Theor Appl Genet (1994) 88:956–964

M. C. Chung · H. K. Wu

Cytological identification of the chromosomes involved in Nishimura's rice translocation lines

Received: 7 June 1993 / Accepted: 5 January 1994

Abstract During the past three decades, Nishimura's reciprocal translocation lines of rice have been used in rice cytogenetics to locate genes on chromosomes, to number extra chromosomes of trisomic series and to associate individual linkage groups with specific chromosomes. In this report, we present our identification of the chromosomes involved in 11 of Nishimura's translocation lines using both meiotic pachytene and mitotic prometaphase chromosome analysis. In addition, the numbering of the 12 linkage groups suggested by Nagao and Takahashi, and modified later by many workers, has been revised to agree with the numbering of the identified chromosomes.

Key words Rice · Chromosome interchange Identification · Pachytene analysis · Karyotype

Introduction

Since Nishimura's pioneering work (1961), the importance of reciprocal translocation (RT) lines has been shown by the fact that they have been used as tools to gain basic information in rice cytogenetics and as aids in breeding. Nishimura described a series of rice reciprocal translocations and arbitrarily numbered the interchanged chromosomes sequentially, in the order in which they were identified in successive translocation lines. Nagao and Takahashi (1963) first proposed 12 linkage groups (I–XII), a number that corresponded well with the haploid chromosome number of *japonica* rice cultivars. Since then, reciprocal translocation lines and trisomics have been used as genetic tools for establishing the relationship between linkage groups and chromosomes (Iwata et al. 1970; Iwata and Omura 1971 a, b, 1975, 1976; Sato et al. 1973, 1975, 1982; Kinoshita et al. 1975; Sato 1976; Omura et al. 1978; Yoshimara et al. 1982). Karyotype analysis has been used in the identification of RT lines (Sato 1981; Chen et al. 1982) and of the extra chromosomes in various trisomic sets (Kurata et al. 1981; Khush et al. 1984; Chung and Wu 1987, 1990). Finally, and almost simultaneously, correspondence between chromosomes and linkage groups has been genetically elucidated in *japonica* rice (Iwata and Omura 1984; Iwata et al. 1984 a, b) as well as in *indica* rice (Khush et al.1984), though the authors were not unanimous in their findings.

In view of the above uncertainty, cytological analysis of the chromosomes involved in Nishimura's RT lines was called for. In the study presented here, we report the cytological identification of the chromosomes involved in the 11 lines of Nishimura's RT heterozygotes by karyotype analysis at both meiotic pachytene of pollen mother cells and mitotic prometaphase of root-tip cells. The chromosome numbers arbitrarily assigned by Nishimura were cytologically determined. They were found to agree with our previous identification of the indica trisomic series (Chung and Wu 1987, 1990) and, with a few exceptions, with that of work based on genetic analysis. A revision of the rice linkage groups has been made on the basis of our direct cytological evidence.

Materials and methods

The 11 lines of reciprocal translocation homozygotes used were a kind gift from Drs. N. Iwata and T. Omura of Kyushu University in 1985; they are listed in Table 1 and were genetically numbered by Nishimura (1961). The RT heterozygotes used for identification were obtained by crossing each RT homozygote to a normal cultivar, 'Taichung 65'. Both young spikelets and seeds from RT heterozygous plants obtained among F_2 segregants were sampled for chromosome preparation which enabled us to have plenty of material for study and the results obtained from spikelet and seeds to be mutually checked. Young spikelets were fixed in acetic alcohol (1:3) fixative containing a trace of ferric chloride, then stored at 4 °C. Both meiotic pachytene chromosome (Wu 1967) and somatic prometaphase chromosome (Kurata and Omura 1978) techniques were used to identify the interchanged chromosomes.

