CHARACTER EXPRESSION OF SOME MAJOR GENES IN RICE AND THEIR AGRONOMIC APPLICATION

— Genetical Studies on Rice Plant, LVI —*

Man-emon TAKAHASHI, Toshiro KINOSHITA

(Plant Breeding Institute, Faculty of Agriculture
Hokkaido University, Sapporo, Japan)

and Kazuyoshi TAKEDA

(Plant Breeding Laboratory, Department of Agriculture
Hirosaki University, Hirosaki, Japan)

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Introduction

In this paper the authors will mention some cases where informations concerning the functioning of major genes and the linkage groups gave clues to understand genetic phenomena of agronomic importance. Before going further the authors wish to express their sincere thanks to Dr. S. SAMOTO, Mr. S. SAITO, Mr. T. SASAKI and Mr. S. SAWADA for their cooperation and help in carrying out experiments related to the studies given in this paper.

I. Inherent Imbalance Between Potential Dimension of Caryopsis and magnitude of Floral Glumes

The first case is that of grain development which is of considerable importance in dealing with the size and shape of grains from a viewpoint of breeding for varieties with good grain quality. It is not so uncommon experience for Japanese rice growers to encounter notched grains or to find plump grains with crocked hulls. In these phenomena a tendency of a varietal characteristics is seen to some extent. However, it has long been considered that such aberrations arise from environmental factors. In the case of the notched grains, its direct cause may be the underdevelopment of the caryopsis due to unfavorable cultivating conditions, while in the

* Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University.

cracked hulls the cause may lie in the overdevelopment of the caryopsis under favorable conditions.

Extreme cases are the character expression of plants that carry the so-called notched genes and the so-called tillering dwarf genes. In these plants notched grains and hull-cracked grains make a regular appearance, respectively. These are genetically controlled but have also been considered to be the results of either underdevelopment or overdevelopment of the caryopsis. In the case of notched character, many workers have proposed its causal major gene or genes, together with some modifyers (MORINAGA and FUKUSHIMA 1943, PORTERS 1946, GHOSE and BUTANY 1952, TAKAHASHI and KINOSHITA 1968, SEETHARAMAN 1967). When the clipping-method is employed for an emasculation of the rice spikelets, the development of the caryopsis is free from the restriction by the floral glumes, since the upper part of the glumes is cut off at the time of flowering. As an incident of hybridization experiment, we noticed that the glume-clipped hybrid seeds produced in the said genotypic plants were invariably longer or larger than the seed which were allowed to develop normally, restricted by the floral glumes.

Our first thought in this respect is as follows. By nature, the caryopsis develops in a state encased in floral glumes ; this means that the size and shape of the rice grain is restricted by the scope of the hull itself. However, since the morphogenesis of the ovary and the floral glumes differ, it may be natural to consider that the developmental path of these separate organs may have a possibility of having some partial differences. And the above-mentioned phenomena may indicate the existence of an inherent imbalance between glumes and caryopsis of these plants. When the potential length and width of the caryopsis far exceed the inner length and width of the caryopsis, the notched grains and the hull-cracked grains may be resulted.

From this angle hundreds of varieties, including Japonica and Indica types, and their hybrid populations were examined. The figure 1 is the schematic expression of grain shapes, and in this figure the conclusive information in the present chapter has already been illustrated diagramatically.

Before going further an explanation of two words, "treated" and "control", whose abbreviations are T and C respectively, is added. In the treated or T group, one to three days after anthesis the upper part of the floral glumes was clipped. In this condition it was expected that the caryopsis would probably grow to its own limit, unrestrained by the scope

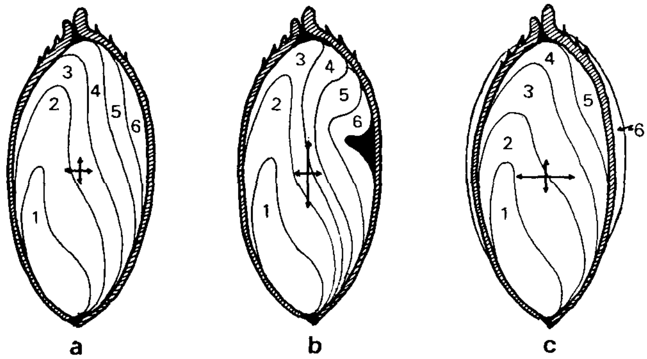


Fig. 1. Diagramatic expression of developmental process of caryopsis.

a : Normal grain; length of caryopsis and that of floral glumes is the same.

b : Notched grain; length of caryopsis exceeds that of floral glumes.

c : Hull-creacked grain; volume of caryopsis exceeds inner size of floral glumes.

Arrows represent rate and direction in growth of caryopsis.

of the floral glumes. While, the caryopsis in the so-called control or C group was allowed to develop normally restricted by the floral glumes. Further, in order to examine the influence of nutritional conditions on the growth of the caryopsis, two additional treatments, that is the thinning of spikelets and the removal of leaves after flowering, were made. The actual procedures in these respects were presented in the previous reports of the authors (TAKAHASHI and TAKEDA 1971, TAKEDA and TAKAHASHI 1970 a, 1970 b, 1972 a, 1972 b).

