The Cytogenetics of F_1 Hybrids from *Oryza nivara* Sharma et Shastry $\times$ *O. sativa* L.

Regina C. Dolores, T. T. Chang and D. A. Ramirez¹

Received October 11, 1977

Oryza nivara Sharma et Shastry, an annual wild species, the prototype of which is most probably the ancestor of the cultivated Asian rice (Chang 1976), is of equal interest to rice geneticists and breeders alike. A strain of *O. nivara* (IRRI Accession No. 101508) collected from northeast Uttar Pradesh state of India is the only strain in the rice taxa known to date that has strong resistance to the grassy stunt virus (Ling et al. 1970). Cytogenetic studies on species relationships between *O. sativa* and its wild relatives, which have a variety of dubious designations such as "*O. perennis*" and "*O. fatua*", have been made by Japanese, Chinese, and American researchers (cf. Chang 1964, Nayar 1973). The relationship between *O. sativa* and *O. nivara* has not been investigated, however, as *O. nivara* was formally described and named as recently as 1965 (Sharma and Shastry 1965).

The primary objectives of this study were to elucidate the chromosome homology between Accession 101508 of *O. nivara* and representative *O. sativa* cultivars of the tropics, to study the morphology of the pachytene chromosomes of the parents and their F_1 hybrids, and to cytogenetically assess the crossability between the two species.

Materials and methods

The strain of *Oryza nivara* Sharma et Shastry (Acc. 101508), which is resistant to the grassy stunt virus, was crossed directly and reciprocally to six cultivars (cv.) of the Indica race of *Oryza sativa* L. The six cultivars were Mudgo, TKM-6, Taichung Native 1 (TNI), Dee-geo-woo-gen (Dgwg), IR5, and IR8. The F_1 hybrids and the parents were planted during the wet season at the International Rice Research Institute (IRRI).

Sporocytes of the parents and hybrids were collected at the early booting stage. For cytological examinations, the modified iron-acetocarmine technique was followed for preparing smears. Individual bivalents at pachynema were identified by their absolute length (in microns), arm ratio (short arm/long arm), and the distribution and pattern of chromomeres. Only the prominent and constant chromomeres were considered as morphological markers and traced as interpretative drawing in Fig. 1. The chromosomes were classified by means of the arm ratios as follows: median (M), having arm ratios ranging from 0.67 to 1.00;

¹ Institute of Plant Breeding, University of the Philippines at Los Baños; International Rice Research Institute, Los Baños, Laguna, Philippines; and Department of Life Sciences, University of the Philippines at Los Baños, respectively.

submedian (SM), from 0.34 to 0.66; and subtelocentric (ST), less than 0.34. Other cytological observations were made at diakinesis, metaphase I, anaphase I, and telophase I stages of meiosis. Photomicrographs were taken from temporary slides.

For counts on pollen and spikelet sterility, the same technique was used as that reported by Dolores *et al.* (1975).

Results

Karyotype analysis at pachytene stage

For purposes of classification, the longest chromosome was identified as number 1 and the shortest, number 12. Remarkable differences in chromatin length, chromomeric pattern and type of chromosome among the varieties and hybrids, and between the two species were found. All the chromosomes of the parents and hybrids have distinct chromomeres on the proximal regions of the centromere.

1. *O. nivara*—Based on arm ratio, the 12 bivalents of this species fell into five median (1, 3, 7, 8 and 9), five submedian (2, 4, 5, 11 and 12) and two subtelocentric (6 and 10). The heterochromatic and euchromatic regions are shown in Fig. 1A.

2. Cv. Mudgo—Chromosomes 1, 2, 5, 10, 11 and 12 are submedian, chromosomes 3, 7, 8 and 9 are median, and chromosomes 4 and 6 are subtelocentric (Fig. 2B).

3. Cv. TKM-6—Heterochromatic segments were observed in nearly all of the chromosomes in the complement (Fig. 1D). On the basis of arm ratio, the 12 bivalents are divided into six median (chromosomes 1, 2, 3, 7, 8 and 9), four submedian (chromosomes 4, 5, 11 and 12), and two subtelocentric (chromosomes 6 and 10).

4. Cv. Taichung Native 1 (TN1)—It was observed that only one chromosome is median (chromosome 3), two are subtelocentric (2 and 6), and all the rest are submedian (Fig. 2D).

5. Cv. Dee-geo-woo-gen (Dgwg)—This variety possesses the shortest chromosomes among the parents and hybrids, ranging from 15.2 microns to 38.0 microns (Table 1). The 12 chromosomes are classified as five median (chromosomes 2, 3, 7, 11 and 12), five submedian (chromosomes 1, 4, 5, 8 and 9), and two subtelocentric (chromosomes 6 and 10) (Fig. 2E).