Communicated by K. Tsunewaki

M. C. Chung · H. K. Wu (✉)
Institute of Botany, Academia Sinica, Nankang, Taipei 115, Republic of China

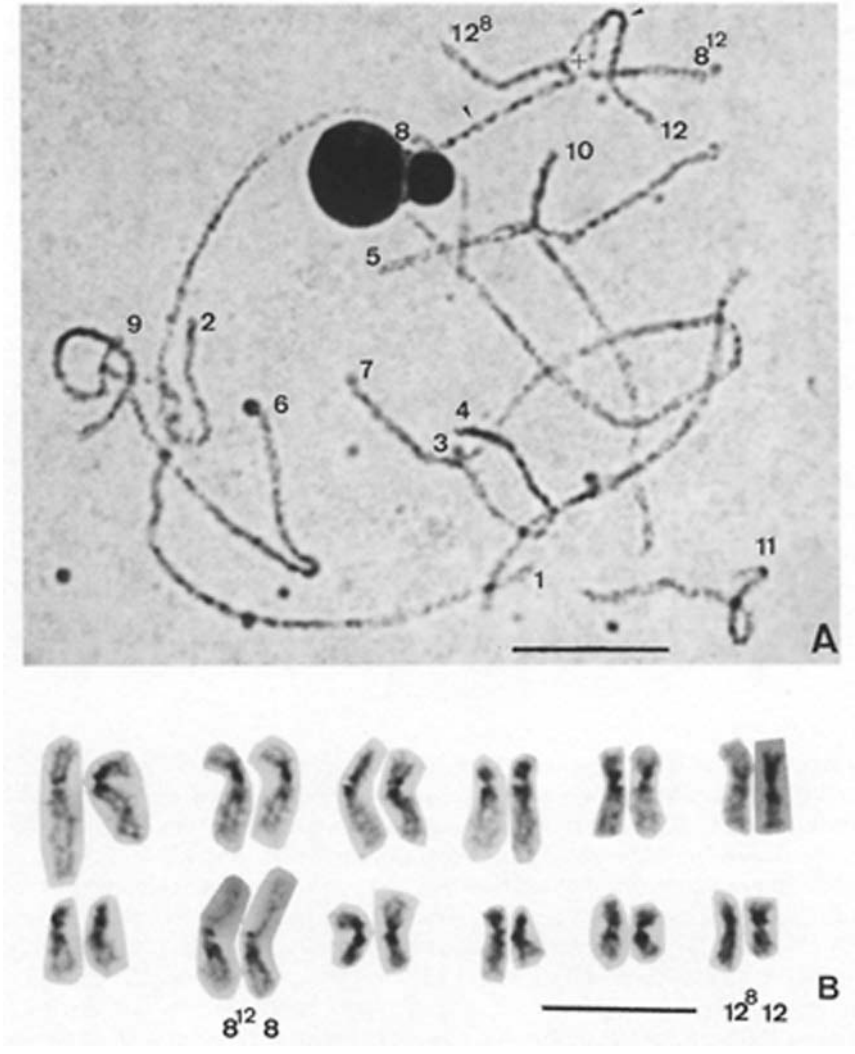

Fig. 1 The karyotype of RT 1-4a in which the long arms of chromosomes 8 and 12 have been interchanged. **A** Pachytene. The cross configuration shows the involvement of chromosome 8, the nucleolar chromosome, and chromosome 12. **B** Mitotic prometaphase. A slight increase in the long arm of 12^8, but a minor decrease in the long arm of 8^{12} can also be ascertained at prometaphase. *Bar*: 10 μm

Table 1 Nishimura's reciprocal translocation lines used in this study

RT line	Genetically numbered	Reference
RT 2	RT 1-3a	Nishimura (1961)
RT 4	RT 1-4a	Nishimura (1961)
RT 85	RT 2-6a	Yoshimura et al (1980)
RT 13	RT 3-11a	Nishimura (1961)
RT 19	RT 5-9	Nishimura (1961)
RT 49	RT 6-7	Iwata (1970)
RT 22	RT 7-8a	Nishimura (1961)
RT 46	RT 7-11	Iwata (1970)
RT 63	RT 7-12	Yoshimura et al (1980)
RT 28	RT 9-10	Nishimura (1961)
RT 31	RT 10-12	Iwata (1970)

The revised karyotype of 'Taichung 65' (Wu and Chung 1989) was used as the standard to identify the interchanged chromosomes involved in the RT heterozygotes. The chromosomes of the revised karyotype were numbered according to their descending order of relative length, as previously described by Chen and Wu (1982) and Chen et al (1982), except for the 10th chromosome, which is the shortest in the complement. The previously designated chromosomes 8, 9, 10, 11 and 12 were consequently renumbered as chromosomes 9, 11, 8, 12 and 10, respectively. The new chromosome 10 in japonica is not a nucleolar chromosome, as it is in the *indica* cultivars, possibly due to its loss of the fragment bearing ribosomal RNA genes (Chung et al 1993). The breakpoint of the interchanges was expressed as the distance from the centromere to the breakpoint divided by the total length of that chromosomal arm (Burnham 1962). The relative length of each interchange segment was then expressed as the percentage of its length in the total length of the chromosomal complements.

Chromosomes shown in the figures, including those of interchanges, are numbered in descending order, except for chromosome 10. The prometaphase chromosomes are so arranged in one to four rows; only those chromosomes involved in an interchange are appropriately numbered. The four ends of a cross configuration (+) are numbered to show the non-translocated or the translocated ones. The centromere is denoted by an arrowhead. In both cases, one chromosome in the neighborhood of either one of the two interchanged chromosomes has been labelled for cross reference. The translocated chromosomes with a segment interchanged from a nonhomologous chromosome are respectively superscribed.

Results

The pachytene chromosome configurations in various RT heterozygotes were examined first. As shown in Fig. 1A,

Table 2 Identification of chromosomes, breakpoints and relative length of the interchanges involved in Nishimura's reciprocal translocation lines

RT line	Identified chromosomes	Involved breakpoints	Relative length of the interchanged	Morphological modification[a] segments(%)	Number of cells observed
1-3a	8; 1	8L 0.54 ± 0.05	2.63	8L+	5
		1L 0.22 ± 0.06	6.60	1L–	
1-4a	8; 12	8L 0.40 ± 0.09	3.43	8L-	13
		12L 0.38 ± 0.08	2.13	12L+	
2-6a	5; 6	5L 0.33 ± 0.15	3.66	5L–	8
		6S 0.40 ± 0.22	2.12	6S+	
3-11a	1; 4	1L 0.89 ± 0.06	0.93	1L+	30
		4L 0.37 ± 0.09	4.64	4L–	
5-9	2; 9	2S 0.64 ± 0.06	1.71	2S+	5
		9L 0.38 ± 0.11	2.52	9L–	
6-7	6; 10	6L 0.66 ± 0.10	1.52	6L+	27
		10L 0.38 ± 0.10	2.52	10L–	
7-8a	10; 3	10S 0.32 ± 0.09	1.10	10S+	29
		3L 0.83 ± 0.05	1.18	3L–	
7-11	10; 4	10L 0.60 ± 0.07	1.63	10L–	16
		4S 0.56 ± 0.04	0.81	4S+	
7-12	10; 7	10S 0.38 ± 0.07	1.00	10S+	16
		7L 0.34 ± 0.07	3.10	7L–	
9-10	9; 11	9L 0.34 ± 0.19	2.69	9L–	20
		1L 0.49 ± 0.16	1.95	11L+	
10-12	11; 7	11L 0.52 ± 0.20	1.83	11L–	7
		7L 0.69 ± 0.09	1.46	7L+	

[a] Morphological modification of an interchanged chromosome is denoted by a change in the length of the involved arms; L+ for longer long arm and S- for shorter short arm compared with their respective normal homologous arms

the configurations of RT 1-4a revealed that the interchange of segments had occurred between chromosomes 8 and 12. As judged from the 13 cells that could be analyzed in which each chromosome could be clearly traced and identified, the two breakpoints occurred at 0.40 of the long arm of chromosome 8 and at 0.38 of the long arm of chromosome12, respectively. This means that the exchanged segments in RT 1-4a are about 3.43% and 2.13% in relative length, respectively. Consequently, the translocated chromosomes in RT 1-4a have a shorter long arm of chromosome 8 and a longer long arm of chromosome 12 than their respective non-translocated homologous chromosomes (Table 2, column 5; also Fig. 1B). The cross configurations observed in the other RT lines (RT 1-3a, 3-11a, 5-9, 6-7, 2-6a, 10-12 and 9-10) are shown in Fig. 2A-G, and the results of the karyotype analysis are summarized in Table 2, including the chromosomal arms involved, the breakpoints and the relative lengths of the interchanged segments.

