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GENE ANALYSIS AND ITS RELATED PROBLEMS *

— Genetical Studies on rice plant, LXXX —

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I. Introduction

It is apparent that without adequate knowledge of the function of each individual gene based on systematically produced crossing examinations, the experimental results on the segregation mode can not be used as a solid basis to elucidate the gene system of complex characters concerned and likewise they would not furnish sufficient data to understand the linkage relationships. In spite of the fact that the rice plant has been used for genetical studies since the pioneering report on xenia of endosperm character by HOSHINO in 1902, and consequently a fairly large number of genes have been postulated, relatively limited affirmed information, as compared with corn and barley, is available on gene systems of some important agronomic characters or on mapping linkage groups. Until recently, little effort has been made to initiate joint and systematically planned research among workers abroad. In addition with special regards to the rice plant, a barrier which precludes the genetic situation in the standard segregation mode exists and as a result the generalization of gene systems and of linkage relationships are blurred. This barrier consist of the various grades of partical sterilities that occur in hybrids and their descendants from crosses between distantly related varieties, especially between *japonica* varieties and the majority of *indica* varieties. This sterility is also recognized to restrict the recombination of genes in subsequent generations (OKA 1955, 1956, 1957, SAMPATH 1959, RICHHARIA *et al*, 1959. 1962, etc). As for the genetic mechanism of the sterility, there is no explanation which would suffice to convince the majority of workers (refer to other chapters).

Such being the case in rice genetics, gene analysis and its accompanying linkage studies have been carried out separately within two varietal groups, *japonica* and *indica*, with the exception of some recent research intentionally planned to encompass both groups. In the present chapter the writer, first intends to review the results obtained on *Japonica* varieties, with special attention paid on reports made in Japan, and to make some critical comparisons with other results obtained in other varietal group abroad. In the later part, some intriguing problems associated with gene analysis of this plant will be described.

To avoid confusion in terminology the proposal appearing CHANG and BARDENAS' paper (1965) was used, and in which terms based on botanical considerations take priority over agronomic terms of extensive usage. In the rice plant, the usage of gene symbols has been a matter of individual preference for a long time, and this added confusion to a common gene nota-

tions. In this article notations are unified to be in accordance with the list of standard gene symbols and nomenclature adopted by the International Rice Commission Working Party of FAO in 1954, whenever it is applicable (I. R. C. 1959, CHANG and JODON 1963, CHANG 1964).

— Acknowledgment —

My work reported here is the 80th report in my series of research on "Genetical Studies on Rice Plants". Since the 1st report of my series of studies was written in 1941, this 80th report is a product of my 40 years of research in this field. Report 1 to Report 20 were the joint efforts of Dr. NAGAO (the then Professor of Plant Breeding Institute of Hokkaido University) and the present writer TAKAHASHI (the then Associate Professor of the said Institute), from Report 21 to Report 30 Dr. KINOSHITA (the then Instructor of the said Institute) joined the team, and from Report 31 to Report 80 the writer TAKAHASHI (the then Professor) and Dr. KINOSHITA (the then Associate Professor) joined their forces to write the series of reports on "Genetical Studies on Rice Plants".

The 80th Report was actually completed as a manuscript seven years ago by the present writer which he intended to publish. But we did not publish this report till now for some reasons. On the occasion of the fulfillment of my duties and on the year of my retirement, the data that we had completed since was added and the Report 80 was written anew in the form of general considerations.

From 1981 Dr. KINOSHITA became Professor of Plant Breeding Institute, and he has contributed largely to this series of publications. Without his valuable assistance and his never ceasing cooperation, the writer could never have continued along the same line. I wish to take this opportunity to thank my excellent collaborator Dr. KINOSHITA for his help in rewriting the present 80th Report. At the same time I wish him all the luck in his future work.

II. Genic schemes of some striking characters

A. Anthocyanin and its related colors

Coloration due to anthocyanin and its related pigments have attracted attention of many workers. The anthocyanin color shows a wide scope of variation from pale pink to purplish black, and its related color expression, the so-called "tawny", ranges from light to dark brown. The aglycone of anthocyanin is usually cyanidin, however, in a rare case, the presence of

malvidin was reported (TAKAHASHI 1957, NAGAI *et al.* 1960, MIZUSHIMA *et al.* 1963).

A survey of color distribution pattern in plant bodies in several varieties may profitably precede the crossing experiments, and this was done by various workers (HECTOR 1916, JONES 1929, NAKAYAMA 1932, RAMIAH 1945, TAKAHASHI 1957, MISRO *et al.* 1960 etc). As a result it was revealed that the color is found in all of the vegetative parts and several floral parts, and that the color develops in these parts only when color occurs in the apiculus, though some exceptions might be in existence. This suggests that the apicular color is important in analyzing color inheritance not only in this part but also in other parts. In this chapter recent genic interpretations on color characters, with an emphasis on the apiculus color, will be made.

For a long time it has been considered that a single locus of gene which by itself produces the apiculus color exists, together with several modifiers which convert color intensities and shades (cf. JODON 1948 and CHANDRARATNA 1964). And further, some workers proposed duplicate genes by which a double recessive is a plant with colorless apiculus (cf. RAMIAH and RAO 1953, CHANDRARATNA 1964). In 1947, NAGAO and TAKAHASHI of Japan briefly accounted for the degree of anthocyanin coloration by conceiving multiple allelic series of two loci. In their later papers, with further evidence, they expressed the view which is given below (NAGAO 1951, TAKAHASHI 1957, 1964, NAGAO *et al.* 1962, etc). According to their genic scheme, the occurrence of the color depends on the complementary action of genes *C* and *A*; *C* produces chromogen and *A* activates *C* and turns the chromogen into anthocyanin. *C* and *A* both comprise multiple allelic series respectively: six alleles were found at the *C*-locus and four at the *A*-locus. They are arranged in the rank of dominancy as $C^B > C^{Bp} > C^{Bt} > C^{Br} > C^{Bm} \geq C^+$ and $A^E > A > A^d > A^+$.

C and *A* are essentially color-producing genes, but with these genes alone coloration is so limited and appears so thinly scattered at the very tip of the apiculus that the apiculus of this genotype is frequently mistaken as colorless. For the distinct coloration, another gene, *P*, which controls the spreading of chromogen over the entirety of the apiculus is necessary to be present. The majority of Japanese varieties possess *P* in common, and the principal color types examined so far are mainly a result of combinations of any alleles of the *C* and *A* loci (NAGAO and TAKAHASHI 1956 a). In the absence of *C* or *A* the anthocyanin color does not appear and the plant is uncolored at the time of flowering. But upon ripening and when

C is present alone or with A^d , that is when it is without A^E or A , C makes the apiculus brown, which is generally referred to as "tawny" in several color intensities, depending on which alleles of the C -locus is involved. This phenomenon is biochemically inferred that C produces such substances as flavon or catechin, or their common precursor, and A is related with the conversion into anthocyanin pigment, or with the prevention of changing of substances into other substances (NAGAO, TAKAHASHI and MIYAMOTO 1965 b. 1957). A^d is less potent than A^E and A , that is, only a fraction of the chromogenic substance can be utilized in the formation of anthocyanin pigment. This is the reason why plants with $C^B A^d$ and $C^{Bp} A^d$ show a particular color type in which the anthocyanin and the tawny colors overlap with each other. The interpretation mentioned so far is diagrammatically represented as given in Fig. 1. In this figure it must be pointed out that, in explaining color intensity, there is no need of proposing modifiers.

Whether or not this genic scheme is most appropriate and adequate to be accepted as a basic system controlling the anthocyanin coloration is a matter of dispute. However, data favoring this scheme are accumulating not only in Japanese varieties but also in foreign varieties of *indica* origin (HSIEH 1960, HSIEH and CHANG 1962 a, GHOSE *et al.* 1963, etc). The segregation patterns, given through *japonica* × *indica* and *indica* × *indica* crosses of extensively produced are intricate. However, they are divided into two cases. In the first case, parental varieties are assumed as to their genotypes on the basis of the C - A scheme and their hybrids given segregation types consistent with this genic assumption. In the second case, the appearance of color types and their segregation modes do not coincide properly with the expectation from the anticipated genotypes of their parents. In explaining this, two directions are possible to consider. One is in a direction to postulate new alleles at the three loci, C , A and P , together with some modifiers including inhibitors (HSIEH and CHANG 1964, NAGAO *et al.* 1962, TAKAHASHI *et al.* 1968 d, MORI *et al.* 1971). To propose plausible explanations which would encompass all the data of TAKAHASHI and his collaborators, the existence of new alleles at the C and P loci was assumed tentatively. They are C^{Bs} , C^{Bc} and C^{Bd} in C , and P^K and P^C in P . The rank of dominance of alleles in these loci are:

$$C^{Bs} > C^B > C^{Bp} > C^{Bt} > C^{Br} \geq C^{Bd} \geq C^{Bk} \geq C^{Bc} \geq C^{Bm} > C^+ \\ P \geq P^K \geq P^C \geq P^+$$

Incidentally, the gene action of P^K shows a lesser spreading ability than that of P , and P^C is lesser than P^K (MORI and TAKAHASHI 1981).

The other is a way to consider the occurrence of structural dissimilarity of chromosomes due to so-called "cryptic" translocation, resulting in duplication and deficiency of either one, two or three loci of the said genes (MIZUSHIMA and KONDO 1959 a, 1959 b, 1960, KONDO *et al.* 1963 a, 1963 b, 1963 c,

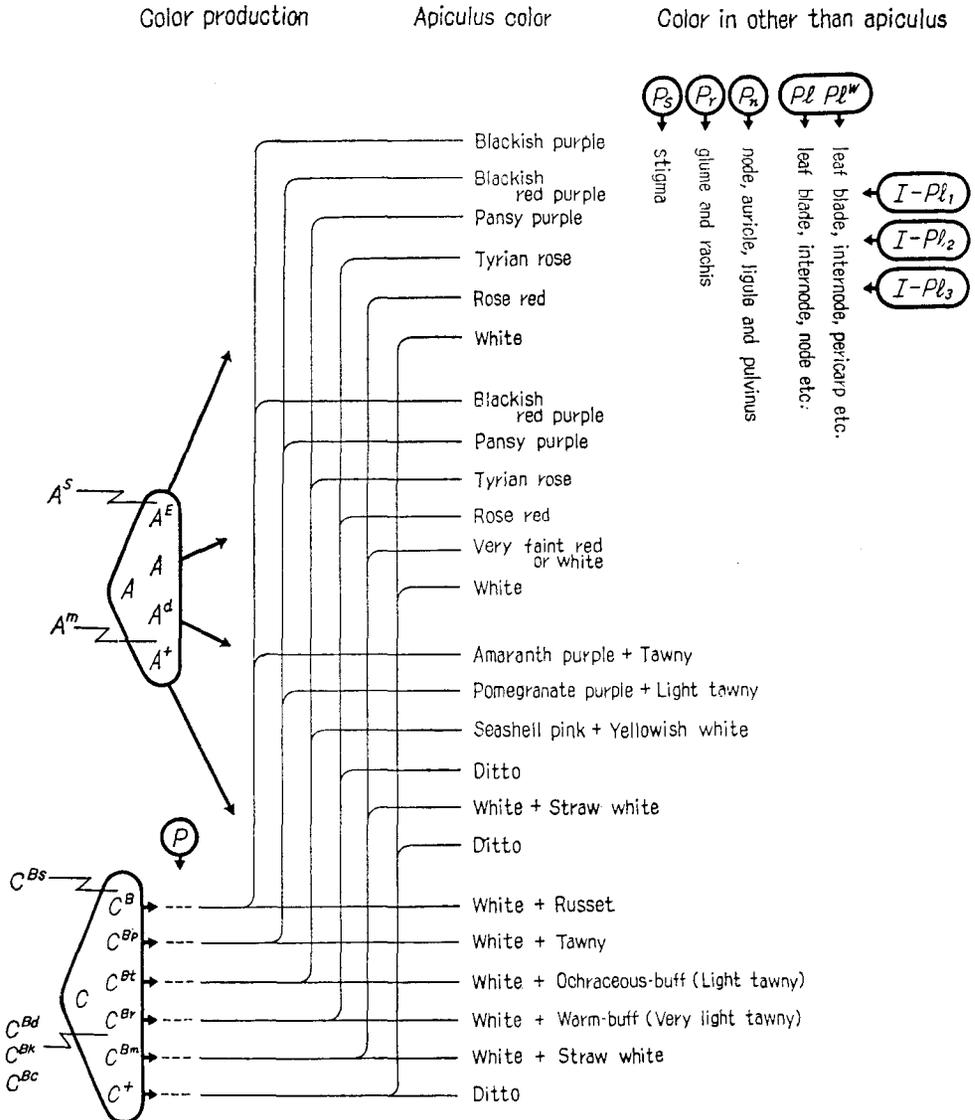


Fig. 1. Diagrammatic illustration of the genic scheme on anthocyanin and its related color, the so-called tawny.

