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PRESENT STATUS OF RICE LINKAGE STUDIES AND SOME INTRIGUING ASSOCIATED PROBLEMS

Genetical Studies on Rice Plant, XXIX¹⁾

By

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I. Introduction

Unlike such crops as corn, barley or wheat, in linkage studies on rice, up to recent years, there had been little or no cooperative efforts in the exchange of genetic materials and information, or efforts to initiate joint research among workers at home and abroad. Consequently, in spite of the fact that a fairly large number of genes have been reported, very little affirmed information have been accumulated on linkage relations or linkage groups.

In the United States, however, JODON (1948) suggested the possibility of the existence of eight linkage groups, based on data reported principally in India and the United States at that time. This was followed by NAGAO (1951) in Japan who published his four linkage groups obtained in Japanese varieties, and in 1953 RAMIAH summarized the results of linkage groups postulated in India. JODON (1956) again made a report, revising his previous linkage grouping of 1948 (eight groups) and of 1955 (six groups) into seven groups to accommodate the linkage relationships reported up to that time. As pointed out by JODON himself, there are some questions and uncertainty regarding grouping and identification of the genes concerned. It is apparent that linkage work would be complicated by inadequate genic information on complex characters.

A barrier which precludes the genetic situation in the standard segregation mode of inheritance, and consequently blurs the intrinsic linkage relations, is the various grades of partial sterilities that occur in hybrids and their descendants from crosses between distantly related varieties, especially between Japonica type

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

varieties and the majority of Indica type varieties. It has been recognized that hybrid sterility restricts segregation and recombination in subsequent generations (OKA 1955, 1956, 1957, SAMPATH 1959, RICHHARIA & MISRO 1959, 1962 and others).

If the principal object of research is to be directed to solve the intrinsic nature of this sterility barrier, hybridization experiments between distantly related varieties, as first step, should be conducted. In this direction, a fairly large amount of works has been accumulated, however, at present there is no explanation which would suffice to convince the majority of workers.

While, in the case where efforts are centered on constructing an outline of rice linkage groups, which corresponds to the haploid number of chromosomes ($n=12$), the actual procedure of this project should be altered, to some extent, as briefly suggested below.

Genic analysis and its accompanying linkage analysis should, at the start, be carried out in two or three varietal groups. These hybridizations are within the Japonica varieties, within the Indica varieties and or within the so-called "Bulu" type varieties. Through these efforts two or three sets of linkage maps will be obtainable without serious difficulty due to intervarietal sterility. And by examining the relative location of apparently identical genes in distantly related varieties, the general situation of rice linkage groups would become clear.

Along this line of thought, and as a first step to initiate cooperative research on rice linkage, the writers, in the present paper, will give their results obtained in Japanese varieties, and make a critical identification of two series of the linkage groups, viz. the groups summarized by JODON and the groups postulated by the writers. And further, in the later part of the present paper, some problems that have attracted the attention of rice workers will be indicated in connection with linkage studies.

II. Present Status of Rice Linkage Groups

In 1960 and 1963 the writers made reports on linkage groups of Japanese varieties, as a trial construction of a complete set of groups which represent the twelve chromosomes, though some of the groups are composed of only two loci. In the data of the present paper new genes, *bl_m*, *drp*, *rl* were added in the three linkage groups, I, II, III respectively and some revisions were made regarding the magnitude of recombination values.

Not only linked inheritance data but also independent data are indispensable to explore linkage relations and demarcate each linkage group. The writers' summarized data of recombination values obtained among genes included in the

linkage groups, are given in Table 1. In this table the genes of each group are arranged in the order of their loci in the linkage maps. A brief résumé