It should also be possible to use the relative lengths of the interchanged segments measured at pachytene to describe the structural changes of the involved chromosomes. For example, in RT 1-3a, the two interchanged segments, 2.6% and 6.6% in relative length (Table 2), from the long arms of chromosome 8 and 1, respectively, would increase the length of the long arm of chromosome 8 and decrease the length of the long arm of chromosome 1. This was confirmed by prometaphase chromosome analysis (Fig. 3 A). The same was true in the case of RT 3-11a (Fig. 3 B). It was possible to identify interchanged chromosomes in the homozygote when the morphological change was substantial. For example, in the RT 3-11a homozygote, the relative length of chromosome 1 increased while that of chromosome 4 decreased; this was also reflected in their arm ratios(Fig. 4). In RT 7-8a, RT 7-11 and RT 7-2, the breaks occurred in a distinctive region, and consequently the chromosomal morphology had changed. In both the RT 7-8a and RT 7-12 lines, interchanges involved a heterochromatin fragment of the short arm of chromosome 10 and a euchromatin fragment from the long arm of chromosomes 3 and 7, respectively, and resulted in a significant, morphological change of the translocated chromosomes (Fig. 5 A–D). In RT 7-11, the interchange involved the heterochromatin fragment of the short arm of chromosome 4 and the euchromatin fragment of the long arm of chromosome 10 (Fig. 5 E, F). From the prometaphase figures it would have been difficult to identify the chromosomes concerned in these RTs if they had not involved the unique, heterochromatic, short arm of chromosome 4. In the case of RT10-12, where the lengths of the interchanged fragments were almost the same, but with no breaks in a heterochromatic segment (Fig. 2 F), identification based on morphological change at prometaphase alone was almost impossible.

On the basis of the above analysis, it was possible to identify the individual chromosomes in 2 RT lines that have 1 chromosome in common. For example, chromosome 8 was involved in the interchanges of both RT 1-3a and RT 1-4a; accordingly, chromosome 1 in Nishimura's system corresponded to chromosome 8 in ours. In addition, the other 2 chromosomes, numbers 3 and 4 in Nishimura's system, corresponded to our chromosome 1 and 12, respectively. Similarly, we could designate chromosomes 6, 2 and 7 in Nishimura's system as chromosomes 6, 5 and 10, respectively, by cytological evidence obtained from RT 2-6a, RT 6-7 and RT 7-8a, and so on. Consequently, the relationship between the two numbering systems was established and is shown in Table 3 (cf. columns 1 and 2).

