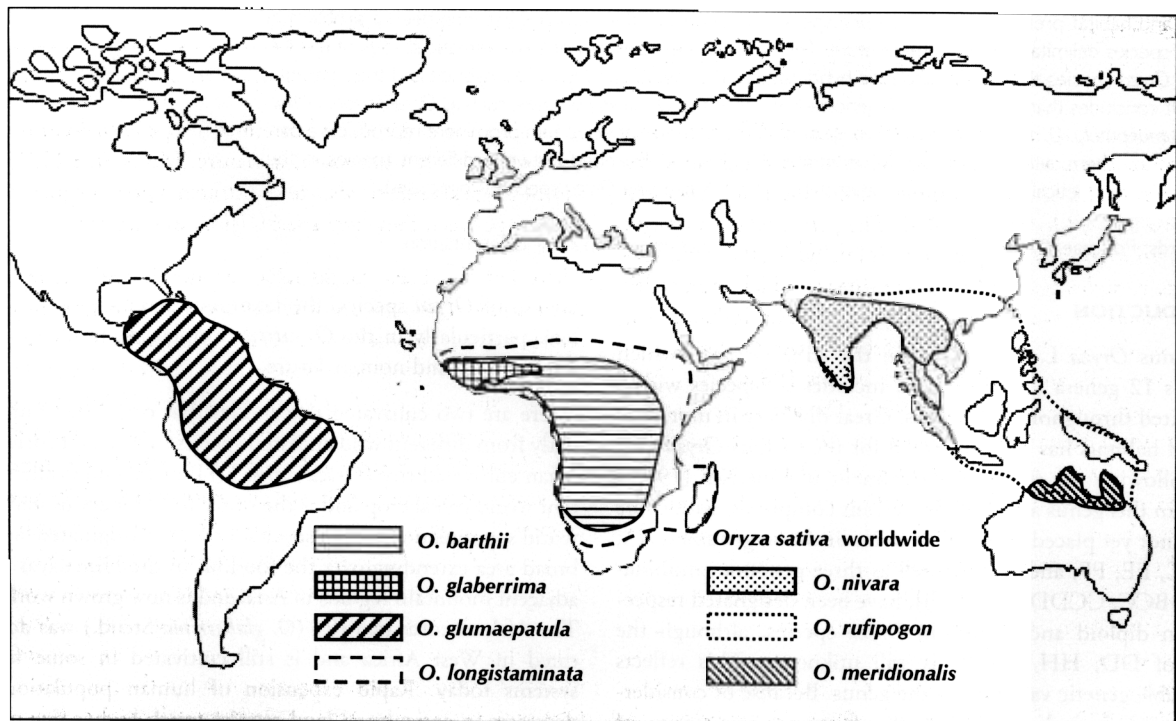


Fig. 1. Distribution of the AA genome *Oryza* species in different geographical regions.

Table 2. Chromosome number, genome content, and distribution of species in the genus *Oryza* (modified from Vaughan 1989)

