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Taxonomic status of *Oryza glumaepatula* Steud. III. Assessment of genomic affinity among AA genome species from the New World, Asia, and Australia

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Abstract

In order to assess affinity of the AA genome in different wild *Oryza* species from Asia, Australia, and South America, chromosome pairing was analyzed at metaphase-I of the F_1 hybrids obtained from interspecific crosses among *O. rufipogon* Griff., *O. nivara* Sharma et Shastry, *O. glumaepatula* Steud., and *O. meridionalis* Ng, and the hybrids produced between different populations of the same species. Both intraspecific and interspecific hybrids showed normal meiosis with remarkably high chromosome pairing at metaphase-I, which was comparable with the meiotic pairing of their respective parental species. An average of higher than 23 chiasmata per pollen mother cell (PMC) was observed in all the intraspecific and interspecific hybrids, except for one *O. glumaepatula* × *O. nivara* hybrid which had an average of 22.6 chiasmata per PMC at metaphase-I. No other meiotic irregularities except for a few bridges and laggards were found in the hybrids. It is concluded from this cytological study that the AA genome is essentially identical in the four *Oryza* species, as well as in different populations of the same rice species. It is therefore not recommended to differentiate the genomic designation of AA genomes by adding superscripts for different species.

Introduction

Six wild species in the genus *Oryza* L. are reported to have AA genome. These are *O. rufipogon* Griff., *O. nivara* Sharma et Shastry (also referred to as the annual form of *O. rufipogon* by some authors, such as Morishima, 1969; Oka, 1991) from Asia, *O. barthii* A. Chev. (Syn. *O. breviligulata* A. Chev. et Roehr.) and *O. longistaminata* A. Chev. et Roehr. from Africa, *O. glumaepatula* Steud. from South America, and *O. meridionalis* Ng from Australia. These wild species of rice are the most accessible germplasm resources in the rice genepool for further improvement of rice varieties, simply because the cultivated rice species, *O. sativa* L. and *O. glaberrima* Steud. also share the same AA genome. Therefore, it should be relatively easy to incorporate useful genes from these wild *Oryza* species into the rice cultigen through interspecific hybridization (Khush, 1977; Shih-Cheng & Yuan, 1980; Dalmacio et al., 1995), where the maximum crossabilities can be obtained between the wild and cultivated species, and the maximum genetic recombination will also occur during meiosis in the interspecific hybrids or their different selfed and backcrossed progenies.

The South America endemic species *O. glumaepatula* is geographically isolated from other AA genome rice species. However, because of the morphological similarities between *O. glumaepatula* and the Asian perennial *O. rufipogon* (also referred to as *O. perennis*), classification of these two species has caused certain taxonomic confusion (see Tateoka, 1962; Morishima, 1969; Vaughan, 1994). A recent comparative study of morphological variation between the South American and Asian AA genome rice species clearly indicated a distinct grouping of *O. glumaepatula* from the Asian AA genome species (Juliano et al., 1998). Data from interspecific hybridization of *O. glumaepatula* with other AA genome *Oryza* species from Asia and Australia further demonstrated strong reproductive barriers between these species (Naredo et al., 1998), confirming the independent taxonomic status of *O. glumaepatula*, and also supporting a previous

Table 1. IRGC accession numbers and origins of the parental taxa used in hybridization (Naredo et al., 1997b) and meiotic analyses.

Species	IRGC accession number	Origin
O. glumaepatula	100968	Surinam, Paramaribo
	100970	Brazil, Amazonas, Manaus
	103812	Venezuela
	105465	French Guiana
	105561	Colombia, Meta
	105687	Brazil, Para, Marcuri
	105689	Brazil, Amazonas, Caceiro
O. rufipogon	100588	Taiwan
	105567	Indonesia, Kalimantan, Handilmanarap
	106135	India, West Bengal, Barddhaman
O. nivara	100593	Taiwan
	105391	Thailand, Central Thailand, Chai Nat
	106185	India, Bihar, Ranchi
O. meridionalis	101147	Australia, Northern Territory, Darwin
	105300	Australia, Queensland, Cooktown
Weedy types[1]	100961	Cuba, Sta Clara
	103810	Venezuela
	104386	Brazil

