

A developmental-genetic study on panicle characters in rice, *Oryza sativa* L.

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1. INTRODUCTION

Interpretation in genetic terms of the differentiation and development of organs of higher plants is one of the most fascinating subjects. Two ways of approach are possible: (1) by enquiring into the effect of mutation of so-called major genes on development, and (2) by quantitative analysis of developmental relations among different characters normal in appearance but variable in quantity.

So far, a large body of studies of the first category have been reported since the early days of genetics. For example, gene mutation is known to bring about abnormal dwarfism or failure to form chlorophyll in many plant species. It is also known that stamens can turn into petals, or male inflorescences can produce female flowers by single gene mutation. For examples of such mutations in corn, the reader is referred to Singleton, Appendix A (1962). All these facts indicate that major genes can be responsible for differentiation or formation of plant organs. Occurrence of abnormal development of a plant organ by a single gene mutation suggests that there is something like a key- or switch-gene, whose sound operation is necessary for normal organ formation.

However, it is reasonable to assume that in addition to such key-genes, there are also genes with individually minor effects but participating co-operatively or co-ordinately in the development of plant parts. Here may belong, for example, the so-called modifiers which are probably responsible for phenotypic variation. These genes, possibly of polygenic nature, may have played an important role either in selective evolution or in domestication of plant species. Thus, it may be of considerable interest to investigate from the genetical standpoint the development of normal characters which show quantitative variation.

Sakai & Suzuki (1964) have succeeded in estimating parameters for pleiotropy in the form of genetic correlation by comparing genetic correlations between progeny lines of X-rayed and those of control populations on the basis of a few assumptions. The same method of analysis has been followed in the present study in order to find

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out to what extent the same genes may participate in the development of some panicle characters. This is the essence of the first part of the present study.

The second part deals with the investigation of developmental relations among the same characters by comparison of their developmental instabilities. It is quite obvious that quantitative characters are likely to show non-hereditary variations in their phenotypes. This may be due, in addition to variation in environmental conditions, to developmental errors happening during the development of the character. The fluctuation in final expression of characters due to these causes will be called in this paper developmental instability, following Jinks & Mather (1955). In fact, a group of geneticists have been interested in this problem. One of the most popular materials for the genetic study of developmental instability has been the bilateral asymmetry of the number of sternopleural chaetae in *Drosophila*. It has been found that the asymmetry is a genetic attribute which can be modified by artificial selection (Mather, 1953; Thoday, 1958; Reeve, 1960). In plants, however, developmental instability has attracted little attention with the exception of *Nicotiana rustica*, in which intraplot-interplant variability in plant height, leaf length, fruit number and flowering date (Jinks & Mather, 1955) or intraplant variability of flower organs and leaf shape (Paxman, 1956) have been investigated. They found concurrently that developmental instability was variable among strains and accordingly a heritable character.

Developmental instability will be of value for the analysis of developmental relations among quantitative characters. If this phenomenon were the outcome of repeated occurrence of errors or noise during the process of development of a character, other closely related characters would show more or less similar instability. Conversely speaking, the degree of correlation of instability between two characters may reveal the developmental relationship between them, provided they are pleiotropic products of the same genes. This hypothesis will be explained with the aid of a schematic diagram in a later section.

2. MATERIALS AND METHODS

(i) *Materials*

Materials for the present study are two groups of lines derived from the same rice variety, 'Norin No. 8', which was itself assumed to contain a certain amount of genetic variability. In 1959, two lots of seeds, two thousand in each, were taken at random from a bulk of its seeds. One lot was irradiated by 20,000 r X-rays, while the other was left untreated as the control. The two lots were cultivated as two separate populations in successive years according to our 'one plant-one offspring' scheme of propagation. That is, each plant in a population was allowed to give only one offspring in the next season. The propagation was continued up to 1961, when the two populations became X_3 and C_3 , i.e. the third generation populations after the treatment. The aim of this propagation scheme was to reduce as far as possible the effect of natural selection within each population. Theoretically, the number of plants in the last generation could in this propagation scheme remain unchanged at