Complex and species	2n	Genome	Distribution
<i>O. sativa</i> complex			
<i>O. barthii</i> A. Chev.	24	AA	Africa
<i>O. glaberrima</i> Steud.	24	AA	West Africa
<i>O. glumaepatula</i> Steud.	24	AA	South & Central America
<i>O. longistaminata</i> Chev. et Roehr.	24	AA	Africa
<i>O. meridionalis</i> Ng	24	AA	tropical Australia
<i>O. nivara</i> Sharma et Shastry	24	AA	tropical & subtropical Asia
<i>O. rufipogon</i> Griff.	24	AA	tropical & subtropical Asia, & tropical Australia
<i>O. sativa</i> L.	24	AA	worldwide
<i>O. officinalis</i> complex			
<i>O. alta</i> Swallen	48	CCDD	South & Central America
<i>O. australiensis</i> Domin.	24	EE	tropical Australia
<i>O. eichingeri</i> Peter	24, 48	CC ^a	South Asia & East Africa
<i>O. grandiglumis</i> (Doell) Prod.	48	CCDD	South & Central America
<i>O. latifolia</i> Desv.	48	CCDD	South & Central America
<i>O. minuta</i> J. S. Presl. et C. B. Presl.	48	BBCC	Philippines & Papua New Guinea
<i>O. officinalis</i> Wall. ex Watt	24, 48	CC ^a	tropical & subtropical Asia, & tropical Australia
<i>O. punctata</i> Kotechy ex Steud.	24, 48	BB & BBCC	Africa
<i>O. rhizomatis</i> Vaughan	24	CC	Sri Lanka
<i>O. meyeriana</i> complex			
<i>O. granulata</i> Nees et Arn. ex Watt	24	GG	South & Southeast Asia
<i>O. meyeriana</i> (Zoll. et Mor. ex Steud.) Baill.	24	GG	Southeast Asia
<i>O. ridleyi</i> complex			
<i>O. longiglumis</i> Jansen	48	HHJJ	Irian Jaya, Indonesia, & Papua New Guinea
<i>O. ridleyi</i> Hook. f.	48	HHJJ	South Asia
Species not assigned to any complex			
<i>O. brachyantha</i> Chev. et Roehr.	24	FF	Africa
<i>O. neocaledonica</i> Morat	24	Unknown	New Caledonia
<i>O. schlechteri</i> Pilger	48	Unknown	Papua New Guinea

^a A tetraploid form with 48 chromosomes has also been found in the species

The close relatives of *O. sativa* have been named differently over time. The species name *O. perennis* Moech was widely used for wild species in the *O. sativa* complex (Sampath 1962; Oka and Morishima 1967; Morishima 1969). The perennial *O. rufipogon* was referred to as Asian *O. perennis*, in line with other wild species of the complex from different continents, which were called African, American, and Oceanian *O. perennis*. This influence has been so significant that many scientists still use *O. perennis* in their recent publications (Pental and Barnes 1985; Oka 1988; Morishima *et al.* 1992; Ishii *et al.* 1996). The annual species was called *O. fatua* Koenig ex A. Chev. or *O. sativa* f. *spontanea* Roshev., and was described as *O. nivara* by Sharma and Shastry (1965) to distinguish it from *O. rufipogon*. But the name *O. nivara* has been interpreted differently. Some scientists have accepted *O. nivara* as an independent species (Chatterjee 1951; Chang 1976; Vaughan 1989, 1994) and considered it as the ancestor of the Asian cultivated rice. Others, however, treated *O. nivara* as a synonym of *O. sativa* (Duistermaat 1987) or the annual form of *O. rufipogon* (Asian *O. perennis*) (Morishima 1969; Oka 1988; Morishima *et al.* 1992). Nevertheless, *O. rufipogon* and *O. nivara* show a continuous array of intergrades

(Morishima *et al.* 1961) and intermediate perennial-annual populations have also been found in nature (Morishima 1986). Our morphological analysis also demonstrated a great degree of overlapping between these two species (Juliano *et al.* 1998).

There has also been considerable taxonomic and nomenclature confusion with the African wild rice species, although morphological differences between these species are significant. The annual *O. barthii*, which has been widely accepted as the ancestor of the African cultivated rice *O. glaberrima* (Chang 1976), was referred to as *O. breviligulata* Chev. et Roehr. (Sampath 1962; Oka and Morishima 1967; Second 1982; Ishii *et al.* 1996) or as African *O. perennis* by some authors (Pental and Barnes 1985). The perennial species *O. longistaminata* was called *O. barthii* (Sampath 1962; Clayton 1968) or *O. perennis* subsp. *barthii* (Oka and Morishima 1967; Clayton 1968). It was also common to name this perennial species as African *O. perennis* (Morishima 1969; Oka 1988; Morishima *et al.* 1992). In the Philippines we use *O. barthii* for the annual species and *O. longistaminata* for the perennial species. Our unpublished data from morphological studies show a clear separation of the two species sampled from different localities.