[1] These accessions are weedy types having either a hybrid origin (100961) or possibly introduced from Asia (104386 and 103810) with cultivated rice (Juliano et al., 1997), and will be referred subsequently as weedy types.

conclusion that species from different continents were geographically and genetically isolated from each other (Chang, 1976). Although some populations of *O. rufipogon* have been found in Australia and possible introgression between this species and the Australian endemic *O. meridionalis* may occur (Vaughan, 1994), most artificial F_1 hybrids between *O. rufipogon* and *O. meridionalis* showed very low spikelet fertility, generally below 5% (Naredo et al., 1997), suggesting the existence of genetic isolation between the Asian and Australian *Oryza* species.

Chromosome pairing data generated from meioses at metaphase-I of the interspecific hybrids and their parents provide a close assessment of genomic relationships between plant species, assuming that genetically controlled chromosome pairing regulation (Riley & Chapman, 1958) is not present. This approach has played an important role in biosystematic and evolutionary studies of rice and many other crop species and their relatives (Morinaga, 1941; Li et al., 1962; Kimber, 1983; Bothmer et al., 1986; Lu & Bothmer, 1990a, b; Katayama, 1992). Meiotic pairing data from artificial hybrids between *O. meridionalis* and other AA genome rice species from Asia demonstrated a high genomic affinity between species from Australia and Asia (Lu et al., 1997), regardless of their morphological differences and reproductive isolation. Based on the above results, the authors confirmed the genomic constitution of *O. meridionalis* and suggested that its genome should not be designated as A^mA^m, as published by Vaughan (1989).

The objective of the present study was to further assess the overall genomic relationship of the South American species *O. glumaepatula* and other AA genome species from Asia and Australia using meiotic pairing data, and to justify whether the designation of genomic constitution of *O. glumaepatula* as $A^{gp}A^{gp}$ (Vaughan, 1989) gains cytological support.

Materials and methods

The parental materials used in the hybridization program were wild *Oryza* species *O. glumaepatula* from South America, *O. rufipogon* and *O. nivara* from Asia, and *O. meridionalis* from Australia, obtained from

Table 2. Meiotic configurations at metaphase-I in the AA genome taxa from the New World, Asia, and Australia.

Species	No. of cells observed	Meiotic configuration				Chiasmata/ PMC
		II			IV	
		Total	Rod	Ring		
O. glumaepatula						
100968	50	11.80	0.78	11.02	0.10	23.22
		(10–12)	(0–3)	(7–12)	(0–1)	(21–24)
105465	50[1]	11.98	0.28	11.70	–	23.68
		(11–12)	(0–2)	(10–12)		(22–24)
105561	50	12.00	0.40	11.60	–	23.60
		(12)	(0–4)	(8–12)		(20–24)
105687	50	11.96	0.14	11.82	0.02	23.86
		(10–12)	(0–1)	(9–12)	(0–1)	(23–24)
105689	50	11.76	0.54	11.24	0.12	23.50
		(10–12)	(0–2)	(9–12)	(0–1)	(22–24)
O. rufipogon						
100588	50	11.96	0.08	11.88	0.02	23.92
		(10–12)	(0–1)	(10–12)	(0–1)	(23–24)
105567	50	11.96	0.16	11.80	0.02	23.84
		(10–12)	(0–2)	(10–12)	(0–1)	(22–24)
106135	50	11.96	0.04	11.92	0.02	23.96
		(10–12)	(0–1)	(10–12)	(0–1)	(23–24)
O. nivara						
100593	50	12.00	0.06	11.94	–	23.94
		(12)	(0–1)	(11–12)		(23–24)
105391	50	11.88	0.10	11.78	0.06	23.90
		(10–12)	(0–1)	(10–12)	(0–1)	(23–24)
106185	17	12.00	0.06	11.94	–	23.94
			(0–1)	(11–12)		(23–24)
O. meridionalis						
101147	50	12.00	0.26	11.74	–	23.74
		(12)	(0–2)	(10–12)		(22–24)
Weedy types						
100961	49[2]	11.63	0.06	11.57	0.18	23.94
		(6–12)	(0–1)	(6–12)	(0–3)	(23–24)
103810	50	11.96	0.04	11.92	0.02	23.98
		(10–12)	(0–1)	(10–12)	(0–1)	(23–24)