1963 d, 1964 a, 1964 b, 1964 c). Conclusive evidence favoring one or the other of the above two has not been forthcoming. There are, in fact, no positive reasons to think that both proposals are mutually exclusive. With respect to the relation between the hybrid sterility and the segregation distortion of apiculus color, there is no direct relationship between them.

As to the coloration in parts other than the apiculus, it is partly explained by a pleiotropic effect of the basic genes (TAKAHASHI 1957). However, the majority of color patterns is the end result of the effect of genes for distributing and localizing of pigment into their respective parts under the coexistence with the basic color-producing genes. Discrepancies of the genes postulated in *japonica* and *indica* rices are shown in Table 1 and Table 2 (NAGAO 1951, NAGAO *et al.* 1962, MORI *et al.* 1981, CHANDRARATNA 1964, CHANG 1964). Coloration of these parts are frequently diminished in several grades by the inhibitors (KADAM 1936, NAGAO *et al.* 1962, KONDO *et al.* 1963 c, 1963 d, etc). These genes for coloration in the plant body are too numerous to mention, however, one of the genes responsible for pericarp color is worthy to note. In some varieties deep purple color is expressed as if it is unconcerned with the presence of the highly potent allele of the *C* and *A* loci (RAMIAH and RAO 1953, HSIEH and CHANG 1962 a, NAGAI *et al.* 1962, NAGAO *et al.* 1962). No plausible explanation has been given as yet, however, in this connection the two reports aforementioned should

TABLE 1. Genic scheme of anthocyanin coloration in plant body

Fundamental gene	Distribution gene	Coloration of plant
<i>C</i> (I), <i>A</i> (III)	(Pleiotropic action)	Coleoptile, leaf sheath (line), internode (line), midrib
"	<i>P</i> (II)	Apiculus, sterile glume, stigma
"	<i>Pr</i> (II)	Lemma, palea
"	<i>Ps</i> ₁ (V), <i>Ps</i> ₂ (II), <i>Ps</i> ₃ (II)	Stigma
"	<i>Pl</i> (II)*	Leaf blade, sheath, collar, pulvinus, internode
"	<i>Plw</i> ** (same locus with <i>Pl</i>)	Leaf blade & sheath, internode, pericarp, part of collar & pulvinus
"	<i>Pn</i> (III)	Pulvinus, collar, leaf margin
"	<i>Pin</i> ₁ (II)	Internode, leaf sheath, part of collar & pulvinus

* *I-Pl*₁: inhibits the coloration of leaf blade.

** *I-Pl*_{2,3,4}: inhibit the coloration of leaf blade and sheath.

*I-Pl*_{5,6}: inhibit the coloration of pericarp.

TABLE 2. Genic hypothesis on anthocyanin coloration in *Indica* rice

Character	F ₂ segregation ratio (P:W or G)*	Factor
Coleptile	9:7 ¹⁾ , 39:25 ⁷⁾ , 195:61 ³⁾	<i>Pc</i> ₁ (III) <i>Pc</i> ₂ <i>I-P</i> <i>Ai-Pc</i> (IV)
Apiculus	3:1 ¹⁰⁾ , 9:7 ^{9,12)} , 39:25 ³⁾ , 9P:3R:4W ⁷⁾	<i>Pa</i> (IV) <i>I-P</i> <i>Ai-P</i> (IV), <i>Ap</i> (IV)
Lemma	9:7 ⁵⁾ , 9:55 ⁴⁾ , 405:619 ⁷⁾	<i>Pr</i> ₁ (X) <i>Pr</i> ₂ <i>Pr</i> ₃ , <i>APra</i> (IV)
Stigma	9:7 ¹²⁾ , 3:13 ¹⁰⁾ , 162:94 ⁵⁾	<i>A</i> <i>Ps</i> _{a1} <i>Ps</i> _{a2} <i>Ps</i> _{a3} , <i>Ps</i> <i>I-Ps</i> (III)
Glume, Outer glume	9:7 ⁵⁾ , 3:13 ¹⁰⁾ , 9:55 ⁴⁾ , 27:37 ¹⁾ , 117:139 ⁷⁾	<i>Pg</i> ₁ (X) <i>Pg</i> ₂ (III) <i>Pg</i> ₃ <i>Ai-Pg</i> (IV) <i>A</i> <i>Pg</i> (IV), <i>Gp</i> <i>I-Gp</i> (III)
Leaf blade	241G:15P ²⁾ , various ⁸⁾	<i>C</i> <i>A</i> <i>Lsp</i> ₁ <i>Lsp</i> ₂ <i>Ilp</i>
Leaf axil	162:94 ⁶⁾ , 567:457 ⁷⁾	<i>Pv</i> (III) (four or five)
Leaf sheath	9:7 ¹⁾ , 27:37 ⁹⁾ , 3:253 ⁷⁾	<i>C</i> <i>A</i> <i>Lsc</i> , <i>Psh</i> (III)
Auricle	9:7 ⁶⁾ , 27:37 ¹⁾ 117:139 ⁴⁾ , 387:637 ⁷⁾	<i>Pau</i> _a (III) <i>Pau</i> _b <i>I-Pau</i> <i>Ai-Pau</i> (IV)
Ligule	45:19 ¹¹⁾ , 27: 229 ⁷⁾ , 117:139 ⁴⁾	<i>Plg</i> (X) <i>Plg</i> _b (X), <i>Ai-Plg</i> (IV)
Junctura	3W:1P ²⁾ , 9:7 ⁷⁾ , 45:19 ³⁾ , 162:94 ⁶⁾ , 243:781 ⁴⁾	<i>Pj</i> _a (IV) <i>Pj</i> _b <i>Pj</i> _c <i>Pj</i> _d <i>Pj</i> _e , <i>Pj</i> _a (III), <i>Pj</i> _{b1} <i>Pj</i> _{b2} , <i>I-Pj</i>
Junctura back	247W:9P ²⁾	
Nodal ring	9:55 ⁴⁾	<i>Pnr</i> ₁ (X) <i>Pnr</i> ₂ <i>Pnr</i> ₃
Node	9:55 ⁴⁾ , 117:139 ^{1,2)} , 9:247 ⁷⁾ , 127:139 ⁴⁾	<i>Pn</i> ₁ (X) <i>Pn</i> ₂ <i>Pn</i> ₃ , <i>Pn</i> (III)
Pulvinus	81:175 ⁶⁾	<i>Pu</i> _a (III) <i>Pu</i> _b <i>Pu</i> _c <i>Pu</i> _d
Septum	9:7 ¹⁾ , 189P:45Y:22W ⁷⁾	<i>Pm</i> _a (III) <i>Pm</i> _b <i>Pm</i> _c <i>Pm</i> _d
Internode	9:7 ^{1,5)} , 9P:6P1:1Y ³⁾ , 9P1:6G:1Y ⁴⁾ , 27:37 ⁷⁾	<i>Pin</i> _a (III), <i>APin</i> _a (IV), <i>Pin</i> _{a1} (IV) <i>Pin</i> _{a2} , <i>Plin</i> _a (X) <i>Plin</i> _b

(1) Reference; 1) DHULAPPANAVAR (1973a), 2) DHULAPPANAVAR (1973b), 3) DHULAPPANAVAR (1977), 4) DHULAPPANAVAR (1979), 5) DHULAPPANAVAR *et al.* (1973a), 6) DHULAPPANAVAR *et al.* (1973b), 7) DHULAPPANAVAR *et al.* (1975), 8) KADAM (1974), 9) KADAM and D'CRUZ (1960), 10) PANDA *et al.* (1967), 11) PAVITHRAN & MOHANDAS (1976), 12) RAO & MISRO (1968).

(2) As to the genes designated before 1967, refer to the following papers; KINOSHITA (1976), MISRO *et al.* (1966), RICHHARIA *et al.* (1960) and TAKAHASHI (1962.)

(3) *P=purple, W=white, G=green, R=red, Pl=purple lines, Y=yellow.

be recalled. Namely only when the pericarp was deeply colored, uliginosin, of which aglycone is malvidin, is detected (NAGAI *et al.* 1960, MIZUSHIMA *et al.* 1963).

B. Colors other than anthocyanin

Although the chemical nature of pigments other than anthocyanin almost remain unsolved, the following colorations have been relatively well known in their causal genes and their assignments in the linkage groups. They are; i) reddish brown color in the pericarp, ii) gold, dark brown and

chalky white colors in the floral glumes, iii) black ripening color in the floral glumes, and iv) various types of mottled discoloration in the leaves.

The pericarp is usually white but may be brown, red or purple. Two genes are recognized for the reddish brown pericarp (cf. NAGAI 1959, TAKAHASHI 1963, CHANDRARATNA 1964, etc). *Rc* causes reddish brown speckles on a brown background, and *Rd*, when coexisting with *Rc*, gives reddish brown selfcoloration in the pericarp and seed coat. A new multiple allele *Rc^s* were found to be located in the locus of *Rc* showing self-coloration of pericarp (TAKAHASHI *et al.* 1972). As to the chemical nature, NAGAO *et al.* (1957) reported it as a series of catechin, catechol tannin and phlobaphane. Besides the action of *Rc* and *Rd*, the reddish brown color is expressed by a pleiotropic effect of leaf color gene, *Pl^w*, when it coexists with *C* in the absence of *A* (NAGAO *et al.* 1962). This is an instance where even when the same tissue of the same organ manifests the same type of color expression, their chemical components and consequently their causal genes are not always the same (TAKAHASHI *et al.* 1967 a).

Gold floral glumes is inherited as a simple recessive, *gh*, white hull, a single dominant, *Wh*, and brown furrows on glumes are caused by a dominant *Bf*. *I-Bf* inhibits *Bf*, resulting normal "straw color" again (cf. RAMIAH *et al.* 1953, JODON 1957, TAKAHASHI 1964). In *indica* varieties PARNEL *et al.* (1917, 1922) and MITRA *et al.* (1928) discovered a multiple allelic series, *H^m* (mottled gold) > *H^{pb}* (piebald gold) > *H^g* (green) > *Hⁱ* (gold), together with their inhibitor, *I-H*. The ripening-black color is multi-genic with a complementary action of which the common basic gene symbol is *Bh* (NAGAO and TAKAHASHI 1954, KADAM and D'CRUZ 1960).