From the comparative experiments of the varieties it has become clear that the grains of the T group were invariably longer than those of the C group, and that the two additional treatments had no noticeable effects on this connection. This is as shown in the figure 2.

In this figure, the latter I of T and I of C mean the length of caryopsis. In this way the letter w which follows the T and C denotes the weight of caryopsis. This result suggests that there is an imbalance in growth between the floral glumes and the caryopsis. The length of the Cl represents the inner length of the floral glumes, so the ratio of the length of Tl to that of the Cl may be used as an index for the degree of imbalance. The varieties with high Tl/Cl rations showed a tendency to produce aberrations such as notched grains or hull-cracked grains, and as given in the figure 3, it is clearly pointed out that in the varieties in which aberrations

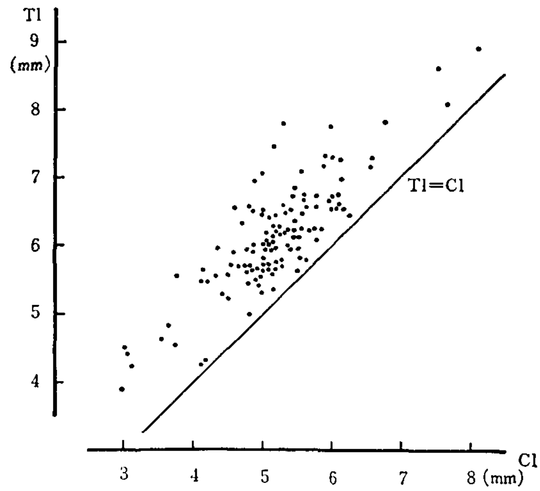


Fig. 2. Relationship between the length of glume-clipped grain (Tl) and non-treated grain Cl, in a survay of varieties.
One dot represents one variety.

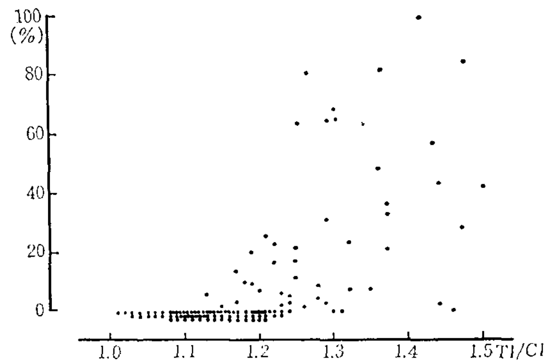


Fig. 3. Relationship between Tl/Cl ratio and frequency of notched grain.
Tl; length of glume-clipped grain.
Cl; length of non-treated grain.
One dot represents one variety.

have a very low appearance the Tl/Cl ratio was relatively low and fell between 1.1 and 1.2.

These are the informations obtained from the varieties or straines whose genotypic states are homozygous. Therefore the whole picture of the genetic situation on the imbarance remains incomplete unless the plants of hybrid or heterozygous state are exposed to the examination.

The main parts of rice kernel are floral glumes, pericarp, seed coat, endosperm and germ. Among them, endosperm is triploid and the remaining four parts ars diploid in their genomic constitutions. At the same time, nuclei in the floral glumes, the pericarp and the seed coat invariably contain the same genotypes as those of nuclei in other parts of the plant body. While, in nuclei of the endosperm and germ the situation in this respect is quite different, since these organs begin to develop after fertilization takes place. Therefore, unless subjected to the selfed seeds of a pure line, genetic situation of two groups, that is the first group of floral glumes, pericarp and seed coat and ihe second group of endosperm and germ, may have a possibility of showing some differences. In this respect the following two examinations were made.

Firstly the variability in length of the glum-clipped grains from varieties and homozygous strains was compared with the variability manifested in filial grains with hybrid state. The data obtained are abridged here; however, they indicate that the variation in the latter group falls into the range of error variance given by the variation in the former group (TAKEDA and TAKAHASHI 1972 a). Secondly, the glume-clipped grains produced in the F_1 plants were subjected to the selection in two grain length, long and short. The results is as given in the table 1.

TABLE 1. Effect of selection for two directions of length, long and short, in glume-clipped grains of F_2 seeds.

items	F_2 seeds (mm)	F_3 seeds (mm)
whole population	5.13	5.49
"L" group	5.91	5.46
"S" group	4.45	5.30

Notes) F_2 seeds and F_3 seeds mean the seeds produced in F_1 and F_2 plants respectively.

Four percent of longest and shortest grains in a sample of 500 grains were selected.

Difference between "L" and "S" of F_3 seeds is not significant ($t=0.93$, $p=0.3$-0.4).

In this table, the difference of grain length between two groups of the selected generation is not statistically significant. This suggests that no noticeable response to the selection appear. Furthermore, the diallel-cross analysis was made, with a view in estimating the influence of paternal

TABLE 2. Analysis of variance for the length and weight of caryopsis obtained in diallel crossing.

source of variance	d.f.	m.s.	
		length	weight
maternal genotypes	2	5.3982***	127.2900***
paternal genotypes	2	0.0713	5.1100
interaction	4	0.0516	2.4800
error	70	0.0406	2.3695

Notes) ***; significant at the 0.1% level.
Interaction between maternal and paternal genotypes is not significant when it was estimated from error variance given by intra varietal (inter plant) variation of parental varieties, H-21, H-346, H-347, N-6, and a big grain variety, Tairyuto.

genotypes upon length and weight of the glume-clipped crossed seeds. The data of the variance analysis is as shown in the table 2. This suggests that no particular contribution of the paternal side is in existence. Thus, as far as the present examinations are concerned, direct effect of male gametes, say, xenia or metaxenia, is hardly detected.