[1] Univalents were 0.04 (0-2), [2] Univalents were 0.02 (0-2)

the International Rice Genebank Collection (designated IRGC) at the International Rice Research Institute (IRRI). The IRGC accession number and origin of these species are listed in Table 1. In this paper, IRGC accessions 103812 and 105561 are considered as true *O. glumaepatula* having been observed to produce fertile hybrids with forms considered to be typical *O. glumaepatula* (Naredo et al., 1998). Three diploid accessions from the New World considered as weedy types were also included. IRGC 100961 was thought to originate from a natural hybrid between *O. sativa* and the South American indigenous diploid *Oryza* species, whereas IRGC 104386 and 103810 were thought to be weedy types of Asian rice, possibly introduced into South America together with the Asian rice (Juliano et al., 1998). The intraspecific and interspecific hybrids used for meiotic analyses were chosen from those produced by Naredo et al. (1998) and maintained in the screenhouse of Genetic Resources Center (GRC) at IRRI.

Table 3. Meiotic configurations at metaphase-I of intraspecific hybrids of *O. glumaepatula*, *O. rufipogon*, *O. nivara*, and *O. meridionalis*

Hybrid combination	No. of cells observed	Meiotic configuration					Chiasmata/ PMC
		I	II			IV	
			Total	Rod	Ring		
O. glumaepatula × *O. glumaepatula*							
105465 × 105687	50	–	11.96	0.18	11.78	0.02	23.82
			(10–12)	(0–2)	(8–12)	(0–1)	(22–24)
105687 × 105465	50	0.04	11.98	0.02	11.96	–	23.94
		(0–2)	(11–12)	(0–1)	(11–12)		(11–12)
100968 × 105561	50	0.08	11.88	0.28	11.60	0.04	23.64
		(0–2)	(10–12)	(0–3)	(8–12)	(0–1)	(19–24)
105561 × 100968	50	0.36	11.78	0.34	11.44	0.02	23.30
		(0–8)	(8–12)	(0–3)	(8–12)	(0–1)	(16–24)
O. nivara × *O. nivara*							
105391 × 100593	34	0.29	11.85	0.03	11.82	–	23.68
		(0–8)	(8–12)	(0–1)	(7–12)		(15–24)
100593 × 105391	37	0.11	11.89	0	11.89	0.03	23.89
		(0–2)	(10–12)		(10–12)	(0–1)	(22–24)
O. rufipogon × *O. rufipogon*							
106135 × 100588	50	–	12.00	0.16	11.84	–	23.84
			(12)	(0–2)	(10–12)		(22–24)
100588 × 106135	50	0.60	11.70	0.12	11.58	–	23.28
		(0–10)	(8–12)	(0–1)	(7–12)		(14–24)
O. meridionalis × *O. meridionalis*							
105300 × 101147	33	0.06	11.97	0.21	11.76	–	23.73
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)

For cytological preparations, immature panicles were collected from both parents and hybrids and fixed in Carnoy's II solution (6 absolute ethanol: 3 chloroform: 1 acetic acid) with a few crystals of ferrous chloride for 24 hours at 4 °C and then stored in 70% ethanol until use. The entire young panicles were stained in alcoholic hydrochloric acid – carmine (Snow, 1963) at 50 °C for 24 hours and at room temperature for at least three days. The stained anthers were squashed in 45% acetic acid. Slides were made permanent by adding modified Hoeyer's medium (Lu & Bothmer, 1990a). Chromosome pairing was analyzed at metaphase-I only in pollen mother cells (PMCs) with complete chromosome sets.

