

PRIMARY TRISOMICS OF RICE: ORIGIN, MORPHOLOGY, CYTOLOGY AND USE IN LINKAGE MAPPING

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ABSTRACT

Twelve primary trisomics of *Oryza sativa* L. were isolated from the progenies of spontaneous triploids and were transferred by backcrossing to the genetic background of IR36, a widely grown high yielding rice variety. Eleven trisomics can be identified morphologically from one another and from diploids. However, triplo 11 is difficult to distinguish from diploid sibs.—The extra chromosome of each trisomic was identified cytologically at pachytene stage of meiosis, and the chromosomes were numbered according to their length at this stage. The major distinguishing features of each pachytene chromosome were re-described.—The female transmission rates varied from 15.5% for triplo 1, the longest chromosome, to 43.9% for triplo 12, the shortest chromosome. Seven of the 12 primary trisomics transmitted the extra chromosome through the male. The low level of chromosomal imbalance tolerated by rice and other evidence are interpreted to indicate that this species is a basic diploid.—Genetic segregation for 22 marker genes in the trisomic progenies was studied. Of a possible 264 combinations, involving 22 genes and 12 trisomics, 120 were examined. Marker genes for each of the 12 chromosomes were identified. The results helped establish associations between linkage groups and cytologically identifiable chromosomes of rice for the first time. Relationships between various systems of numbering chromosomes, trisomics, linkage groups and marker genes are described, and a revised linkage map of rice is presented.

RICE is the principal food of more than half of mankind; yet, our knowledge of its genetics lags far behind that of other major food crops such as wheat, maize, barley and tomato. Twelve linkage groups corresponding to the haploid chromosome number of rice were suggested by NAGAO and TAKAHASHI (1963). However, these linkage groups have not been associated with the cytologically identifiable chromosomes, and their independence has not been tested.

Primary trisomics from the progenies of rice triploids were obtained by RAMANUJAM (1937), YUNOKI and MASUYAMA (1945), KARIBASAPPA (1961), KATAYAMA (1963), SEN (1965), HU (1968), IWATA, OMURA and NAKAGAHARA (1970) and WATANABE and KOGA (1975). However, none of these workers have identified the extra chromosomes of the trisomics cytologically, and only IWATA and OMURA (1975) have utilized their trisomics in genetic investigations.

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IWATA and OMURA (1975) determined the associations between eight of their primary trisomics and marker genes. By trisomic tests, they showed that three linkage groups previously considered independent were, in fact, located on the same chromosome (IWATA and OMURA 1976). However, genetic studies revealed that the trisomic series established by IWATA, OMURA and NAKAGAHARA (1970) contained trisomics for nine chromosomes only. Independence of all of the linkage groups, therefore, could not be tested.

This study was undertaken to establish all of the primary trisomics of rice, to identify cytologically the extra chromosome of each trisomic and to utilize these trisomics in testing the independence of each linkage group and associating linkage groups with the respective chromosomes.

ORIGIN OF TRISOMICS

A triploid rice plant was found in a pedigree nursery planted in January 1969 on the experimental farm of the International Rice Research Institute (IRRI), Los Baños. The semidwarf experimental breeding line IR841-36-2-2, in which the triploid plant was found, originated from the cross of another breeding line IR262-43-8 and a high-grain-quality Thai variety Khao Dawk Mali 4-2-105. The triploid plant was very distinct, as it was slightly taller and had larger and sterile spikelets with awns. The cytological examination of the plant in June 1969 revealed 36 chromosomes. The plant was uprooted, pruned and divided into several clones. New tillers were pollinated with pollen from IR22, a bacterial blight-resistant variety. The 92 seeds obtained were planted in the greenhouse in January 1971. Of those, 81 germinated; however, nine seedlings were too weak and deformed and died at an early age. The surviving 72 plants were remaining plants had 2, 3, 4 or 5 extra chromosomes (Table 1). This chromosome distribution agrees well with the chromosome distribution observed in the progenies of triploids by other investigators (Table 1). Individuals with $2n + 1$ and $2n + 2$ chromosomes predominate in the progenies of rice triploids studied to date, and the maximum number of extra chromosomes tolerated by rice is

TABLE 1

Chromosome numbers in the progenies of autotriploid plants of rice

Reference	Rice plants with given chromosome number							Total
	24	25	26	27	28	29	30	
RAMANUJAM (1937)	6	9	8	9	11	4	3	50
	12.0	18.0	16.0	18.0	22.0	8.0	6.0	100
KATAYAMA (1963)	3	6	8	1	2	1		21
	14.3	28.5	38.1	4.8	9.5	4.8		100
HU (1968)	20	42	61	14	1	0	1	139
	14.4	30.2	43.9	10.1	0.7	0	0.7	100
WATANABE <i>et al.</i> (1969)	6	35	31	12	2	1		87
	6.9	40.2	35.6	13.8	2.3	1.1		100
This study	2	20	25	14	8	3		72
	2.8	27.8	34.7	19.4	11.1	4.2		100

First value in each pair is number of rice plants. Second value is percent of total.

six. Tolerance limits for extra chromosomes in rice are narrow; very few rice plants with more than four extra chromosomes have been obtained.

Twenty-five trisomic plants were categorized into 14 morphological groups. Open-pollinated seeds from one plant of each of the 14 groups, four plants of the $2n + 2$ group and two plants of the $2n + 4$ group were planted in the greenhouse in June 1973. The progenies were again categorized into 14 distinct trisomic lines. Because infestation of the brown plant hopper was serious during 1971–1972, representative $2n + 1$ plants of each line were pollinated with pollen from brown plant hopper-resistant line IR3265-193-3 to avoid infestation on the trisomic progenies. On the basis of cytological examination, 11 of the 14 trisomic lines isolated were classified as primary trisomics, and the remainder were classified as secondary trisomics. Another triploid rice plant was found in 1974 in the F_2 population of IR3478, a topcross of three breeding lines. This triploid plant was clonally propagated and pollinated with pollen from IR3265-193-3. The pollinations yielded a progeny of 26 plants, which included previously identified trisomics as well as two sterile plants that had $2n + 1$ and $2n + 2$ chromosomes, respectively. The two plants were morphologically different from the 11 primary trisomics. The $2n + 1$ plant was clonally propagated as the 12th primary trisomic. No progenies could be obtained even with repeated pollination of this trisomic with pollen from diploid parents. Another trisomic plant resembling this trisomic was isolated from the progeny of a triploid plant of IR36. This plant produced a few seeds when pollinated with pollen of IR36. After 1976, all 12 primary trisomics were transferred to IR36 background by five backcrosses. IR36 has short growth duration and multiple disease and insect resistance and is grown widely in Asia.

RICE KARYOTYPE

Before the extra chromosomes of each of the primary trisomics could be cytologically identified, it was necessary to adopt one of the three proposed systems for numbering rice chromosomes. ISHII and MITSUKURI (1960) and HU (1964) measured the somatic chromosomes of rice, and the longest chromosome of the complement was numbered 1, the second longest as 2 and so on. However, the somatic chromosomes of rice are very small and lack any distinguishing features. Barring one or two chromosomes, it is impossible to identify individual members of the somatic complement. A variation of this system was proposed by KURATA and OMURA (1978), who numbered the somatic chromosomes as *K1* to *K12*, *K1* being the longest and *K12* the shortest. They pointed out the differential staining features of chromosome arms after staining with Giemsa.

NISHIMURA (1961) assigned numbers *I* to *XII* to the rice chromosomes involved in translocations in the order in which the translocations were discovered. Later on, the roman numerals were changed to arabic numerals. NISHIMURA's system of numbering chromosomes is not based on cytological identification and could not be utilized for cytological identification of the extra chromosome of the trisomics.