As the last step of this serial examination two types of crosses from four varieties were made, and their F_1s and F_2 segregating populations were observed. The cross combinations are H-347×H-346 and H-21×N-62. H-347 is a large sized grain variety with well balanced Tl/Cl ratio, and no aberration appeared. In contrast with this, H-346 is one of the smallest grain varieties in which the Tl highly exceeds the Cl, and it develops aberrant grains frequently. Thus the cross of H-347×H-346 is a case where both the parents are strikingly different from each other in their grain size and degree of imbalance. H-21 and N-62 show almost an equal size of grains to that of cultivars, but in H-21 the Tl exceeds the Cl in most of grains, while N-62 is well balanced in the two dimensions of Tl and Cl.

In an F_2 segregating population from H-347×H-346, a major genic segregation mode was observed clearly in Cl and some ambiguously in Tl, Cw and Tw (Fig. 4). While in an F_2 population from H-21×N-62, the variation was completely continuous and the mean value of the F_2 population almost perfectly coincided with the mid-parent values in respect of Tl, Cl, Tw and Cw. In this combination it may be naturally considered that genes for quantitative effect participate in the inheritance of these characters.

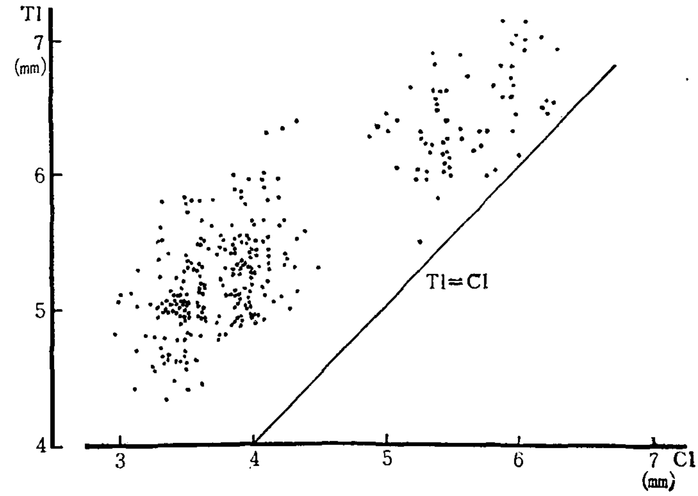


Fig. 4. Comparison of Tl and Cl in an F_2 population from H-347×H-346.

As to the ratios of Tl/Cl and Tw/Cw, they were widely segregated. The range of Tl/Cl was from 1.07 to 1.58 in the cross of H-21×N-62, and 1.00 to 1.71 in the cross of H-347×H-346. This trend held true in the case of Tw/Cw. The heritability values in a broad sense of these indices were calculated as 0.67 and 0.93 in Tl/Cl, and 0.56 and 0.64 in Tw/Cw. In these crosses, their F_2 plants with a high degree of imbalance in Tl/Cl and/or Tw/Cw tended to produce notched grains and/or hull-cracked grains. This is presented in the table 3. The figure 5 is the scattered diagram of an F_2 population from H-347×H-346. In this figure,

TABLE 3. Relationship between the frequency of notched or hull-cracked grain and Tl/Cl or Tw/Cw ratio.

		H-21×N-62		H-347×H-346	
		Tl/Cl	Tw/Cw	Tl/Cl	Tw/Cw
notched (%)	0	1.26	0.96	1.17	0.94
	1～29	1.29	0.95	1.35	0.99
	30～100	1.32	0.98	1.43	1.07
cracked (%)	0	1.23	0.97	1.26	0.97
	1～29	1.26	0.96	1.35	1.02
	30～100	1.29	0.96	1.39	1.06

a threshold-like phenomenon is seen in respect of the relationship between the Tl/Cl ratio and the frequency of notched grains. Nothched grains can only be found in such plants whose Tl/Cl, that is a degree of imbalance, is over 1.2.

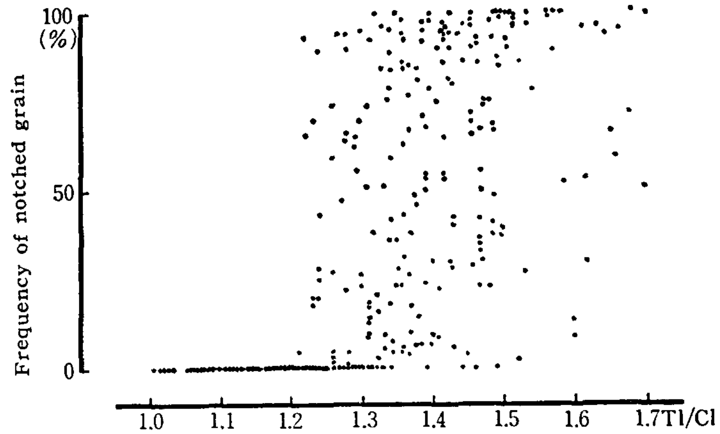


Fig. 5. Relationship between Tl/Cl ratio and frequency of notched grain in an F_2 population from H-347×H-346.