Several kinds of mottled discoloration were reported by many workers (JONES 1952, JODON 1957, NAGAO *et al.* 1963, 1964, TAKAHASHI *et al.* 1968 c, etc). The discoloration of chlorophyll appears first in the leaves as black, brown, red or yellow spots, sometimes as fine speckles, resembling fungus lesions. So far reported, they are simple recessive to the normal.

C. The presence of floral structures

Among several floral structures, awning, pubescence, long empty glumes have attracted attention of geneticists. In awn development, there is a marked variation within the same panicle and inconsistent results may appear from the confusing data. However, when demarcation is made as awned vs. awnless, the awn development of Japanese varieties appears to be under the control of triplicated dominant genes (IKENO 1972, cf. NAGAO 1951). Besides this, a ratio of two complementary genes was obtained in Chinese varieties (KUANG *et al.* 1964), and an inhibitor was postulated in Indian

varieties (MISRO *et al.* 1954). The basic gene symbol of this character is *An*. Degree of awn development is affected by environmental conditions and the level of polyploidy (SAHADEVAN 1959).

Pubescence commonly shows dominance to the glabrous condition (KADAM and RAMIAH 1943, JODON and CHILTON 1946, etc). To bring under one general gene scheme of the pubescence in glumes and leaves, NAGAO *et al.* (1960) and KINOSHITA *et al.* (1968) postulated four genes; *gl* for glabrous glumes and leaves, *Hla* and *Hlb* for long pubescence of leaves, and *Hg* for long pubescence of glumes.

In some varieties empty glumes are as long as, or longer than the lemma and palea. These types are governed by the respective single gene, *g* and *Gm* (CHAO 1928 a, NAGAO 1951, JODON 1957), though a case of digenic inheritance was reported (BUTANY *et al.* 1962). When the *g* coexists with an inhibitor, *Su-g*, the empty glume on the lemma side is markedly reduced to the normal short (NAGAO *et al.* 1960). Extra glume is born by the action of *eg* (NAGAMATSU *et al.* 1965 a).

D. Modified or deformed structures

There are various kinds of modified or deformed structures. Among them the causal genes of the following traits have been assigned their loci in the linkage groups. They are; clustered spikelets (*Cl*), claw shaped spikelet (*clw*), depressed palea (*dp*), triangular hull (*tri*), extra glume (*eg*) cleistogamous spikelets (*d₁*), dense panicle (*Dn*), Lax panicle (*lx*), Exerted panicle (*Ex*), short panicle (*sp*), verticillate rachis (*ri*), neck leaf (*nl*), liguleless (*lg*), lazy growth habit (*la*), grain shattering (*Sh*), rolled leaf (*rl*), narrow leaf (*nal*), dripping-wet of leaf (*drp*), lopped leaf (*lop*) fine stem (*fc*) and twisted stem (*ts₁*). Some detailed genetic natures of them and many other traits are reviewed in publications presented by KUANG (1951), RAMIAH and RAO (1953), JODON (1955, 1957), NAGAI (1959), GHOSE *et al.* (1960), CHANDRARATNA (1964), CHANG (1964) and TAKAHASHI *et al.* (1977).

In Japanese varieties, *lg* is considered to be responsible for the deficit of the junctura, the auricle, as well as the ligule. However, CHOSE *et al.* (1957) concluded from their studies in Indian varieties that the presence or absence of each of these characters is controlled by each of three set of genes, which are closely linked with each other. The grain shattering is either major genic or polygenic (SAKAI and NILES 1957, NAGAI 1959).

E. Dwarfness

Several forms have been recorded, however, they may be roughly classified into two main types, one is the "daikoku" type which is more common,

and the other is the "bonsai" type. In the former, leaves are upright, short and rigid, having a deep green color. The panicle is short and compact and the grains are usually small. The latter is characterized by many tillers with slender leaves and with not so small grains (cf. NAGAO 1951, NAGAI 1959, CHANDRARATNA 1964, etc). Dwarfs are generally single recessive and their common basic gene symbol is *d*, accompanied with numerical subscripts for different gene loci. Dwarf genes in *japonica* rice are listed in Table 3. As a general rule, a cross between two dwarf forms gives a normal plant in the F_1 , and a double dwarf form in the F_2 . The first reporter of this phenomenon is AKEMINE (1925) in Japan. In some cases a dwarf is expressed by multiple recessive genes (NAGAO 1951, BUTANY *et al.* 1959), and in one case it was inherited as a single dominant (SUGIMOTO 1923). Multiple dwarfs which carry more than two different dwarf genes are not only very weak but also highly sterile owing to the imperfect development of reproductive organs (NAGAO and TAKAHASHI (1963)).

TABLE 3. List of dwarf genes identified by allelic tests in *japonica* rice

Gene	Character	Gene locus	Chromosome	Remark	Reference
d_1	Daikoku d.	VI 18	2		1)
d_2	Ebisu d.	II 0	11		1)
d_3		II 25	11	Triplicate genes	11)
d_4	Bunketsu-waito or tillering d.	I 0	6	"	11)
d_5		X 43	8	"	11)
d_6	Ebisumochi or lop-leaved d. or Tankan-shirasasa d.	IV 0	10	equivalent with d_{34}	12)
d_7	Heiei-daikoku or cleistogamous d.	IV 39% from d_6	10		13)
d_9	Shinatoh d.	I 75	6		14)
d_{10}	Tillering d.	III 31	3	equivalent with d_{15}, d_{16}	6)
d_{11}	Shinkane-aikoku or Norin-28 d.	II 160	11	equivalent with d_8	7)
d_{12}	Yukara d.				17)
d_{13}	Short grained d.				17)
d_{14}	Kamikawa bunwai or tillering d.	XI 32% from lop_2	5		18)
d_{17}	Slender d.				18)
d_{18}^h	Hosetsu d. or Akibare d.	III 3	3	$d_{18}^h > d_{18}^k > +$ (multiple allele)	15)

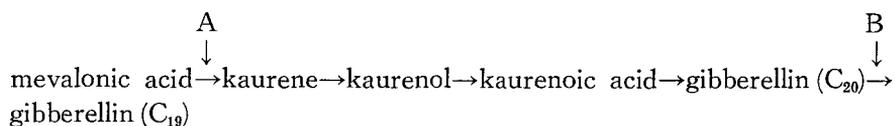
Gene	Character	Gene locus	Chromosome	Remark	Reference
d_{18}^k	Kotaketamanishiki d.	III 3	3		15)
d_{19}	Kamikawa d.				10)
d_{20}	Hayayuki d.	XII 12% from <i>Hg</i>			10)
d_{21}	Aomorimochi-14 d.	I 8% from <i>wx</i>	6		10)
d_{22}	Jokei 6549 d.				18)
d_{23}	AH-7 d.				18)
d_{24}	m-7 d.				18)
d_{26}	7237 d.	III 37% from <i>A</i>	3		3)
d_{27}	Bunketsuto or tillering d.	VII 13	9		19)
d_{28}	Chokeidaikoku or long stemmed d.	VIII 18	9		19)
d_{29}	Short uppermost internode d.	X 14% from bl_1	8		9)
d_{30}	Waisei-shirasasa d.	X 101	8		6)
d_{31}	Taichung-155-irradiated d.	II 131	11		20)
d_{32}	Kyudai-4 d.	X 15% from d_{30}	8		5)
d_{32}	Bonsaito d.		4		8)
d_{35}	Tanginbozu d.				16)
d_{42}	Liguleless d.	II 102	11		4)
d_{47}	Taichung Native-1 d.				
d_{49}	Reimei type d.				2)
d_{50}	Fukei 71 type d.				2)

Reference :

1) AKEMINE (1925), 2) FUTSUHARA (1968), 3) HSIEH (1960), 4) HSIEH (1965), 5) IWATA and OMURA (1970), 6) IWATA and OMURA (1971 a), 7) IWATA and OMURA (1971 b), 8) IWATA and OMURA (1975), 9) IWATA and OMURA (1977), 10) KINOSHITA, *et al.* (1974), 11) NAGAO and TAKAHASHI (1943), 12) NAGAO and TAKAHASHI (1946), 13) NAGAO and TAKAHASHI (1954), 14) NAGAO *et al.* (1966), 15) SHINBASHI *et al.* (1976), 16) SUGE and MURAKAMI (1968), 17) TAKAHASHI *et al.* (1968) TAKAHASHI and KINOSHITA (1974), 19) TSUZUKI *et al.* (1971), 20) YEN *et al.* (1968).

Many dwarf forms of different simple recessives are revealed to be different in the specificity of their response to gibberellins (NAGAMATSU *et al.* 1965 c, HARADA *et al.* 1968). Thus, these dwarf can be used as a "multiple plant assay" to detect gibberellins with similar structures. MURAKAMI (1968, 1969) have inferred that in the process of the gibberellin synthesis, "tanginbozu" dwarf fails to activate the enzyme necessary to carry out the reaction labeled A, while "kotaketamanishiki" dwarf is connected with the failure

of the reaction B.



Dwarfs of intermediate stature, normal panicle and grains, and consequently are valuable materials in breeding for lodging resistance were produced by irradiation (JODON 1955, HUANG 1961, SHAH *et al.* 1961, HSIEH 1962 b, FUTSUHARA *et al.* 1967, TAKAHASHI *et al.* 1968 c).

F. Modified composition

Since the description of the waxy character of rice by HOSHINO (1902) and of corn by COLLINS (1909) this property of endosperms and pollen grains in many cereals has been used in genetical and radiobiological studies (cf. ERIKSSON 1969). In rice waxy starch is frequently called glutinous starch, thus in addition to the designation *wx*, the gene symbol *gl* was used. The waxy endosperm, comprised largely of amylopectin, is contrasted with the non-waxy type containing both amylopectin and amylose. A monogenic difference has been recognized in them, the waxy type being a single recessive. Since the endosperm is triploid in constitution, four genotypes can be expected in seeds from a genotypic plant of *wx/wx*⁺. Endosperms with *wx*⁺, at least one, are non-waxy, showing that one dominant allele masks the effect of three recessive alleles. However, spectrophotometric and iodine color test show that there is some additivity in the action of the *wx* allele (SUGAWARA 1953, NAGAI 1959, SHIBUYA 1962). SEETHARAMAN (1959, 1964) ascribed the difference in the contents of amylose and amylopectin to one pair of genes and several modifiers.