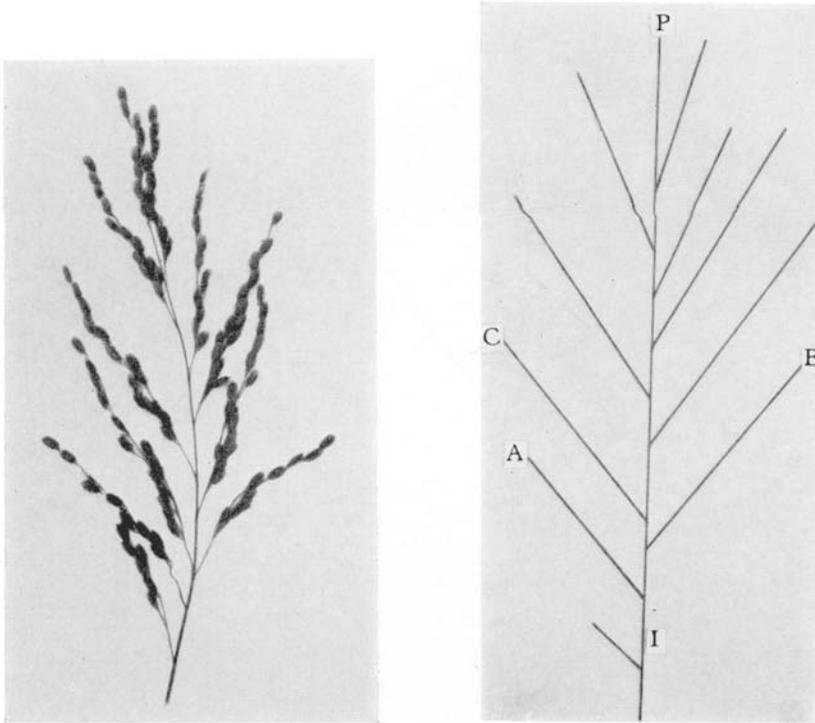


Fig. 1. Photograph and schematic diagram of a panicle of rice.

I: Basal internode. A: Second rachilla. B: Third rachilla.
C: Fourth rachilla. P: Main rachis.

2000, but actually it decreased in both to approximately 1500, due to uncontrollable causes involving incidental loss by chance, seed sterility or failure in germination.

In 1962, 46 lines selected at random were grown from each of the two populations. Each line was planted in a row of 16 plants, of which 12 were used for examination. The characters examined, for all panicles in every plant, were lengths of main rachis (P), basal internode (I) and the second (A), third (B) and fourth (C) rachillas counted from the base. From these measurements, within plant variation of each character, in units of standard deviation, was computed as a measure of its developmental instability. Plate I, Fig. 1, shows the conformation of a rice panicle.

(ii) *Method of estimation of pleiotropic parameters*

This method has already been described by Sakai & Suzuki (1964), but a brief account will be given here for the reader's convenience.

Genetic correlation between two characters in a given population is expected to consist mainly of (1) gene linkage effects, (2) pleiotropy effects, and (3) effects of conscious or unconscious selection due to repeated sampling of seed, which may yield disequilibrium in the combination of characters. If the same computation is made for an X-rayed population, irradiated several generations back and inbred thereafter, the genetic correlation thus obtained should involve an additional effect of pleiotropy of newly mutated genes besides the above three. Effect of linkage disequilibrium, if any, could be considered negligible. Then, the difference between the two genetic correlations will give the estimate of a parameter measuring the pleiotropic effect of genes. This new parameter is designated as p^G , and actual computation is made by the following formula:

$$p_{AB}^G = \frac{W_{AB}^{G(X)} - W_{AB}^{G(C)}}{\sqrt{[(V_A^{G(X)} - V_A^{G(C)})(V_B^{G(X)} - V_B^{G(C)})]}}$$

where A and B are two characters, and V^G and W^G stand for genetic variance and covariance, respectively, X and C denoting X-rayed and control.