TABLE 2. Linkage Groups of Japonica-type Rice

Group	Gene	Character expression
I	<i>d₄</i>	one of the multiple genes for "tillering" dwarf
	<i>wx (m, gl)</i>	waxy (glutinous) endosperm
	<i>C</i>	Chromogen for anthocyanin color
	<i>bl_m</i>	black leaf spot
	<i>Cl (Scl)</i>	Clustered spikelets
	<i>Lf</i>	Maturity (YAMAGUCHI 1928)
	<i>sm</i>	male sterile (HARA 1947)
	<i>Pla</i>	Purple leaf apex and margin (NAGAO 1951)
	<i>X₁</i>	Gamete development (OKA 1953)
	<i>Y₁</i>	ditto (ditto)
	<i>dp</i>	depressed palea (NAGAMATSU & OHMURA 1961)
<i>ws (v)</i>	white striped seedling (ditto)	
II	<i>d₂</i>	"ebisu" dwarf
	<i>d₃</i>	one of the multiple genes for "tillering" dwarf
	<i>Pl</i>	Purple leaf
	<i>lg</i>	liguleless
	<i>Ph</i>	Phenol staining
	<i>Pr (Rp)</i>	Purple hull
	<i>P (A)</i>	Completely colored apiculus
	<i>Xe (R)</i>	<i>Xanthomonas</i> resistance (NISHIMURA 1960)
	<i>lop</i>	lopped leaf (NAGAMATSU & OHMURA 1961)
	<i>drp (nu)</i>	dripping-wet of leaves (NAGAO, TAKAHASHI & MORIMURA)
<i>Pi</i>	<i>Piricularia</i> resistance (HSIEH 1961)	
III	<i>rl</i>	rolled leaf
	<i>A (Sp)</i>	Anthocyanin activator
	<i>Rd</i>	Red pericarp
	<i>Pn</i>	Purple node
	<i>lax</i>	lax panicle (MORINAGA & NAGAMATSU 1942)
	<i>ts₁</i>	twisted stem (HSIEH 1960)
	<i>d</i>	dwarf (ditto)
	<i>lgt</i>	long twisted grain (ditto)
	<i>Pp</i>	Purple pericarp (HSIEH 1964)

Group	Gene	Character expression
IV	<i>d</i> ₆ <i>g</i> <i>Rc</i> <i>d</i> ₇	"lop-leaved" dwarf recessive long empty glumes Brown pericarp "cleistogamous" dwarf
V	<i>I-Bf (df)</i> <i>Ps</i>	Inhibitor for dark or brown furrows in lemma and palea Purple stigma
VI	<i>grw</i> <i>d</i> ₁ <i>gh (rg)</i> <i>An</i> ₃	green-and-white striped "daikoku" dwarf gold hull Awn
VII	<i>Ur</i> <i>fs</i> <i>Dn</i>	Undurate rachis fine stripes in leaf margin of young plants Dense (barnyard-grass-like) panicle
VIII	<i>la</i> <i>sh</i> <i>d</i>	"lazy" growth habit shattering or easy threshing "long-stemmed" dwarf (NAGAMATSU & OHMURA 1961)
IX	<i>nl (hk)</i> <i>ri</i>	neck leaf, bract leaf at the basal node of panicle verticillate arrangement of rachis
X	<i>bl</i> ₁ (<i>mt, mg</i>) <i>d</i> ₅	physiological disease showing dark brown discoloration of leaves one of the multiple genes for "tillering" dwarf
XI	<i>bc</i> <i>d</i> ₈ <i>An</i> ₁	brittle culm "nohrin-28" dwarf Awn
XII	<i>gl</i> <i>An</i> ₂ <i>Hg</i>	glabrous glume and leaf Awn Hairy glumes (Long pubescence on floral glumes)

of character expressions of these genes are listed in Table 2, together with genes and their character expressions recently reported by other workers in Japan and adjacent countries, mostly in Taiwan.

Other linkage groups suggested by JODON (1955, 1956) are briefly presented in Table 3. His later experimental finding and that of other workers who employed exotic, not Japanese, varieties are added properly in this table.

TABLE 3. Linkage Groups of Rice, Summarized by JODON

Group	Gene	Character expression
I	<i>C (Ap)</i>	Colored apiculus (Chromogen)
	* <i>Lmp (Pla)</i>	Colored leaf apex and margin
	* <i>d₃</i>	dwarf
	<i>Hf</i>	Colored hull-furrows (Dark furrows)
	* <i>Anr</i>	Red apiculus (Modifier)
	<i>wx</i>	waxy
	<i>Fl₁</i>	Maturity
	<i>v</i>	virescent
	<i>Cl</i>	Clustered spikelets
	<i>fm (sf)</i>	sterility
	* <i>Fl₃</i>	Maturity
* <i>Lp</i>	Colored leaf blade	
II & III	<i>A (Apb)</i>	Colored apiculus (Activator)
	<i>Pr (Rd)</i>	Red pericarp
	<i>Sp (Ps)</i>	Purple stigma
	<i>Np (Pn)</i>	Purple node
	<i>Pa</i>	Purple auricle ?
	<i>Lax</i>	Colored leaf axil
	<i>Lsp</i>	Purple sheath
	<i>hg (gh)</i>	gold hull
	<i>Ntp</i>	Colored internode
	<i>Gp</i>	Purple empty glumes
	<i>Lgp</i>	Purple collar (ligule)
	<i>Lmp</i>	Purple leaf margin
	<i>Hp</i>	Purple hull (caryopsis and lemma)
	<i>Hw (Wh)</i>	White hull
	<i>lg</i>	liguleless
	<i>Ph</i>	Phenol staining
	<i>Lbp (Pl)</i>	Purple leaf blade
	* <i>d₂</i>	dwarf
* <i>sk</i>	semi sterile ?	
IV	<i>Pbr (Rc)</i>	Brown pericarp (bran)
	<i>g</i>	recessive long empty glumes
	* <i>d₆</i>	dwarf
	<i>Ntp (Pin)</i>	Colored internode
	<i>Fl</i>	Maturity