Results

From the cytological observations, we confirmed that all the parental species from Asia, South America, and Australia, as well as the weedy types, had a consistent chromosome number of 2n=2x=24 in meiotic PMCs. All the *Oryza* parental species presented normal meiosis in the PMCs (Table 2) with predominant ring bivalent formation at metaphase-I. An average of 11.76–12.00 bivalents per cell was found in different accessions of *O. glumaepatula*, 11.96 bivalents per cell in *O. rufipogon*, 11.88–12.00 bivalents per cell in *O. nivara*, and 12.00 bivalents per cell in the single accession of *O. meridionalis*. The two weedy type accessions also had high meiotic pairing with an average of bivalents ranging from 11.63–11.96 per cell. No univalents were found in any of the parental species, except for one accession each of *O. glumaepatula* (IRGC 105465) and a weedy type (IRGC 103810), where a low frequency (0.02 and 0.04 per cell, respectively) of univalents was observed. A low number of quadrivalents, ranging from 0.02-0.18 per cell, was scored in some accessions of *O. glumaepatula* and *O. nivara*, and in all accessions of *O. rufipogon* and the weedy types. Chiasma frequency varied between 23.22–23.98 per cell in the parental species (Table 2). Chromosomes were

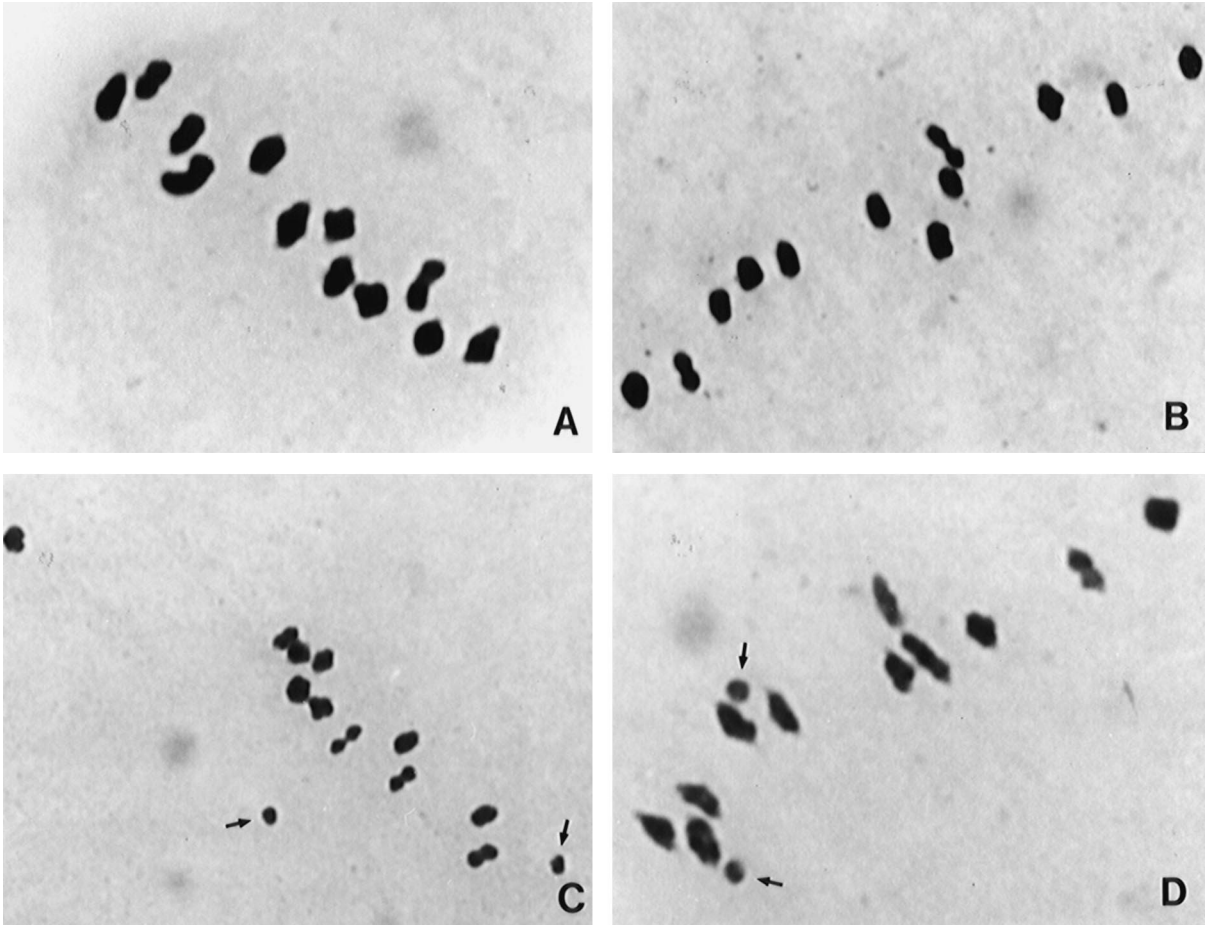

Fig 1. A-1D. Meiotic configurations at metaphase-I of the intraspecific (1A) and interspecific (1B-1D) hybrids.
1A. *O. rufipogon* (106135) × *O. rufipogon* (100588), with 12 ring bivalents; 1B. *O. glumaepatula* (100968) × *O. rufipogon* (100588), with 12 ring bivalents; 1C. *O. glumaepatula* (105465) × *O. rufipogon* (100135), with 2 univalents (arrows) and 11 ring bivalents; and 1D. *O. nivara* (106185) × *O. glumaepatula* (105687), with 2 univalents (arrows) and 11 ring bivalents.