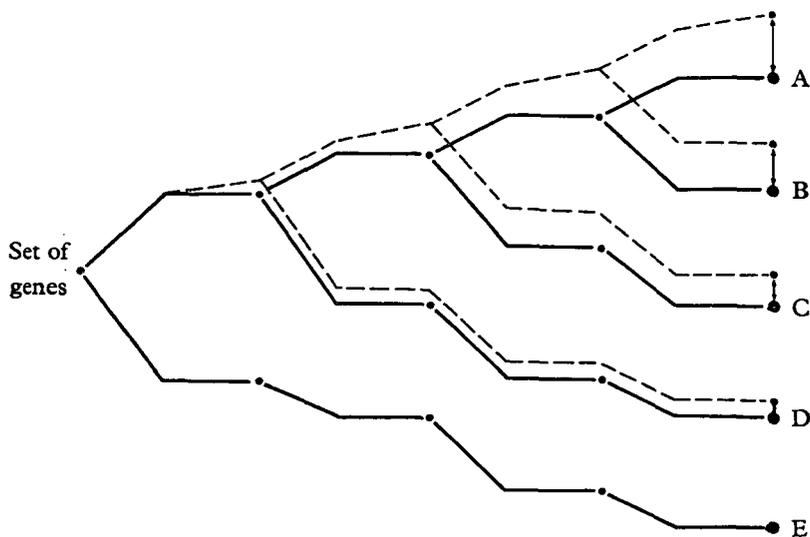
(iii) *Conjecture on developmental relations among characters based on developmental instabilities*

Two quantitative characters which are found to be pleiotropically controlled by the same genes, may each follow its own developmental path separately from an early stage of development or they may develop together in a single process until a certain stage when they differentiate. If developmental instability in a full-grown character is the reflection of accumulated effects of developmental errors occurring during its development, then it is expected that characters differentiated from a common predecessor at a late stage may have a good part of their instabilities in common, while an early differentiation may make their instabilities more or less independent from each other.

Text-fig. 1 shows a hypothetical diagram of five developing characters controlled by the same set of genes. It is assumed in this diagram that development of a single

character involves four stages. Each stage consists of two processes, one expressed by an oblique line is assumed to represent the process of differentiation, while the other by a horizontal line indicates the process of growth of the differentiated substance. As the figure shows, A and B differentiated at a very late stage while E had differentiated from other characters at the very beginning of their development. C and D differentiate in intermediate stages.

Granting that intraplant variation or developmental instability results from growth variation during development due to either chance or environment, we can propose the following hypothesis. On the assumption that effects of 'noise' in each process of development are cumulative, we should expect the correlation between A and B with regard to developmental instability to be high, while that between A



Text-figure 1. A diagram demonstrating the hypothesis that genetic correlations between instabilities of characters may reveal their developmental relations in so far as the characters concerned are pleiotropically controlled by the same set of genes. Detailed explanation is given in the text.

and E should be very low. Genetic correlation coefficients between developmental instabilities of two characters may then disclose the genetically controlled developmental relationship between them.

On this assumption, correlations between any two characters should always be positive. There is, however, a possibility of obtaining a negative correlation, e.g. when two characters comprise a third character and instability in the former two would compensate to bring about stability in the latter.

3. EXPERIMENTAL RESULTS

(i) *Estimation of pleiotropic parameters*

Results of analysis of variance of data obtained in C_4 and X_4 line-groups are presented in Table 1. The Table shows that interline variation is statistically significant for all characters investigated in both line-groups.

Table 1. Analysis of variance of some characters of panicles in control and X₄ lines of rice

Source of variation	d.f.	Mean squares				
		Length of main rachis (P)	Length of basal internode (I)	Length of second rachilla (A)	Length of third rachilla (B)	Length of fourth rachilla (C)
Control						
Between lines	45	2.3265**	0.2119**	0.6908**	0.6596**	0.5648**
Within lines	500	0.5096	0.0345	0.1546	0.1318	0.1026
X₄						
Between lines	45	3.6535**	0.2314**	1.2370**	0.7947**	0.8248**
Within lines	502	0.5098	0.0348	0.1693	0.1574	0.1534

** Significant at the 1% level.

Table 2 shows the frequency distribution of line means for the main rachis, basal internode and second, third and fourth rachilla. It is of interest to find that mean values for both line-groups are approximately the same, while variation is greater

Table 2. Distribution of 46 control and 46 X₄ lines for some panicle-characters of rice