Therfore, as a whole, it is concluded that the appearance of notched grains and cracked hulls is mainly attributed to the inherent imbalance between the potential dimension of caryopsis and the magnitude of floral glumes.

2. Distribution Pattern of Elongated Internodes

The next case is that of distribution pattern of elongated internodes. More than one hundred of varieties and strains, including short-stemmed mutants, were subjected to the present examination. They are much the same in their maturity giving panicle emergence from the beginning to the middle of august in the northern part of Japan. A majority of them gives rise to four elongated internodes accompanied by several reduced basal internodes. The successive internodes from top downward were designated as In_1, In_2, In_3 and In_4, respectively, in which the last one consists of many nodes, they being contiguous. In order to express their differential relative size in terms of metric indices, a numerical measure, tentatively called as internode ratio, was proposed. This is an arcsined percentage of the respective internode which shows a degree of contribution to a final culm length.

In the course of genic analysis in dwarf forms, and also when some short-stemmed mutants were happened to deal with, it was noticed that the internode ratio seemed to be attributed to the intense genetic control. In this direction, many varieties and strains were examined, and, at least, five basic types of the internode distribution patterns, the ideograms, were succeeded in demarcating. They are dubbed as N, dn, dm, d_6 and nl. They are as shown in the figure 6. The N is the most popular type, whose internodes generally become decreasingly shorter from the top to the base of the culm. The dn is similar to the N, but the dm is an singular type in which the In_2 is strikingly shortened. The d_6 is an another marked type whose internodes, except the In_1, are so shortened that the In_1 is much longer than the total length of other internodes. The last type, nl, attracts attention in its counter-balancing effect of reduction in the In_1 and slight elongation in the In_4.

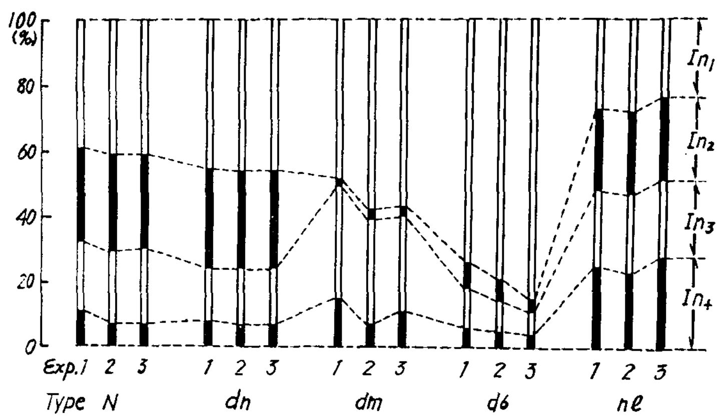


Fig. 6. Ideograms of internode patterns of Japanese varieties and strains.

These types of internode patterns remain constant as long as they are obtained within ordinary cultivating conditions. It goes without saying that considerable variations of actual culm length among varieties are seen, but they are isometric among each internode of the same type. Actual procedures employed for the demarcation among respective types are omitted here; however as reported in the previous papers, DUNCAN's multiple-range test and an ellipse with equal probability were applyed (TAKAHASHI and TAKEDA 1969 a, TAKEDA and TAKAHASHI 1969 b). A part of the results given by the latter method is as demonstrated in the figure 7.

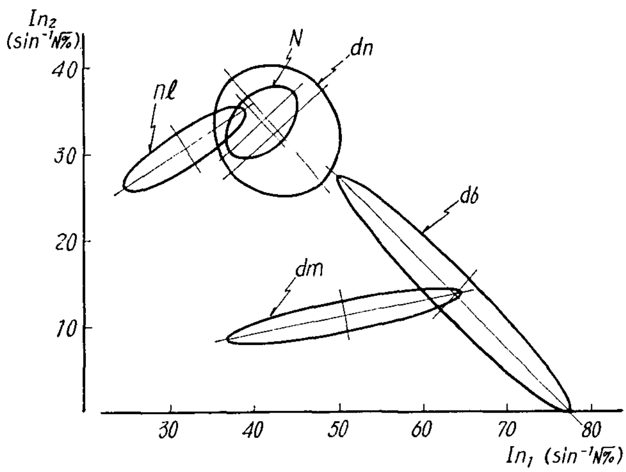


Fig. 7. Ellipse with equal probability (P=0.95) of each internode pattern in regard to In_1 and In_2.