Group	Gene	Character expression
V	<i>Jp</i>	Purple junctura or collar
	<i>Prp</i>	Purple pericarp
	<i>Lsp</i>	Purple sheath
	<i>O</i>	Scent or aroma in grain
VI	<i>Hb</i>	Colored hull (black)
	<i>Ntv</i>	Purple internode
	<i>An</i>	Awn
	<i>d</i>	dwarf
VII	<i>Lh (gl)</i>	Pubescence
	<i>An</i>	Awn
VIII	<i>Ce</i>	<i>Cercospora</i> resistance
	<i>d</i>	dwarf

* Gene of which location is estimated by Japanese data alone.

Figure 1 is a diagrammatic illustration of linkage groups arranged in the sequence of the groups proposed by the writers.

Through these tables and diagrams it can be pointed out that these two series of linkage groups do not coincide with respect to the loci of some genes, and thus it is apparent that they can not be brought under one general series of rice linkage groups. Especially, the differences are seen in the location of *A*, *P*, *Pl*, *Pn*, *Pr* and *gh*. In Japanese rice, these genes belong to three different linkage groups, viz. (*P*, *Pl*, *Pr*), (*A*, *Pn*) and (*gh*), while in other varieties, genes which are probably identical with those genes in Japanese rice have been assigned positions in the group termed as the combined (II-III) group of JODON.

This discrepancy can not be convincingly explained as yet, since only limited information has been available in the comparison of gene system and identification of genes in distantly related rice varieties. Whether this discrepancy is due to structural differences of chromosomes or brought about by the different gene systems or based on some difficulties which lie in the proper identification of characters and the causal genes involved, remains to be solved.

III. Beneficial Side-effects Expected from Establishment of Linkage Groups

As briefly pointed out in the introduction, intervarietal sterility has been the subject of a great deal of research and has attracted the attention of both

the rice breeders and geneticists. Divergent views of interpretations on the basis of the nature of sterility has been proposed by many workers; among them the sharpest controversy comes from a difference of opinions as to whether the sterility is genic or chromosomal.

Such workers, as HENDERSON (1959, 1963), YAO et al (1958), SHASTRY et al (1960, 1961, 1963) and others, indicated the possible roles of inversions, translocations, deletions and duplications. According to HENDERSON'S view both his cytological and genetic data indicate stronger evidence that the sterility is due to the structural differences in chromosomes, probably of the included inversion type. SHASTRY stated that the differential segments, which are most common in the hybrids and which are interpreted as brought about by translocations, may account for sterility and non-recovery of some recombinants in hybrid progenies. The genic explanation of sterility is redundant since the basic premise of normal homologous pairing was not satisfied at pachytene.

On the other hand, OKA (1953, 1957, 1962, 1963) based on hybrids and their subsequent generations, arrived at an opinion that, in explaining the sterility patterns and segregation distortions, there is no particular reason for assuming the chromosomal differentiation in structure. He postulated a series of gene system termed as "gametic-development genes" and "duplicate-fertility genes". According to him, the F_1 sterility might be the so-called haplontic and can be accounted for by the presence of duplicate genes for gamete development, which also bring gametic selection and consequently result in the modification of segregation ratio and a restriction on recombination of independent genes. Duplicate genes of diplontic effect were also postulated to account for the true breeding partial sterile lines obtained in the F_1 and later generation. In regard to the above, through a cytological basis HSIEH (1957, 1958) supports OKA'S hypothesis. OKA (1963), further, suggested that the occurrence of these duplicate genes might be mainly due to the possible nature of secondary-balanced polyploidy of rice. However, whether or not rice may have latent homologous chromosomes in the haploid phase and, therefore whether or not rice may be a secondary polyploid in nature is still a matter of dispute, even though quite a few reports of the secondary association in meiotic chromosomes have been accumulated both in the diploid and the haploid level of somatic chromosomes (SAKAI 1935, NANDI 1936, HU 1957, 1958, 1960 and others). The validity and the significance of the secondary association in rice also has attracted interest of rice geneticists.

