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GENETICAL STUDIES ON RICE PLANT, XXIV

Preliminary Report of Twelve Linkage Groups in Japanese Rice[1)]

By

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Introduction

Notwithstanding the fact that rice is the worlds' most important food crop and the fact that various practical and fundamental genetic studies have been made, some important phases in this field are still unexplored. Especially in the phase of linkage relationships, only a fraction of the possible paired combinations between recognized characters has been tested, and no comprehensive search has been undertaken. This is mainly due to the reason that the linkage analysis on rice plant hitherto have usually been incidental to studies for a different purpose, and thus have seldom found their way into literature—in other words, linkage analysis in this plant has not been subjected to systematic studies.

During the past several years the writers have engaged in studies of genic analysis in rice plant, at the Plant Breeding Institute of Hokkaido University. In the process, strains became available that were segregating simultaneously for two or more monogenically inherited characters, and some multiple marker stocks were built up. These segregations, supplemented with hybrids made specifically for the study of linkage, have been useful in analysing linkage relationships.

Experimental works of the writers conducted at the said Institute provide data on the linkage of 37 gene loci in 12 groups corresponding to the haploid chromosome number. In this report the writers present representative crossing over data for genes in each group and show diagramatically the linear relationships of the genes within each group. Linkage intensities were calculated with the use of IMMER's tables, except as noted.

1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

[Journ. Facul. Agr., Hokkaido Univ., Sapporo, Vol. 51, Pt. 2, 1960]

Not all the possible gene combinations have been tested, and additional data are needed to verify linkage or independence between other combinations. The writers desire, however, to make their results available at this time in connection with the report of the Committee on Gene Symbolization and Linkage presented at the 1959 meeting of the FAO International Rice Commission, held in Ceylon. Present knowledge of linkage in rice is very incomplete and intensive genetic studies are needed in this important cereal crop.

In the present paper the writers will use the new gene symbols. These are based on the list of standard gene symbols and nomenclature which was presented at the I.R.C. meeting of FAO, through N. E. JODON, representing the co-workers mentioned below, pending approval as "Recommended I.R.C. Standard Symbols for Rice Genes". As a basis for determining characters for which standard gene symbols should be established, the following workers have tabulated results of genetic studies published since about 1940. N. E. JODON tabulated the results of studies conducted in the United States, R. SEETHARAMAN with the advice of K. RAMIAH made the tabulation for work done in India, and M. TAKAHASHI with the suggestion and guidance of S. NAGAO tabulated the Japanese work. Based on these tabulations and the report of the International Committee on Genetic Symbols and Nomenclature (adopted by the Tenth International Genetics Congress held in Canada in 1958), JODON has made the above mentioned trial list of standard gene symbols for rice, under the support, cooperation and assistance of these four workers. In order to avoid confusion, the writers, in the present paper, put their previously used symbols in parentheses and have listed them at the end of the descriptive notes of genes referred to.

Before going further, the writers express their special thanks to Mr. Nelson E. JODON, United States Department of Agriculture, for encouragement in their endeavor. They wish to thank Mr. Toshiro KINOSHITA, Research Assistant of our Institute, for his help during the course of the studies. The cost of the present work was partly defrayed by a Grant in Aid for Fundamental Scientific Research from the Ministry of Education.

Linked Genes and Their Segregation Modes

1. "*wx*" Linkage Group

wx : waxy (glutinous) endosperm; (*m* or *gl*)
C (*C^B*, *C^Bp*, *C^Bt*, *C^Br*, *C^+*): Allelic basic genes for anthocyanin color; higher alleles have pleiotropic expression in internode.
C alone: Tawny apiculus
Pla: Purple leaf apex and margin
d_4 : one of the multiple genes for "tillering" dwarf
Cl : Clustered spikelets