6. Cv. IR8—Chromosomes 1, 2 and 4 have median centromeres, 6 and 10 have subterminal centromere, and the other seven have submedian centromeres (Fig. 2F).

7. Cv. IR5—Among the parents and hybrids, IR5 has the longest chromosomes (Table 1). Chromosomes 1, 2, 4, 5, 6 and 8 are submedian, chromosomes 3, 7, 11 and 12 are median, and chromosomes 9 and 10 are subtelocentric (Fig. 2G).

8. F₁ hybrid of *O. nivara* × Mudgo—Most of the chromosomes are submedian

Fig. 1. Photomicrographs and interpretative drawings of pachytene chromosomes of: A, *O. nivara*; B, TKM-6; C, *O. nivara* × Mudgo and D, Dgwg × *O. nivara*.

(1, 4, 5, 7, 9, 10, 11 and 12). Chromosomes 2 and 3 are median. Only chromosome 6 has its centromere near one end of the chromosome arm (Figs. 1C and 3A). The length of chromosome 1 was only 39.2 microns, the shortest for chromosome 1 among all of the hybrids examined (Table 1).

9. F_1 hybrid of *O. nivara* $\times$ TKM-6—The chromosomes are equally distribu-

Fig. 2. Karyograms of the parents: A, *O. nivara*; B, Mudgo; C, TKM-6; D, TNI; E, Dgwg; F, IR8; G, IRS. IR5.

Table 1. Absolute length and arm ratio of the different chromosomes at pachytene in the parents and F_1 hybrids

Parents and hybrids	Chromosomes											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Oryza nivara</i>	75.0 ^a 0.88 ^b	66.0 0.61	65.0 0.86	43.8 0.36	43.5 0.56	41.0 0.32	39.0 0.86	35.0 0.89	34.2 0.78	33.5 0.07	32.6 0.58	31.0 0.51
Mudgo	105.2 0.46	73.0 0.51	66.8 0.87	47.2 0.34	44.0 0.38	37.0 0.12	35.6 0.83	31.2 0.89	31.0 0.72	29.0 0.38	28.8 0.57	13.0 0.44
TKM-6	89.0 0.87	81.8 0.75	78.3 0.97	77.0 0.47	76.8 0.57	57.2 0.11	48.5 0.67	47.8 0.75	42.0 0.68	39.5 0.22	22.5 0.55	17.0 0.48
Taichung Native 1 (TN1)	80.5 0.38	65.0 0.15	42.7 0.88	41.5 0.43	41.2 0.51	41.0 0.11	40.5 0.37	34.6 0.60	32.8 0.38	22.5 0.41	21.0 0.45	19.0 0.41
Dee-geo-woo-gen (Dgwg)	38.0 0.35	30.0 0.90	24.0 0.85	22.8 0.54	22.0 0.59	21.6 0.08	21.2 0.93	20.5 0.55	20.0 0.54	19.0 0.15	17.8 0.82	15.2 0.67
IR8	63.0 0.75	60.8 0.83	60.5 0.57	48.0 0.78	36.3 0.63	34.0 0.21	31.6 0.50	31.0 0.66	30.8 0.41	30.5 0.18	27.0 0.41	24.8 0.60
IR5	107.0 0.53	94.0 0.34	92.4 0.70	76.8 0.43	59.5 0.51	54.0 0.50	51.0 0.76	50.5 0.40	44.7 0.17	31.0 0.11	30.0 0.94	28.4 0.89
<i>O. nivara</i> $\times$ Mudgo	39.2 0.34	36.2 0.79	34.0 0.94	27.8 0.52	27.0 0.55	24.6 0.09	23.0 0.59	22.5 0.55	22.0 0.38	21.5 0.39	19.2 0.37	18.0 0.64
<i>O. nivara</i> $\times$ TKM-6	67.2 0.67	54.2 0.68	46.5 0.72	39.5 0.25	35.6 0.43	32.4 0.08	31.3 0.76	29.5 0.64	29.0 0.33	27.6 0.12	22.8 0.40	14.5 0.53
<i>O. nivara</i> $\times$ IR5	57.7 0.55	46.5 0.52	44.7 0.39	39.0 0.59	31.2 0.99	27.7 0.06	24.0 0.85	22.0 0.57	20.5 0.52	19.0 0.46	15.2 0.97	13.0 0.58
Mudgo $\times$ <i>O. nivara</i>	69.5 0.93	63.3 0.85	60.9 0.65	52.5 0.37	52.3 0.84	46.2 0.38	44.0 0.91	41.2 0.76	38.6 0.89	36.3 0.43	26.0 0.33	22.5 0.29
TN1 $\times$ <i>O. nivara</i>	93.0 0.31	63.5 0.57	63.0 0.42	60.0 0.20	53.0 0.26	45.5 0.12	45.0 0.74	43.2 0.36	35.0 0.59	31.0 0.06	29.0 0.32	25.0 0.66

Table 1. (Cont'd.)