In the third numbering system proposed by SHASTRY, RANGA RAO and MISRA (1960), the chromosomes are numbered in decreasing order of length at pachy-

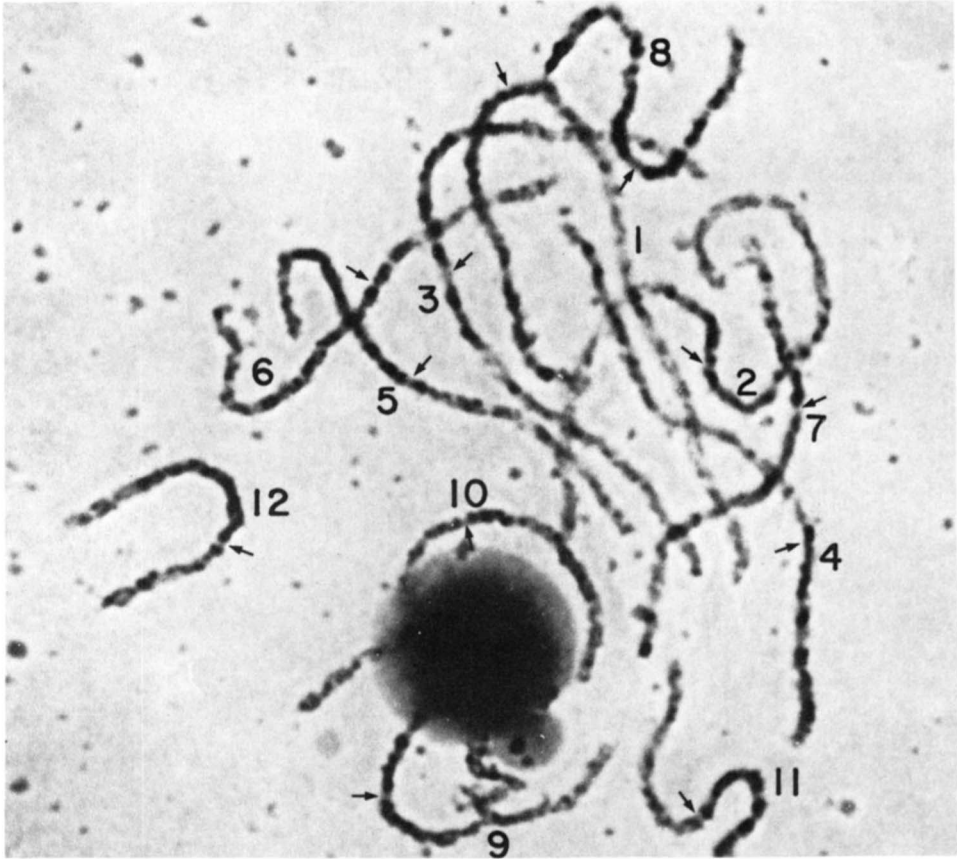


FIGURE 1.—A photomicrograph of pachytene chromosome complement of rice. Centromere of each chromosome is indicated by an arrow.

tene stage of meiosis. The longest chromosome is called chromosome 1, the next longest, chromosome 2 and so on. We adopted this system of numbering for identifying the extra chromosomes of each of the 12 primary trisomics. A chromosome-numbering system based on pachytene length has also been adopted in other genetically well-known species such as maize (MCCLINTOCK 1929) and tomato (BARTON 1950; RICK and BARTON 1954).

The individual pachytene chromosomes of rice can easily be identified in cells in which chromosomes are well spread and have optimal staining. In addition to length and centromere position, size, number, stainability and position of chromomeres are helpful in identification. For example the chromomeres of short arms of chromosomes 4 and 11 stain darkly, and these two arms appear almost entirely heterochromatic. Similarly, chromosome 8 is easily identified because of its distinctly darkly stained chromomeres. Chromosome 9 is the nucleolar organizing chromosome, but some nucleolar organizing activity is also shown by chromosomes 1 and 11, and chromosome 10 is quite frequently attached to the nucleolus. The entire pachytene chromosome complement of rice is shown in Figure 1. The rice karyotype with the distinguishing features of each chromo-

some is shown in Figure 2. The centromere location of some members of the complement is difficult to determine with certainty. However, pachytene trivalent configurations in the trisomics were helpful in delimiting the position of the centromere. The main features of the pachytene chromosomes are given in Table 2 and supplement the description already published by SHASTRY, RANGA RAO and MISRA (1960).

CYTOLOGICAL IDENTIFICATION OF TRISOMICS

The distinguishing features of the individual members of the complement given in the last section were utilized in identifying the extra chromosome of each trisomic. Several trivalent associations of each trisomic were observed at pachytene stage. By and large, two by two pairing was observed. The univalent portions were sometimes paired nonhomologously. The trisomic having chromosome 1 in triplicate was called triplo 1, that having an extra chromosome 2 was called triplo 2 and so on. A representative pachytene trivalent association of each trisomic is shown in Figure 3.

It should be noted that a small nucleolus is associated with the extra chromosome in triplo 2. In triplo 12, in addition to the main nucleolus, several small nucleoli were also observed. The number of these nucleoli varied from cell to cell.

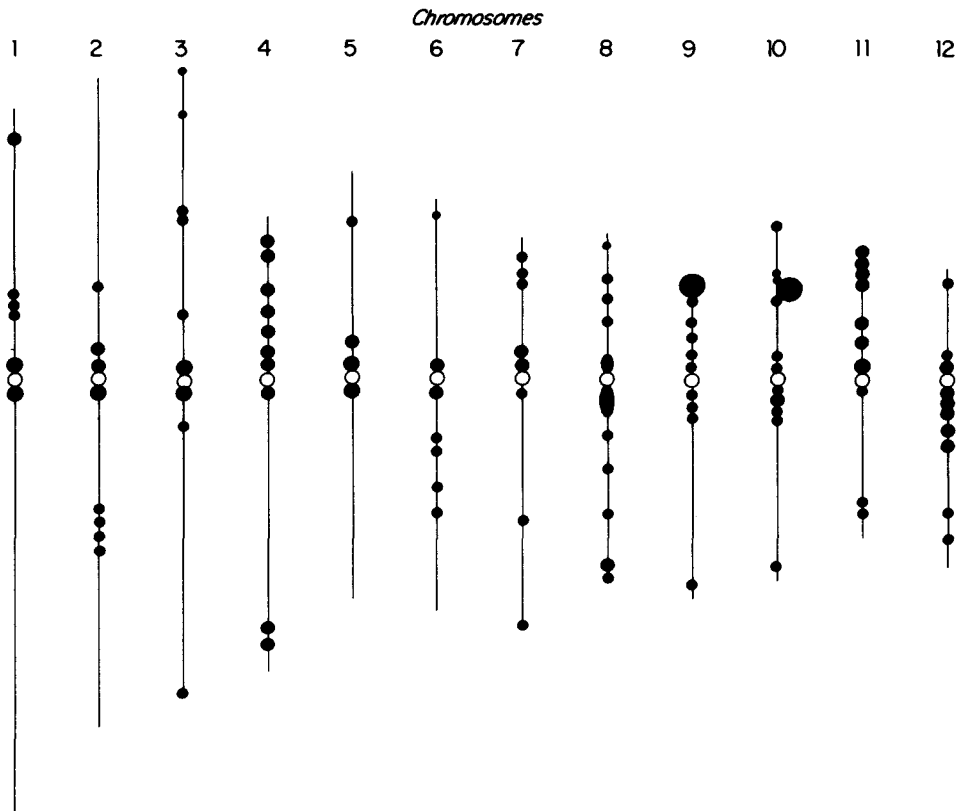


FIGURE 2.—Idiogram of rice pachytene chromosomes ($\times 2000$).

TABLE 2

Diagnostic cytological features of rice pachytene chromosomes

Chromosome	Centromere position	Chromomeres						Remarks
		Centric		Median		Terminal		
		L	S	L	S	L	S	
1	Submedian	1	1		4			Occasional puff-like structure on long arm
2	Median	1	2	4	1			
3	Median	1	1	1	4	1	1	
4	Submedian	1	2	2	5			Short arm largely heterochromatic
5	Median	1	2		1			
6	Median	1	1	4	1			
7	Submedian	1	2	1	3	1		
8	Median	1	1	3	4	2		Chromomeres stain darkly
9	Subterminal	3	2	1	2		1	Nucleolus organizing chromosome
10	Submedian	4	2	1			1	Sometimes attached to the nucleolus
11	Median	1	1	2	2		4	Short arm largely heterochromatic
12	Submedian	2	1	4	3			

L, long arm; S, short arm.