Gene pair	Phase	Segregation mode					Recombination value	χ^2 [1]	n	*p*
		AB	Ab	aB	ab	Total				
d_4—*wx* (3:1) (3:1) (21.5%)	r	309 (285.45)	122 (133.05)	122 (133.05)	5 (6.45)	558	21.5 ±2.70	2.937	3	0.50–0.30
wx—*C* (3:1) (3:1) (22.8%)	c	1148 (1124.06)	167 (174.94)	175 (174.94)	242 (258.06)	1732	22.8 ±0.79	1.870	3	0.70–0.50
d_4—*C* (3:1) (3:1) (38.2%)	r	295 (298.82)	127 (118.93)	114 (118.93)	21 (20.32)	557	38.2 ±2.41	0.824	3	0.90–0.80
Pla—*wx* (3:1) (3:1) (44.7%)	c	385 (388.53)	123 (116.97)	113 (116.97)	53 (51.53)	674	44.7 ±1.83	0.520	3	0.95–0.90
Cl—*C* (3:1) (3:1) (40.3%)	c	360 (360.53)	114 (98.47)	84 (98.47)	54 (54.53)	612	40.3 ±1.81	4.582	3	0.30–0.20

1) χ^2 for goodness of fit, under respective linkage intensities.

2. "*Pl*" Linkage Group

Pl : Purple leaf
d_3 : one of the multiple genes for "tillering" dwarf
d_2 : "ebisu" dwarf
lg : liguleless (auricle and collar also absent)
Ph : Phenol staining
Pr : Purple hull (colored lemma and palea due to anthocyanin distribution); (*Rp*)
P : Completely colored apiculus (complementary action with *C* and *A*); (*A*)

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	*p*
		AB	Ab	aB	ab	Total				
d_2—d_3 (3:1) (3:1) (25.4%)	r	207 (194.58)	86 (88.17)	79 (88.17)	5 (6.08)	377	25.4 ±3.21	1.992	3	0.70–0.50
d_3—*Pl* (15:1) (3:1) (35.2%)	r	354 (349.71)	125 (121.85)	21 (27.54)	3 (3.90)	503	35.2 ±5.53	1.894	2	0.50–0.30
Pl—*lg* (3:1) (3:1) (29.5%)	c	1203 (1229.78)	234 (247.72)	273 (247.72)	260 (244.78)	1970	29.5 ±0.85	4.869	3	0.20–0.10

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
lg—*Ph* (3:1) (3:1) (7.4%)	c	218 (229.30)	13 (11.45)	11 (11.45)	79 (68.80)	321	7.4 ±1.03	2.297	3	0.70–0.50
Ph—*Pr* (3:1) (3:1) (24.2%)	c	333 (346.28)	55 (57.22)	64 (57.22)	86 (77.28)	538	24.2 ±1.47	2.383	3	0.50–0.30
d_2—*Pl* (3:1) (9:7) (38.1%)	c	232 (223.78)	157 (152.01)	51 (58.07)	59 (65.14)	499	38.1 ±2.80	1.905	3	0.70–0.50
d_3—*lg* (15:1) (3:1) (39.7%)	c	146 (149.14)	44 (47.74)	13 (8.36)	7 (4.76)	210	39.7 ±7.13	3.988	3	0.30–0.20
lg—*Pr* (3:1) (3:1) (28.2%)	c	486 (497.44)	93 (95.81)	103 (95.81)	109 (101.94)	791	28.2 ±1.31	1.374	3	0.80–0.70
Pl—*Pr* (3:1) (3:1) (48.6%)	c	341 (325.11)	99 (112.89)	114 (112.89)	30 (33.11)	584	48.6 ±2.06	2.789	3	0.50–0.30
d_2—*lg* (3:1) (3:1) (47.2%)	c	920 (886.45)	297 (280.55)	243 (280.55)	96 (108.45)	1556	47.2 ±1.24	8.689	3	0.05–0.02
d_2—*Ph* (3:1) (3:1) (50.0%)	c	165 (165.94)	65 (55.31)	48 (55.31)	17 (18.44)	295	51.5 ±2.99	2.781	3	0.50–0.30
d_2—*Pr* (3:1) (3:1) (50.0%)	c	341 (325.12)	121 (108.38)	90 (108.38)	26 (36.12)	578	54.9 ±2.22	8.192	3	0.05 –0.02
Pl—*P* (3:1) (3:1) (2.1%)	c	580 (550.31)	4 (7.69)	13 (7.69)	147 (178.31)	744	2.1 ±0.36	11.854	2	0.005 –0.001