Parents and hybrids	Chromosomes											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Dgwg</i> × <i>O. nivara</i>	1000.5	64.0	57.0	41.0	39.0	36.0	35.0	33.0	29.0	27.0	26.5	20.4
	0.61	0.69	0.97	0.55	0.63	0.70	0.92	0.69	0.54	0.17	0.56	0.32
<i>IR8</i> × <i>O. nivara</i>	106.0	93.5	70.0	64.5	50.2	49.0	45.0	42.0	41.0	40.8	35.0	24.5
	0.61	0.85	0.67	0.77	0.89	0.26	0.73	0.22	0.74	0.14	0.52	0.81
<i>IR5</i> × <i>O. nivara</i>	50.0	48.6	48.0	40.0	30.5	30.0	29.6	28.8	26.4	24.5	23.5	17.0
	0.85	0.38	0.75	0.57	0.63	0.07	0.70	0.49	0.52	0.11	0.81	0.30

^a The upper row refers to the absolute length.^b The lower row refers to the arm ratio.Table 2. Chromosome types and behavior at pachynema in the parents and F₁ hybrids

Parents and hybrids	Chromosome types	Total no. of cells observed	Percent cells observed						
			Normal	Loose pairing	Frag-ments	Deficiency and inver-sion loop	Reciprocal transloca-tions	Unequal bivalent	Trivalent associa-tion
<i>Oryza nivara</i>	5-5-2*	61	91.8	4.9	—	3.2	—	—	—
<i>Mudgo</i>	4-6-2	71	87.3	12.7	—	—	—	—	—
<i>TKM-6</i>	6-4-2	72	93.1	6.9	—	—	—	—	—
<i>Taichung Native 1</i>	1-9-2	74	100.0	—	—	—	—	—	—
<i>Dee-geo-woo-gen</i>	5-5-2	73	98.6	1.4	—	—	—	—	—
<i>IR8</i>	3-7-2	67	98.5	1.5	—	—	—	—	—
<i>IR5</i>	4-6-2	65	100.0	—	—	—	—	—	—
<i>O. nivara</i> × <i>Mudgo</i>	2-9-1	100	88.0	11.0	1.0	—	—	—	—
<i>O. nivara</i> × <i>TKM-6</i>	4-4-4	52	96.2	3.8	—	—	—	—	—
<i>O. nivara</i> × <i>IR5</i>	3-8-1	61	98.4	—	—	—	1.6	—	—
<i>Mudgo</i> × <i>O. nivara</i>	6-4-2	57	100.0	—	—	—	—	—	—
<i>TN1</i> × <i>O. nivara</i>	1-5-6	55	94.5	—	5.5	—	—	—	—
<i>Dgwg</i> × <i>O. nivara</i>	5-5-2	61	85.2	11.5	—	—	—	—	—
<i>IR8</i> × <i>O. nivara</i>	7-2-3	34	67.6	23.5	—	—	—	3.3	—
<i>IR5</i> × <i>O. nivara</i>	4-5-3	57	96.5	1.7	1.7	—	5.9	—	2.9

* Number of median-submedian-subtelocentric chromosomes.

ted into median (1, 2, 3 and 7), submedian (5, 8, 11 and 12), and subtelocentric (4, 6, 9 and 10) types (Fig. 3B).

10. F_1 hybrid of *O. nivara* $\times$ IR5—Chromosome 8 has a knob-like supernumerary nucleolus at the distal end of its short arm (Fig. 3C). Chromosomes 5, 7 and 11 have median centromeres, chromosome 6 has a subterminal centromere, and

Fig. 3. Karyograms of the F_1 hybrids: A, *O. nivara* $\times$ Mudgo; B, *O. nivara* $\times$ TKM-6; C, *O. nivara* $\times$ IR5; D, Mudgo $\times$ *O. nivara*; E, TN1 $\times$ *O. nivara*; F, Dgwg $\times$ *O. nivara*; G, IR8 $\times$ *O. nivara*; H, IR5 $\times$ *O. nivara*.

the rest are all submedian.

11. F_1 hybrid of Mudgo $\times$ *O. nivara*—Chromosomes 1, 2, 5, 7, 8 and 9 are median, 3, 4, 6 and 10 are submedian, and 11 and 12 are subtelocentric (Fig. 3D).