equally segregated to the two poles at anaphase-I and -II.

Meiosis in intraspecific hybrids

Meiosis was regular in all intraspecific hybrids with high chromosome pairing at metaphase-I (Table 3 and Figure 1A). Compared with meiosis of the parental species, the frequency of univalents was noticeably higher in the different intraspecific hybrids, with an average between 0.04–0.36 per cell in *O. glumaepatula* × *O. glumaepatula* hybrids, 0.11–0.29 per cell in *O. nivara* × *O. nivara* hybrids, 0.06 per cell on *O. rufipogon* × *O. rufipogon* and *O. meridionalis* × *O. meridionalis* hybrids, respectively. Ring bivalents was predominantly found in all intraspecific hybrids. The total number of bivalents varied from 11.51–12.00 per cell in *O. glumaepatula* intraspecific hybrids, 11.85–11.89 per cell in *O. nivara* intraspecific hybrids, 11.70–12.00 per cell in *O. rufipogon* intraspecific hybrids, and 11.97 per cell in the single *O. meridionalis* intraspecific hybrid. The frequency of quadrivalents did not change significantly, compared with their parents. Chiasma frequency varied from 23.28–23.96 per cell in various hybrids. Chromosomes were equally segregated to the two poles at anaphase-I and -II in most PMCs.

Meiosis in interspecific hybrids

All interspecific hybrids also showed regular meiosis (Table 4). Chromosome configurations at metaphase-I of the interspecific hybrids did not differ appreciably

Table 4. Meiotic configurations at metaphase-I of interspecific hybrids among *O. glumaepatula*, *O. rufipogon*, *O. nivara*, *O. meridionalis*, and weedy types.