3. "*A*" Linkage Group

A (*A*, A^d, A^+): Allelic anthocyanin activator genes (complementary action with *C* produces red or purple in apiculus; (*Sp*)

Rd: Red pericarp (complementary action with *Rc*)

Pn: Purple node

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
A—*Rd* (3:1) (3:1) (0.33%)	c	2298 (2326.71)	4 (5.04)	10 (5.04)	797 (772.21)	3109	0.33 ±0.07	5.950	2	0.10–0.05
Rd—*Pn* (3:1) (3:1) (26.8%)	r	241 (270.89)	132 (121.36)	137 (121.36)	13 (9.39)	523	26.8 ±2.70	7.634	3	0.10–0.05
A—*Pn* (3:1) (3:1) (29.9%)	r	333 (358.85)	173 (156.40)	162 (156.40)	19 (15.35)	687	29.9 ±2.31	4.692	3	0.20–0.10

4. "*g*" Linkage Group

g : recessive long empty glumes
d_6 : "lop-leaved" dwarf
Rc : Brown pericarp (basic to *Rd*)
d_7 : "cleistogamous" dwarf

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	*p*
		AB	Ab	aB	ab	Total				
d_6—*g* (3:1) (3:1) (14.0%)	r	383 (363.53)	178 (176.47)	156 (176.47)	3 (3.53)	720	14.0 ±2.45	3.424	2	0.20–0.10
g—*Rc* (3:1) (3:1) (29.1%)	c	831 (832.14)	157 (165.36)	174 (165.36)	168 (167.14)	1330	29.1 ±1.03	2.701	3	0.50–0.30
d_6—*Rc* (3:1) (3:1) (29.9%)	c	1557 (1573.94)	319 (321.31)	330 (321.31)	321 (310.44)	2527	29.9 ±0.76	0.793	3	0.90–0.80
d_6—d_7 (3:1) (3:1) (39.4%)	r	192 (206.28)	85 (80.22)	87 (80.22)	18 (15.28)	382	39.4 ±2.62	2.332	3	0.70–0.50

5. "*I-Bf*" Linkage Group

I-Bf: Inhibitor for dark (or brown) furrows in lemma and palea; (*I-F* or *df*)
Ps : Purple stigma (complementary action with *C*, *A* and *P*)

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	*p*
		AB	Ab	aB	ab	Total				
I-Bf—*Ps* (3:1) (3:1) (42.1%)	c	114 (116.76)	35 (33.24)	33 (33.24)	18 (16.76)	200	42.1 ±3.25	0.252	3	0.98–0.95

6. "d_1" Linkage Group

d_1 : "daikoku" dwarf *gw*: green and white striped
gh : gold hull (golden yellow hull, recessive to straw color); (*r-g*)
An: Awned d_8 : "norin-28" dwarf