MORPHOLOGY AND REPRODUCTIVE FEATURES OF TRISOMICS

Primary trisomics of rice differ from the normal diploids in numerous characters. Trisomics for the long chromosomes are more distinct from the diploid as well as from each other. They are also slower in growth. This is expected as the longer chromosomes cause more imbalance than the shorter ones. Some, such as triplo 1 and triplo 8, can be distinguished at seedling stage (two- to three-leaf stage). Triplo 1 seedlings have narrow, light green leaves with mottled appearance. Triplo 8 seedlings have narrow, dark green, rolled leaves. Triplo 2, triplo 3, triplo 4, triplo 5, triplo 6, triplo 7 and triplo 9 can be distinguished from their diploid sibs as well as from each other, 2-3 wk after transplanting. Their growth rates are slower, and they have distinct leaf features. At seedling stage triplo 10, triplo 11 and triplo 12 are difficult to distinguish as their growth rates are almost normal. At flowering stage, however, triplo 10 and triplo 12 can easily be distinguished. Triplo 10 has finer foliage and stems and narrow slender grains. Triplo 12 is about 20% taller than its diploid sibs and has a somewhat spreading habit. We have not been able to identify triplo 11 with certainty at any stage. Therefore, cytological examination is necessary to identify the $2n + 1$ plants in the progenies of triplo 11. Occasionally we have found that triplo 11 plants have brownish glumes at the time of anthesis.

Trisomics for the longer chromosomes (triplo 1 to triplo 4) have very low seed fertility. As the data in Table 3 show, triplo 1, triplo 2 and triplo 3 give low seed set when open pollinated. Triplo 4 is completely self-sterile. We have never observed any seed set in the open-pollinated plants of true breeding stocks of triplo 4. In the BC_1 progenies of triplo 4 and *dl* where triplo 4 plants were surrounded by diploid sibs, a few seeds were formed on the triplo 4 plants presumably because of outcrossing. The pollen fertility of triplo 4 plants is fairly

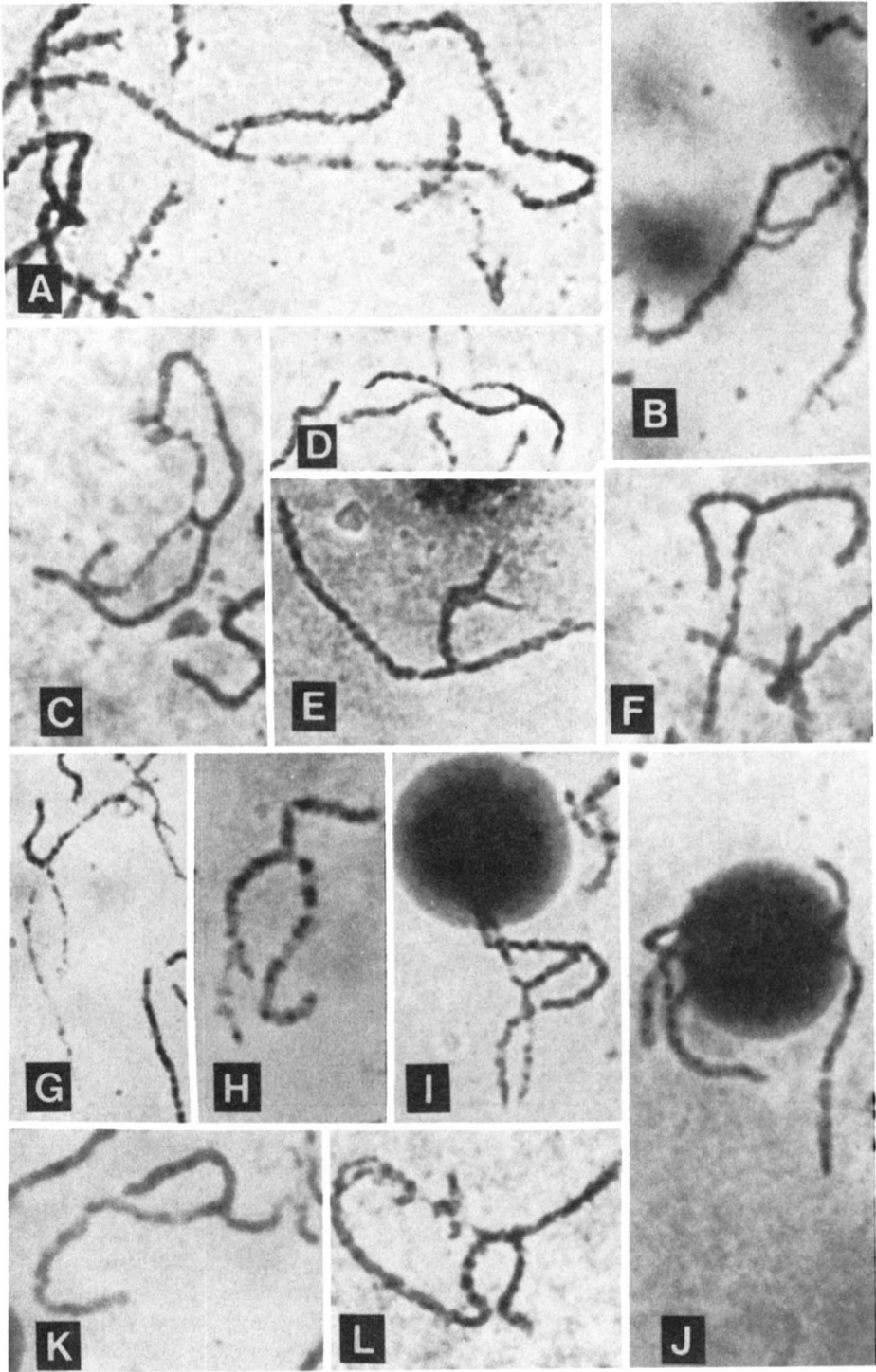


FIGURE 3.—Photomicrographs of rice chromosomes at pachytene stage of meiosis. Each figure shows the trivalent configuration from a trisomic complement. A, Chromosome 1; B, chromosome 2; C, chromosome 3; D, chromosome 4; E, chromosome 5; F, chromosome 6; G, chromosome 7; H, chromosome 8; I, chromosome 9; J, chromosome 10; K, chromosome 11; L, chromosome 12 (all $\times 1600$).

TABLE 3
Morphological and reproductive features of primary trisomics of rice

Trisomic	Plant height (cm)	Leaf length (cm)	Leaf width (mm)	Ligule length (mm)	Panicle length (cm)	Spikelets per panicle	Fertile spikelets (%)	Grain length (mm)	Grain width (mm)	100-grain weight (g)
1	52.0	15.7	6.0	4.7	17.5	51.7	11.7	9.1	2.3	1.7
2	64.0	19.8	9.0	11.0	21.8	128.1	1.3	8.1	2.7	1.7
3	68.5	33.8	11.8	30.0	21.3	79.0	6.8	8.8	2.6	2.0
4	48.0	27.0	11.0	14.0	18.2	88.0	0.0	8.2	2.8	1.4
5	66.0	24.4	11.3	5.4	15.9	75.2	61.4	7.4	2.4	1.7
6	69.6	39.1	11.6	19.1	21.7	67.0	76.6	10.8	2.3	2.0
7	62.7	35.1	11.6	10.6	23.0	80.2	46.4	9.9	2.0	1.8
8	56.5	23.6	4.8	8.5	14.6	71.2	78.4	8.2	2.6	2.0
9	84.6	33.5	13.0	14.6	23.3	135.8	70.2	9.9	2.5	2.6
10	74.1	33.0	12.4	15.1	23.1	100.8	81.5	9.9	1.9	1.7
11	78.0	38.1	12.7	17.3	26.2	119.3	88.3	10.0	2.5	2.3
12	100.7	36.4	12.0	24.0	23.7	116.2	85.4	8.8	2.0	1.6
IR36	82.3	41.2	15.5	17.1	23.2	138.5	96.2	9.5	2.4	2.0