TABLE 4. List of cross combination

cross combination		type of cross
N-62	×H-21	dn×N
"	×H-123	"
"	×H-143	"
"	×Shimada-mochi	"
"	×Yukara	"
"	×Himehonami	"
H-61	×Yukara	"
C-19	×H-129	dm×N
N-58	×H-75	"
A-23	×Furen-bozu	"
N-58	×N-62	dm×dn
H-135	×N-56	"
H-126	×Norin 9	d_6×N
N-45	×Somewake	"
"	×Yukara	"
H-69	×Yukara	nl×N
N-62	×H-69	dn×nl
N-7	×N-62	dn×dn
N-4	×Wasenishiki	N×N
Ju-4	×Himehonami	"
Yukara	×A-58	"
N-62	×N-45	dn×d_6
"	×H-100	"

To look into the inheritance mode of these ideograms, cross experiments were made. The list or cross combinations are as shown in the table 4. Among the crosses within the N-type varieties no noticeable segregation of the internode pattern was observed, indicating that no difference existed among parental varieties, as far as a major gene or genes for the internode types are concerned. The dn-type was subdivided into two types of dn_7 and dn_{12}, the former being the typical dn type and the latter being characterized with a slight reduction of the lower internode. From the results of F_2 segregation modes given in possible cross combination among six types, it was revealed that these types are principally governed by the respective causal major gene which extends its effect into the determination of internode pattern. The figure 8, is a case of crosses whose combination was dn_{12} and dm. In this figure, it may well be demonstrated that new phenotyges were segregated which were the resultant products of an interaction between genes of both parents. This held true in other cross combinations, and therefore, it may be concluded that the internode pattern, one of the discriptive characters of rice plant, is principally inherent.

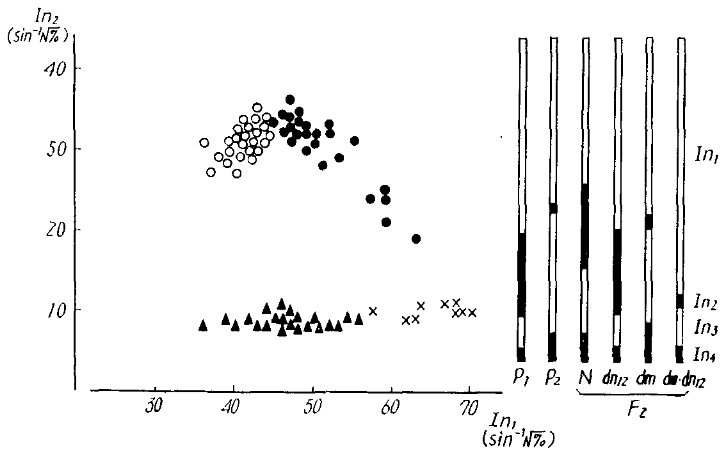


Fig. 8. F_2 segregation in a dn-type × a dm-type.
○ N-type; ● dn-type due to d_{12} gene; ▲ dm-type due to d_8 gene; × a type with d_8+d_{12}

The total culm length, a final character, should be discussed in the light of relative length or growth rate of each internode, since the culm length can be analyzed by breaking it into its primary components, length of each internode, number of elongated internodes, and further each internode may comprise an isometric and an allometric phase of genetic effect.

This line of examinations will offer valuable informations to both phases of rice genetics and breeding, finding a developmental pathway by which a final manifestation of plant type can be reached, and improving varieties suitable for lodging resistance and yielding capacity.

3. Initation of Internode Elongation

In connection with the number of elongated internodes, some additional informations will be made. Rice varieties in the northern part of Japan usually have four elongated internodes, while Japanese varieties in all the internode number is four to six. In these varieties a beginning of the internode elongation has been recognized to be closely related with the panicle initiation, which is a start of the so-called generative or reproductive growth. And thus, the change of the developmental phase is considered to act as a trigger mechanism in starting the internode elongation (TAKEDA and TAKAHASHI 1972 c).

However, when varieties of world wide scope and of very diverse cultural conditions were dealt with this was not always true. In our observation these varieties showed such a wide magnitude of character expression as 5～21 in leaf number of main stem, 3～12 in number of elongate internodes and 40～220 in days from seeding to flowering. On the examination of these varieties and some of their hybrid populations the following points were manifested. The plants which bring forth less than *fifteen leaves consistently bear three to five elongated internodes and* in these plants a beginning of internode elongation seems to be governed by

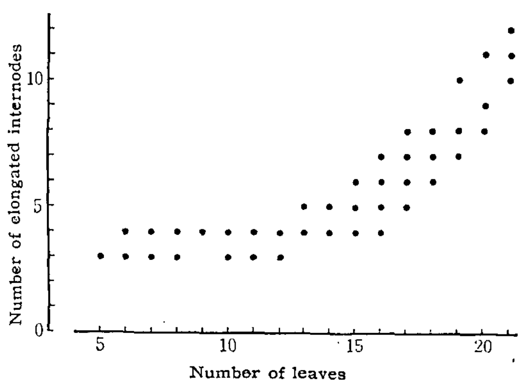


Fig. 9. Diagramatic representation of the relationship between number of leaves on main stem and node order from which internode elongation initiates.

a start of panicle initiation. While in the plants whose number of leaves are more than fifteen, a beginning of internode elongation precedes the panicle initiation and thus many internodes, up to nine, have already elongated at the time of panicle initiation. The beginning of internode elongation in these plants was not influenced by the short day treatment but remained unchanged, though the date of flowering was markedly shifted. Thus the internode elogation of these varieties might arise from some stimuli which have something to do with coming of a particular developmental stage and not with a panicle initiation. These two types of pattern of internode elongation are shown in the figure 9.