Hybrid combination	No. of cells observed	Meiotic configuration					Chiasmata/ PMC
		I	II			IV	
			Total	Rod	Ring		
O. glumaepatula × *O. rufipogon*							
100968 × 100588	50	0.12	11.94	0.12	11.82	–	23.76
		(0–4)	(10–12)	(0–1)	(10–12)		(20–24)
105465 × 106135	50	0.48	11.76	0.06	11.70	–	23.46
		(0–4)	(10–12)	(0–1)	(10–12)		(20–24)
103812 × 106135	50	0.60	11.70	0.36	11.34	–	23.04
		(0–8)	(8–12)	(0–3)	(8–12)		(16–24)
O. rufipogon × *O. glumaepatula*							
100588 × 100968	50	0.40	11.80	0.08	11.72	–	23.52
		(0–14)	(5–12)	(0–1)	(5–12)		(10–24)
106135 × 105465	50	0.28	11.86	0.02	11.84	–	23.70
		(0–10)	(7–12)	(0–1)	(7–12)		(14–24)
106135 × 100968	50	0.12	11.90	0.32	11.58	0.02	23.56
		(0–4)	(10–12)	(0–2)	(10–12)	(0–1)	(22–24)
O. glumaepatula × *O. nivara*							
105687 × 106185	40[1]	0.42	11.70	0.85	10.75	0.02	22.62
		(0–4)	(9–12)	(0–6)	(4–12)	(0–1)	(17–24)
O. nivara × *O. glumaepatula*							
105391 × 105465	50	–	12.00	0.44	11.56	–	23.56
			(12)	(0–2)	(10–12)		(22–24)
106185 × 105687	50	0.24	11.88	0.28	11.60	–	23.48
		(0–2)	(11–12)	(0–2)	(10–12)		(22–24)
O. glumaepatula × *O. meridionalis*							
105465 × 105300	50	–	12.00	0.26	11.74	–	23.74
			(12)	(0–2)	(10–12)		(22–24)
105687 × 105300	50	–	12.00	0.34	11.66	–	23.66
			(12)	(0–2)	(10–12)		(22–24)
O. meridionalis × *O. glumaepatula*							
105300 × 105465	50	0.04	11.98	0.44	11.54	–	23.52
		(0–2)	(11–12)	(0–3)	(9–12)		(21–24)
105300 × 100970	50	0.04	11.98	0.16	11.82	–	23.80
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)
O. glumaepatula × weedy type							
100968 × 103810	50	–	12.00	0.04	11.96	–	23.96
			(12)	(0–1)	(11–12)		(23–24)
105561 × 103810	47	0.98	11.51	0.28	11.23	–	22.74
		(0–8)	(8–12)	(0–1)	(8–12)		(16–24)
weedy type × *O. glumaepatula*							
103810 × 100968	50	0.28	11.86	0.10	11.76	–	23.62
		(0–6)	(9–12)	(0–1)	(10–12)		(23–24)
104386 × 105689	31	0.25	11.87	0.58	11.29	–	23.16
		(0–2)	(11–12)	(0–2)	(9–12)		(20–24)
103810 × 105561	26	0.23	11.88	0.08	11.81	–	23.69
		(0–6)	(9–12)	(0–1)	(9–12)		(18–24)

Table 4. (Continued).

Hybrid combination	No. of cells observed	Meiotic configuration					Chiasmata/ PMC
		I	II			IV	
			Total	Rod	Ring		
O. rufipogon × *O. nivara*							
100588 × 105391	50	0.04	11.98	0.12	11.86	–	23.84
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)
O. nivara × *O. rufipogon*							
105391 × 106135	31	0.06	11.97	0.03	11.94	–	23.90
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)
100593 × 100588	50	0.08	11.96	0.06	11.90	–	23.86
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)
O. rufipogon × weedy type							
100588 × 104386	47	0.13	11.94	0.02	11.91	–	23.85
		(0–2)	(11–12)	(0–1)	(11–12)		(22–24)
weedy type × *O. rufipogon*							
104386 × 100588	50	0.04	11.94	0.20	11.74	0.02	23.72
		(0–2)	(11–12)	(0–1)	(10–12)		(21–24)

[1] Trivalent observed at a frequency of 0.03 (0-1) per PMC

from those of the parental species and intraspecific hybrids. The bivalent formation was generally high in all the interspecific hybrids (Figures 1B to 1D). The total number of bivalents ranged from 11.51–12.00 per cell in various hybrids. Univalents were observed in almost all hybrids, with a slightly higher value in some hybrids, up to 0.98 per cell. Quadrivalents were only found in three hybrids and their number (0.02 per cell) was slightly lower than in the parents and intraspecific hybrids. A low frequency of trivalents (0.03 per cell) was also observed in one *O. glumaepatula* × *O. nivara* hybrid. No significant differences in chromosome configurations were found between hybrids derived from reciprocal crosses (Table 4). Chiasma frequency varied from 22.62 (in *O. glumaepatula* × hybrid) to 23.96 per cell in various hybrids. Chromosomes were equally segregated to the two poles at anaphase-I and -II in most PMCs.