	Class interval (cm.)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Mean (cm.)
Main rachis X (P)	C 0.25				3	5	7	11	9	6	3	1	1			18.20 ± 0.068
	X 0.25	1	1	1	4	6	9	13	7	2	1				1	18.20 ± 0.081
Basal internode (I)	C 0.10		1	3	7	17	11	4	2	1						2.38 ± 0.020
	X 0.10	1	3	8	13	16	2	2	1							2.38 ± 0.021
Second rachilla (A)	C 0.20			1	1	10	16	13	3	2						6.94 ± 0.035
	X 0.20	1		3	4	15	14	5	2	2						7.00 ± 0.047
Third rachilla (B)	C 0.20					1	4	13	16	9	2	1				7.47 ± 0.035
	X 0.20			1			5	12	18	6	4					7.44 ± 0.038
Fourth rachilla (C)	C 0.20							5	17	13	7	4				7.65 ± 0.033
	X 0.20					1	1	5	9	20	7	2	1			7.65 ± 0.038

in X₄ than in the control. It is found that among X₄ lines, a few showed apparent inferiority in most characters.

Genetic variances and covariances have been estimated from the analysis of variance and covariance and the differences between the X₄ and the control were obtained, from which the pleiotropic parameters, p^G, were computed (Table 3).

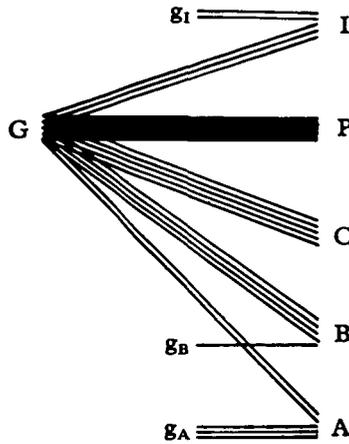
Table 3 shows that p^G values between the main rachis and the other four characters are moderately to extremely high, indicating that genes responsible for the main rachis are more or less pleiotropically controlling the other four characters. For

example, p^G between main rachis and fourth rachilla is as high as 0.94, while that between main rachis and the second rachilla is 0.63. It means that the fourth rachilla is strongly governed by genes operating on the main rachis, while the lower

Table 3. Genetic variances and covariances between length of main rachis and lengths of other panicle parts, and the degree of pleiotropy controlling them in rice

	V^G			W^G			p^G
	X	C	Diff.	X	C	Diff.	
Main rachis (P) and Basal internode (I)	0.2639	0.1531	0.1108	0.0465	0.0362	0.0103	0.7721
Basal internode (I) and Second rachilla (A)	0.0165	0.0149	0.0016	0.1209	0.0763	0.0446	0.6348
Second rachilla (A) and Third rachilla (B)	0.0897	0.0452	0.0445	0.0969	0.0569	0.0400	0.8527
Third rachilla (B) and Fourth rachilla (C)	0.0535	0.0336	0.0199	0.1074	0.0662	0.0412	0.9368

rachillas are less influenced. Pleiotropic control between main rachis and basal internode is intermediate between those of the second and the third rachilla. A diagrammatic illustration of pleiotropic relations between the main rachis and the other four characters is given in Text-fig. 2.



Text-fig. 2. A diagrammatic illustration of pleiotropic relations among different characters. G: Set of genes concerned. g_i : Different genes for i th character. I: Basal internode. P: Main rachis. C: Fourth rachilla. B: Third rachilla. A: Second rachilla. It is not yet known whether the genes pleiotropically controlling P and C are the same as those controlling P and B, P and A or P and I. This diagram is constructed as a tentative one before the question is solved by further studies.

This figure is drawn on the assumption that the same genes are concerned in all these characters, but it is not yet known whether or not this assumption is correct. In Text-fig. 2, the number of lines connecting G, which represents a set of genes governing main rachis formation (P), with the four characters, I, C, B and A, on the right side, indicates the strength of pleiotropic control on an arbitrary basis. For

example, only two lines connecting G with A indicate that pleiotropic effect of G on A is weak in comparison with others. We may be allowed to suppose that some other independent set of genes, say g_A , might be operating on A as shown by three short lines in the figure.

(ii) *Conjecture on developmental relations*

The result of analysis of variance of developmental instability in panicle-forming characters of the control line-group is presented in Table 4. (The X-line group was not investigated because of a possible occurrence of a remnant within-line segregation for the polygenes concerned.)