4. Heterotic Effect of Divergent Alleles

The fourth case is the presentation of a cumulative action of divergent alleles in a single gene locus of major gene. Up to the present, reports on clear-cut cases of the overdominance or heterotic effect, 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 homozygous state, are not numerous. And this has been a deterrent to the general acceptance of the overdominance theory of heterosis.

A color type called "Murasaki-ine" which, in Japanese, means purple rice plant is a resultant color pattern by a distribution gene *Pl*, in conjunction with the anthocyanin producting genes of such genotypes as $C^{B}A$ and $C^{Bp}A$. The *Pl* distributes the color over the entire surface of the leaf blade, leaf sheath, junctura, auricle, ligule and pulvinus. Rice plants outside of Japan are abundant in purple-leaved varieties. Among them a color type characterized with purple wash in leaf and deep purple color in stem and pericarp has been recognized to be governed by a distribution gene Pl^{W}. The color type caused by the Pl^{W} was introduced into the Japanese germplasma through hybridization between Japanese tester varieties and foreign varieties. In the process, strains were built up that were keeping the Pl^{W} and were giving rise to fertile F_1 when crossed with Japanese gene stocks (NAGAO, TAKAHASHI and KINOSHITA 1962, 1968).

To ascertain that Pl^{W} and *Pl* are really allelic, and to examine the actual working realms of their distribution effects, the said strains were crossed with Japanese testers, basic genotypes of which are $C^{B}A$ and $C^{Bp}A$, and consequently two genotypic plants, $C^{B}APl^{W}$ and $C^{Bp}APl^{W}$ were bred true. Then these plants were crossed with gene stocks, genotypes of which are $C^{B}APl$ and $C^{Bp}APl$, and their hybrid descendants were examined up

TABLE 5. Pattern of anthocyanin coloration in the three genotypic plants, Pl^W/Pl^W, Pl^W/Pl and Pl/Pl.

P_1 & F_1	genotype	leaf					stem		pericarp
		blade		sheath	collar	ligule	pulvinus (node)	internode	
		early	late						
H-120	Pl^W/Pl^W	++	+	++		+		++	+
H-127	Pl/Pl	+	++	++	+	+	+		
F_1	Pl^W/Pl	++	++	++	+	+	+	++	+

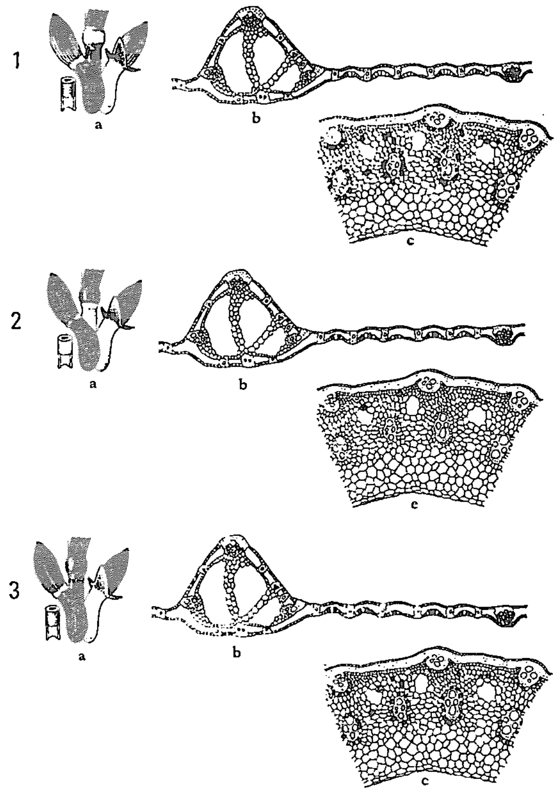


Fig. 10. Histological location of anthocyanin color developed in genotypic plants of Pl^W/Pl^W, Pl/Pl and Pl^W/Pl, in cooperation with apiculus genes, C^{Bp} and A.

1; Pl^W/Pl^W a; outward appearance
2; Pl/Pl b; midrib of leaf blade
3; Pl^W/Pl c; internode

to the F_6 generation. The table 5 shows the coloration pattern in three states of gene combinations, Pl^w/Pl^w, Pl^w/Pl and Pl/Pl. In the table it is pointed out that the Pl^w/Pl, the F_1 type, exceedingly abounds with color realm. In F_2s of these crosses, three color types in this table, that is a type with Pl^w/Pl^w, a type with Pl^w/Pl and a type with Pl/Pl, appeared in a ratio of 1 : 2 : 1, suggesting that the Pl^w and the Pl are allelic. Pedigree culture of the hybrid populations were made for several gemerations, and in every generation segregates which phenotypically were assumed to possess such genotypes as Pl^w/Pl^w and Pl/Pl gave rise to offsprings all of which are identical with their predecessors. While, segregates which showed widest realm of coloration and were assumed to have a genotype of Pl^w/Pl were segregated again into the three color types. As far as the present examination was continued, this was true in every generation up to the F_6. Thus it may be concluded that the color type with the widest realm of the anthocyanin coloration cannot be bred ture.

The location of the pigmental cells by two alleles, Pl^w and Pl, was histologically observed. A part of this is as demonstrated in the figure 10. This account for a cumulative effect of Pl^w and Pl when they are coexistent in a heterozygous state, Pl^w/Pl. It may easily be understood that the color type and the histological location of pigmental cells in a genotypic plant of Pl^w/Pl coincide with an expectation that the realm of coloration by the Pl^w/Pl^w and that of Pl/Pl unite together.