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	*p*
		AB	Ab	aB	ab	Total				
gw—d_1 (3:1) (3:1) (17.8%)	r	745 (701.44)	304 (334.31)	323 (334.31)	9 (10.94)	1381	17.8 ±1.75	6.124	3	0.20–0.10
d_1—*gh* (3:1) (3:1) (27.8%)	r	350 (336.00)	138 (149.25)	148 (149.25)	11 (12.50)	647	27.8 ±2.42	1.622	3	0.70–0.50
gw—*gh* (3:1) (3:1) (41.0%)	r	282 (275.89)	101 (105.86)	106 (105.86)	20 (21.39)	509	41.0 ±2.46	0.449	3	0.95–0.90
gh—*An* (3:1) (3:1) (42.9%)	c	265 (259.35)	70 (75.15)	77 (75.15)	34 (36.35)	446	42.9 ±2.20	0.674	3	0.90–0.80
An—d_8 (3:1) (3:1) (5.4%)	c	840 (831.56)	23 (30.19)	39 (30.19)	247 (257.06)	1149	5.4 ±0.46	4.764	3	0.20–0.10

7. "*fs*" Linkage Group

fs : fine stripes in leaf margin of young plant
Ur: Undulate rachis (Sinuous panicle branch)
Dn: Dense (vs. normal)panicle

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
Ur—fs (3:1) (3:1) (27.5%)	c	414 (433.78)	90 (81.47)	80 (81.47)	103 (90.28)	687	27.5 ±1.39	3.614	3	0.50–0.30
fs—Dn (3:1) (3:1) (41.1%)	c	511 (531.58)	147 (147.92)	160 (147.92)	88 (78.58)	906	41.1 ±1.51	2.918	3	0.50–0.30

Hence the gene *Dn* is epistatic over the gene *Ur*, the recombination value in *Ur–Dn* was calculated by FISCHER's Maximum Likelihood Method. This is as follows.

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
Ur—Dn (1:2:1)(3:1) (46.2%)	r	246 (252.75)	27 (24.43)	44 (41.88)	20 (17.94)	337	46.2 ±4.99	0.794	3	0.90–0.80

8. "*la*" Linkage Group

la : lazy (spreading growth habit of plant)
sh : recessive shattering as in difficult or intermediate threshing vs. drop-seed type

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
la—sh (3:1) (3:1) (38.7%)	r	215 (216.05)	98 (85.45)	74 (85.45)	15 (15.05)	402	38.7 ±2.82	3.383	3	0.50–0.30

9. "*nl*" Linkage Group

nl : "neck leaf" character; bract leaf at the basal node of panicle; (*hk*)
ri : verticillate (whorled) arrangement of rachis ("rinshi" character in Japanese)

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
nl—ri (3:1) (3:1) (33.5%)	r	636 (654.79)	282 (275.21)	284 (275.21)	38 (34.79)	1240	33.5 ±5.30	1.284	3	0.80–0.70

10. "*bl*" Linkage Group

bl : physiologic diseases showing dark brown or blackish mottled discoloration of leaves ; (*mt* or *mg*)

d_5 : one of the multiple genes for "tillering" dwarf

Gene pair	Phase	Segregation mode					Recombination value	χ^2	n	p
		AB	Ab	aB	ab	Total				
bl—d_5 (3:1)(15:1) (25.1%)	c	215 (200.15)	6 (7.60)	50 (59.54)	6 (9.71)	277	25.1 ±2.09	4.835	3	0.30–0.20