As in the situation in corn, striking segregation distortion mostly characterized with a deficit of waxy endosperm is also known. The degree of the distortion varies from cross to cross, but in general, it may be said that it is most frequently brought about from crosses between distantly related varieties, especially in the crossing phase of *japonica* (*wx*) × *indica* (*wx*⁺) (OKA 1953 b, MIZUSHIMA *et al.* 1961 a, 1962, NAKAGAHARA *et al.* 1968, MORI *et al.* 1969). This can not directly be ascribed to a distorted pollen ratio in the heterozygote, because of the fact that the number of waxy pollens are equal to that of non-waxy pollens. To explain this various hypothesis have been suggested. They are ; i) the certation due to the lesser vitality of the waxy pollens (CHAO 1928 b), ii) the existence of a linkage between the *wx* gene and lethal, gametic-development or some modifying

genes (OKA 1953 b, TSAI and OKA 1965), iii) the existence of complementary genes which depreciate fertilization activity of the *wx* pollens (MIZUSHIMA and KONDO 1961 a, 1962, IWATA *et al.* 1964, NAKAGAHARA *et al.* 1970), iv) the gene mutations from the recessive to the dominant which occur in the gamete (YAMAGUCHI 1963), and v) some role of cytoplasmic effect (MORI, KINOSHITA and TAKAHASHI 1969). Among them, ii) and iii) seem to be favored, however, which is the most appropriate explanation is not determined as yet, since the data in hand seems insufficient to definitely establish the causes of the deviations herein involved. In this connection, and for further studies, strict criterion on the use of the χ^2 -test should also be employed simultaneously, with respect to the demarcation between normal and distorted segregation patterns. MORI and TAKAHASHI (1970) devised a scale, a part of which is shown in Fig. 2. This is an application of the binominal probability paper designed by MOSTELLER and TUKEY (1949), followed by FERGUSON (1956) and others. In this figure, if there is a sample and it is not known whether it belongs to the 3:1 ratio of the intrinsic nature, and if

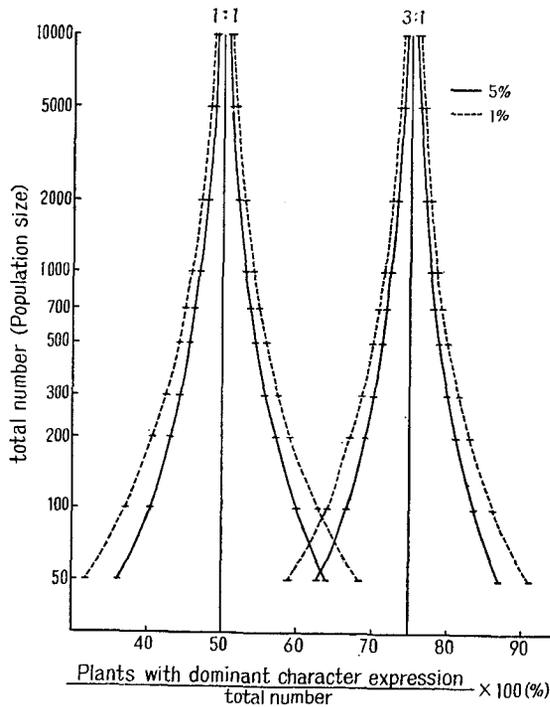


Fig. 2. Fitness of segregation ratio (χ^2 test) and its fiducial limit in relation to population size.

this paired count falls within the critical region, that is outside the steeped lines, the given hypothesis of 3:1 may be rejected at a significance level of 0.05 or 0.01.

Since the attractive reports of NELSON (1959, 1962) on corn endosperm, fine structures of the gene locus became a point of academic interest. As to problems on the intracistron recombination at *wx*-locus of rice plant, little information is available (NAGAMATS and IWATA 1968). Sectorial chimera endosperms composed of waxy and non-waxy parts and their possible causation were reported by TSUNODA *et al.* (1964, 1965).

Scented or aromatic grains and fragrance at blooming are dependent on one, two or three complementary genes (JODON 1944, cf. CHANG 1964). Brittle plant body, which is presumably caused by a low α -cellulose content in the cell wall, is controlled by a single recessive gene, *bc* (JONES 1933, TAKAHASHI 1964). Recently another gene with the same character expression as *bc* was discovered (TAKAHASHI *et al.* 1968 c). It is known that a single dominant gene, *Ph*, is connected in the presence of a substance by which the pericarp and floral glumes are stained with a brownish purple color when treated with an aqueous solution of phenol (MORINAGA *et al.* 1943 a, NAGAO and TAKAHASHI 1952, 1954). KURIYAMA and KUDO (1967) showed that *Ph* is identical with *Bh*, one of the complementary genes for ripening black glume color. They inferred that *Ph* produces phenol-oxidizing enzyme, while the other black-glume genes are responsible for the phenol substance. The majority of *Ph* are distributed among *indica* varieties, while *Bh* are found in *japonica* varieties (OKA 1953 a, TAKAHASHI 1963, etc).

G. Chlorophyll deficiency

Almost every conceivable form of chlorophyll abnormalities have been observed, however they may fall into the following types.

lethal deficiencies	{	lethal white (albinos) lethal yellow (xantha, lutescent and tip-burn yellow) lethal chlorotic
non-lethal deficiencies	{	virescent striped chlorotic (chlorina)

The majority of chlorophyll-defective mutants are simple or double recessive to the normal, although there are some mutants that show cytoplasmic inheritance. The character expression of some mutants are to a large extent dependent on the environmental conditions, especially upon temperature (TAKAHASHI 1950, KATAYAMA *et al.* 1951, NAGAO *et al.* 1963). Studies on

chemical properties associated with chlorophyll mutants are not so abundant, however, with respect to the relative amount of such fractions as chlorophyll-a, chlorophyll-b, two xanthophylls and carotene marked differences are shown between mutants and their original varieties (KATAYAMA and SHIDA 1965, 1970).

H. Other characters

In this paragraph a brief description will be made on some types of sterility. Reports of sterility arising from morphological abnormalities in reproductive or non-reproductive organs of the spikelets have been reviewed by NAGAI (1959), KINOSHITA *et al.* (1977) in Japan and GHOSE *et al.* (1960) in India. Most of the abnormalities are inherited as simple recessive. Sterility caused by cytoplasmic factors has also been noticed. A well known case is the nucleo-cytoplasmic interaction which affects intervarietal hybrid sterility (SAMPATH 1963, KATSUO *et al.* 1958, MIZUSHIMA 1961 b, KITAMURA 1960, 1962 a, 1962 b, SHINJO *et al.* 1966, 1968, 1969 a, 1969 b, KINOSHITA *et al.* 1980, etc). In SHINJO's studies, the sterile cytoplasm (cms-boro) and its restorer *Rf* originally came from an India variety and a series of experiments were made by the isogenic lines having a genetic background of a Japanese variety. When a plant with sterile cytoplasm (cms-boro) has *Rf/Rf*, it is completely male fertile, when it has $+/Rf$, it is partially male fertile, and when it has $+/+$, it is completely male sterile. F_1 plants from (cms-boro) $+/+ \times Rf/Rf$ have a 90% or higher seed setting, though they are semi-sterile in pollen grains. This source may be of some use in breeding material for "hybrid rice". While in KITAMURA's results, no abortion was seen in either male or female gametes but due to interruption of anther dehiscence the flowers became sterile.

III. Linkage groups

A. Trial construction of linkage groups

The first instance of linkage, that between black floral glumes and purple internodes, was reported by PARNELL *et al.* in 1917 in India, however, the best known linkage is that between the apiculus color and the waxy endosperm. This was first found in Japan by YAMAGUCHI (1921, 1926) and was confirmed both in *japonica* and *indica* varieties by many workers (CHAO 1928 a, RAMIAH *et al.* 1931, TAKAHASHI 1935, JODON 1940, NAGAO *et al.* 1942, COMEAUX 1946, etc). Based on this the first linkage group was settled. The next known group of Japanese rice, which is termed as the second linkage group, is based upon linkages among purple leaf, liguleless and phenol

staining characters (MORINAGA *et al.* 1942, 1943 a). As early as 1948, JODON provided a deserving integration of linkage data previously reported and recognized eight linkage groups. Since then attempts have been made for advocating linkage groups by such workers as JODON (1955, 1964) in the U. S. A., MISRO, RICHHARIA and THAKUR (1966) in India, NAGAO and TAKAHASHI (1963, 1964) and TAKAHASHI (1964) in Japan. Through these efforts recognition with some degree of reliability of the twelve groups, corresponding to the haploid number of chromosomes, has now become possible, although the prospect of a precise map is still remote.

Tables 4, 5 and Figure 3. line up of genes with the possibility of being

TABLE 4. Gene located to the twelve linkage groups of *japonica* rice (an alteration of TAKAHASHI and KINOSHITA 1977)

Group	Gene	Character expression
I	<i>al</i> ₁	albino (lethal)
	<i>alk</i>	alkali (1.7% KOH) degeneration
	<i>bl</i> ₂	black leaf spot
	<i>bl</i> ₃	brown leaf spot
	<i>bl</i> ₁₅	brown spotted leaf
	<i>C</i>	Chromogen for anthocyanin color
	<i>chl</i> ₁	chlorina
	<i>Cl</i>	Clustered spikelets
	<i>d</i> ₄	one of multiple genes for "tillering" dwarf
	<i>d</i> ₉	"shinato" dwarf
	<i>d</i> ₂₁	"aomorimochi-14" dwarf
	<i>dp</i> ₁	depressed palea
	<i>Est</i> ₂	Esterase isozymes
	<i>ga</i> ₁	gametophyte gene
	<i>ga</i> ₄	do.
	<i>ga</i> ₅	do.
	<i>gf</i>	gold furrows on glume
	<i>I-Pl</i> ₂	Inhibitor for purple leaf
	<i>I-Pl</i> ₄	Inhibitor for purple pericarp
	<i>Lf</i> ₁	Late flowering
<i>ms</i> ₁	male sterile	
<i>Pla</i>	purple leaf apex and margin	
<i>Pi-i</i>	<i>Piricularia</i> resistance	

Group	Gene	Character expression
I	<i>Pi-z</i>	do.
	<i>Rsv₁</i>	Resistance to rice stripe disease
	<i>s_{A1}</i>	duplicate gametophytic lethal
	<i>s_{B1}</i>	do.
	<i>s_{C1}</i>	do.
	<i>s_{E1}</i>	Photosensitivity
	<i>v₁</i>	virescent seedling
	<i>ws</i>	white stripe leaves
	<i>wx</i>	waxy (glutinous) endosperm
II	<i>al₅</i>	albino (lethal)
	<i>al₇</i>	do.
	<i>d₂</i>	"ebisu" dwarf
	<i>d₃</i>	one of the multiple genes for "tillering" dwarf
	<i>d₁₁</i>	"shinkane-aikoku" or "nohrin 28" dwarf
	<i>d₃₁</i>	"taichung-155-irradiated" dwarf
	<i>d₄₂</i>	"liguleless" dwarf
	<i>drp₁</i>	dripping-wet of leaves
	<i>lg</i>	liguleless
	<i>lop₁</i>	lopped leaf
	<i>nal₁</i>	narrow leaf
	<i>nal₄</i>	do.
	<i>nal₅</i>	do.
	<i>nk</i>	splitted grain or notched
	<i>P</i>	Completely colored apiculus
	<i>Pb</i>	purple pericarp
	<i>Ph</i>	Phenol staining
	<i>Pi-1</i>	<i>Piricularia</i> resistance
	<i>Pin₁</i>	purple internode
	<i>Pl₁</i>	purple leaf
	<i>Pl₂</i>	do.
	<i>Pr</i>	Purple hull
	<i>Ps₂</i>	Purple stigma
	<i>Ps₃</i>	do.
	<i>rk₁</i>	round kernel
<i>rl₂</i>	rolled leaf	
<i>sd₂</i>	duplicate gametophytic lethal	

Group	Gene	Character expression
II	<i>ssk</i>	malformed semi-sterile
	<i>Wh</i>	White hull
	<i>Xe₁</i>	<i>Xanthomonas</i> resistance
	<i>Xe₂</i>	do.
	<i>ylm</i>	yellow leaf margin
III	<i>A</i>	Anthocyanin activator
	<i>al₄</i>	albino (lethal)
	<i>bl₇</i>	brown leaf spot of "Banshinriki-type"
	<i>d₁₀</i>	tillering dwarf
	<i>d₁₈</i>	"kotaketamanishiki" dwarf
	<i>d₂₆</i>	"7237" Jodon's dwarf
	<i>eg</i>	extra glume
	<i>lgt</i>	long twisted grain
	<i>lx</i>	lax panicle
	<i>Pn</i>	Purple node
	<i>Prp₂</i>	Purple pericarp
	<i>Rd</i>	Red pericarp
<i>rl₁</i>	rolled leaf	
<i>ts_a</i>	twisted stem	
IV	<i>bl₁₆</i>	brown spotted leaf
	<i>d₆</i>	"Ebisumochi" or "lop-leaved" dwarf
	<i>d₇</i>	"cleistogamous" dwarf
	<i>g</i>	long empty glumes
	<i>Gh</i>	Gold hull
	<i>gl₂</i>	glabrous
	<i>I-An</i>	Inhibitor for awning
	<i>Lf₂</i>	Late flowering
	<i>ls</i>	leaf spot
	<i>Mi</i>	Minute spikelet
	<i>Pi-2</i>	<i>Piricularia</i> resistance
<i>Rc</i>	Brown pericarp	
<i>se</i>	Photosensitivity	
V	<i>I-Bf</i>	Inhibitor for brown furrows in glume
	<i>Ps₁</i>	purple stigma