12. F_1 hybrid of TNI $\times$ *O. nivara*—The chromomeric pattern of the chromosomes is shown in Fig. 3E. This hybrid has the largest number of subtelocentric chromosomes (1, 4, 5, 6, 10 and 11). Only chromosome 7 had a median centromere. Chromosomes 2, 3, 8, 9 and 12 are submedian.

13. F_1 hybrid of Dee-geo-woo-gen $\times$ *O. nivara*—Chromosomes 1, 4, 5, 9 and 11 are submedian, chromosomes 2, 3, 6, 7 and 8 are median, and chromosomes 10 and 12 are subtelocentric (Fig. 3F). The chromomeric pattern including the heterochromatic and euchromatic regions of the chromosomes in this hybrid are shown in Fig. 1D.

14. F_1 hybrid of IR8 $\times$ *O. nivara*—Most of the chromosomes are median (2, 3, 4, 5, 7, 9 and 12). Only two chromosomes are submedian (1 and 11) and three others are subtelocentric (6, 8 and 10) (Fig. 3G). Among the hybrids, it has the longest chromosomes (Table 1).

15. F_1 hybrid of IR5 $\times$ *O. nivara*—Chromosomes 1, 3, 7 and 11 are metacentric, chromosomes 2, 4, 5, 8 and 9 are acrocentric, and chromosomes 6, 10 and 12 are subtelocentric (Fig. 3H).

Pachytene chromosomes of *O. nivara* $\times$ TNI, *O. nivara* $\times$ Dgwg, and *O. nivara* $\times$ IR8 were not analyzable because they were clumped. There were no PMCs available for the analysis of TKM-6 $\times$ *O. nivara* hybrid due to the non-viability of F_1 seeds.

Meiotic behavior of the parents and hybrids

Table 2 shows the chromosome behavior of the parents and hybrids at pachytene. TNI, IR5 and Mudgo $\times$ *O. nivara* did not show any abnormality at that stage. IR8 $\times$ *O. nivara* had the lowest number of normal cells among the parents and hybrids. This hybrid had as high as 23.5 percent of loose pairing, 5.9 percent reciprocal translocations, and it is the only cross with trivalent association of the chromosomes. Deficiency and inversion loops were observed only in *O. nivara* (3.2%), and unequal bivalent was observed only in Dgwg $\times$ *O. nivara* (3.3%). Fragments were also observed but found at low frequencies only in three of the hybrids (*O. nivara* $\times$ Mudgo, TNI $\times$ *O. nivara* and IR5 $\times$ *O. nivara*). The most common aberration was loose pairing.

Both parents and hybrids had low percentages of abnormalities at diakinesis and metaphase I. Table 3 shows that the range of normal cells was from 81.2 percent in IR5 to 95.8 percent in *O. nivara* among the parents, and from 82.3 percent in *O. nivara* $\times$ IR5 to 90.0 percent in *O. nivara* $\times$ TKM-6 among the hybrids.

One to two quadrivalents were found in all the hybrids, and only Mudgo and Dgwg did not show this kind of aberration among the parents. Trivalents, pentavalents, and hexavalents were also observed in some hybrids and in one of the parents (Dgwg), but with very low frequencies. *O. nivara* showed an association of eight chromosomes.

Some of the hybrids showed instances of aneuploid chromosome numbers

ranging from $2n-7$ to $2n+2$. In one cell out of 406 in *O. nivara* $\times$ Mudgo and one cell out of 514 in TN1 $\times$ *O. nivara*, only 17 to 21 chromosomes plus fragments were found. Some of the chromosomes were probably lost in the cytoplasm before metaphase I stage. Some cells of *O. nivara* and IR8 have 26 chromosomes. Five of the 12 F₁ hybrids had one to two cells with 26 chromosomes. The frequency of these aneuploid cells however, was very low in all cases.

Table 3. Chromosome behavior at diakinesis and metaphase I in the parents and F₁'s