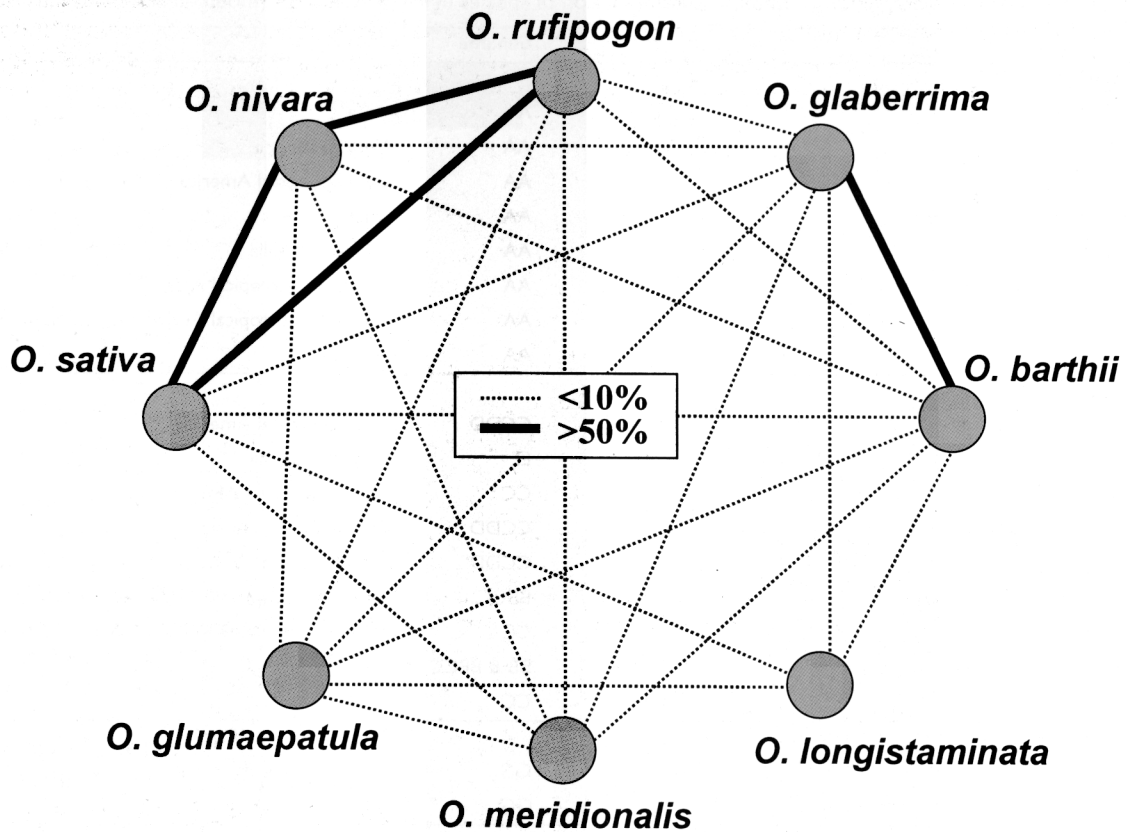


Fig. 2. Spikelet fertility (%) of F_1 hybrids between various AA genome *Oryza* species.

Oka and Morishima (1967) and Morishima (1969, 1986) suggested certain strains of wild rice from New Guinea and Australia as the Oceanian form of *O. perennis*, which Oka and Morishima (1967) indicated contained perennial and annual types. Through a comprehensive study, Ng *et al.* (1981) recognized the Australian annual strain as an independent species, *O. meridionalis*, on the basis of its unique morphological characteristics, distinct from the Asian AA genome wild *Oryza* species. In some Australian herbaria and publications, however, *O. meridionalis* was included in *O. rufipogon*. This taxonomic confusion is obviously caused by the fact that both *O. meridionalis* and *O. rufipogon* are found in Australia, and insufficient morphological characters have been used by Australian scientists to separate the two species (B. K. Simon pers. comm.).