Table 4. *Analysis of variance of intraplant variability measured in terms of σ in length of main rachis, basal internode, second, third and fourth rachillas in the control population of rice*

Source of variation	d.f.	Mean squares for lengths of				
		Main rachis (P)	Basal internode (I)	Second rachilla (A)	Third rachilla (B)	Fourth rachilla (C)
Between lines	45	0.3892**	0.0355*	0.1645**	0.1036**	0.0846**
Within lines	500	0.1944	0.0228	0.0600	0.0532	0.0423

*Significant at the 5% level.

** Significant at the 1% level.

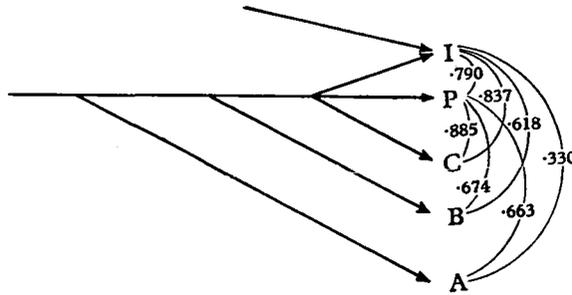
Table 4 shows that inter-line variation in developmental instability is statistically significant in all characters investigated. This indicates that some lines are unstable while others are stable for any particular panicle character. Genetic correlations between developmental instabilities in different panicle characters are computed, and the values are given in Table 5.

Table 5. *Genetic correlation coefficients among developmental instabilities of various parts of a panicle of rice*

	Basal internode (I)	Second rachilla (A)	Third rachilla (B)	Fourth rachilla (C)
Main rachis (P)	0.7896	0.6630	0.6736	0.8848
Basal internode (I)		0.3301	0.6176	0.8373

From Table 5, we find that the highest value is the genetic correlation between main rachis and fourth rachilla with $r^G = 0.88$, while the lowest ones are between main rachis and the second or third rachilla, with $r^G = 0.66$ or 0.67 . Genetic correlation between instability in the main rachis and that in the basal internode is intermediate with $r^G = 0.79$.

Based on the hypothesis suggested before, genetically controlled developmental relations among these characters are diagrammatically drawn up in Text-fig. 3.



Text-fig. 3. Developmental relations among panicle-forming organs based on the diagram given in Text-fig. 2 and the data of Table 5. I: Basal internode. P: Main rachis. C: Fourth rachilla. B: Third rachilla. A: Second rachilla. The figures on the right side represent genetic correlation coefficients between developmental instabilities of corresponding organs.

The figure shows that main rachis (P) is developmentally closely related to the fourth rachilla (C) and basal internode (I), while the third (B) and second (A) rachillas are less closely related to the main rachis.

4. DISCUSSION

To what extent different parts of a plant body are controlled pleiotropically by the same genes is an interesting subject, because it may give a key to a genetic interpretation of differentiation and development of plant organs. It may be a way of approach to developmental genetics in plants.

The method of analysis of pleiotropic effects of genes by the aid of X-ray treatment, suggested by Sakai & Suzuki (1964), was used in the present study. The results indicate that of the three rachillas investigated, the highest one is more strongly affected than the lower ones by genes governing the main rachis formation. If we assume that genes responsible for the main rachis formation are of primary importance in panicle formation because, without their function, the panicle itself could not be formed, then we may conclude that the development of a higher rachilla is the more essential than that of the lower ones. It is inferred that the development of the lower rachillas is under a partial control of genes other than those of the main set responsible for main rachis formation.

Developmental instability can contribute to detecting developmental relationships among quantitative characters. If we assume that developmental instability is the result of errors happening during the developmental process of a character and also that these errors accumulate their effects, then two characters which take the same path of development should show associated behaviour of developmental instability. In other words, if two characters are pleiotropically controlled by the same genes and genetic correlation of instability between them is high, then we may conclude that these two characters take the same developmental path for a long way before they differentiate.