Parents and hybrids	Total no. of cells observed	Percent cells observed						
		12 II	2-10 I + 7-11 II	8-10 II + 1-2 IV	9 II + VI	11-12 II + nucleolar bodies	13 II	Others*
<i>Oryza nivara</i>	334	95.8	1.5	1.5	—	0.3	0.6	0.3 ^d
Mudgo	307	93.8	6.2	—	—	—	—	—
TKM-6	163	84.7	10.4	4.9	—	—	—	—
Taichung Native 1	348	82.2	16.1	1.1	—	0.6	—	—
Dee-geo-woo-gen	401	84.5	9.5	—	0.2	5.7	—	—
IR8	215	88.3	10.2	0.5	—	0.5	0.5	—
IR5	388	81.2	17.8	0.5	—	0.5	—	—
<i>O. nivara</i> $\times$ Mudgo	406	82.5	10.8	3.9	0.2	2.0	—	0.2 ^a ; 0.2 ^e ; 0.2 ^g
<i>O. nivara</i> $\times$ TKM-6	380	90.0	6.3	1.8	—	1.3	—	0.5 ⁱ
<i>O. nivara</i> $\times$ TN1	401	85.5	9.5	3.0	—	1.5	0.2	0.2 ^c
<i>O. nivara</i> $\times$ Dgwg	494	82.4	9.7	3.0	0.2	3.0	—	0.8 ^a ; 0.2 ^c ; 0.2 ^b ; 0.4 ^j
<i>O. nivara</i> $\times$ IR8	281	88.6	9.9	0.4	—	—	0.4	0.4 ^a ; 0.4 ⁱ
<i>O. nivara</i> $\times$ IR5	361	82.3	16.3	1.1	—	—	—	0.3 ^e
Mudgo $\times$ <i>O. nivara</i>	442	87.8	2.7	0.2	—	—	—	0.2 ^b ; 0.2 ^k
TN1 $\times$ <i>O. nivara</i>	514	82.7	4.2	1.3	—	11.0	0.4	0.2 ^b ; 0.2 ^e
Dgwg $\times$ <i>O. nivara</i>	290	87.5	9.3	1.7	—	1.4	—	—
IR8 $\times$ <i>O. nivara</i>	336	88.1	7.4	2.1	—	1.5	0.3	0.3 ^f ; 0.3 ⁱ
IR5 $\times$ <i>O. nivara</i>	232	84.9	12.5	1.3	0.4	—	0.4	0.4 ⁱ

^a, 7-9 II + 2 I + 1-2 IV; ^b, 8-10 II + 1-5 I + III; ^c, 7 II + IV + VI; ^d, 8 II + VIII; ^e, 8-10 II + I + f's; ^f, 9 II + I + V; ^g, 9 II + IV + f's; ^h, 10 II; ⁱ, 11 II; ^j, 12 II + f; ^k, II forming a bridge; ^l, persistent nucleolus.

A bivalent forming a bridge at metaphase I (0.2%) was observed in Mudgo $\times$ *O. nivara*. Persistent nucleolus was observed in *O. nivara* $\times$ TKM-6 (0.5%) and *O. nivara* $\times$ IR8 (0.4%). Nucleolar bodies were also observed in most of the parents and hybrids among which TN1 $\times$ *O. nivara* showed the highest percentage (11.0%).

Table 4 shows the chromosome behavior at anaphase I and telophase I. The parents and hybrids had almost the same percentage of normal cells (85.9%–99.5%),

Table 4. Chromosome behavior at anaphase I and telophase I in the parents and their F_1 's

Parents and hybrids	Total no. of cells observed	Percent cells observed										
		Normal	Unequal segregation	Bridges (1-3)	Bridge + fragments	Bridge + lag-gard	Lag-gards (1-2)	Lagging fragments	Late disjunction	Early div. of chromosomes	Persistent nucleolus	With nucleolar bodies
<i>Oryza</i>												
<i>nivara</i>	149	85.9	—	3.4	—	—	1.3	—	9.4	—	—	—
Mudgo	163	87.7	—	—	—	0.6	1.2	—	0.6	9.8	—	—
TKM-6	162	87.7	0.6	—	—	—	—	—	—	11.7	—	—
Taichung Native 1	336	93.2	—	1.2	—	—	—	—	2.7	2.9	—	—
Dee-geo-woo-gen	195	96.9	—	—	—	—	—	—	3.1	—	—	—
IR8	207	99.5	—	0.5	—	—	—	—	—	—	—	—
IR5	143	97.9	—	0.7	—	—	—	—	1.4	—	—	—
<i>O. nivara</i>												
× Mudgo	314	86.3	—	3.8	0.3	—	5.4	0.3	2.9	0.3	—	0.6
<i>O. nivara</i>												
× TKM-6	412	93.9	—	0.7	—	0.5	0.7	—	1.7	0.7	0.2	1.5
<i>O. nivara</i>												
× TN1	503	98.0	—	1.2	—	—	0.2	—	0.6	—	—	—
<i>O. nivara</i>												
× Dgwig	248	89.9	0.4	4.0	0.4	—	1.6	0.4	0.8	2.4	—	—
<i>O. nivara</i>												
× IR8	156	92.9	—	1.9	0.6	—	1.3	0.6	1.9	0.6	—	—
<i>O. nivara</i>												
× IR5	149	85.9	—	6.7	0.7	—	1.3	—	4.0	1.3	—	—
Mudgo ×												
<i>O. nivara</i>	185	90.8	—	1.1	0.5	—	0.5	0.5	6.5	—	—	—
TN1 ×												
<i>O. nivara</i>	183	61.2	—	1.1	—	—	1.6	0.5	2.2	—	—	33.3
Dgwig ×												
<i>O. nivara</i>	185	96.2	0.5	2.2	—	—	—	—	1.1	—	—	—
IR8 ×												
<i>O. nivara</i>	244	96.7	—	—	—	—	—	—	2.5	—	—	0.8
IR5 ×												
<i>O. nivara</i>	238	87.0	0.4	3.8	—	—	0.4	—	4.2	4.2	—	—