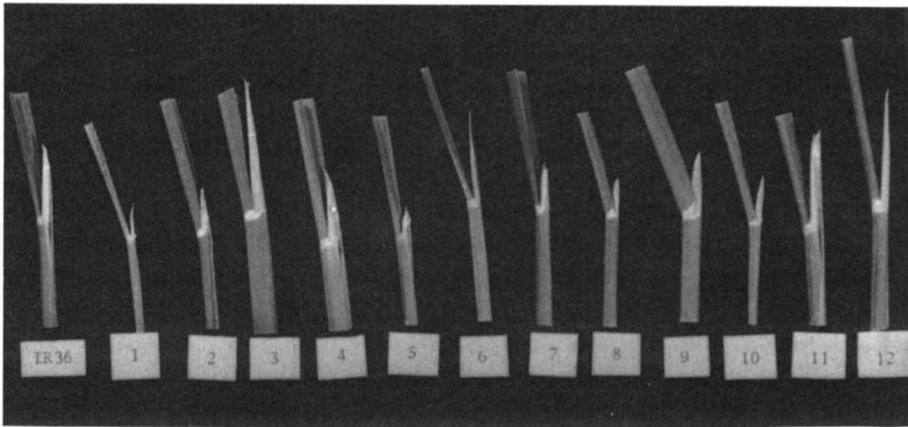


FIGURE 4.—Segments of uppermost leaves of IR36 and primary trisomics of rice showing differences in ligule length. Numbers below the leaves correspond to the respective trisomics.

good, but the anthers fail to dehisce. This probably accounts for the complete self-sterility. The remaining trisomics produce abundant seed, although most of them have varying sterility (Table 3).

Ligule length can be used in distinguishing the different trisomics (Figure 4). Triplo 1, triplo 5 and triplo 8 have much reduced ligules, whereas the ligules of triplo 3, triplo 6 and triplo 12 are longer than those of the diploid (Table 3).

The grain size and shape of each trisomic are also characteristic (Figure 5). The grains of triplo 1 are slender and somewhat triangular, and the glumes do not close properly. Triplo 2, triplo 4, triplo 5 and triplo 8 have short grains. The grains of triplo 6 and triplo 10 are longer than those of the diploid (Table 3). Long awns are a constant feature of triplo 3. One of the trisomics of most of the other trisomic series has been reported to be awned [trisomic B of IWATA, OMURA and NAKAGAHARA (1970), trisomic E of WATANABE and KOGA (1975) and trisomic awned of HU (1968)]. Some of the grains of triplo 7 and 12 have small trip awns (Figure 5), but IR36 is completely awnless. The grains of triplo 9 are largest (Table 3).

The outstanding features of each trisomic are enumerated as follows.

Triplo 1 (grassy): Triplo 1 is a slow growing trisomic with reduced height and high panicle sterility. It has slender grains of somewhat triangular appearance. The tips of the lemma and palea are often open, and the kernel is partially exposed. The trisomic's narrow and pale green leaves give it a grassy appearance (Figure 6). It flowers much later than the diploid sibs and other trisomics.

Triplo 2 (dwarf): Plant height and tiller number of triplo 2 are reduced to 75% of the normal. This trisomic has short spikelets with longer empty glumes, which are twice the length of those in the normal. The lemma and palea are sometimes open at the tips. Triplo 2 has short anthers and reduced filament. The plants are characterized by high self-sterility but produce abundant seed when crossed with a diploid. It has dark green and short leaves (Table 3), which are often twisted near the base and have short ligules.

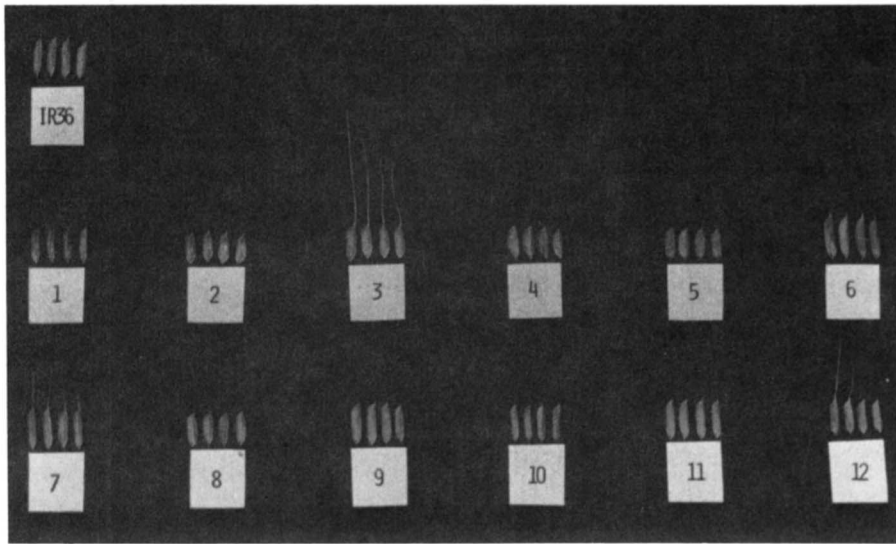


FIGURE 5.—Grains of IR36 and primary trisomics of rice. Numbers below the grains correspond to the respective trisomics.

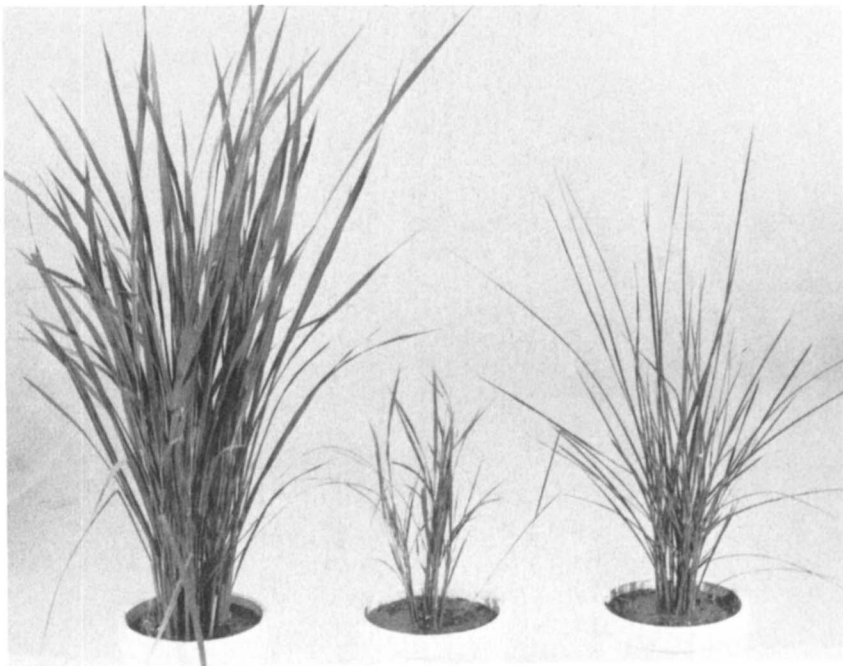


FIGURE 6.—Plants of IR36 (left), triplo 1 (center) and triplo 8 (right).