11. "*bc*" Linkage Group

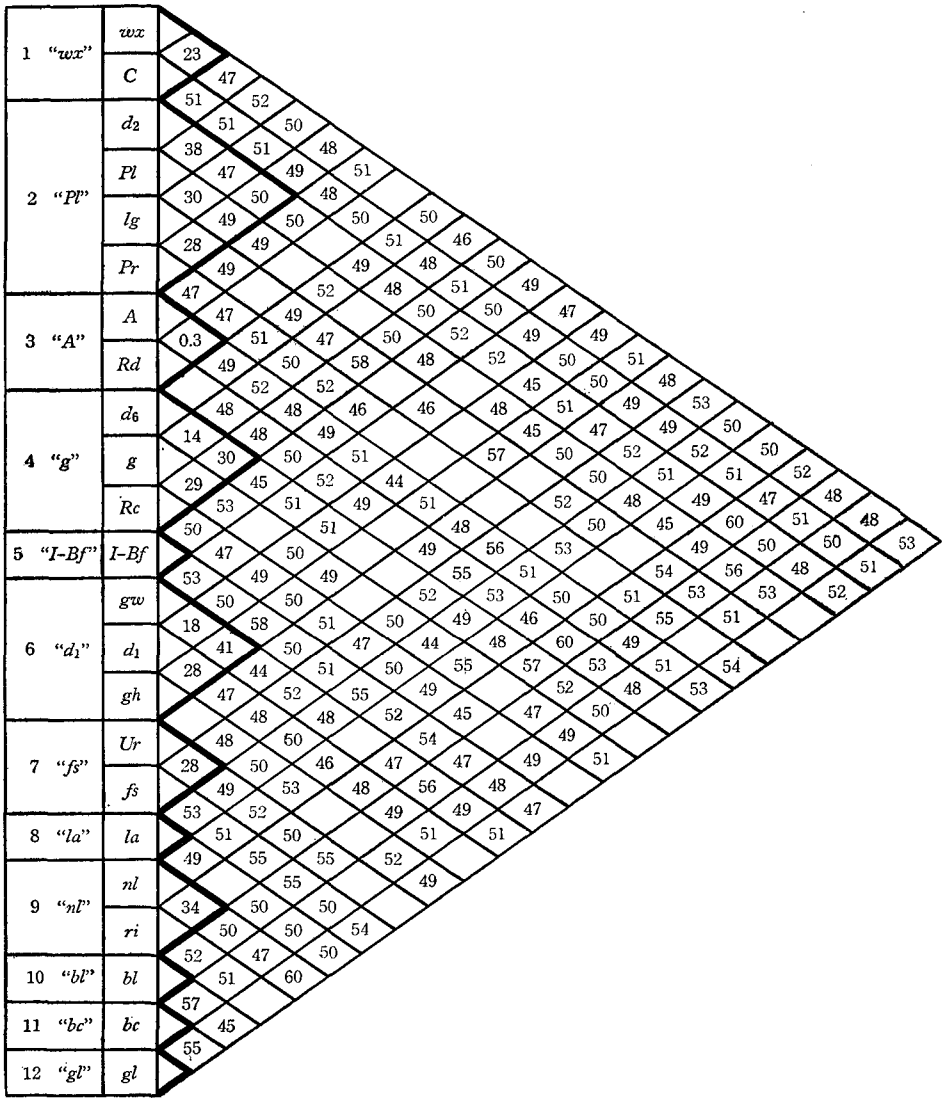
bc : brittle culm

12. "*gl*" Linkage Group

gl : glabrous (non-hairy) leaf

List of Recombination Values

The recombination values from which the linkage groups were estimated are listed in the next table on page 8.


1 "wx"
wx
C
2 "Pl"
d2
Pl
lg
Pr
3 "A"
A
Rd
4 "g"
d6
g
Rc
5 "I-Bf"
I-Bf
6 "d1"
gw
d1
gh
7 "fs"
Ur
fs
8 "la"
la
9 "nl"
nl
ri
10 "bl"
bl
11 "bc"
bc
12 "gl"
gl

Trial Construction of Linkage Maps

Based on the above mentioned data, the genes of every linkage groups appear to be arrenged in the order as shown in Figure 1 and 2.