Group	Gene	Character expression
VI	<i>An</i> ₃	Awn
	<i>d</i> ₁	"daikoku" dwarf
	<i>er</i>	erect growth habit
	<i>gh</i> ₁	gold hull and internode
	<i>gw</i>	green-and-white striped
	<i>I-P</i> ₁	Inhibitor for purple leaf
	<i>nl</i> ₂	neck leaf
	<i>ops</i> ₁	open-palea-sterile
VII	<i>Bp</i>	Bulrush-like panicle
	<i>Dn</i>	Dense (barnyard-grass-like) panicle
	<i>dp</i> ₂	depressed palea
	<i>drp</i> ₂	dripping wet leaves
	<i>fs</i> ₁	fine stripe in leaf margin
	<i>Hl</i> _a	Hairy leaf
	<i>Pi-ta</i>	<i>Piricularia</i> resistance
	<i>sl</i>	"sekiguchi" lesion
	<i>Ur</i>	Undulate rachis
VIII	<i>d</i> ₂₇	tillering dwarf
	<i>d</i> ₂₈	long stemmed dwarf
	<i>Ef</i>	Earliness
	<i>la</i>	"lazy" growth habit
	<i>nal</i> ₂	narrow leaf
	<i>Pi-a</i>	<i>Piricularia</i> resistance
	<i>Pi-f</i>	do.
	<i>Pi-k</i>	do.
	<i>Pi-m</i>	do.
	<i>Pi-4</i>	do.
	<i>Pi-7</i>	do.
	<i>sh</i>	shattering
	<i>sp</i>	short panicle
	<i>z</i> ₁	zebra-striped seedling
	<i>z</i> ₂	do.
IX	<i>al</i> ₂	albino (lethal)
	<i>al</i> ₃	do.
	<i>al</i> ₆	do.

Group	Gene	Character expression
IX	<i>nl₁</i>	neck leaf
	<i>Pi-3</i>	<i>Piricularia</i> resistance
	<i>ri</i>	verticillate rachis
	<i>ylb</i>	yellow banded leaf margin
X	<i>bc₃</i>	brittle culm
	<i>bl₁</i>	brown discoloration of leaves and glumes
	<i>bl₁₃</i>	brown spotted leaf
	<i>d₅</i>	one of the multiple genes for tillering dwarf
	<i>d₂₉</i>	short uppermost internode dwarf
	<i>d₃₀</i>	"waisei-shirasasa" dwarf
	<i>d₃₂</i>	dwarf (Kyudai-4)
	<i>gh₂</i>	gold hull
	<i>gh₃</i>	do.
	<i>Pi-s</i>	<i>Piricularia</i> resistance
<i>tri</i>	tirangular hull	
XI	<i>An₁</i>	Awn
	<i>bc₁</i>	brittle culm
	<i>bl₄</i>	"m-25" brown leaf spot
	<i>bl₁₁</i>	brown spotted leaf
	<i>bl₁₄</i>	do.
	<i>chl₂</i>	chlorina
	<i>d₁₄</i>	tillering dwarf
	<i>fc</i>	fine culm
	<i>ga₂</i>	gametophyte gene
	<i>ga₃</i>	do.
	<i>lop₂</i>	lopped leaf
	<i>op</i>	"over-developed" palea
	<i>sd₁</i>	duplicate gametophytic lethal
<i>v₂</i>	virescent seedling	
XII	<i>An₂</i>	Awn
	<i>d₂₀</i>	"hayayuki" dwarf
	<i>gl₁</i>	glabrous leaf and hull
	<i>Hg</i>	Hairy glume

TABLE 5. Genes assigned to twelve different groups of *indica* rice (cited from MISRO, RICHHARIA and THAKUR, 1966)

Group	Gene	Character expression
I	<i>wx</i>	glutinous endosperm
	<i>Ap</i>	Apiculus purple
	<i>Cl</i>	Clustered spikelets
	<i>Fs</i>	Fuzziness of fertile glume
	<i>C</i>	Chromogen for anthocyanin colour
	<i>v</i>	virescent
	<i>Se</i>	Photoperiod sensitiveness
II	<i>Plm</i>	Purple leaf margin
	<i>Plx (Px)</i>	purple leaf axil
	<i>Gp (Pg)</i>	Purple sterile glume
	<i>Ap</i>	Apiculus purple
	<i>Psh</i>	Leaf sheath purple
	<i>Pl</i>	Purple leaf
	<i>lg</i>	liguleless
	<i>Wh</i>	White hull
III	<i>Psh</i>	Leaf sheath purple
	<i>Plx (Px)</i>	Leaf axil purple
	<i>Pin</i>	Internode purple
	<i>Ap</i>	Apiculus purple
	<i>Sp</i>	Septum purple
	<i>Ps</i>	Purple stigma
IV	<i>Rc</i>	Brown pericarp
	<i>Pin</i>	Internode purple
	<i>A</i>	Apiculus purple
	<i>Gl</i>	Short sterile glume
	<i>g</i>	long sterile glume
	<i>Kra</i>	Short round grain
	<i>Gp (Pg)</i>	Purple sterile glume
	<i>Ap</i>	Apiculus purple
	<i>Pr</i>	Purple stigma
	<i>mp</i>	multipistillate

Group	Gene	Character expression
V	<i>Psh</i> <i>Jp</i> <i>Prp</i> <i>Sk</i>	Leaf sheath purple Juntura purple Purple pericarp Scented kernel
VI	<i>gh</i> <i>Pr</i>	gold hull Red pericarp
VII	<i>I-Gp</i> <i>glb</i> <i>glh</i> <i>I-Ps</i> <i>Ap</i>	Inhibitor for purple glume glabrous blade glabrous hull Inhibitor for purple stigma Apiculus purple
VIII	<i>Lp</i> <i>Kr</i> <i>Rd (Pr)</i> <i>Sh</i>	Long palea Short round grain Red pericarp Shattering or easy threshing
IX	<i>Ps</i> <i>Gp</i> <i>I-Jp</i>	Purple stigma Purple sterile glume Inhibitor for purple juntura
X	<i>fh (dw)</i> <i>fl</i>	floating habit flowering duration
XI	<i>Cl</i> <i>Lx</i> <i>An</i> <i>Kr</i>	Clustered grains Lax panicle Awning Short round grain
XII	<i>gl</i> <i>An</i> <i>Nk</i> <i>Bd</i>	glabrous hull Awning Notched kernel Beaked lemma

assigned to the twelve linkage groups of *japonica* and *indica* rice, respectively (TAKAHASHI and KINOSHITA 1968 a, MISRO, RICHHARIA and THAKUR 1966). In these tables and figures there is some disagreement between the two grouping, of which conceivable reasons will be mentioned later. A diagra-

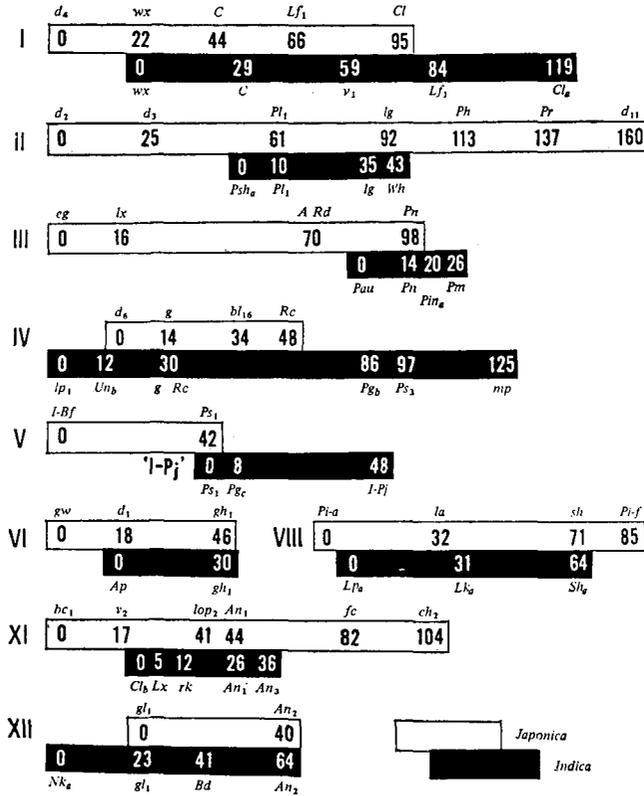


Fig. 3. Comparison of *Japonica* and *Indica* linkage maps.

mmatic illustration of the linkage map was also presented by TAKAHASHI and KINOSHITA (1977 a), which is given in Fig. 4 and 5. This is focussed on data mainly obtained from *japonica* rice and is largely due to the experiments of NAGAO and TAKAHASHI. The group's number in the *japonica* group, is in accordance with NAGAO and TAKAHASHI's proposal (1963, 1964), however as seen in the diagram, the affixed chromosome's number, which was designated by NAGAMATSU *et al.* (1962, 1965 b), does not coincide with it.

B. Cytological basis of linkage groups

Another important phase of linkage studies is the assignment of specific linkage groups to specific morphologically identifiable chromosomes. In other crops various techniques have been used in this respect. The linkage between established interchange break points of reciprocal translocation and marker genes have been helpful. Primary trisomics and tertiary ones, and further,