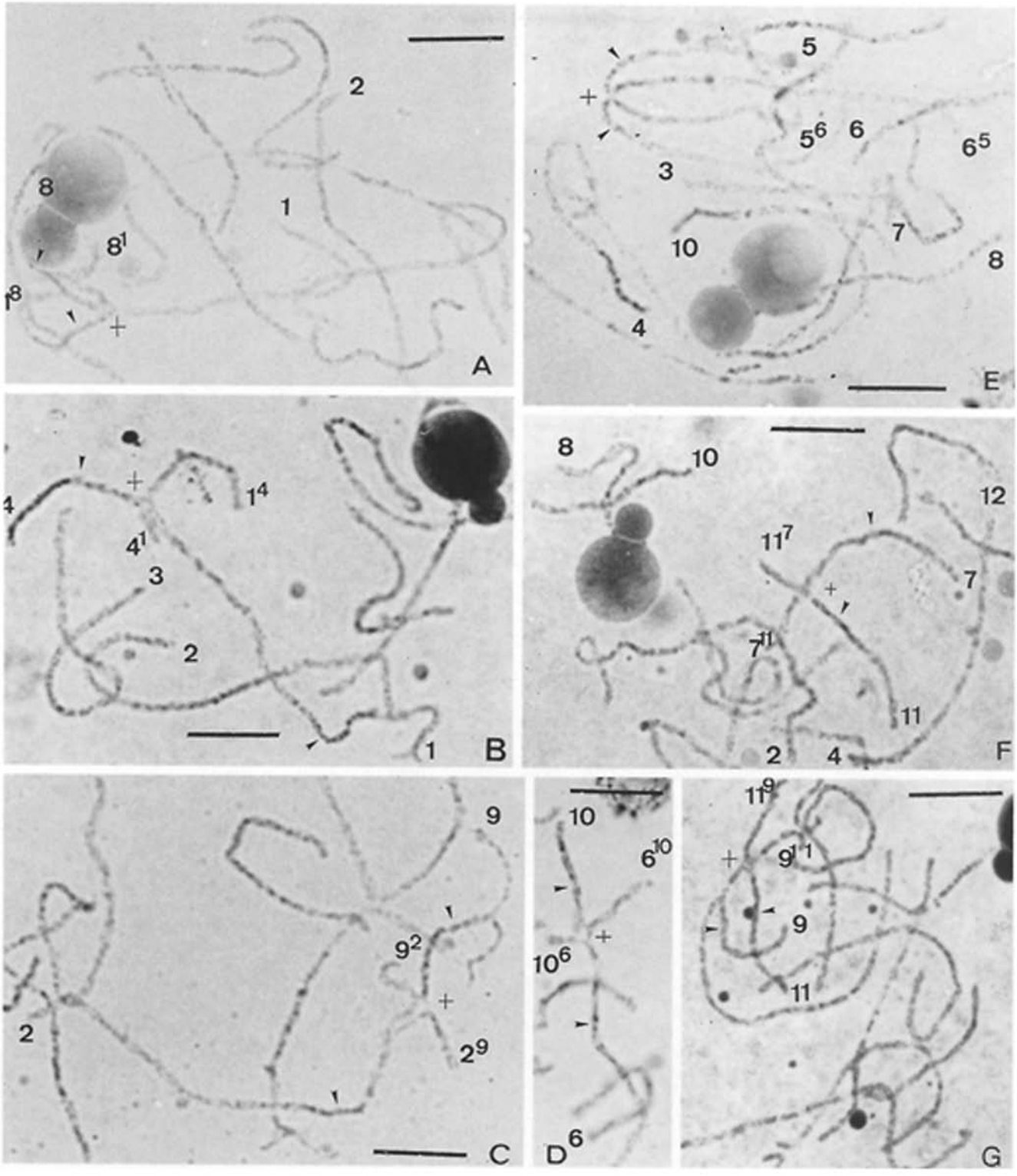

Fig. 2A–G Seven cross configurations at pachytene are exhibited, each showing two nonhomologous chromosomes involved in a RT line. **A** RT 1-3a; the long arms of chromosomes 1 and 8 have been interchanged. The karyotype of this RT line at prometaphase is shown in Fig. 3A. **B** RT 3-11a; the long arms of chromosome 1 and 4 are involved. As a result, 1^4 and 4^1; had a longer and shorter long arm, respectively. The karyotype at prometaphase is shown in Fig. 3B. **C** RT 5-9; interchange occurred between the short arm of chromosome 2 and the long arm of chromosome 9. **D** RT 6-7; the long arms of chromosomes 6 and 10 are involved in the interchange. The difference in the length of the two interchanged segments is obvious. **E** RT 2-6a; the long arm of chromosome 5 and the short arm of chromosome 6 are involved. As a result, the long arm of 5^6 became shorter while the short arm of 6^5 became longer. **F** RT 10-12; center of the cross was highly synaptic in comparison with that of the others (**C**, **D**). Both long arms of chromosomes 7 and 11 were involved but the lengths of the interchanged segments were quite similar. **G** RT 9-10; both long arms of chromosome 9 and 11 were involved. The interchange made the long arm of 9^{11} shorter but that of 11^9 longer. This is discernible in the cross configuration. *Bar*: 10 μm

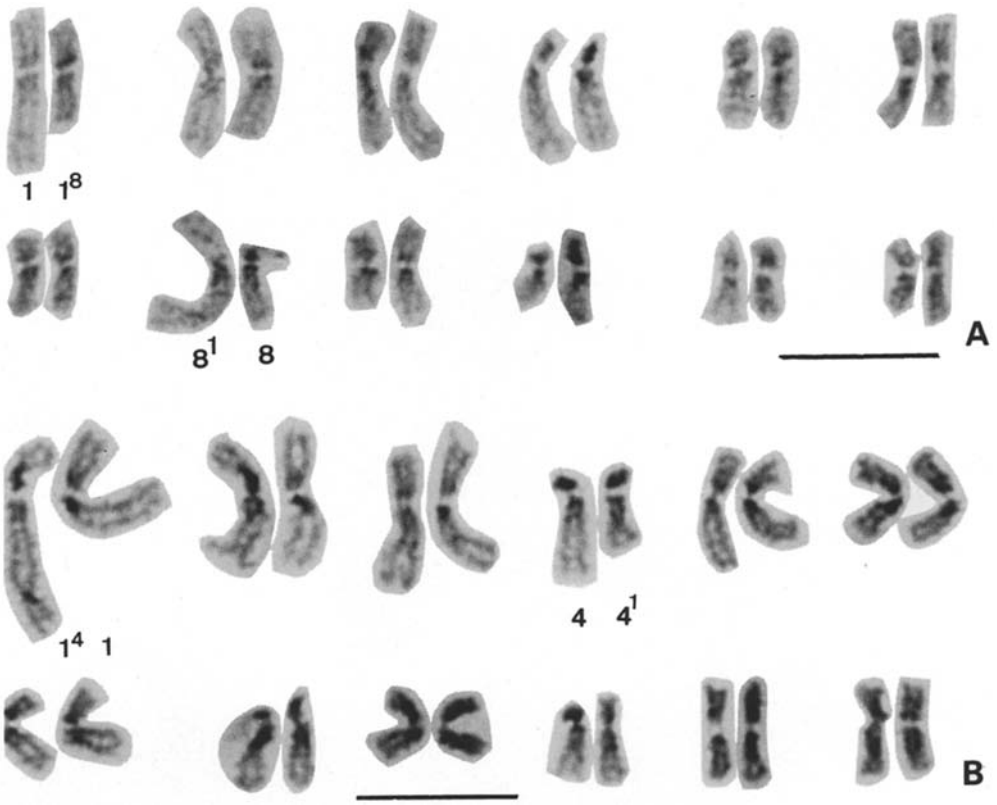

Fig. 3A, B Mitotic prometaphase preparations of RT 1-3a and RT 3-11a heterozygotes. **A** Chromosome 1^8 and 8^1 had their long arms respectively, decreased and increased. **B** Karyotype of RT 3-11a heterozygote. The long arms of chromosome 1 and 4 have been interchanged. The resulting $1^4$and 4^1 had longer and shorter long arms, respectively. *Bar*: 10 μm

Table 3 The corresponding relationship between rice chromosomes and linkage groups