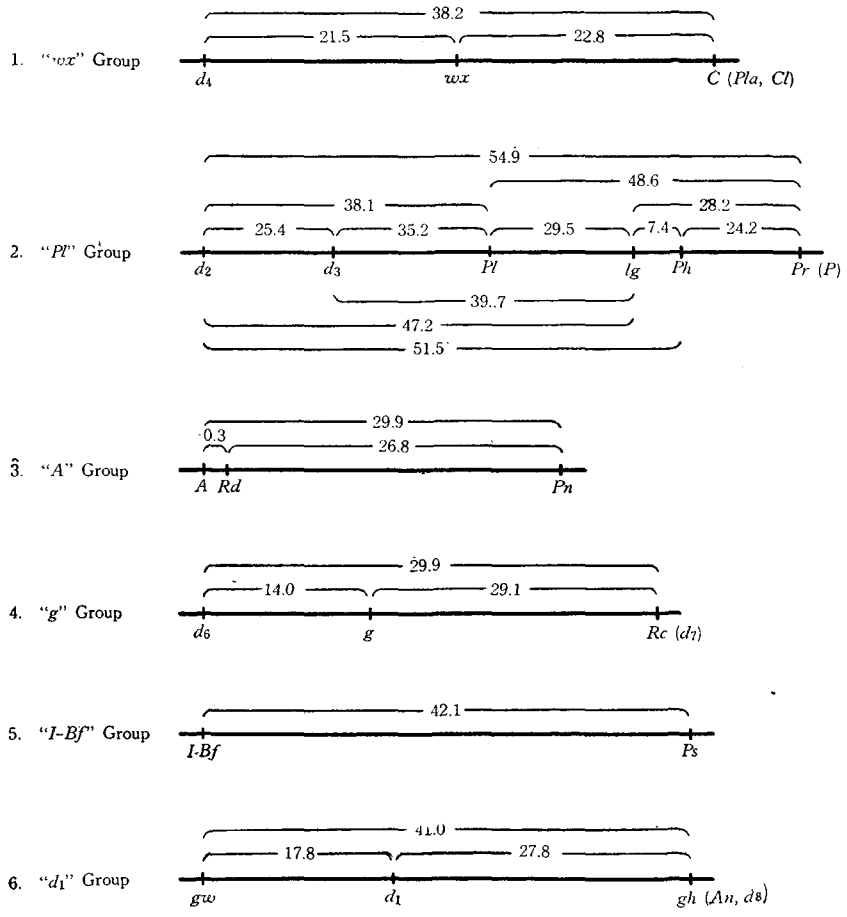


Fig. 1. Linkage maps of "1st to 6th" groups.

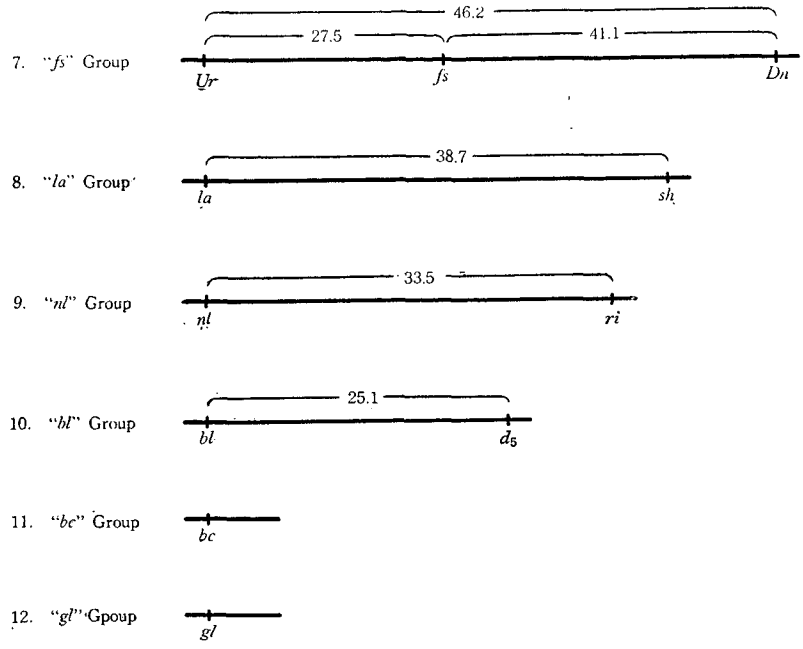


Fig. 2. Linkage maps of "7th to 12th" groups.

Key Literature on Rice Linkage, since 1940

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