The Latin American species *O. glumaepatula* has been clarified as the American form of *O. perennis* (Oka and Morishima 1967; Morishima 1969; Pental and Barnes 1985) or *O. cubensis* Ekman (in Vaughan 1989; Morishima *et al.* 1992). Because the American *O. glumaepatula* and the Asian *O. rufipogon* have great morphological similarity and are both perennial species, Tateoka (1962) maintained no significant morphological distinction between them, and gave these two species conspecific status. In his most recent taxonomic treatment, Vaughan (1994) classified *O. glumaepatula* in *O. rufipogon*. However, through our study on morphological analysis of more than 60 samples of *O. glumaepatula* from South and Central America, and *O. rufipogon* and *O. nivara* from Asia, we have confirmed that typical *O. glumaepatula*

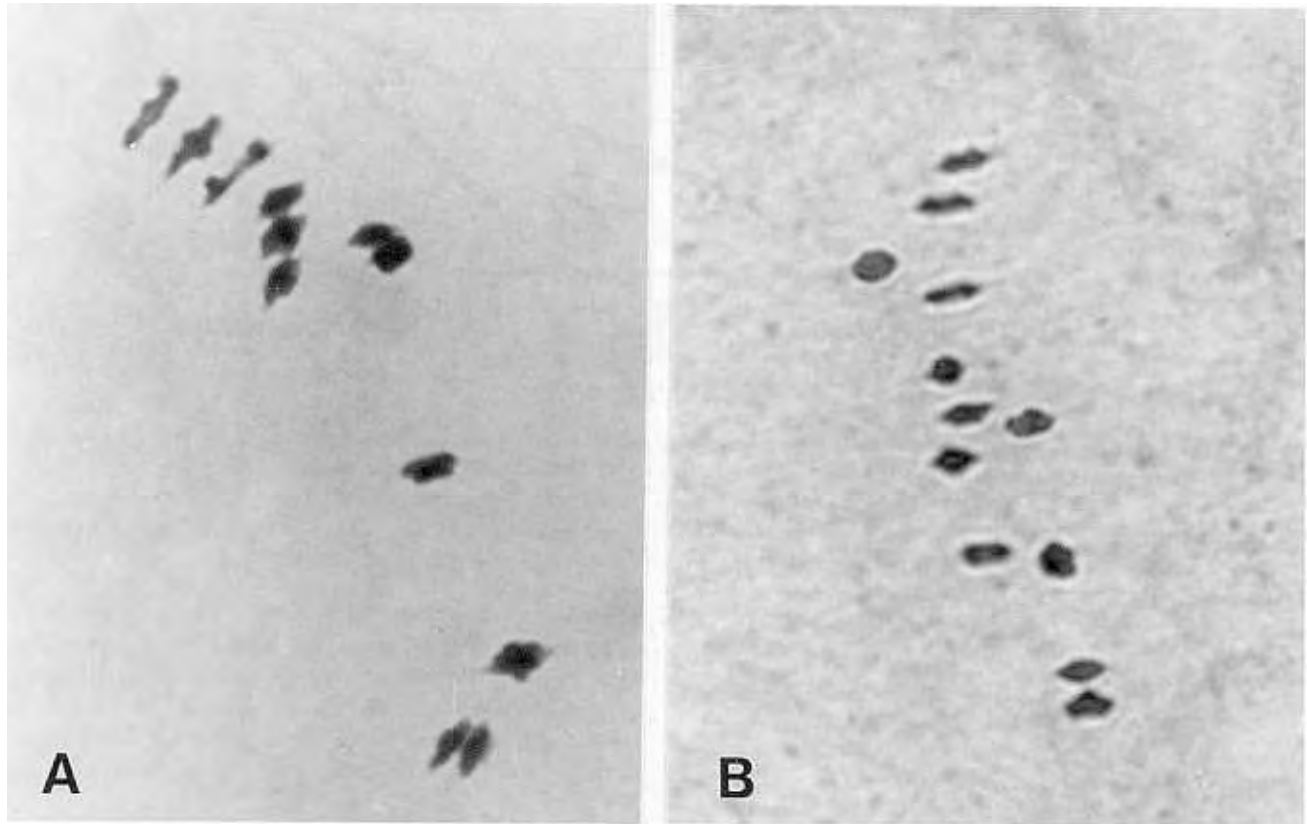
accessions do form a clear cluster distinct from the Asian wild rice species. We have concluded that *O. glumaepatula* warrants an independent taxonomic status (Juliano *et al.* 1998). This conclusion has gained support from our studies on interspecific hybridization and meiotic analysis (Naredo *et al.* 1998; Lu *et al.* 1998).