Chromosome						Linkage group	
Nishimura's RT lines		Trisomic series					
Nishimura, (1961)	This study	IRRI (Chung and Wu 1987,1990)	IRRI (Khush 1990)	IRRI (Kurata 1988)	Kyushu (Iwata 1985)	Compiled (Kinoshita 1990)[a]	Revised (this study)
1 (1-3a, 1-4a)	8	$8^{n\,b}$	9^n	9^n	$K10^n$	V, VII	VIII
2 (2-6a)	5	$5^{11\,c}$	5	5	K 9	VI, IX	V
3 (1-3a, 3-11a)	1	1	1	1	K 1	III	I
4 (1-4a)	12	12	12	11	K 5	d-33	XII
5 (5-9)	2	2	3	2	K 3	XI, XII	II
6 (2-6a, 6-7)	6	6^9	6	6	K 6	I	VI
7 (6-7, 7-8a)	10	10^n	10^n	10^n	K12	fgl	X
8 (7-8a)	3	3	2	3	K 2	X	III
9 (5-9, 9-10)	9	9	11	8	K 8	VIII	IX
10 (9-10)	11	11^7	7	7	K11	IV	XI
11 (3-11a, 7-11)	4	4	4	4	K 4	II	IV
12 (7-12, 10-12)	7	7	8	12	K 7	sug	VII

[a] See the text for description
[b] Nucleolar chromosome
[c] The extra chromosome in a trisomic was identified as a translocated chromosome, i.e., chromosome 5 with a segment translocated from chromosome 11, and so on (Chung and Wu 1990)

Discussion

In Japan, there are 52 lines of reciprocal translocation available for linkage studies (Iwata and Omura 1971 a, b; Yoshimura et al. 1982; Iwata et al. 1984 a, b), providing one of the most useful tools for the establishment of a rice linkage map. However, before the present study was conducted the chromosomes involved in these lines had not been determined. We have undertaken karyotype analysis of 11 of Nishimura's RT lines and have determined the chromosomes involved in the interchanges (Table 3, column 2).

Long before the availability of rice trisomic series (Iwata 1970; Khush et al. 1984), 12 linkage groups were proposed on the basis of genetic studies (Nagao and Takahashi 1963). Later, attempts were made to relate linkage groups and corresponding chromosomes by crossing a

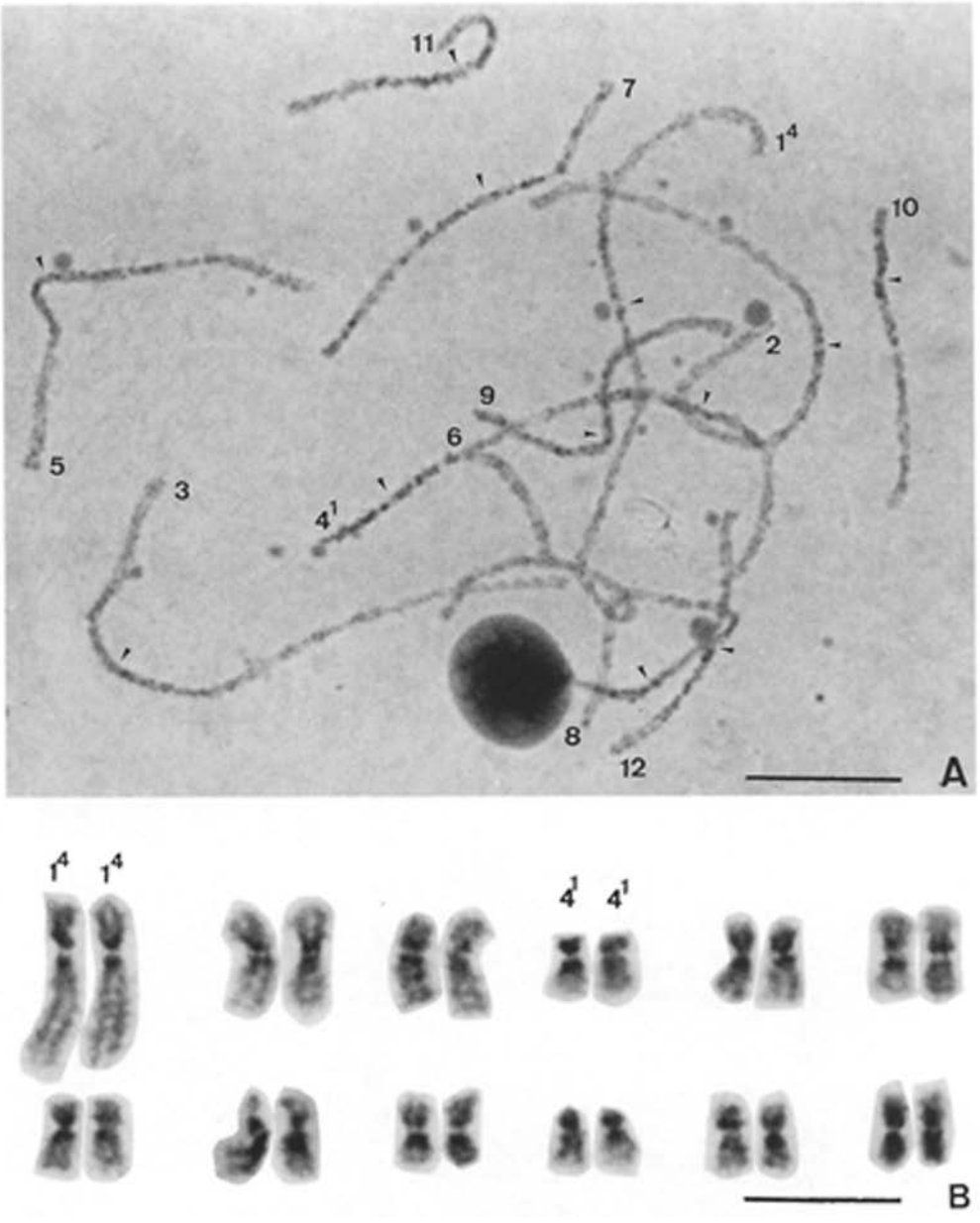

Fig. 4A, B Karyotypes of the RT 3-11a homozygote. The morphology of the chromosome pairs of ($1^4 1^4$) and ($4^1 4^1$) have substantially changed at both pachytene (**A**) and prometaphase (**B**) compared with that of the nontranslocated chromosomes 1 and 4 at pachytene (Fig. **2B**) and prometaphase (Fig. **3B**). *Bar*: 10 μm