Triplo 3 (awned): The most distinctive feature of triplo 3 is the presence of awns on all grains. Grain length is reduced, however. This trisomic has thick, semirolled dark green leaves with long ligules. Plant height is reduced, and growth rate is slower. However, the tillers are increased. It flowers earlier but is

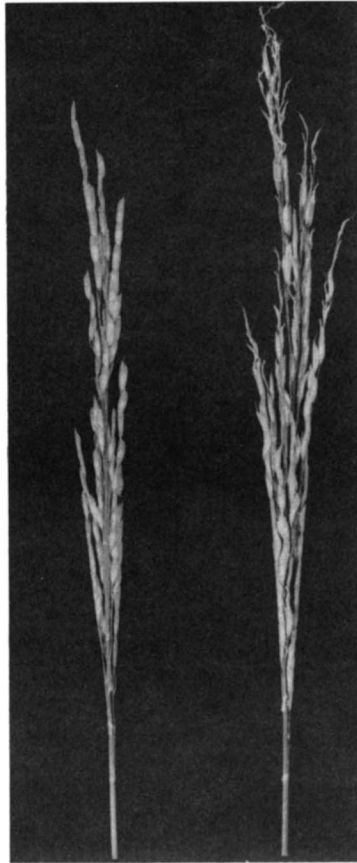


FIGURE 7.—Panicles of IR36 (left) and triplo 6 (right). Several florets in the panicle of triplo 6 are degenerated.

observed at different growth stages, and chromosome counts were made in June through July 1971. The population had two diploid plants and 20 trisomics. The highly self-sterile (Table 3).

Triplo 4 (sterile): Triplo 4 is the shortest, with reduced tiller number. It has short, dark green and thick leathery leaves with prominent midribs. The panicles are incompletely exerted. Spikelets are short and cleistogamous. This trisomic is completely self-sterile.

Triplo 5 (twisted leaf): Triplo 5 is also short in stature. It has short twisted leaves with fine hairs. The leaves appear more hairy than those of a disomic. The ligule is very short (Figure 4). This trisomic has short compact panicles with high fertility.

Triplo 6 (bushy): The profuse tillering habit of triplo 6 gives it a bushy appearance. It has lighter green foliage, especially at booting stage. This trisomic has long slender grains and high seed fertility. Degenerated spikelets at the tips of panicles are a unique feature of triplo 6 (Figure 7).

Triplo 7 (narrow leaf): Triplo 7 has narrow, dark green and semirolled leaves, which give it a characteristic appearance. The ligule is short. This trisomic is low

tillering with incompletely exerted and somewhat lax panicles, which are partially fertile. Some grains have short awns (Figure 5).

Triplo 8 (rolled leaf): Triplo 8 is very slow growing at seedling stage and is easily identified because of its narrow, dark green, rolled leaves (Figure 6) and short ligules (Figure 4). This trisomic has short, dense and fully exerted panicles. The grains are short and bold with partial fertility.

Triplo 9 (stout): Triplo 9 is characterized by thick, dark green leaves and thick stems that give it a stout appearance. Leaf blades are slightly folded. The plants have a somewhat spreading habit. This trisomic has the largest spikelets among the trisomics and the highest 100-grain weight (Table 3).

Triplo 10 (short grain): Triplo 10 has fine foliage and stems at flowering stage. The leaves are erect with hairy auricles. The grains are slender and slightly longer. This trisomic is fully fertile. It can be distinguished only after flowering.

Triplo 11 (pseudo-normal): Triplo 11 is morphologically indistinguishable from the diploid sibs, although the trisomic plants in the population tend to be slightly reduced in vigor and late in flowering. It is fully fertile.

Triplo 12 (tall): Triplo 12 is taller than all of the other trisomics as well as diploid sibs (Table 3). The leaves are light green and droopy with long ligules, imparting a spreading appearance to the plants. It is a vigorous trisomic with many tillers and is fully fertile. The grains at the tips of the panicles have small awns (Figure 5).

TRANSMISSION RATES OF THE EXTRA CHROMOSOME

The transmission rates of the extra chromosome of the trisomics through the female are fairly high (Table 4). Triplo 3, triplo 6, triplo 11 and triplo 12 transmitted at a high frequency. Transmission rates were lowest for triplo 1 and triplo 4 (15.5 and 17.8%). However, the female transmission rates reported here

TABLE 4

Female and male transmission rates of the extra chromosome in the primary trisomics of rice

Trisomic	Transmission rates							
	Total	$(2n + 1) \times 2n$			$2n \times (2n + 1)$			
		2n	2n + 1	%2n + 1	Total	2n	2n + 1	%2n + 1
Triplo 1	194	164	30	15.5	162	162	0	0.0
Triplo 2	364	247	114	31.6	20	20	0	0.0
Triplo 3	2414	1499	915	37.9	20	20	0	0.0
Triplo 4	326	268	58	17.8	0	0	0	0.0
Triplo 5	2067	1392	675	32.7	197	195	2	1.6
Triplo 6	1868	1176	692	37.1	209	198	11	5.6
Triplo 7	1404	967	437	31.1	113	113	0	0.0
Triplo 8	1755	1307	448	25.5	192	168	24	14.3
Triplo 9	1199	773	426	35.5	168	132	36	27.3
Triplo 10	1932	1402	530	27.4	209	206	3	1.5
Triplo 11	199	120	79	39.7	192	187	5	2.7
Triplo 12	1521	853	668	43.9	196	195	1	0.5

have been calculated from the F_2 or backcross progenies of trisomics and marker genes. Thus, the populations were highly heterozygous. This heterozygosity may have favored the transmission rates of the extra chromosome. As pointed out by KHUSH (1973), transmission rates are affected by genetic background.

Data on transmission rates through the male are also given in Table 4. Progenies from the crosses of 11 trisomics when used as pollen parents with IR36 as female were obtained. Seven transmitted their extra chromosome through the male. Triplo 8 and triplo 9 gave the highest transmission through the male (14.3 and 27.3%). These observations are borne out by the consistently observed occurrence of a few tetrasomic plants in the selfed progenies of triplo 8 and triplo 9. The longer chromosomes of the complement do not transmit through the pollen, as they probably cause greater imbalance. In this respect the behavior of the trisomics of rice parallel that of tomato and maize trisomics (KHUSH 1973).

GENETIC SEGREGATION IN TRISOMICS

The linkage groups of rice described by NAGAO and TAKAHASHI (1963) were associated with the cytologically identifiable chromosomes of the complement through the modified ratio technique characteristic of the trisomic segregations. For this purpose, representative marker genes of each linkage group were crossed with the trisomics. Except for one case, the trisomics are homozygous for the normal alleles of the marker genes that we studied. When we found that some marker genes belonging to different linkage groups were located on the same chromosome, we tested several marker genes that had not been assigned to any linkage group. This was done to identify the new linkage groups for the unmarked chromosomes.

We studied 22 marker genes (Table 5). As soon as a marker was located on a specific chromosome, its tests with the remaining chromosomes were discontinued. Because of its high sterility, triplo 4 could be tested with only two marker genes. Some marker genes, for example ch_1 , were tested with all trisomics; others, such as z_2 , were tested with only one. We tested 120 of 264 possible combinations involving 22 genes before markers for all of the chromosomes were identified. Table 5 lists all of the combinations studied and the type of segregation obtained for each combination.

Segregation data for 17 recessive genes and one dominant gene ($I-Bf$) that gave trisomic segregations are presented in Table 6. Trisomic F_1 plants of triplo 1 \times eg , triplo 4 \times dl and triplo 4 \times ch_1 were highly sterile and were backcrossed with the respective marker genes. F_2 populations were grown from the remaining combinations. The trisomic individuals in the segregating populations of triplo 1 to triplo 9 could be identified at seedling stage. Therefore, segregation data for the $2n$ and $2n + 1$ fractions of the populations involving triplo 1 to triplo 9 are given separately. Triplo 10, triplo 11 and triplo 12 can only be identified at flowering stage. The F_2 populations involving these trisomics were classified into normal and mutant fractions at seedling stage and then discarded. Therefore, segregation data for the marker genes tested with triplo 10, triplo 11 and triplo 12 given in Table 6 are for the entire population only.