INTERSPECIFIC HYBRIDIZATION AND FERTILITY IN HYBRIDS

The AA genome wild *Oryza* species not only have remarkable morphological similarities but also show some introgression in nature between sympatric populations, and with cultivated species. This spontaneous intercrossing has caused the formation of many intermediate types between the cultivated and wild species, as well as between the annual and perennial forms based on our own field observations and those of others (Morishima 1969; Oka 1988; Morishima *et al.* 1992; Majumder *et al.* 1997). To estimate crossability and the degree of reproductive isolation among the different AA genome rice species, we have undertaken an extensive interspecific hybridization program, involving more than three populations of each AA genome rice species from different origins. Table 3 summarizes data on seed set for interspecific hybridization involving pollination of more than 70,000 spikelets. It is evident that crossability between the AA genome species was generally low, with a range of seed set from 4.1% to 52.0% between interspecific crosses and 11.1% to 31.5% between intraspecific crosses. Seed set of most combinations did not show significant differences between the reciprocal crosses. This indicates different degrees of pre-fertilization barriers

Table 3. Seed set (%) from intraspecific and reciprocal interspecific crosses among AA genome rice species (modified from Naredo *et al.* 1997, 1998, and our unpublished data).

Combination	<i>O. barthii</i>	<i>O. glaberrima</i>	<i>O. glumaepatula</i>	<i>O. meridionalis</i>	<i>O. nivara</i>	<i>O. rufipogon</i>
<i>O. barthii</i>	31.0					
<i>O. glaberrima</i>	27.4					
<i>O. glumaepatula</i>	16.1	28.4	31.5			
<i>O. longistaminata</i>						
<i>O. meridionalis</i>	16.8	52.0	11.4	11.1		
<i>O. nivara</i>	21.7	24.9	29.3	6.1	23.5	
<i>O. rufipogon</i>	22.8		19.2	7.7	21.7	13.4
<i>O. sativa</i>	28.2			4.1		

**Fig. 3A-B.** Meiotic chromosome pairing at metaphase I of the *O. barthii* x *O. glumaepatula* hybrid with 10 ring and 2 rod bivalents in A and the *O. barthii* x *O. nivara* hybrid with 12 ring bivalents in B.

between various AA genome rice species, particularly between those from different continents, and between certain populations of the same species. Figure 2 summarizes data for spikelet fertility of the F₁ interspecific hybrids which was generally less than 10%, except for the F₁ hybrids among *O. rufipogon*, *O. nivara*, and *O. sativa*, and those between *O. glaberrima* and *O. barthii*, for which more than 50% spikelet fertility was observed in each combination (Naredo *et al.* 1997, 1998; Naredo *et al.*, unpublished data). In contrast, spikelet fertility of the parental species included varied between 60%-80%. This indicates different degrees of reproductive isolation between different AA genome species, and comparatively strong isolation between those from different continents, supporting previous studies on hybrid fertilities of *O. perennis* from different geographical origins (Morishima 1969; Oka 1988).

GENOME RELATIONSHIP THROUGH MEIOTIC CHROMOSOME PAIRING

It is generally agreed that species in the *O. sativa* complex have essentially the same AA genome (Richharia 1960; Chu *et al.* 1969; Morishima *et al.* 1992). Some authors have used different superscripts to differentiate the AA genomes in some species, such as *O. longistaminata* (A¹A¹), *O. glumaepatula* (A^{EP}A^{EP}), and *O. meridionalis* (A^mA^m) (Chang 1985; Vaughan 1989). However, this differentiation cannot be supported from cytogenetic studies. To assess genomic relationships, particularly between the wild AA genome rice species, we analyzed all the available F₁ hybrids generated from the interspecific crosses. Data from chromosome configurations in meioses of different interspecific hybrids showed almost full pairing between the parental genomes (Figure 3A-B), except for some hybrids with *O. meridionalis*, in which a slightly lower value of