MIZUSHIMA and KONDO'S view (1960, 1961, 1963, 1964) is a rather eclectic case of the above two. In explaining the anomalous segregation mode of inheritance which they have obtained in hybrids from crosses of Japanese and

Figure 1. Diagrammatic Illustration of Linkage Data Arranged in the Order of Linkage Groups in Japanese Rice

	JAPONICA TYPE VARIETIES	VARIETIES IN TAIWAN & OTHERS	INDICA TYPE VARIETIES
I	<p>YAMAGUCHI (1928) HARA (1947) NAGO (1951) OKA (1953) NAGAMATSU & OHMURA (1962) NAGO, TAKAHASHI & MORIMURA (1964)</p>	<p>HSIEH (1961) (<i>Pla?</i>)</p>	<p>JODON (1948-1957) CHANDRARATNA (1953) RICHHARIA et al (1960)</p>
II	<p>NAGO & TAKAHASHI (1956) NISHIMURA (1960) NAGAMATSU & OHMURA (1961) NAGO, TAKAHASHI & MORIMURA (1964)</p>	<p>HSIEH (1961) HSIEH (1961) HSIEH (1961) HSIEH (1964)</p>	<p>JODON (1948-1957) RICHHARIA et al (1960) RICHHARIA et al (1960) CHAO (1928) D'CRUZ (1960) SHAFI & AZIZ (1959) GOUYON & GOUYON (1946)</p>
III	<p>MORINAGA & NAGAMATSU (1942)</p>	<p>HSIEH (1960)</p>	<p>RAMIAH & RAO (1953) RAMIAH et al (1960) SHAFI & AZIZ (1959) KADAM & D'CRUZ (1960)</p>
IV	<p>NAGO & TAKAHASHI (1963) YAMAGUCHI (1929) NAGAMATSU & OHMURA (1960)</p>		<p>JODON (1948-1956) KADAM & D'CRUZ (1960) RAMIAH & RAO (1959)</p>
V	<p>I-Bf Ps</p>		<p>SHAFI & AZIZ (1959) D'CRUZ (1960)</p>
VI	<p>NAGO & TAKAHASHI (1963)</p>		<p>JODON & CHILTON (1946)</p>
VII	<p>Ur fs Dn</p>		
VIII	<p>NAGAMATSU & OHMURA (1961)</p>		
IX	<p>nl ri</p>		
X	<p>bl₁ d₅</p>		
XI	<p>bc d₈ An₁</p>		
XII	<p>NAGO, TAKAHASHI & KINOSHITA (1960)</p>	<p>ANANDAN (1928) KUANG (1951) KUANG (1951)</p>	<p>BREAUX (1948)</p>

Indian varieties, they advocated an explanation that there might be structural differences of chromosomes between parental varieties. In their experiments, however, the chromosomal differences did not directly affect the gametic sterility in F_1 . As to the possible causation of the sterility, they postulated that it might be due to a complementary action of genes or to a deficiency of genes brought about by structural hybridity.

Still another opinion, though not so pronounced, was made by such workers as SAMPATH (1963), KITAMURA (1960) and others. SAMPATH suggests the possible role of cytoplasmic factors as one of the causes of sterility.

Such being the case of research regarding the intervarietal hybrid sterility of rice, further studies should be made to reach a convincing elucidation. In this connection, and as one of the approaches toward this target, an examination of the relative location of apparently identical genes in the distantly related varieties would be worth consideration. Valuable results may be brought to light after each set of linkage maps are established. During the course of these studies, data useful for discussing the intrinsic nature of secondary associations will also be obtainable.

Another beneficial side effect associated with linkage analysis of rice is the revealing of correlations or linkages between marker genes and agronomic characters. This will provide a positive method for improving varieties in some important characters that are difficult to identify among the segregation products of hybrids. In rice, only a few instances have been reported in this respect; however, a case of particular interest was described by TORIYAMA (1960). He found that cool tolerance in Japanese varieties is correlated with the glume color gene, *Pr*, which is located in the writers' Group II. He further indicated that the cool tolerance is also associated with an awning gene, *An*.

A phase of studies regarding the cytological basis of linkage groups is nearly unexplored; and, as far as the writers are aware, only two such investigations which are systematically planned, have been made public. According to NISHIMURA (1961, 1963), his chromosomes No. VI and No. XI bear two series of genes which belong to Group I and Group II of the writers' respectively.

— Postscript —

In laying plans for the future studies of the writers, the writers should, at first, ask themselves how to make the most of the informations obtained from their past work toward their future studies. The present paper was prepared in answer to this question. We should like to add here that future studies will be made with emphasis on the clarification of the relative locations

of identical genes in distantly related varieties. This direction, in the writers belief, also, corresponds with one of the resolution discussed at the symposium on rice genetics and cytogenetics, held at the International Rice Research Institute (IRRI), in the Philippines, 1963 (CHANG 1963).

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