TABLE 5

Summary of primary trisomic segregation tests^a in rice

Gene	Linkage group	Primary trisomic and type of segregation obtained											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>bc</i> ₁ (brittle culm)	XI	D	D	D	-	D	D	D	D	D	D	D	D
<i>ch</i> ₁ (chlorina-1)	XI	D	D	D	T	D	D	D	D	D	D	D	D
<i>Cl</i> (clustered spikelets)	I	-	-	T	-	-	-	-	-	-	-	-	-
<i>dl</i> (droopy leaf)	XI	D	-	D	T	D	D	D	-	D	-	D	D
<i>dp</i> ₂ (depressed palea-2)	VII	-	-	D	-	-	D	-	-	T	-	-	-
<i>eg</i> (extra glume)	III	T	D	-	-	D	D	D	D	D	D	-	D
<i>fl</i> (faded leaf)		-	-	-	-	-	D	-	-	-	T	-	-
<i>g</i> (long empty glume)	IV	D	D	-	-	-	-	T	D	D	-	D	-
<i>gh</i> ₁ (gold hull-1)	VI	-	-	D	-	T	D	D	D	-	D	-	-
<i>gl</i> ₁ (glabrous-1)	XII	D	D	D	-	T	D	D	D	D	D	D	D
<i>I-Bf</i> (inhibitor of brown furrow)	V	-	-	-	-	-	-	-	-	T	-	-	-
<i>la</i> (lazy)	VIII	D	-	-	-	-	D	D	D	D	-	T	D
<i>lax</i> (lax panicle)	III	-	-	D	-	-	D	-	D	-	D	-	-
<i>lg</i> (liguleless)	II	-	D	D	-	D	D	D	D	D	D	D	T
<i>nl</i> ₁ (neck leaf-1)	IX	-	-	-	-	T	D	-	-	-	-	D	-
<i>pgl</i> (pale green leaf)		-	-	-	-	-	D	-	-	-	T	-	-
<i>Ps</i> ₁ (purple stigma)	V	-	-	T	-	D	-	D	D	D	D	-	D
<i>spl</i> ₁ (spotted leaf-1)		-	-	-	-	-	T	-	-	-	-	-	-
<i>tri</i> (triangular hull)	X	-	T	D	-	D	D	-	D	D	D	D	D
<i>v</i> ₈ (virescent-8)		-	-	-	-	-	-	-	T	-	-	-	-
<i>ws</i> (white stripes)	I	D	-	T	-	D	-	-	-	-	-	-	D
<i>z</i> ₂ (zebra striped leaves-2)	VIII	-	-	-	-	-	-	-	-	-	-	T	-
No. of genes tested		8	7	12	2	11	15	10	12	12	11	10	10

^a D, disomic segregation; T, trisomic segregation; -, not tested.

As discussed by KHUSH (1973), the diploid portion of the trisomic F₂ populations for the recessive genes should segregate in a ratio of 8:1 instead of 3:1, irrespective of rates of transmission of the extra chromosome or the distance of the marker gene from the centromere. Similarly, the diploid portion of the backcross population segregating in a trisomic fashion should give a ratio of 2:1 instead of 1:1. As shown in Table 6, the segregation ratios for the normal and mutant plants in the diploid fractions agreed with the expected trisomic ratios. The segregation data of the trisomic portion of each population further confirmed these conclusions. As expected, all of the trisomic plants, barring exceptional individuals in four populations, showed normal phenotypes—clear proof of the association of the marker gene with the extra chromosome of the trisomic. Exceptional individuals with recessive phenotypes in four populations undoubtedly resulted from double reduction. The segregation data for the total population ($2n$ and $2n + 1$) of all of the F₂ populations segregating in a trisomic fashion agreed with the ratio of 12.5:1 expected on the basis of 33.3% transmission of the extra chromosome (KHUSH 1973). The segregation data for the three backcross populations agreed with the ratio of 3.5:1 expected on the basis of 33.3% transmission of the extra chromosome.

TABLE 6
Segregation ratios for marker genes in the F₂ or BC generation of primary trisomics of rice

Trisomic	Gene	F ₂ or BC	Progeny						χ ² 12.5:1
			2n		2n + 1		Total		
			Normal	Mutant	Normal	Mutant	Normal	Mutant	
Triplo 1	<i>eg</i>	BC	49	20	22	1	71	21	0.02 ^b
Triplo 2	<i>tri</i>	F ₂	109	13	58	0	167	13	0.01
Triplo 3	<i>ws</i>	F ₂	53	6	34	0	87	6	0.12
Triplo 4	<i>dl</i>	BC	57	19	23	1	80	20	0.29 ^b
Triplo 4	<i>ch₁</i>	BC	33	10	7	0	40	10	0.14 ^b
Triplo 5	<i>gh₁</i>	F ₂	205	31	98	2	303	33	2.85
Triplo 5	<i>gl₁</i>	F ₂	84	8	54	0	138	8	0.79
Triplo 5	<i>nl₁</i>	F ₂	56	6	42	0	98	6	0.41
Triplo 6	<i>spl₁</i>	F ₂	91	11	87	0	178	11	0.69
Triplo 7	<i>g</i>	F ₂	131	11	69	0	200	11	1.48
Triplo 8	<i>vs</i>	F ₂	84	12	31	0	115	12	0.77
Triplo 9	<i>dp₂</i>	F ₂	208	15	128	0	336	15	5.03
Triplo 9	<i>I-Bf</i>	F ₂	59	6	46	1	105	7	0.22
Triplo 10	<i>pgl</i>	F ₂					363	19	3.30
Triplo 10	<i>fl</i>	F ₂					165	15	0.22
Triplo 11	<i>la</i>	F ₂					211	12	1.23
Triplo 11	<i>z₂</i>	F ₂					268	15	1.83
Triplo 12	<i>lg</i>	F ₂					215	18	0.03

^a χ² for 2:1.
^b χ² for 3.5:1.

A word regarding the segregation of *I-Bf* (inhibitor of brown furrows on the glumes) is in order. IR36 and all of the trisomics have the genotype *Bf Bf I-Bf I-Bf*. Hence, they do not show brown furrow phenotype. When brown furrow (*Bf Bf + +*) is crossed with IR36, an F_2 segregation ratio of three normal to one brown furrow is obtained. In the cross of triplo 9 \times brown furrow, this ratio was modified to 8:1 in the diploid fraction, all:0 in the trisomic fraction and 12.5:1 for the entire population, thus showing that *I-Bf* is located on chromosome 9. An F_2 population from the disomic F_1 plant of the cross triplo 9 \times brown furrow segregated 333 normal to 117 brown furrow, which agreed with the expected 3:1 ratio.

Two dominant genes, *Cl* (clustered spikelets) and *Ps₁* (purple stigma-1), gave trisomic ratios with triplo 3. As expected, the F_2 ratios of both crosses were modified to four normal to five mutant (instead of 1:3) in the diploid fraction (Table 7). In the trisomic fraction of the F_2 of triplo 3 \times *Ps₁*, the ratio agreed with the expected two normal to seven mutant. However, the ratio of normal to mutant in the trisomic portion of the F_2 population of triplo 3 \times *Cl* was 7:2. This apparent reversal was due to the fact that *Cl + +* individuals have normal phenotype (as determined from trisomic F_1 phenotypes) instead of mutant. Therefore, the expected genotypic ratio of 2 *Cl Cl +*:5 *Cl + +*:2 *+ + +* was expressed into seven normal to two mutant.

ASSOCIATION BETWEEN LINKAGE GROUPS AND CHROMOSOMES

Trisomic segregation data given in Tables 6 and 7 were useful in associating the linkage groups of rice proposed by NAGAO and TAKAHASHI (1963) with the respective chromosomes. Gene *eg* gave a trisomic ratio with triplo 1. Thus, linkage group III is located on chromosome 1. Gene *tri* of linkage group X segregated in a trisomic fashion with triplo 2. Therefore, linkage group X finds its home on chromosome 2. Similarly, linkage group I was associated with chromosome 3, group XI with chromosome 4, group IV with chromosome 7, group VIII with chromosome 11 and group II with chromosome 12 (Table 8). Three markers (*gh₁*, *nl₁*, *gl₁*) belonging to three different linkage groups (VI, IX and XII) gave trisomic segregations with triplo 5. Thus, these three linkage groups belong to chromosome 5. Similar results were obtained by IWATA and OMURA (1976) who obtained trisomic ratios for *d₁* (another marker of linkage

TABLE 7

Segregation ratios for two dominant genes in the F₂ population of triplo 3 of rice

Gene	Progeny					
	2n		χ^2 4:5	2n + 1		χ^2 7:2 or 2:7
Normal	Mutant	Normal		Mutant		
<i>Cl</i>	104	110	1.49	126	40	0.33 ^a
<i>Ps₁</i>	66	85	0.03	20	54	0.99 ^b

^a χ^2 for 7:2.