except the hybrid of TN1 × *O. nivara*, which produced 61.0 percent normal cells. This particular cross had as high as 33.3 percent of nucleolar bodies in its cytoplasm. Aberrations that occurred most frequently in both parents and hybrids were late disjunction and bridges.

Laggards were observed in two of the parents (*O. nivara* and Mudgo) and occurred at 1.3 and 1.2 percent, respectively. Among the hybrids, *O. nivara* × Mudgo had the highest frequency of laggards (5.4%) and the lowest frequency is in two F₁'s Dgwg × *O. nivara* and IR8 × *O. nivara*. Unequal segregation of chromosomes occurred only in TKM-6 (0.6%), *O. nivara* × Dgwg (0.4%), Dgwg × *O. nivara* (0.5%), and IR5 × *O. nivara* (0.4%).

The major nucleolus persisted up to anaphase I in one cell of *O. nivara* × TKM-6. The nucleolar bodies disappeared at late metaphase in most of the parents and hybrids but they persisted in *O. nivara* × Mudgo (0.6%), *O. nivara* × TKM-6 (1.5%), TN1 × *O. nivara* (33.3%), and IR8 × *O. nivara* (0.8%).

Pollen and spikelet sterility

Pollen and spikelet sterility in F₁ hybrids and their parents are shown in Table 5. The F₁ hybrid of *O. nivara* × Dgwg had the highest mean percentage for both pollen and spikelet sterility (64.1% and 58.1%, respectively). Mudgo was the least pollen-sterile among the parents (15.1%) and *O. nivara* × IR5 was least pollen-sterile among the hybrids (18.6%). For spikelet sterility, TKM-6 had the lowest mean (30.1%) among the parents, and *O. nivara* × IR8 (32.5%) was the lowest among the hybrids.

Table 5. Mean percentage of pollen and spikelet sterility in the parents and F₁ hybrids

<i>O. nivara</i>	<i>O. sativa</i> varieties					
	Mudgo	TKM-6	TN1	Dgwg	IR8	IR5
<i>O. nivara</i> × <i>O. sativa</i> cv.	24.8 ^a	30.9	49.1*	64.1*	37.7*	18.6
	33.5 ^b	40.7	44.4	58.1*	32.5	38.9
<i>O. sativa</i> cv. × <i>O. nivara</i>	26.7 ^a	—	35.6	20.2	21.2	25.8
	33.7 ^b	—	40.5	43.4	40.3	38.0
Parents	45.2 ^a	15.1	22.7	20.0**	25.9**	16.0**
	39.5 ^b	37.4	30.1	42.5	53.8	48.1**
						43.2

^a Mean percent pollen sterility.

^b Mean percent spikelet sterility.

* Significantly different from the reciprocal cross at 5%.

** Significantly different from the direct cross at 5%.

It was further observed that the mean pollen sterility of *O. nivara* × TN1, *O. nivara* × Dgwg and *O. nivara* × IR8 hybrids were significantly different from their reciprocal crosses. All the other reciprocal crosses had no significant differences.

O. nivara and two F₁ hybrids (*O. nivara* × TN1 and *O. nivara* × Dgwg) were partially pollen sterile (40 to 65% sterility). All the other hybrids were fertile (less than 40% sterility).

In most crosses and parents, spikelet sterility was higher than pollen sterility.

This may be due to external factors such as heavy rains and pest attacks, which could affect seed set.

Unfortunately, spikelet seed set of F_1 's was not recorded. However, about 70 percent of the spikelets set seed. This indicates that the strain of *O. nivara* used in this study is cross-compatible with the six *O. sativa* cultivars.

Discussion

The chromomeric pattern, chromatin length, and degree of symmetry vary among the *O. sativa* varieties, between the *O. nivara* strain and *O. sativa* cultivars, between the parents and hybrids, and also between the direct cross and its reciprocal. The differences in their chromomeric pattern might be due to the coalescence of two or more microchromomeres to form a macrochromomere or knob and sometimes resulting to a heterochromatic region. Hence, the knob or heterochromatic region found in the direct cross could be equivalent to two or more microchromomeres in the reciprocal cross or vice versa. Since the pairing of chromosomes was essentially normal in the F_1 hybrids, the same interpretation may apply to the differences between the parents and hybrids, between the cultivated and wild species, and between the *O. sativa* cultivars. The above situation is similar to that observed by Ourecky (1963) and Misra and Shastri (1967). Pokmeljnych (1974) has also pointed out that the size and position of knobs and macrochromomeres depend on the number and size of constituent chromomeres and the length of euchromatic zones separating the chromomeres.