On the whole therefore, the effect of the *Pl*-locus may be a sort of direct evidence of locus at which the heterozygote is superior to the either homozygote.

5. Cool Tolerance

The last case in the present article is connected with some beneficial side effects of analysis of linkage markers. It may be needless to say that correlation or linkage relationship between marker genes and agronomic characters will provide a positive method for improving varieties in some important characters that are difficult to identify amony the segregation products of hybrids, under ordinary cultivating conditions. Cool weather damage is not so infrequent in the northern part of Japan. The damage becomes severe when cool temperature comes over at the germination and the ensuing seedling stage and then at the reproductive growth stage. Testing methods to evaluate the degree of cool tolerance at the above respective stages have been devised in Japan (TORIYAMA 1962a, TAKAHASHI 1968).

TABLE 6. Association between marker genes and cool tolerance.

L. Group	I		II		III		IV			V	VI	VII			VIII	IX		X	XI	XII
Cross Combi. \ G. Marker	*C*	*wx*	*Pr*	*Pl*	*A*	*Pn*	*g*	*Rc*	*ds*	*I-Bf*	*gh*	*Ur*	*fs*	*Dn*	*la*	*nl*	*ri*	*gl*	*bc*	*Hg*
N-4×NOHRIN-9	⧺ ⧺ ⧺ ⧺ ⧺ +						— — — — —													
NOHRIN-9×H-68																	—	⧺		
〃 ×H-126	—								⧺											+
A-58×WASENISHIKI	+	⧺	— — —		— — —	— — —														
A-58×TOYOHIKARI			⧺		⧺ +	+														
H-158× 〃														— —					+	
H-89×WASENISHIKI													—			—				
TOYOHIK.×H-75	—							⧺			— —									
KANMASAR.×H-69																—				
〃 ×N-4	—						—													
〃 ×H-126	—			—					+											+
TOYOHIKA.×A-32	—											—								
A-5×TOYOHIKARI										—										
TORIYAMA's	—		+	+	—	—	—	—			+				—	+		—	+	

Notes) "L. Group" and "G. Marker" stand for Linkage group and Marker gene, respectively.

Crosses were made between linkage markers and varieties with several degree of cool tolerance in the respective stages and their hybrid populations were assorted with their genotypes of marker genes and with degree of tolerance. As a result, cool tolerance at the reproductive stage was correlated with seven marker genes of four linkage groups. This was done by other workers (TORIYAMA and FUTSUHARA 1962 b). In our examination at least eleven markers of seven linkage groups are connected with cool tolerance. To sum up, as shown in the table 6, nine of twelve linkage groups are connected with cool tolerance. From this table it may be suggested that the inheritance mode of this character would be complex, and that different varieties possess different genes for this character.

As to the germinability at low temperature there was very high correlation with markers of two linkage groups, the first and the second group, and fairly high correlation with markers of other two linkage groups, the fourth and the seventh group. In connection with the above said results it must be added that in a majority of cross combination, the results obtained in the present approach were fairly well consistent with results obtained MATHER's procedure which is capable of an estimation of the number of effective factors in this character.

References

GHOSE, R. L. M. and W. T. BUTANY (1952). Studies on the inheritance of some characters in rice. Indian J. Genet., 12: 25-30.

MORINAGA, T. and E. FUKUSHIMA (1943). Heritable character in rice I. Abnormal mutation characters and their mode of inheritance. Bull. Sci. Dept. Agric., Kyushu Imp. Univ., 10: 301-339.

POTERS, R. (1946). The notched rice. Agron. Trop. 1-2: 69-72.

NAGAO, S., M. TAKAHASHI and T. KINOSHITA (1968). Heterotic effect of alleles at *Pl*-locus in rice plant. J. Facult. Agric., Hokkaido Univ. 56(1): 45-56.

SEETHARAMAN, R. (1967). Inheritance of notch in rice pernels. Indian J. Genet. and Plant Breed. 27: 465-472.

TAKAHASHI, M. (1968). Studies on promotion of seletion efficiency in self-pollinated crops, II. (Japanese). Special Rep. Plant Breed. Inst., Hokkaido Univ., Japan: 58 pp.

——— and T. KINOSHITA (1968). Present statur of rice linkage map. (Japanese). Ann. Rep. Farm., Hokkaido Univ. 16: 33-41.

——— and K. TAKEDA (1969). Type and grouping of internode pattern in rice culm. (Japanese). Mem. Facult. Agric., Hokkaido Univ. 7(1): 32-43.

——— and ——— (1971). Unbalanced growth between caryopsis and floral glumes in rice. SABRAO Newsletter 3: 35-37.

TAKEDA, K. and M. TAKAHASHI (1969). Preliminary report on cross experiments in six types of internode pattern in rice culm. (Japanese). Mem. Facult. Agric., Hokkaido Univ. 7(1): 44-50.

TAKADE K. and M. TAKAHASHI (1970 a). Some genetical considerations on appearance of notched grains and hull-cracked grain in rice. (Japanese). Ditto 7(4): 449-453.