^b χ^2 for 2:7.

TABLE 8

Relationships between various systems of numbering chromosomes, trisomics, linkage groups and marker genes of rice

Chromosomes			Trisomics		Linkage groups	
SHASTRY, RANGA RAO and MISRA (1960)	NISHIMURA (1971)	KURATA and OMURA (1978)	This study	IWATA and OMURA (1975)	NAGAO and TAKAHASHI (1963)	Marker genes
1	3		1		III	<i>eg, lax</i>
2	8		2		X	<i>tri</i>
3	6	K6	3	B	I	<i>wx, ws</i>
4	5		4		XI	<i>bc₁, ch₁, dl</i>
5	2	K9	5	L	VI, IX, XII	<i>gh₁, nl₁, gl₁</i>
6	4	K5	6	A		<i>spl₁, rl₁</i>
7	10	K11	7	F	IV	<i>g</i>
8	12	K7	8	D		<i>v₈, su</i>
9	1	K10	9	H	VII, V	<i>dp₂, drp₂, I-Bf</i>
10	7	K12	10	C		<i>pgl, fl</i>
11	9	K8	11	G	VIII	<i>la, z₂</i>
12	11	K4	12	E	II	<i>lg, Pl</i>

group VI), *nl₁* and *gl₁* with their trisomic L. More recently SATO, MURAOKA and SANO (1982) associated these three linkage groups with chromosome 2 of NISHIMURA's designation, through the use of translocations. The gene *dp₂* of linkage group VII and *I-Bf* of linkage group V gave trisomic segregations with triplo 9. Thus, these two linkage groups belong to the same chromosome.

It is clear that the 12 linkage groups of NAGAO and TAKAHASHI (1963) are located on nine of the 12 chromosomes. To find the marker genes for the remaining three chromosomes, seeds of several useful marker genes were obtained through the courtesy of NOBUO IWATA and TAKESHI OMURA of Kyushu University, Fukuoka, Japan. The markers were transferred to indica background by backcrossing to IR36. When tested with the unmarked chromosomes, marker genes were found for all of them. Thus, *spl₁* (spotted leaf-1) gave trisomic segregation with triplo 6, *v₈* (virescent-8) gave trisomic segregation with triplo 8 and *pgl* (pale green leaf) and *fl* (faded leaf) gave trisomic segregation with triplo 10 (Table 6). Thus, we now have marker genes for all of the chromosomes.

CORRESPONDENCE BETWEEN DIFFERENT CHROMOSOME-NUMBERING SYSTEMS

The correspondence between the chromosome-numbering system of NISHIMURA (1961) and that of SHASTRY, RANGA RAO and MISRA (1960) used in this study was determined by crossing each of our primary trisomics with the translocation stocks. Trisomic F₁ populations were cytologically examined to determine whether an association of five chromosomes or an association of four chromosomes and a trivalent were formed during meiosis. Presence of a pentavalent indicated that one of the two chromosomes involved in the translocation was the extra chromosome in that trisomic. When the same trisomic formed an association of five in crosses with two translocations, we concluded that the extra

chromosome of the trisomic corresponded with the chromosome involved in both of these translocations. The relationships between the extra chromosomes of each trisomic and the chromosomes of NISHIMURA's designation were ascertained by using this technique (IWATA and KHUSH, unpublished results) and are shown in Table 8.

The associations between the linkage groups of NAGAO and TAKAHASHI (1963) and the chromosomes of NISHIMURA's system were determined by IWATA and OMURA (1971a,b). They studied the linkage relations between the translocation break points and representative markers of the linkage groups. Using this translocation technique they determined associations between eight chromosomes and linkage groups. Through further studies using the primary trisomic series of Kyushu University, IWATA and OMURA (1975, 1976) and IWATA, SATOH and OMURA (1981) established associations between nine chromosomes of NISHIMURA's designation and 12 linkage groups. The extra chromosomes of these nine trisomics were identified according to the numbering system of KURATA and OMURA (1978) by KURATA, IWATA and OMURA (1981). The available information on the correspondence between various chromosome-numbering systems, trisomics, linkage groups and marker genes is summarized in Table 8.

LINKAGE MAP OF RICE

The associations between the linkage groups and the cytologically identifiable chromosomes of rice have been established for the first time. Marker genes for each of the 12 chromosomes have been identified. Following the convention in other crop species and to remove the confusion between the different chromosome-numbering systems and the linkage groups of old nomenclature, it is suggested that the numbering system of SHASTRY, RANGA RAO and MISRA (1960) be followed, as the chromosomes are easiest to identify at pachytene stage. The linkage group corresponding to chromosome 1 should be called linkage group 1, that corresponding to chromosome 2, linkage 2, and so on. Relevant information about each of the linkage groups is given, and an up-to-date linkage map is presented in Figure 8.

Linkage group 1 (eg group): Linkage group 1 corresponds to linkage group III. The gene order and linkage data are based on the summary of KINOSHITA (1972). The gene for semidwarf stature (*sd*₁) from variety DGWG, present in semidwarf high yielding varieties, was located in this linkage group by SUH and HEU (1978). Our data show that *sd*₁ is very closely linked with *lax* (Table 9).

Linkage group 2 (tri group): Linkage group 2 corresponds to linkage group X. Other good markers of this group are *bl*₁ and *gh*₂. The gene order and linkage data are based on the summary of TAKAHASHI (1982).

Linkage group 3 (wx group): Linkage group 3 corresponds to linkage group I and has several well-known markers such as *Ps*₁, *Cl* and *ws*. The gene order and linkage data are based on the summarized report of TAKAHASHI (1982).

Linkage group 4 (dl group): Linkage group 4 corresponds to linkage group XI. Other good markers are *bc*₁, *ch*₁, *v*₁ and *ch*₂. OMURA, IWATA and SATOH (1978) provided useful information on gene order and linkage data for this group.