The large differences in the chromatin length between the parents and hybrids and even between the direct and reciprocal hybrids might be due to the differential rate of contraction of the chromosome arms as reported by Misra and Shastri (1967). They pointed out that the differences in chromatin length cannot be taken as indication of real differences because of condensation differences.

Though all the materials studied vary in their arm ratios, all three types of chromosomes—median, submedian, and subtelocentric—were found in the complement of each of the parents and hybrids. Most of the parents and hybrids have seven submedian (chromosome number 1, 4, 5, 8, 9, 11 and 12), three median (number 2, 3 and 7), and two subtelocentric chromosomes (number 6 and 10). Our findings agree to those reported by Shastri *et al.* (1960) except for chromosome 2, which is classified as median in the present study and considered as submedian by Shastri *et al.* (1960). On the other hand, our observations differ from those of Das and Shastri (1963) and Misra and Shastri (1967) because they reported only two types of chromosomes, median and submedian. Our observations also differ from the reports of Chu (1967) and Sur (1975) in which they observed eight submedian, three median and one subtelocentric types. Khan (1974) found 11 submedian and one subtelocentric chromosomes. Like chromatin length, the variability in the arm ratios among the rice strains studied could be due to the differential rate of contraction in the chromosome arms.

Pairing of chromosomes from pachytene to metaphase I stage in all of the F_1 hybrids is essentially normal. The minor meiotic abnormalities observed in the par-

ents and hybrids are the same. The types and frequencies of meiotic aberrations observed in the interspecific hybrids were no greater than those found in interracial hybrids in *O. sativa* (Demeterio *et al.* 1965, Engle *et al.* 1969). These indicate that the strain of *O. nivara* most likely has the same genome as the *O. sativa* cultivars. Hence, Acc. 101508 of *O. nivara* and *O. sativa* can be considered as closely related.

The partial sterility observed in two hybrids (*O. nivara* $\times$ Dgwg and *O. nivara* $\times$ TN1) and the *O. nivara* parent could not be accounted for by the meiotic aberrations, because similar abnormalities with nearly the same frequencies were also found in the fertile hybrids and parents.

Partial sterility was commonly observed in the *O. nivara* parent. However, because this characteristic was not transmitted to all of the hybrids, sterility in the two partially sterile F_1 's cannot be considered as due to genes inherited from *O. nivara*. Similar observations in the interspecific hybrids were reported by Richharia (1960). The works of Morinaga and Kuriyama (1956, 1957) further showed that sterility in the interspecific hybrids might not be entirely caused by structural differences in the chromosomes but may be genically controlled. Complex genic interactions could also contribute to partial sterility.

About 70 percent of the artificially cross-pollinated spikelets in our six reciprocal crosses set seed. Therefore, it can be inferred that Accession 101508 of *O. nivara* is cross-compatible with all the six cultivars of *O. sativa*. On the other hand, Ng Quat (1977) found other accessions of *O. nivara*, which were not as cross-compatible with *O. sativa* cultivars as Accession 101508. In view of its unique virus resistance and high affinity with *O. sativa*, Accession 101508 may not be a typical strain of *O. nivara*.

Summary

IRRI Accession 101508 of the wild species *Oryza nivara* Sharma *et* Shastry was crossed directly and reciprocally to six varieties of the cultivated species, *O. sativa* L. This accession was cross-compatible with the six *O. sativa* cultivars.

Each of the parents and hybrids have median, submedian, and subtelocentric chromosomes. A combination of three median (chromosome number 2, 3 and 7), seven submedian (number 1, 4, 5, 8, 9, 11 and 12), and two subtelocentric chromosomes (number 6 and 10) were the most common set. The parents and hybrids differed markedly in their chromomeric pattern, chromatin length, and arm ratio.

The most frequent chromosomal aberrations observed were loose pairing at pachytene, univalents, and quadrivalents at diakinesis and metaphase I, bridges and late disjunction at anaphase I, and bridges and laggards at telophase I.

Based at pollen and spikelet counts, only *O. nivara*, *O. nivara* $\times$ TN1 and *O. nivara* $\times$ Dgwg were partially sterile. The other F_1 hybrids were fertile. The difference between the pollen and spikelet sterilities in most hybrids and parents may be due to environmental effects. There was no direct relationship between the meiotic aberrations observed and the sterility of the F_1 plants.