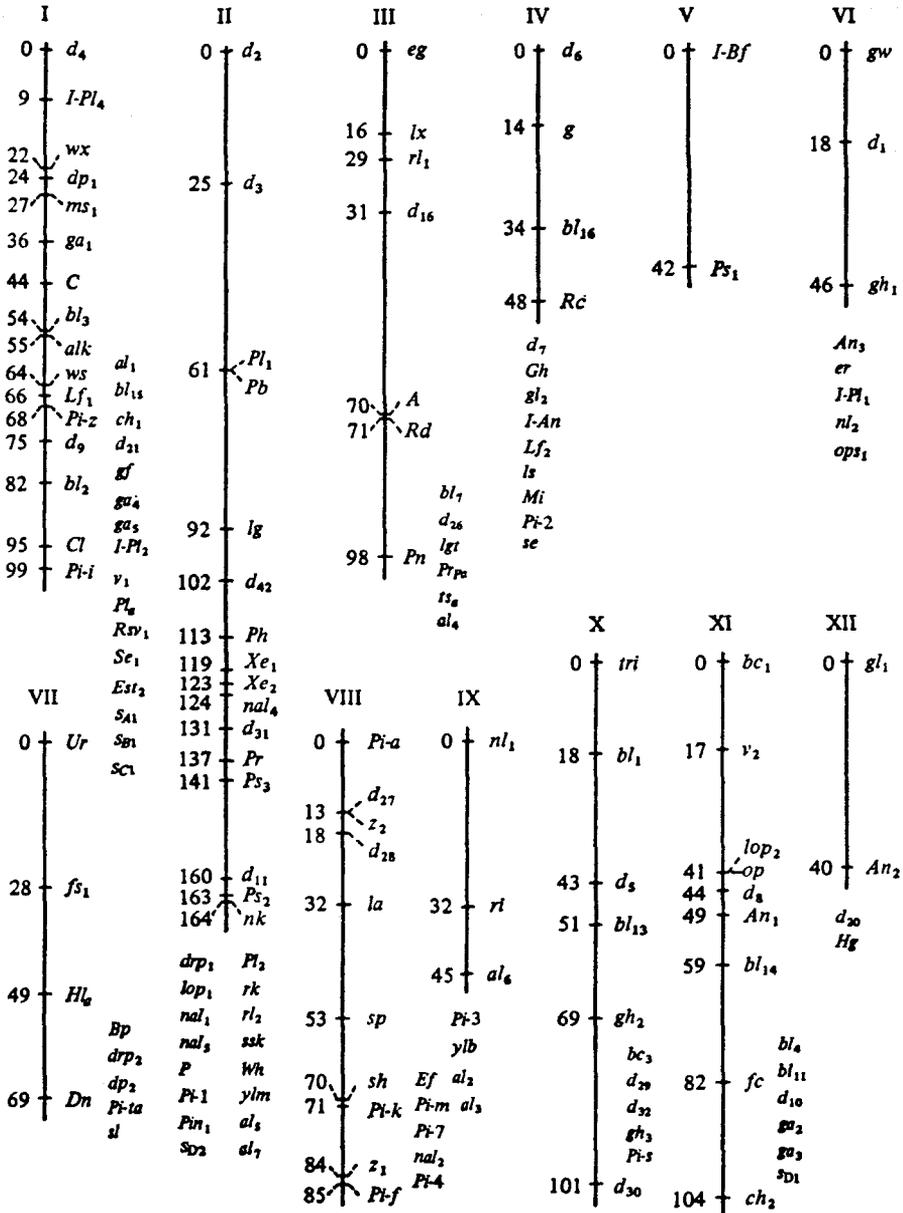


Fig. 4. Trial construction of linkage maps in Japanese rice.

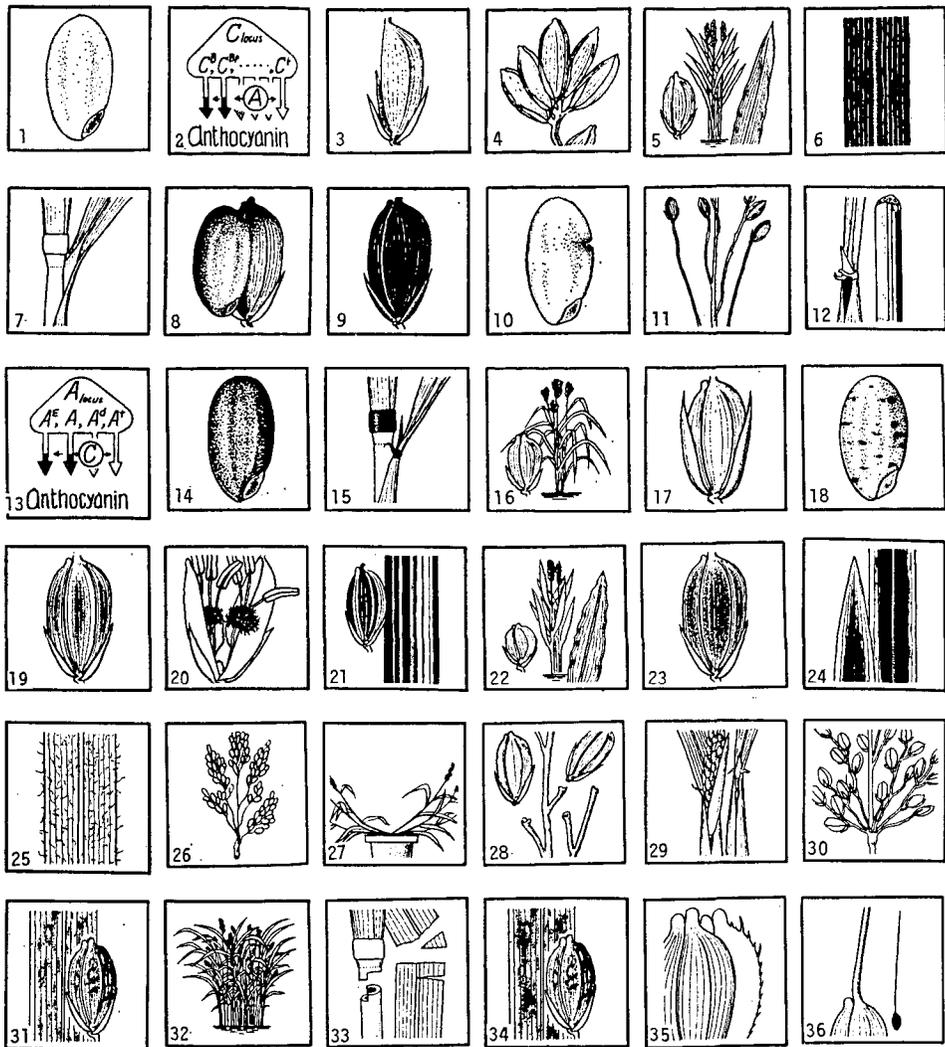


Fig. 5. Character expression of marker genes located in 12 linkage groups

1. waxy (*wx*, I-22), 2. Anthocyanin chromogen (*C*, I-44), 3. depressed palea (*dp*₁, I-24), 4. Clustered spikelets (*Cl*, I-95), 5. "ebisu" dwarf (*d*₂, II-0), 6. Purple leaf (*Pl*₁, II-61), 7. liguleless (*lg*, II-92), 8. Phenole reaction (*Ph*, II-113), 9. Purple hull (*Pr*, II-137), 10. notched kernel (*nk*, II-164), 11. lax panicle (*lx*, III-16), 12. *rl*₁, III-29), 13. Anthocyanin activator (*A*, III-70), 14. Red pericarp (*Rd*, III-71), 15. Purple node (*Pn*, III-98), 16. "lop-leaved" dwarf (*d*₆, IV-0), 17. long empty glumes (*g*, IV-14), 18. Brown pericarp (*Rc*, IV-42), 19. Inhibitor for brown furrows in glume (*I-Bf*, V-0), 20. Purple stigma (*Ps*₁, V-42), 21. green-and-white striped (*gw*, VI-0), 22. "daikoku" dwarf (*d*₁, VI-18), 23. gold hull and internode (*gh*₁, VI-46), 24. fine stripe in leaf margin (*fs*₁, VII-28), 25.

inversion could also be used. The first report on the cytological basis of rice linkage groups was made by NISHIMURA (1960, 1964). He, from the progeny of Japanese rice subjected to irradiation from the atomic bomb explosion and by x-ray, obtained 34 strains homozygous for reciprocal translocation, which could be identified to contain 23 translocations with different interchanges of chromosomes. By using these stocks the relationship of gene loci to the interchanged segment of chromosomes were examined. This was followed by NAGAMATSU *et al.* (1962, 1965 a, 1966) and SATO *et al.* (1973) and at present ten out of twelve linkage groups have been assigned to the relevant chromosomes. This line of studies has also been underway in Taiwan (CHANG 1955, HSIE *et al.* 1959, 1962 c).

However, neither by this method, nor by the conventional genetic method was it possible to know the linkage relationships of genes located apart from each other. In this connection trisomics are being use. HU *et al.* (1963, 1968) in Taiwan obtained many trisomic plants and classified them into twelve types. In Japan attempts have also been made since the first work by ICHIJIMA in 1935. Recently WATANABE *et al.* (1969) and IWATA *et al.* (1981) presented twelve types of primary trisomics. From the observation in the PCMs of F₁s from crosses between trisomics and reciprocal translocation lines, the latter workers were able to identify five types of trisomics with their relevant extra, viz, supernumerary chromosomes and linkage groups. They are as follows :

type of trisomics	A	B	C	D	E	F	G	H	L
chromosomes	4	6	7	12	11	10	9	1*	2
linkage groups		I	<i>fgl</i>		II	IV	VIII	VII (V**)	VI (IX, XII)**

(* nucleolar chromosome, ** a part of the group is included)

C. Comparison of genic systems and linkage relationships between *japonica* and *indica* rice

Intensive and systematically produced studies in an attempt to render experimental elucidation of the differences of genic systems of the *japonica* and the *indica* are not so abundant, and consequently the availability of information along this line are limited. Nevertheless it seems probable that there exists some differences between these varietal groups.

Especially in view of the fact that the *indica* has a wider range than

Hairy leaf (*Hla*, VII-49), 26. Dense (barnyard-grass-like) panicle (*Dn*, VII-69), 27. "lazy" growth habit (*la*, VIII-32), 28. shattering (*sh*, VIII-70), 29. neck leaf (*nl*₁, IX-0), 30. Verticillate rachis (*ri*, IX-32), 31. brown discoloration of leaves and glumes (*bl*₁, X-18), 32. tillering dwarf (*d*₅, X-43), 33. brittle culm (*bc*₁, XI-0), 34. brown spotted leaf (*bl*₁₄, XI-59), 35. glabrous leaf and hull (*gl*₁, XII-0), 36. Awn (*An*₂, XII-40).

the *japonica* in terms of variability of major genes. Some examples in this respect will be given. i) New alleles at the *C*, *A* and *Rc* loci were found in *indica* varieties, by KONDO (1961), NAGAO, TAKAHASHI and KINOSHITA (1962) and MORI *et al.* (1981). ii) Restricted color types in floral glumes are governed by duplicate or triplicate genes with a suppressive effect, in cooperation with the basic genes *C*, *A* and *P*, and this restricting effect is diminished again by another genes. These genes are involved not in *japonica* but in *indica* (TAKAHASHI and KINOSHITA 1967 a). This type of genic diversity in color characters in *indica* varieties is ascertained in such organs as the stigma, leaf, stem node and pericarp (GHOSE *et al.* 1957, D'CRUZ 1960, HSIEH 1960, TAKAHASHI 1958, etc). Therefore, in *indica* rice, and even when parents are colorless or have inconspicuous coloration, they frequently involve several alleles or genes. iii) Further, and even when the both varietal groups give the same type of character expression, their causal genes frequently are different. This may well be demonstrated in the stem node and pericarp colors (TAKAHASHI *et al.* 1968 d, HSIEH *et al.* 1964). iv) Another point of interest is the difference in gene distribution and differentiation. The black color in floral glumes results from the complementary action of genes, and each counterpart of them is seen in *japonica* and *indica* separately (KAMATH 1956, KURIYAMA *et al.* 1967, MAEKAWA *et al.* 1981). The gametic development genes by OKA (1953 b, 1957, 1963, 1964 etc), recessive sterility genes by MIZUSHIMA and KONDO (1962), or gametophyte genes by IWATA and OMURA (1964) and NAKAGAHRA and IWATA (1970) may also be the genes of the same case. Purple leaf genes, *Pl^w* of *indica* and *Pl* of *japonica*, are an instance of differentiation of alleles in a single locus at which the alleles differentiated and evolved a new function (NAGAO, TAKAHASHI and KINOSHITA 1968).

As a whole, it may be said that *indica* and *japonica* have at least same basic gene systems in common, however the latter is a derivative of the former and at the same time, the latter has differentiated to some extent.