Discussion

Chang (1976) reported that the AA genome wild *Oryza* species from different continents were geographically and genetically isolated. Data from hybridization between and within the AA genome *Oryza* species from different origins also showed relatively strong reproductive barriers between species, usually with remarkably low spikelet or pollen fertility in most interspecific hybrids (Chu et al., 1969; Naredo et al., 1997, 1998). Studies of morphological variation (Morishima & Oka, 1960; Morishima, 1969; Juliano et al., 1998), isozyme electrophoresis (Second, 1985), restriction fragment length polymorphism (RFLP) (Wang et al., 1992; Doi et al., 1996), and random amplified polymorphic DNA (RAPD) (Ishii et al., 1996; Martin et al., 1997) also suggested a diverged relationship between the AA genome rice species, particularly the Australian *O. meridionalis* and African *O. longistaminata*, which have shown remarkably different patterns of diversity from all other AA genome rice species. Therefore, the general conclusion from these studies was that the AA genomes *Oryza* species from different continents have differentiated to a considerable extent.

However, it is evident from the present cytological observation that the interspecific hybrids showed remarkably high chromosome pairing at metaphase-I, although a low frequency of univalents was observed. All the hybrids had an average of chiasmata higher than 23 per cell in meiosis, except for one combination, *O. glumaepatula* × *O. nivara*, which had an average of 22.62 chiasmata per cell. This value is comparable with the chromosome pairing level of various parental species. Even for such species, which differ in morphology, isozyme pattern and molecular markers, as *O. glumaepatula* and *O. meridionalis*, chro-

mosome pairing in their hybrids was almost as high as that in their parental species. Hybrids between the weedy type from the New World and other AA genome rice species from different continents also had similar amount of chromosome pairing in comparison with other hybrids. These data indicate high chromosome homology between the AA genomes in all the rice species studied, given the fact that no or extremely low chromosome pairing has been recorded in diploid *Oryza* hybrids containing distantly related genomes, such as AB, AC, AE, CE or BC (Nezu et al., 1960; Morinaga, 1964; Ogawa & Katayama, 1971). This indicates that the assessment of genome relatedness using diploid hybrids is essentially reliable in the genus *Oryza*. In other words, the genomes in *O. rufipogon*, *O. nivara*, *O. glumaepatula*, and *O. meridionalis* are essentially identical with limited differentiation even though they are geographically isolated and possess relatively strong reproductive barriers, and some of them have prominent morphological differences and molecular variation patterns. It is therefore not justifiable to give the genome designation as $A^{gp}A^{gp}$ for *O. glumaepatula* as suggested in earlier publications (Vaughan, 1989). Furthermore, cytological analyses of a large number of cell samples indicated that only few chromatid bridges and fragments were detected at anaphase-I and -II, and extremely low multivalents were observed at metaphase-I of the various interspecific hybrids. This suggests that no evident chromosome structural changes, such as chromosome inversion or translocation, have occurred between the AA genomes in the different parental species.

Meiotic pairing in hybrids from intraspecific crosses was also very high, although as in the interspecific hybrids, a slightly higher frequency of univalents than the parents was present at metaphase-I. This suggests that the AA genomes in different populations of the same rice species possess high chromosome homology, and no substantial genomic differentiation has occurred at the population level. In some reported artificial *O. meridionalis* and *O. nivara* intraspecific hybrids, spikelet fertility was substantially lower ($\leq$ 3%) than that of other intraspecific hybrids (Naredo et al., 1997), but full chromosome pairing at the metaphase-I was still evident in these hybrids, suggesting that sterility of these hybrids was not caused by meiotic abnormality like in many other inter-population or interspecific hybrids (Lu & Bothmer, 1990b). Instead, it has more likely occurred at the gene level. It therefore seems that certain genetic mechanisms have been established at the gene level to isolate populations of the same species, as has occurred between species, where the interspecific hybrids presented low spikelet fertility (Chu et al., 1969; Naredo et al., 1997, 1998).

It is noticeable that the chromosome pairing data showed no significant differences between the hybrids from reciprocal crosses. This suggests no maternal effect on chromosome pairing in these rice species, as observed in some other interspecific and intergeneric hybrids (Dahleen & Joppa, 1991; Lu, 1997).

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