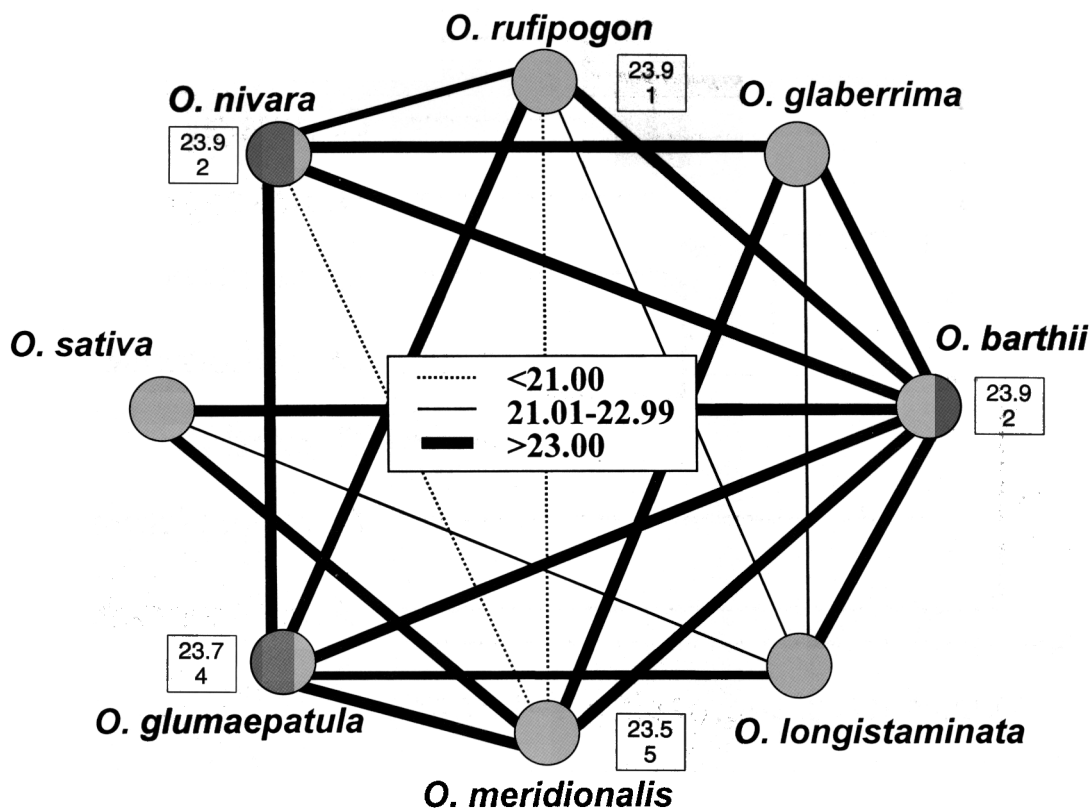


Fig. 4. Meiotic pairing of the F₁ hybrids between various AA genome *Oryza* species. Numbers in the middle box indicate chiasma frequency per pollen mother cell (PMC), and numbers in the small boxes indicate chiasma frequency per PMC of the wild parental species.

chromosome pairing was observed. Figure 4 summarizes the average chiasma frequencies per pollen mother cell (PMC) at meiotic metaphase I in the available F₁ hybrids (including the reciprocal crosses) between different AA genome rice species, and in the wild parental species (Lu et al. 1997, 1998; Lu et al., unpublished data). The chiasma frequencies are generally higher than 20 per PMC in the F₁ hybrids (many F₁ hybrids had more than 23 chiasmata per PMC). The chromosome pairing level is almost as high as in their parental accessions, although it is slightly lower in a few combinations. This result suggests limited differentiation of the AA genome in the different species of the *O. sativa* complex, regardless of the geographical isolation of these species.

CONCLUSIONS

The wild AA genome species in the *O. sativa* complex, such as *O. rufipogon*, *O. barthii*, *O. glumaepatula*, *O. meridionalis*, and *O. longistaminata*, are distinct species with prominent degrees of reproductive isolation between them. Our interspecific hybridization studies (Naredo et al. 1997, 1998; Naredo et al., unpublished data) strongly support the conclusion that these wild rice species warrant specific taxonomic status.