As can be seen in Table 1 and 2, these two series of linkage groups do not coincide in respect to the assignment of some genes. This discrepancy cannot be satisfactorily explained at present, however, as to the probable nature of such differences, the following presumption is possible to consider. i) It may be due partly to the existence of some structural differences of chromosomes. MIZUSHIMA *et al.* (1959 b, 1960, 1961 a, 1962), KONDO (1963 a, 1964 b), RICHHARIA *et al.* (1962) and SEETHARAMAN (1964) made *japonica-indica* crosses and observed an anomalous mode of segregations. They ascribed this to the structural differences of chromosomes between parental

varieties. Some cytologists are inclined to assume the presence of structural differences (YAO *et al.* 1958, HEDERSON 1959, 1964, SHASTRY *et al.* 1961, 1964), however others are not convinced of this (HSIEH 1957, 1958, OKA 1964, etc). ii) JODON (1955) suggested that color character may be controlled by different genic constitutions in different varietal groups. It also appears that complex gene loci are involved in certain cases. iii) More probable reasons or causation, however, seems to be the difficulties which lie in the proper identification of characters and the causal genes involved. If the reported data merely indicate that a certain character shows association with purple leaf color, for example, it is actually impossible to determine which gene, chromogen (*C*), activator (*A*), localization (*Pl*) or inhibitors ($I-Pl_1 \sim I-Pl_n$), is linked with the causal gene of the said character. Inadequate genic information on complex characters complicates linkage work.

Such being the present status of rice linkage groups, further studies should be made with more emphasis on the coordination of cytological and genetic approach, in pursuit of more complete mapping and genetical placement of the centromere.

IV. Related problems

A. Areas requiring new efforts

In the two preceding sections, recent research on the analysis of major genes and linkage groups in the rice plant were reviewed. As compared with work in such crops as corn, barley and tomato research on the rice plant is somewhat delayed. However, from the trend seen in recent years for international cooperation and the actual work done along this line, it may be expected that research will be promoted and in the very near future the level of work in the rice plant may become comparable with that in other crops.

As a staple rice is the most important single crop in the world and has an extraordinarily wide geographic distribution. It is also known for its tremendous variability in morphological and physiological characteristics and in the production of progeny no hindrance is seen either by selfing or crossing of usual varietal combinations. It is even possible to induce clonal propagation. Thus it may well be said that this plant is most suitable as research material for fundamental aspects of genetics and breeding science work. The results of gene analysis of this plant will throw additional light on the concept of the nature and action of genes. These informations may also be useful in the research of evolution dynamics of crops or breeding schemes or even breeding procedures of self-pollinated crops. To achieve this we

must endeavour to bring about additional clarification of the pattern of action of the major genes and to find more examples of the mode of gene interaction.

In this regard and to make clear the fine structure of genes, it is necessary to find cases of gene clusters, pseudo-alleles or isoalleles. And further, it is necessary to prepare numerous iso-genic lines in order to obtain detailed information on the pleiotropic or manifold effects of major genes. Further, it may be pointed out that the investigation of the nature of heterotic loci may be useful for building the basis of the theory of heterosis, and also comparative studies on gene distribution may well provide valuable information for phylogenetic studies. It goes without saying that a compilation of as many cases as possible in which important agronomic characters are governed by major genes with large, easily recognizable stable effects is necessary.

Now, here an attempt will be made to list problematic points in linkage studies with special reference to possible studies in the rice plant. One of the first problems is to provide data for the linkage of major genes and polygenes, next, cases of correlated response should be compiled, and additionally the position effect should be proven.

As mentioned before, if the present linkage map can be filled in to a greater extent, this would firstly serve to clarify or otherwise elucidate the nature and genetic mechanism of hybrid sterility in distantly related varieties. In this respect, divergent views of interpretations has been proposed; among them the sharpest controversy comes from a difference of opinions as to whether the sterility is genic or chromosomal. Some workers indicate the possible role of inversions, translocations, deletions and duplications. On the other hand, other workers insist that there is no particular reason for assuming the chromosomal differences in structure, postulating a series of duplicate gene system termed as "gametic-development genes" and "duplicate fertility genes" In this connection some workers suggest 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 is still a matter of dispute. Thus to reach a convincing elucidation on the above problems further studies, with emphasis on examinations of the relative location of apparently identical genes in *japonica* and *indica*, should be made. Valuable results may be brought to light after each set of linkage map are established. Another beneficial side effect associated with linkage analysis of rice is the revealing of correlation or linkage 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 the following paragraphs, and along the above mentioned line of thought, some interesting studies being made in Japan will be reviewed.

B. Relation between major genes and modifiers or polygenes

In general, breeders are interested in the maximum expression of the characters with which they work. Consequently modifiers and polygenes are likely to become increasingly important as more and more major genes are concentrated in single lines. However, clear cut instances of this sort of gene cooperation are rather scarce.

The clustering habit of rice means a clumped arrangement of the spikelets on the panicle. The clustering has been considered partially dominant over nonclustering with a single gene locus (*Cl*) of the first linkage group (JODON 1947, NAGAO *et al.* 1964). However, through recent studies (MORIMURA *et al.* 1969 a, TAKAHASHI *et al.* 1968 e), it was indicated that while this character is essentially governed by a major gene, at the same time several modifiers contribute to the degree of character expression. The cumulative effect of polygenes are also ascertained in this character (MORIMURA and TAKAHASHI 1969 b). In ordinary varieties that lack *Cl*, their panicle branches generally bear solitary spikelets, however, some varieties are not always free from the occurrence of clustering though the degree of character expression is relatively low. Intense cross examination gave support to the presence of polygenes in this character. This type of gene cooperation was also reported in "rachis deficiency" character (WASANO and SAKAI 1966, 1967).

C. Finding of new descriptive character

Agronomic characters, in the point of breeding studies, are not always directly measurable ones. If a certain numerical expression is possible to be deduced through the interrelationship between two or more contributing characters, and at the same time, if varietal differences are detected in this numerical value, genetic analysis on this "new descriptive character" may be worthy to carry on.

Varietal differences of internode length have been recognized to be inherent and some morphological (NAGAMATSU *et al.* 1961) and genetical (MORISHIMA and OKA 1968, OKA and MORISHIMA 1968) studies were made. A majority of Japanese rice gives rise to four elongated internodes accompanied by several reduced basal internodes. The successive internodes from

top downward may be designated as In_1 , In_2 , In_3 and In_4 respectively, in which the last one consists of many nodes being contiguous. In order to express their differential relative size in terms of metric indices, TAKEDA and TAKAHASHI proposed the "internode ratio" (TAKAHASHI and TAKEDA 1969, TAKEDA and TAKAHASHI 1969). This is an arcsin percentage of the respective internode which shows a degree of contribution to a final culm length. Employing this, they classified varieties of their collections into five basic types of "internode distribution pattern"; N, dn , dm , d_6 and $n1$. The idiogram of this is as shown in Fig. 6. Though considerable variations of

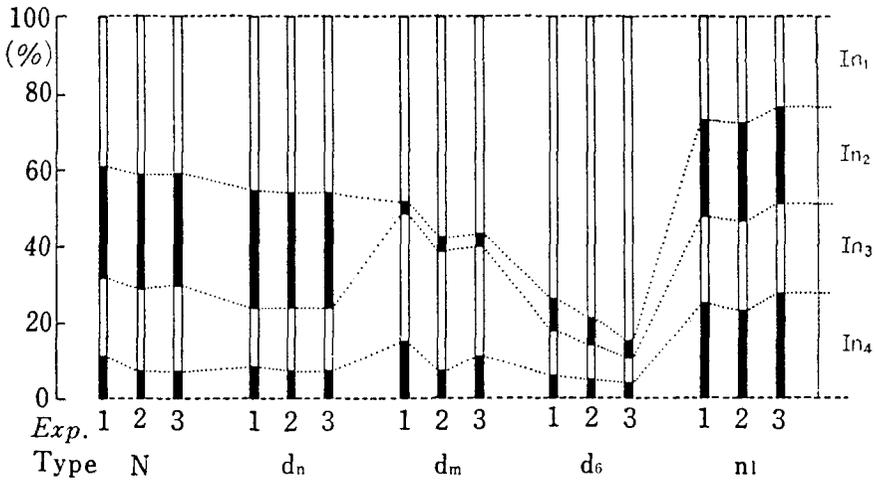


Fig. 6. Idiogram of the five internode patterns.

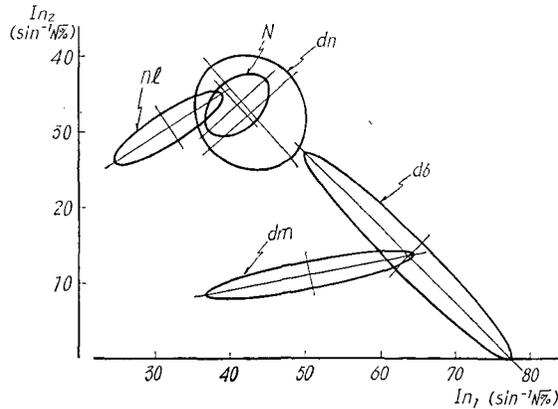


Fig. 7. Ellipse with equal probability ($p=0.95$) of internode pattern in regard to In_1 and In_2 .

actual culm length among varieties are seen, they are isometric among each internode of the same type under the same cultivating conditions, suggesting that this new descriptive character is stable. For the purpose of demarcation among five types an ellipse with equal probability in regard to any of two internodes was applied, part of which is as given in Fig. 7. From segregation modes in crosses of five types it was concluded that these types are principally controlled by the respective major gene. New distribution patterns which are the resultant products from an accumulative interaction between these major genes were obtained.

D. Functioning of major genes as an aid in understanding genetic events

The articles in this paragraph are chosen to demonstrate how informations concerning the function of a major gene is useful in understanding genetic events or phenomenon.

The gene stocks that carry "notched genes" and genes for "tillering dwarf" are characterized with a regular appearance of notched grains and cracked hulls, respectively (GHOSE and BUTANY 1952, CHANG and JODON 1963, TAKAHASHI and KINOSHITA 1968 a). By nature, the caryopsis develops in a state encased in floral glumes, which means that the size and shape of the rice grain, hulled rice, is restricted by the scope of hull itself. However, since the morphogenesis of ovary and floral glumes differ, it may be natural to consider that the genetic pathway which governs the development of these separate parts may well have a possibility of having some partial differences. TAKEDA and TAKAHASHI (1970) found out that when the upper parts of the floral glumes of these gene stocks are clipped after anthesis, allowing for the development of caryopsis to grow up unrestricted by the floral glumes, the matured grains were strikingly longer or larger than the hulled grains. This indicates the existence of inherent unbalance between glumes and caryopsis of these plants. They pursued examinations in many varieties, since it has widely been accepted that such aberrations arise from environmental factors; the underdevelopment causes notched grains, while the over development causes cracked hulls. However, as a matter of fact, it was revealed that in varieties with a higher degree of this type of unbalance a tendency of appearance of the notched grains and cracked hulls was more pronounced. From crosses with a high degree of appearances in size of grains, segregates with a high degree of appearance of aberrations were also obtained.

Reports on clear-cut cases of the overdominance in which different alleles in an identical locus actually perform different effects and the sum of their different products indeed is superior to the single product produced

by either allele in a homozygous state are not numerous. This seems to have been a deterrent to the general acceptance of the overdominance theory of heterosis. A color type called "murasaki-ine" in Japanese, which means purple rice plant, is a resultant anthocyanin color pattern by a distribution gene *Pl*, in conjunction with the basic genes of such genotypes as $C^B A$ or $C^{Bp} A$ (TAKAHASHI 1957). The *Pl* distributes the color over the entire surface of the leaf blade, leaf sheath, junctura, auricle, ligule and pulvinus. While, in Indian varieties, a color type with purple wash of leaf and deep purple color in stem and pericarp is known. A distribution gene Pl^W is responsible for this color type. The Pl^W was transferred into the *japonica* germplasm and the genotypic plants of $C^B A Pl^W$ and $C^{Bp} A Pl^W$ were bred true. They were crossed with $C^B A Pl$ and $C^{Bp} A Pl$ and their hybrid progenies were investigated up to F_6 generation (NAGAO, TAKAHASHI and KINOSHITA 1968). Through examination, including histological observation, it was clarified that Pl^W behaves as an allele of the *Pl*-locus, and that a heterozygous state of this locus, viz. Pl^W/Pl , is superior in its working scope of coloration than those of either homozygotes, Pl^W/Pl^W and Pl/Pl .