strain with markers on a known linkage group to a trisomic strain (Iwata and Omura 1975, 1976, 1977, 1978, 1984; Iwata et al. 1978, 1984 a, b; Khush et al. 1984) or to a set of Nishimura's reciprocal translocation lines (Sato et al. 1973, 1975, 1982; Sato 1976; 1981; Kinoshita et al. 1975; Iwata and Omura 1971 a, b; Yoshimura et al. 1982), or by crossing identified trisomics to Nishimura's reciprocal translocation lines (Iwata and Khush 1983; Khush and Singh 1985). Unfortunately, there were discrepancies between the results of these studies, and a unified correspondence of chromosomes and linkage groups did not merge.

The discrepancies may have been due to the fact that the numbering of the extra chromosomes in the two trisomic series, one of which is *indica* and another is *japonica*, are different. It is also possible that a mutant from different linkage groups may have been used in correlating linkage groups and extra chromosomes (Iwata et al. 1984 a, b; Khush et al. 1984). However, even when the same *indica* trisomic series was used, chromosomal identifications from three laboratories were still different (Khush et al. 1984; Chung and Wu 1987, 1990; Kurata 1988); a technical problem in chromosome identification thus existed. Although C. M. Rick suggested in a meeting (1985) the use of pachytene chromosomes in rice karyotyping, our experience over the past two decades leads us to believe that it is better to use both meiotic pachytene and mitotic prometaphase chromosomes. The total consistency between the results of our two independent experiments (Table 3, columns 2 and 3) may give support to this point.

It was mentioned that the discrepancies may have arisen from the use of different numbering systems that appeared