———— and ———— (1970 b). Unbalanced growth in floral glumes and caryopsis in rice, I. (Japanese). Jap. J. Breed. 20(6): 337-343.

———— and ———— (1972 a). Ditto, II. (Japanese). Mem. Facult. Agric., Hokkaido Univ. 8(2): 125-131.

———— and ———— (1972 b). Relationship between the number of leaves and that of elongated internodes on the main stem of rice plant. (Japanese). Jap. J. Breed. 22(1): 25-32.

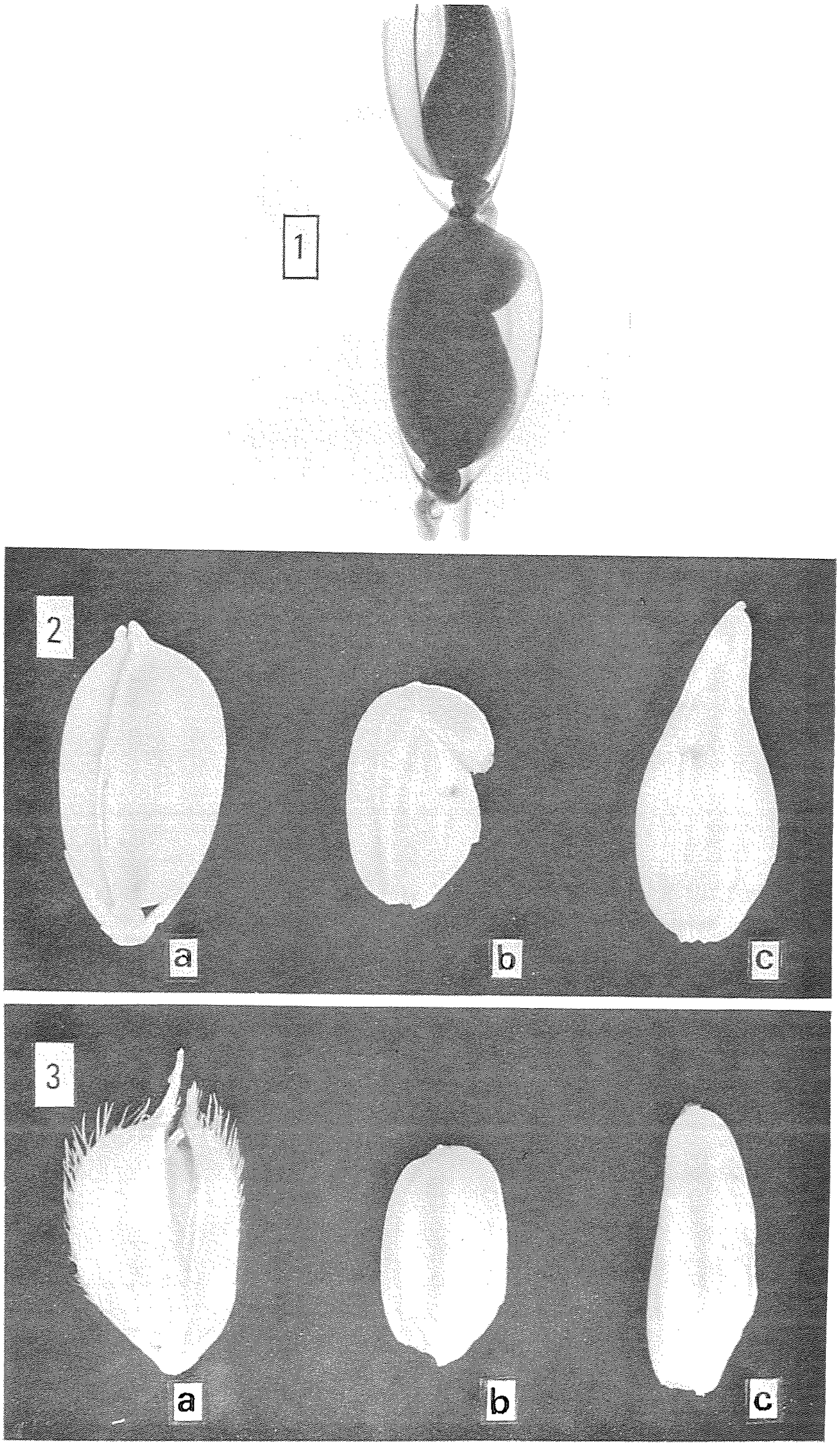
———— and ———— (1972 c). Unbalanced growth in floral glumes and caryopsis in rice, III. (Japanese). Ditto 22(2): 67-74.

TORIYAMA, K. (1962 a). Studies on the cool-tolerance of rice varieties, with special reference to testing methods and its inheritance. (Japanese). Rep. Aomori Pref. Agric. Exp. Sta., Japan 7: 109-153.

———— and Y. FUTSUHARA (1962 b). Genetic studies on cool tolerance in rice, II. Relation between cool tolerance and other characters. (Japanese). Jap. J. Breed. 11: 191-198.

Plate I. Developmental process of aberrant grains.

1; X-ray photograph of notched caryopsis
2; notched grains
3; hull-cracked grains
a; hull
b; grain developed in a state, encased by floral glumes
c; grain developed in a glume-clipped spikelet


1
2
a
b
c
3
a
b
c