Chromosome pairing was essentially normal in all F_1 plants and most of

them are fertile, indicating that the *O. nivara* accession and the *O. sativa* cultivars have the same genome composition (AA). There is close affinity between IRRI Acc. 101508 and the *O. sativa* cultivars.

References

- Chang, T. T. 1964. Present Knowledge of Rice Genetics and Cytogenetics. Tech. Bull. 1. Int. Rice Res. Inst., Los Baños, Laguna, Philippines. 96 p.
- 1976, The origin, evolution, cultivation, dissemination and diversification of Asian and African rices. *Euphytica* **25**: 425-441.
- Chu, Y. E. 1967. Pachytene analysis and observations of chromosome association in haploid rice. *Cytologia* **32**: 87-95.
- Das, D. C. and Shastry, S. V. S. 1963. Pachytene analysis in *Oryza* VI. Karyomorphology of *O. perennis* Moench. *Cytologia* **28**: 36-43.
- Demeterio, E. G. V., Ando, S., Ramirez, D. A. and Chang, T. T. 1965. Cytological and histological studies of sterility in F_1 hybrids of twelve indica-japonica crosses. *Phil. Agric.* **49**: 248-259.
- Dolores, R. C., Chang, T. T. and Ramirez, D. A. 1975. Cytogenetics of sterility in F_2 hybrids of Indica $\times$ Indica and Indica $\times$ Javanica varieties of rice (*Oryza sativa* L.). *Cytologia* **40**: 639-647.
- Engle, L. M., Chang, T. T. and Ramirez, D. A. 1969. The cytogenetics of sterility in F_1 hybrids of Indica $\times$ Indica and Indica $\times$ Javanica varieties of rice (*Oryza sativa* L.). *Phil. Agric.* **53**: 289-307.
- Khan, S. H. 1974. The identification of a complete set of twelve primary trisomics in rice (*Oryza sativa* L.). Diss. Abst. **B35** (6): 2813-2814-B.
- Ling, K. C., Aguiero, V. M. and Lee, S. R. 1970. A mass screening method for testing resistance to grassy stunt disease of rice. *Plt. Dis. Repr.* **54**: 565-569.
- Misra, R. N. and Shastry, S. V. S. 1967. Pachytene analysis in *Oryza* VIII. Chromosome morphology and karyotypic variation in *O. sativa*. *Ind. J. Genet. Pl. Breed.* **27**: 349-368.
- Morinaga, T. and Kuriyama, H. 1956. Cytogenetical studies on *Oryza sativa* L. VIII. The F_1 hybrid of *O. sativa* L. and *O. cubensis* Ekman. *Japan. J. Breed.* **6**: 133-141.
- and — 1957. Cytogenetical studies on *Oryza sativa* L. IV. The F_1 hybrid of *O. sativa* L. and *O. glaberrima* Steud. *Japan. J. Breed.* **7**: 57-65.
- Nayar, N. M. 1973. Origin and cytogenetics of rice. *Adv. Gen.* **17**: 153-292.
- Ng, Q. N. 1977. A biosystematic study of the Asian wild and cultivated taxa in the "sativa species-complex" of genus *Oryza*. Unpublished Ph. D. Thesis, University of Birmingham, U. K.
- Ourecky, D. K. 1963. Pachytene chromosome morphology in *Cynodon dactylon* (L.) Pers. *Nucleus* **6**: 63-82.
- Pokmeljnych, G. A. 1974. On the nature of heterochromatic knob regions in maize chromosomes. I. Comparative study of chromosomes of somatic cells stained with Giemsa dye and pachytene chromosomes of a maize line characterized by a multitude of knobs. *Genetika* **10**: 14-24.
- Richharia, R. H. 1960. Origins of cultivated rices. *Ind. J. Genet. Pl. Breed.* **20**: 1-14.
- Sharma, S. D. and Shastry, S. V. S. 1965. Taxonomic studies in genus *Oryza* L. III. *O. rufipogon* Griff. *sensu stricto* and *O. nivara* Sharma *et* Shastry *nom. nov.* *Ind. J. Gen. Pl. Breed.* **25**: 157-167.
- Shastry, S. V. S., Rango Rao, D. R. and Misra, R. N. 1960. Pachytene analysis in *Oryza* I. Chromosome morphology in *O. sativa*. *Ind. J. Genet. Pl. Breed.* **20**: 15-21.
- Sur, S. C. 1975. Identification and cytogenetic studies of primary trisomics in rice (*Oryza sativa* L.). Unpublished Ph. D. Thesis, University of the Philippines at Los Baños, Philippines.