The Asian cultivated rice *O. sativa* and its putative ancestral taxa, *O. rufipogon* and *O. nivara*, have very limited reproductive isolation, although the ‘typical’ samples of *O. sativa*, *O. rufipogon*, and *O. nivara* are morphologically distinct. But intermediate types from introgression of the three taxa are found in nature and continuous morphological variation can be observed between

them. A similar situation is found between the African cultivated rice *O. glaberrima* and its ancestor *O. barthii*.

The differentiation of the AA genome in rice species of the *O. sativa* complex is extremely limited judging from the chromosome pairing ability of the parental genomes in interspecific hybrids. More detailed studies at the molecular level should be conducted to determine the degree of homology shared by the AA genome in different species in the *O. sativa* complex.

Based on the results from our morphological studies, interspecific hybridization, and meiotic analysis of the interspecific hybrids, in combination with reports from other molecular studies (Doi et al. 1996; Ishii et al. 1996; Martin et al. 1997), a tentative biosystematic relationship of the AA genome species in the *O. sativa* complex is illustrated in Figure 5. The Asian *O. sativa*, *O. nivara*, and *O. rufipogon* share close biosystematic relationships. The African *O. glaberrima* and *O. barthii* have the highest affinity, and the Latin American *O. glumaepatula* joins this African group. *O. longistaminata* and the Australian *O. meridionalis* have relatively distant relationships with the other AA genome rice species.

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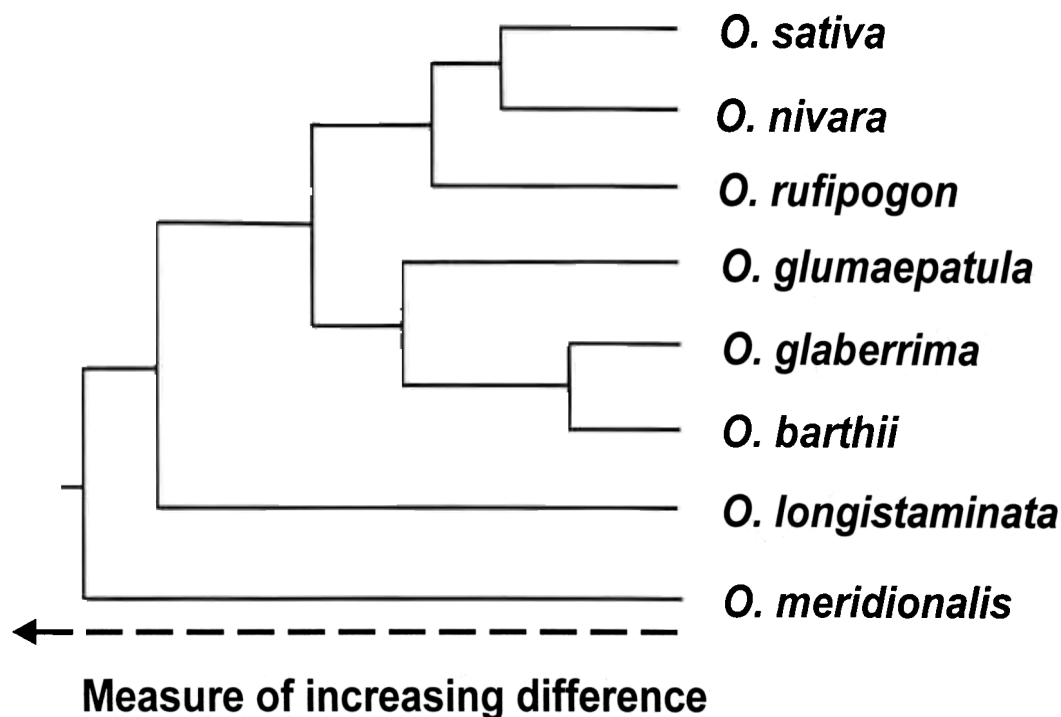


Fig. 5. A tentative biosystematic relationship of the AA genome *Oryza* species.

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