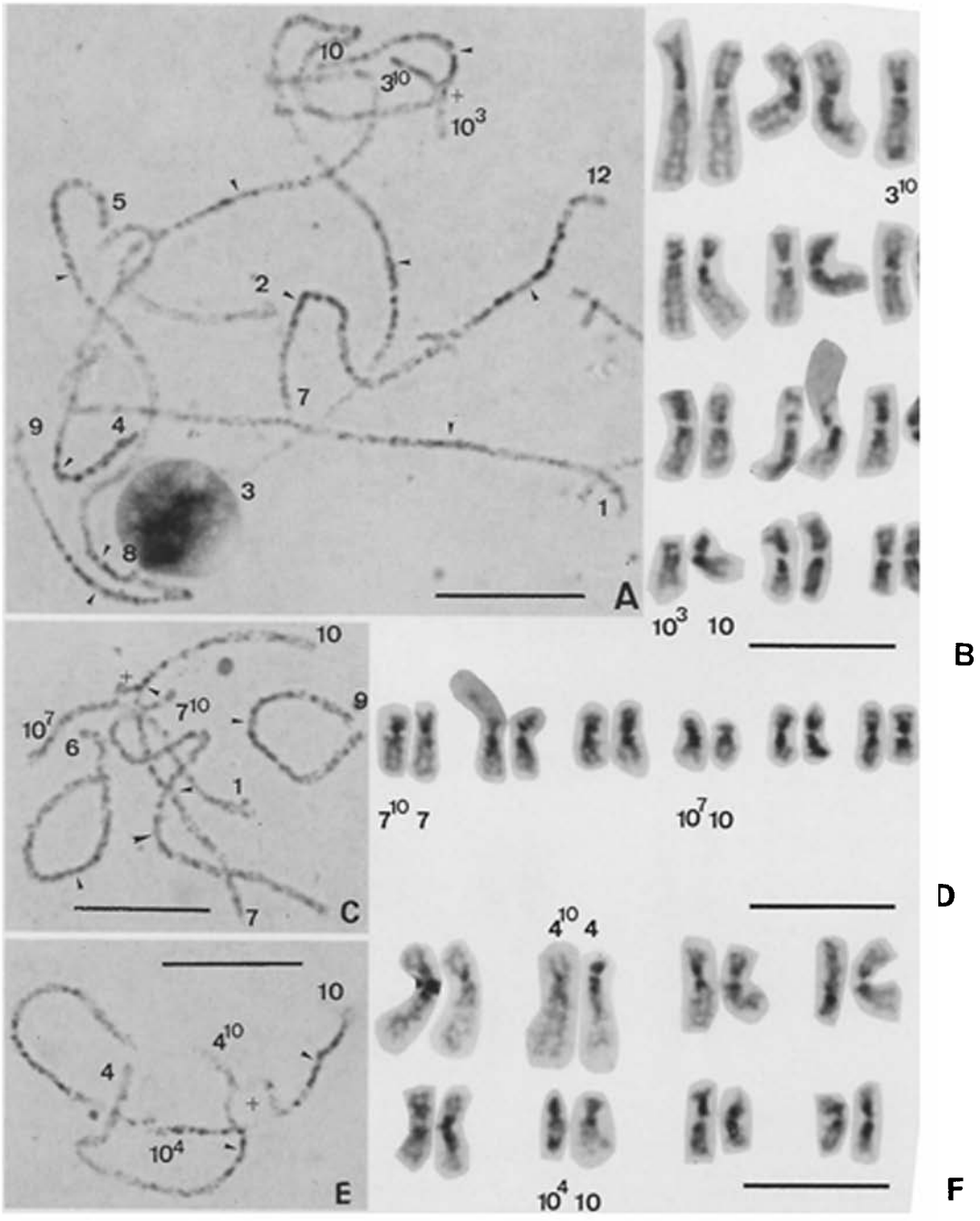

Fig. 5A–F Karyotypes of RT 7-8a, RT 7-12 and RT 7-11. **A** and **B** RT 7-8a showing the interchange between the short arm of chromosome 10 and the long arm of chromosome 3 at pachytene (**A**) and at prometaphase (**B**) resulting in an increase in the length of the short arm of chromosome 10 and a decrease in that of the long arm of chromosome 3. The difference in length between the two translocated segments was the minimum among all of the 11 lines observed. However, the translocation of the heterochromatic segment of chromosome 10 is obvious. **C** and **D** RT 7-12 showing that the heterochromatic segment of chromosome 10 has been interchanged at pachytene (**C**) and at prometaphase (**D**) with the euchromatic segment of chromosome 7 resulting in a longer short arm of chromosome 10 and shorter long arm of chromosome 7. **E** and **F** RT 7-11 showing a similar heterochromatic and euchromatic interchange that has made the morphological change distinct occurred between the short arm of chromosome 4 and the long arm of chromosome 10 (**F**).The cross configuration of the interchange is shown in **E**. *Bar*: 10 μm

to be unified (Iwata 1985; Khush and Singh 1985). In fact, except for Nishimura (1961), investigators have all used a system in which the chromosomes were arranged in a descending order of length. It seems more pertinent and practical to unify rice karyotype identification in a particular trisomic series, in a single species or subspecies. With regard to this point, we have reported the karyotype of *japonica* 'Chianung 242' (Chen et al. 1982), 'Taichung 65' (Chen and Wu 1982) and of *indica* 'IR36' (Wu et al. 1985), which was used as a recurrent parent in backcrossing dur-

ing the establishment of the *indica* trisomic series (Khush et al. 1984).

It is to be regretted that the earlier reported karyotypes were not considered during meetings (1985, 1986 and 1987 at IRRI; 1989 at Tsukuba, Japan; 1990 at Kurahsiki City, Japan and finally 1990 at IRRI again) held for discussions on rice chromosome numbering systems (Khush 1990). If the reported karyotype of 'IR36' had been considered or adopted in identifying extra chromosomes in *indica* trisomic series, discrepancies would have not been so encountered.

These results lead us to revise the linkage groups that have been so far constructed since Nagao and Takahashi (1963) and compiled by Kinoshita (1990). Table 3 gives a summarized comparison of the present results, and those of some earlier workers, on the numbering of rice chromosomes and their corresponding linkage groups. Columns 1 and 2 show, respectively, Nishimura's (1961) arbitrary chromosome numbers and those produced in this study of his RT lines. Columns 3, 4, 5 and 6 show the various proposals arising from studies of trisomics; the proposals of column 3 (Chung and Wu 1987, 1990), but not the other columns, are entirely consistent with those of column 2 (this study). Finally, because the relationship between the compiled linkage groups (column 7) and Nishimura's chromosomes had been well elucidated (Iwata and Omura 1971 a, b; Sato et al. 1973, 1975; Kinoshita et al. 1975; Sato 1976; Sato et al. 1982; Yoshimura et al. 1982; Iwata et al. 1984 a, b; Iwata 1985), we were able to make the revised linkage groups (column 8) corresponding to the identified chromosomes (column 2).

Acknowledgements We thank Prof. J. A. Roper, Department of Molecular Biology and Biotechnology, Genetics Section, University of Sheffield, UK, for critical reading of this manuscript. This work was funded by the Academia Sinica.

References

Burnham R (1962) Discussions in cytogenetics. Burgess Publ, Mineapolis, Minn.

Chen JT, Lai HC, Hwang YH, Chung MC, Wu HK (1982) Identification of rice reciprocal translocation and the location of lazy gene (in Chinese/English). Bot Bull Acad Sin 23:71–87

Chen YJ, Wu HK (1982) A comparison of karyotypes among six *Oryza* species. Bot Bull Acad Sin 23:163–183

Chung MC, Wu HK (1987) Karyotype analysis of 'IR36' and two trisomic lines of rice. Bot Bull Acad Sin 28:289–304

Chung MC, Wu HK (1990) Scrutiny of trisomics from an *indica* rice, *Oryza sativa*.. Proc. Natl. Sci. Counc. B. ROC 14:166–174.

Chung MC, Ning CN, Wu HK (1993) Localization of rRNA genes on rice chromosomes. Bot Bull Acad Sin 34:43–55

Iwata N (1970) Cytogenetical studies on the progenies of rice plants exposed to atomic radiation in Nagasaki (in Japanese/English). Sci Bull Fac Agric Kyushu Univ 25:1–53

Iwata N (1985) The relationship between cytologically identified chromosomes and linkage groups in rice. In: Proc. Rice Genet Symp. IRRI, Manila, The Philippines, pp. 229–237. Ed. Island Publishing House, Inc. Manila, Philippines

Iwata N, Khush GS (1983) Identification of the extra chromosomes of IRRI trisomic series which have been obtained from *indica* varieties in rice. Jpn J Breed 33 [Suppl 2]:208–209

Iwata N, Omura T (1971 a) Linkage analysis by reciprocal translocation method in rice plants (*Oryza sativa* L.). I. Linkage groups corresponding to the chromosome 1, 2, 3 and 4 (in Japanese/English). Jpn J Breed 21:19–28

Iwata N, Omura T (1971 b) Linkage analysis by reciprocal translocation method in rice plants (*Oryza sativa* L.). II. Linkage groups corresponding to the chromosome 5, 6, 8, 9, 10 and 11 (in Japanese/English). Sci Bull Fac Agric Kyushu Univ 25:137–153

Iwata N, Omura T (1975) Studies on the trisomics in rice plants (*Oryza sativa* L.). III.Relation between trisomics and genetic linkage groups. Jpn J Breed 25:363–368

Iwata N, Omura T (1976) Studies on the trisomics in rice plants (*Oryza sativa* L.). IV. On the possibility of association of three linkage groups with one chromosome. Jpn J Genet 51:135–137