E. Use of isogenic lines in a study of pleiotropic gene effects

Use of isogenic lines is a positive method for identifying manifold or pleiotropic effects of major genes, and knowledge in this respect may also serve as a basis for studying problems related to adaptation of plants in which self-fertilization is the mode of reproduction.

Two types of isogenic lines in a Ponlai rice variety of Taiwan, Taichung-65 (abridged as T-65), having i) the *wx* and ii) the earliness gene (or gene block, dubbed as *E*), were bred true by TSAI (1961) and TSAI and OKA (1965). Data showed that the waxy gene in the genetic background of T-65 did not affect the yielding capacity or other characters. This attracted notice of other workers, since it has been believed that the waxy gene directly affected the yield (MORINAGA 1943). Further, in hybrids between T-65 and its waxy isogenic lines the segregation distortion was not so pronounced as in ordinary varietal crosses. This seems to form the basis of OKA's opinion that certation might be due not only to the delaying effect of the *wx* itself on pollen tube growth but also to other modifying genes which magnify the effect. In contrast the above isogenic lines, the isogenic lines with "*E*" gene differed in many respects from the original strains, indicating that the replacement of a gene for earliness involves pleiotropic changes of characters related to the physiology and adaptation to environment (TSAI and OKA 1966, 1968). That is, the *E* promotes flower initiation and subsequent growth of certain flower organs. And this results in an increase

or decrease of the growth rate, growth duration and final size of various organs that develop after flower initiation.

F. Application of zymography to comparative gene analysis

Electrophoretic analysis of enzyme protein into isozymes has been conducted in various materials and in many cases an isozyme bands were found to be determined by genes. Thus isozyme analysis of an enzyme seems to enable us to look into the differentiation of certain relevant genes. In rice plants, peroxidase isozymes in the vegetative organs have been investigated using starch-gel electrophoresis (CHU 1967, SHAHI, CHU and OKA 1969). CHU stated that most *indica* varieties had the band 4C in leaves, while most *japonica* leaves did not. SHAHI *et al.* compared the zymograms of *Oryza sativa*, *O. perennis* of Asian form, and their interspecific hybrid populations. The data showed that the genes controlling peroxidase variation between *sativa* and *perennis* are at two independent loci. One of them has two alleles $Pe^{2A} : Pe^{AA}$, and produces in heterozygotes a hybrid dimmer band, 3 A. The other locus has the alleles $Pe^{4C} : Pe^{4C-}$, the former specifying band 4 C while the latter produces no active band. Since they produce no hybrid band in heterozygotes, these may be considered to be "structural" genes. From diallel crosses in *perennis* populations the presence of a gene repressing the active band, 4 C, was found. This gene, R^{4C} , is considered to be a "regulatory" gene. In these respects the variation in isozymes of cultivated rice seems to be relatively limited, while the Asian form of *perennis* carries a much wider variability.

G. Correlation between marker genes and agronomic important characters

Among the correlation or linkage between linkage markers and agronomic important characters that are difficult to identify under ordinary cultivating conditions, three cases are briefly described. They are cool tolerance, resistance to rice blast disease and to rice stripe disease.

Cool weather damage is not so infrequent in the northern part of Japan, however genetic studies in this phase are not so abundant. TORIYAMA *et al.* (1960, 1962 a, 1962 b) and FUTSUHARA *et al.* (1966) devised a testing method by which the degree of cool tolerance is clearly evaluated by the sterile index of panicles under cool water (18°C) of irrigated fields. Crosses were made between linkage markers and varieties with tolerance to coolness and their hybrid descendants were assorted with respect to their genotypes of marker gene and degree of sterility index. As a result, cool tolerance was correlated with seven markers of four linkage groups. This line of studies was followed by TAKAHASHI (1967 b, 1968 f). In his examinations

at least eleven markers of seven linkage groups showed association with cool tolerance. To sum up, nine of twelve linkage groups are connected with cool tolerance, suggesting that the inheritance mode of this character would be complex, and that different varieties possess different genes for this character.

Several major genes for resistance to rice blast disease have been advocated in Japan. These are based on the assumption that the resistance phenomenon is a result of the interaction of specific pathogenicity of parasite races and the corresponding genotypes for resistance of the host plant. Nine different gene loci have been relatively well identified to date. They are *Pi-a*, *Pi-k*, *Pi-i* (YAMASAKI *et al.* 1966), *Pi-b*, *Pi-t*, *Pi-ta*, *Pi-z* and *Pi-m* (KIYOSAWA 1966, 1967 a, 1967 b, 1968). These loci also consist of some multiple alleles respectively (KIYOSAWA 1969 a, 1969 b, 1969 c, 1969 d, YOKOO *et al.* 1969). Through examinations of relationships between these genes and linkage markers it has become more probable that these resistance genes are assembled in the limited linkage groups, which are given below (KIYOSAWA 1967 b, TAKAHASHI 1967 b, 1968 f, SINODA *et al.* 1969, FUKUYAMA *et al.* 1970, SAITO *et al.* 1970, etc):

linkage group	gene locus	allele
I	<i>Pi-i</i>	
	<i>Pi-z</i>	<i>Pi-z^t</i>
VII	<i>Pi-ta</i>	<i>Pi-ta²</i>
VIII	<i>Pi-a</i>	
	<i>Pi-k</i>	<i>Pi-k^s</i> , <i>Pi-k^p</i> , <i>Pi-k</i> , <i>Pi-k^mPi-kⁿ</i>
	<i>Pi-m</i>	

Though it is only one case, *Pi-k* links with *Pi-m* in such an intensity as eleven crossover units (KIYOSAWA 1968). With these genes entering as the cross in the coupling phase, more than 93% of the resistant plants in F_2 are expected to carry both genes. Each gene imparts resistance to races of the fungus not covered by the other so that lines with both alleles for resistance in the coupling phase are valuable materials in breeding for blast resistance.

In major genes of resistance to rice stripe disease St_1 is located on the first linkage group and St_2^i on the fifth or twelfth groups (WASHIO *et al.* 1967, 1968 a, 1968 b).

V. Addendum

Recently, the writer's collaborator T. KINOSHITA is constructing a new

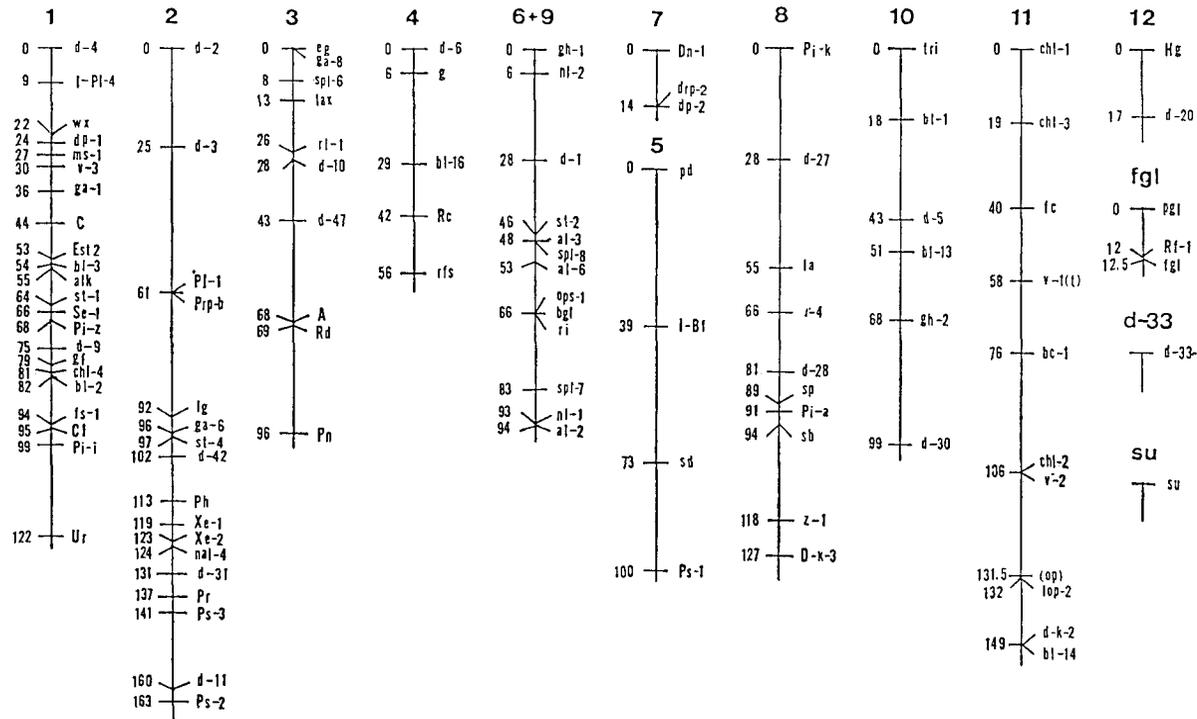


Fig. 8. Revised linkage maps in Japanese rice.

TABLE 6. Location on marker genes, interchange points and centromere in the respective chromosome

Linkage group-I (Chromosome 6)
<i>wx-dp-1-6-11-C-6-10-fs-Cl-5-6-6-7-3-6-Ur</i>
Linkage group-II (Chromosome 11)
<i>3-11 b-d₂-3-11 a-Pl-10-11 a-lg-6-11-centromere-Ph-Pr-3-11 a-d₁₁</i>
Linkage group-III (Chromosome 3)
<i>1-3 b-3-12-A-Rd-1-3 a-centromere-1-3 b-3-4 b-3-6-Pn</i>
Linkage group-IV (Chromosome 10)
<i>6-10-d₆-g-centromere-9-10 a-8-10 a-Rc-11-10-8-10 b</i>
Linkage group-VI+IX (Chromosome 2)
<i>2-5-gh₁-d₁-st₂ (gw)-2-3-1-2-centromere-2-3 c-nl₁-2-6 a-2-7 a-2-3 b-2-10 a-2-3 d-gl₁</i>
Linkage group-VII (Chromosome 1)
<i>1-11-centromere-Dn₁-1-2-drp₂-1-8-dp₂-1-3 b-1-10-1-3 a</i>
Linkage group-VIII (Chromosome 9)
<i>9-10 a-la-7-9-5-9</i>
Linkage group-X (Chromosome 8)
<i>tri-7-8 a-3-8 b-1-8-8-10 a-d₃₀-7-8 b-gh₂</i>
Linkage group-XI (Chromosome 5)
<i>bc₁-2-5-lop₂-5-9</i>
Linkage group-(<i>fgl</i>) (Chromosome 7)
<i>7-9-pgl-7-8 b-Rf₁-fgl-6-7-3-7</i>

linkage maps with some alteration and additions of the TAKAHASHI-KINOSHITA's maps in Figure 4 and Table 4.

Further, through the effort of S. SATO (the then post graduate student of our laboratory) valuable informations on the physical location of marker genes in relation to the translocation interchange points and centromere in the respective chromosome are partly revealed (unpublished).

The outlines of them are given in Figure 8 and Table 6, respectively.

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