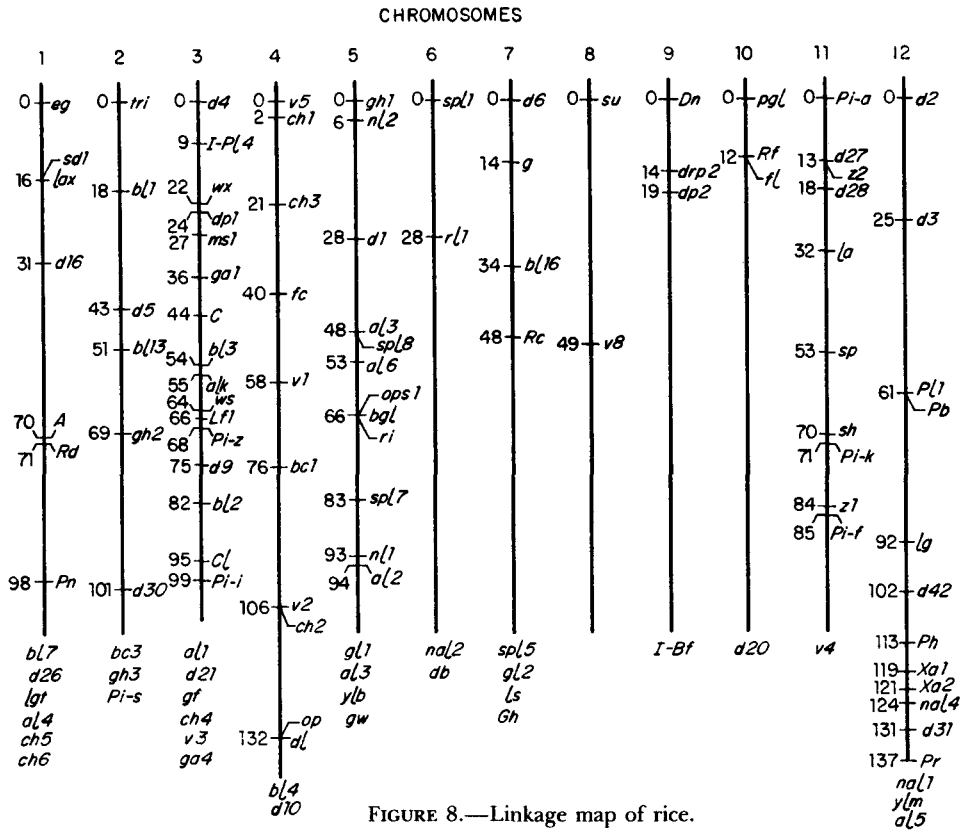


FIGURE 8.—Linkage map of rice.

Linkage group 5 (nl₁ group): Three linkage groups, VI, IX and XII, are consolidated in linkage group 5. Other useful marker genes are *gh*₁, *gl*₁, *gw* and *ri*. Gene order of this group was studied by SATO, MURAOKA and SANO (1982). Gene *gl*₁, which along with *An*₂ constituted linkage group XII, has not been mapped. In our tests (Table 9), *gl*₁ segregated independently of *gh*₁.

Linkage group 6 (spl₁ group): Linkage group 6 is composed of two marker genes, *spl*₁ and *rl*₁, located 27.5 map units apart (Table 9). IWATA and OMURA (1975) also associated *spl*₁ and *rl*₁ with their A trisomic, which corresponds to our triplo 6. Marker *rl*₁ was earlier located on linkage group I by NAGAO, TAKAHASHI and MORIMURA (1964), but the *rl*₁ gene that we studied is undoubtedly located on chromosome 6.

Linkage group 7 (g group): Linkage group 7 corresponds to linkage group IV, and the linkage information is based on the summary report of KINOSHITA (1972).

Linkage group 8 (su group): Linkage group 8 is new. Association between *v*₈ and chromosome 8 was found in this study. ISONO, SATOH and OMURA (1978) located *su* on the D trisomic which corresponds to triplo 8. Thus, linkage group 8 has two good markers. No linkage between *v*₈ and *su* was detected (Table 9).

Linkage group 9 (dp₂ group): Linkage group 9 corresponds to linkage group

TABLE 9

Linkage relations between some marker genes of rice

Gene pair	Phase	Segregation data				No. of Plants	Recombination value (%)
		AB	Ab	aB	ab		
<i>rl₁-spl₁</i>	Repulsion	225	90	97	7	420	27.5
<i>v₈-su</i>	Repulsion	236	64	52	15	367	≥50.0
<i>sd₁-lax</i>	Repulsion	139	75	84	0	298	0.0
<i>gh₁-gl₁</i>	Coupling	567	154	172	53	946	49.7

VII, and the gene order and linkage data are based on the report of IWATA and OMURA (1971a). Dominant gene *I-Bf* of linkage V gave trisomic segregation with triplo 9. Linkage group V consisting of *I-Bf* and *Ps₁* was proposed by NAGAO and TAKAHASHI (1963) on the basis of weak linkage between these two markers. We tested *Ps₁* with seven trisomics (Table 5), and it gave trisomic segregation with triplo 3. Thus, the two markers of linkage group V are located on two different chromosomes, and this is not a valid linkage group. SASTRY, PRAKASARAO and SEETHERAMAN (1975) added genes *Pd* for gall midge resistance and *sd* for semidwarf stature to linkage group V. The linkage between *Pd* and *I-Bf* is very weak, and, as discussed earlier, *sd₁* is located on linkage group 1. Thus, the linkage group proposed by SASTRY, PRAKASARAO and SEETHERAMAN (1975) is also not valid.

Linkage group 10 (pgl group): Linkage group 10 is a new group consisting of two markers, *pgl* and *fl*, both of which showed trisomic segregation with triplo 10. IWATA and OMURA (1975) located these markers on their trisomic C, which corresponds to our triplo 10. SHINJYO (1975) reported that fertility-restoring gene *Rf* belongs to this linkage group. The gene order and linkage data for this group are based on SHINJYO's report.

Linkage group 11 (la group): Linkage group 11 corresponds to linkage group VIII. Other suitable markers of this group are *z₁* and *z₂*. Gene order and linkage data are based on the summary of TAKAHASHI (1977).

Linkage group 12 (lg group): Linkage group 12 corresponds to well-known linkage group II. Gene order and linkage information follow the summary of KINOSHITA (1972).

LINKAGE GROUPS IN INDICA AND JAPONICA RICES

Several workers, especially MISRO, RICHHARIA and THAKUR (1966), have suggested that linkage groups of indica rice differ from those of japonica rice. They even suggested that separate linkage groups should be established for indica, japonica and javanica rices. This opinion seems to have been based on insufficient information available at that time. However, we have systematically transferred marker genes from japonica and indica varieties into improved indica variety IR36 by backcrossing and determined gene chromosome relationships through trisomic tests. Complete correspondence between the linkage groups of japonica and indica rice was found. We have not observed a single case in which a gene was located on one chromosome in japonica rice and on

another chromosome in indica rice. Similarly, the gene order in indica and japonica varieties is the same for the markers that we have studied. The map distances may vary, but commensurate variation is observed in the varieties of the same group. Genotypic background and environmental conditions, such as temperature, are known to influence the recombination values. Therefore, we should study linkage groups of rice and not of varietal groups of rice.

NATURE OF RICE GENOME

On the basis of observations on somatic chromosome morphology, several workers, especially NANDI (1936), have suggested that rice is a secondary polyploid. However, our studies with trisomics reveal that rice is a diploid species. KHUSH (1973) pointed out that the trisomics of polyploid species are morphologically indistinct; they are fully fertile, and their transmission rates are very high. Moreover, extra chromosomes are transmitted through the male, and tetrasomics are obtained. Consistently in the progenies of triploids of polyploid species, plants with all possible chromosome numbers from $2n$ to $3n$ are obtained because polyploids have much higher tolerance for duplications, and plants with one or two extra chromosomes have normal morphology and fertility. However, the tolerance limits for extra chromosome in diploid species, such as tomato, barley and datura, are narrow. The trisomics are morphologically distinct, their productivity is impaired, transmission rates are low, transmission through the male is very poor and only a small number of extra chromosomes are tolerated in the triploid progenies. In this respect rice resembles the other diploid species, although tolerance limits for extra chromosomes in rice are slightly higher than those in tomato and datura.

FUTURE OF RICE GENETICS

There is very little coordination among rice geneticists. Consequently, different chromosome-numbering systems are used. Similarly, there is no coordination in assigning gene symbols: completely different gene symbols are assigned by different workers to the same gene. Many mutants have been described, and gene symbols have been assigned, but the seeds of the mutants have not been maintained. Linkage studies in rice have lagged because of lack of coordination. A rice genetics newsletter for sharing information, similar to those for tomato or barley, is needed. It is high time that world rice geneticists started cooperative studies along lines similar to those in tomato genetics. For this purpose: (1) A rice genetics newsletter should be published annually. (2) A commonly accepted nomenclature for rice chromosomes should be followed. (3) Rules for gene symbolization suggested by the INTERNATIONAL RICE COMMISSION (1959) should be strictly followed, and coordinators to monitor the gene symbols should be designated. (4) Two rice genetic stock centers should be established: one for maintaining the markers, translocation and trisomic stocks in japonica background and the other for markers and trisomics in the indica background. (5) Linkage mapping should be done cooperatively by assigning one linkage group to one cooperator.

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