Iwata N, Omura T (1977) Linkage studies in rice (*Oryza sativa* L.). On some mutants derived from chronic gamma irradiation. J Fac Agric Kyushu Univ 21:117–127

Iwata N, Omura T (1978) Linkage studies in rice (*Oryza sativa* L.). Some albino genes and their linkage relations with marker genes. Sci Bull Fac Agric Kyushu Univ 33:11–18

Iwata N, Omura T (1984) Studies on the trisomics in rice plants (*Oryza sativa* L.). VI. An accomplishment of a trisomic series in *japonica* rice plants. Jpn J Genet 59:199–204

Iwata N, Omura T, Nakagahra M (1970) Studies on the trisomics in rice plants (*Oryza sativa* L.). I. Morphological classification of trisomics. Jpn J Breed 20:230–236

Iwata N, Omura T, Satoh H (1978) Linkage studies in rice (*Oryza sativa* L.). On some mutants for physiological leaf spots. J Fac Agric Kyushu Univ 22:243–251

Iwata N, Omura T, Satoh H (1984 a) Studies on the trisomics in rice plants (*Oryza sativa* L.). V. Relationship between the twelve chromosomes and the linkage groups. Jpn J Breed 34:314–321

Iwata N, Satoh H, Omura T (1984 b) Studies on the trisomics in rice plants (*Oryza sativa* L.) VII. Some marker genes located on chromosome 2 and their sequence on the linkage map. J Fac Agric Kyushu Univ 29:139–144

Khush GS (1990) Report of meetings to discuss chromosome numbering system in rice. Rice Genet Newsl 7:12–15

Khush GS, Singh RJ (1985) Relationships between linkage groups and cytologically identifiable chromosomes of rice. In: Proc Rice Genet Symp. IRRI, Manila, The Philippines, pp 239-248. Ed. Island Publishing House, Inc. Manila, Philippines

Khush GS, Singh RJ, Sur SC, Librojo AL (1984) Primary trisomics of rice: origin, morphology, cytology and use in linkage mapping. Genetics 107: 141–163

Kinoshita T (1990) Report of committee on gene symbolization, nomenclature and linkage groups. Rice Genet Newsl 7:16–50

Kinoshita T, Takahashi M, Sato S (1975) Genetical studies on rice plant. LXIV. Linkage analysis by reciprocal translocation method, with special references to the first linkage group (in Japanese/English). Memo Fac Agric Hokkaido Univ 9:259–263

Kurata N (1988) Identification of trivalent chromosomes of IR36 tripo plants. Rice Genet Newsl 5:54–59

Kurata N, Omura T (1978) Karyotype analysis in rice. I. A new method for identifying all chromosome pairs. Jpn J Genet 53:251–255

Kurata N, Iwata N, Omura T (1981) Karyotype analysis in rice. II. Identification of extra chromosomes in trisomic plants and banding structure on some chromosomes. Jpn J Genet 56:41–50

Nagao S, Takahashi M (1963) Genetical studies on rice plant. XXVII. Trial construction of twelve linkage groups in Japanese rice. J Fac Agric Hokkaido Univ 53:72–130

Nishimura Y (1961) Studies on the reciprocal translocations in rice and barley (in Japanese/English). Bull Natl Inst Agric Sci Jpn Ser D9:171–235

Omura T, Iwata N, Satoh H (1978) Linkage studies in rice (*Oryza sativa* L.). On some virescent and chlorina mutants. J Fac Agric Kyushu Univ 23: 85–93

Rick CM (1985) Report of Interim Comittee on Chromosome Numbering to the International Rice Genet Syposium Rice Genet Newsl 2:16

Sato S (1976) Linkage analysis of rice plant, by the use of reciprocal translocation lines (in Japanese/English). Bull Coll Agric Univ Ryukyus 23: 73–104

Sato S (1981) Identification of interchanged chromosomes in isogenic translocation lines of a rice variety, 'Taichung 65' (in Japanese/English). Bull Coll Agric Ryukyus Univ. 28:41–47

Sato S, Kinoshita T, Takahashi M (1973) Genetical studies on rice plant. LIV. Linkage analysis of rice plant, by the use of Nishimura's reciprocal translocation lines (in Japanese/English). Memo Fac Agric Hokkaido Univ 8:367–376

Sato S, Kinoshita T, Takahashi M (1975) Genetical studies on rice plant. LXII. Linkage analysis of rice plant by the use of reciprocal translocation lines induced from linkage testers. Memo Fac Agric Hokkaido Univ 9:193–199

Sato S, Kinoshita T, Takahashi M (1980) Genetical studies on rice plant. LXXI. Location of centromere and interchange break points in the pachytene chromosome of rice. Jpn J Breed 30:387–398

Sato S, Muraoka K, Sano Y (1982) Reconstruction of a linkage group corresponding to the Nishimura's second chromosome in rice, *Oryza sativa* L. Jpn J Breed 32:232–238

Wu HK (1967) Note on preparing of pachytene chromosomes by double mordant (in Chinese/English). Sci Agric 15:40–44

Wu HK, Chung MC (1989) The interchanged chromosomes involved in Nishimura's translocation lines. In: Proc Congr SABRAO. pp 183-186. Eds. Lyamas, Takeda G, Aug. 21–25, 1989. Tsukuba, Japan

Wu HK, Chung MC, Chen MH (1985) Karyotype analysis of cultivar 'IR36'. Rice Genet Newsl 2:54–57

Yoshimura A, Iwata N, Omura T (1980) Identification of interchanged chromosomes in isogenic reciprocal translocation lines originated from rice variety 'Taichung 65'. Sci Bull Fac Agric Kyushu Univ 34:97–104

Yoshimura A, Iwata N, Omura T (1982) Linkage analysis by reciprocal translocation method in rice plants (*Oryza sativa* L.). III. Marker genes located on chromosomes 2, 3, 4 and 7. Jpn J Breed 32:323–332