We have estimated developmental relationships among the five panicle-forming

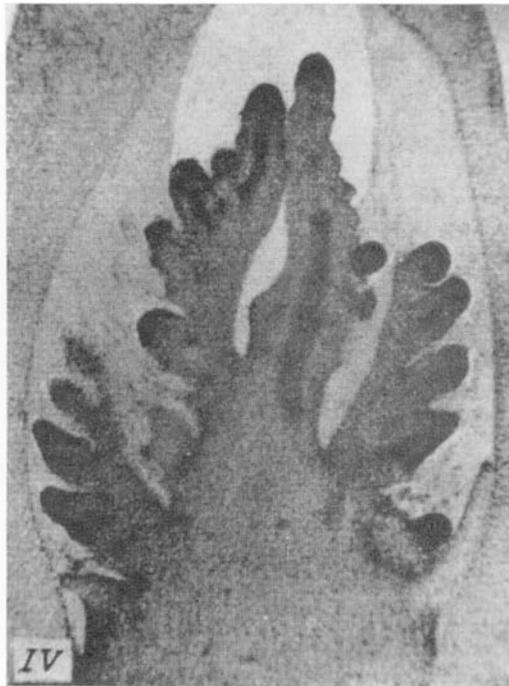


Fig. 2. A microscopic photograph of a young panicle of rice, showing that the upper rachillas have started their development in line with the main rachis, while the lower ones are just about to start their development. (Reproduced from Akimoto & Togari (1939) by the courtesy of the authors.)



Fig. 3. Panicles of a mutant strain (left) and a normal one (right). The arrows indicate the nodes on the main rachis where rachillas could have developed. The mutant strain is maintained by Dr Nagamatsu in Kyushu University, with whose permission this photograph was taken.

characters on the basis of our hypothetical diagram of character development. It is very interesting to find that the genetic relations among them estimated from the pleiotropy of genes are in accord with the diagram of genetic development-relations estimated from developmental instabilities.

The conclusion drawn from the present study is that the set of genes responsible for the main rachis formation in rice strongly governs the formation of the middle rachilla, but influences less the lower rachillas of a panicle. The basal internode seems to be to some extent also controlled by the same set of genes.

It will be of interest to seek for evidences from other sources for panicle formation in rice. Plate II, Fig. 2, is a microscopical photograph of an early stage of development of a young panicle of rice, reproduced from Akimoto & Togari (1939). This picture shows that the development of lower rachillas is apparently lagging behind. In other words, the main rachis and upper rachillas are developing more or less synchronously, while the developmental tempo of lower rachillas is somewhat different from that of the main rachis.

Another fact of interest is disclosed by Plate III, Fig. 3. It is a photograph of three panicles of a mutant strain (left), and two of a normal one (right), though they do not derive from the same variety. This mutant strain is maintained in the laboratory of Professor Nagamatsu, Kyushu University, who kindly gave us the specimens. The higher rachillas in a panicle of this mutant rice are developing normally while the lower rachillas remain undeveloped, leaving only small traces. It seems that this development-inhibiting effect of genes is not operative on the higher rachillas, but affects seriously the lower ones. The genetic behaviour of this mutant strain is not well known yet, but there may be something like inhibition of the so-called switch- or key-gene responsible for the development of rachillas, affecting those which are less controlled by the set of primary genes governing main rachis formation. Whatever the mechanism may be, both figures seem to support our conclusion that primary genes govern the formation of main rachis and higher rachillas, while formation and development of lower rachillas are more or less independent from them.

Higher plants possess very intricate differentiation and organization of body parts in comparison with lower ones. This intricate organization is of course due to structural and mechanical differentiation of organs. It is true that in some cases differentiation and development of some body parts are controlled by a simple Mendelian gene which may behave as a key to open the gate to the developmental path. However, normal development of body parts following the operation of the key-gene may most likely be under the control of genes of polygenic nature, because normally built plants may show quantitatively variable development of body parts. Inquiry into the genetic mechanism of differentiation and development of quantitative characters may open the way into developmental genetics of higher plants.

Sakai & Suzuki (1964) concluded from their studies on the effect of X-rays on such quantitative characters as tillering capacity, plant weight, grain yield, etc. in rice that X-ray induced mutation of polygenes was most likely unidirectional in a minus direction. Data presented in Table 2 of the present study give, however, a different

impression. They show that X-rays cause increase in genetic variation (see Table 3), but without shifting the mean values either in plus or minus direction (Table 2). This inconsistency between the two studies may be explained when we consider that the characters dealt with in the two papers are somewhat different in nature.

Number of tillers or number of panicles per plant, plant weight and grain yield are characters directly related to growth vigour of plants, while lengths of main rachis, basal internode, or rachillas may not be directly related to it. The panicle length in Sakai & Suzuki's paper and length of main rachis in the present paper are two measures of the same thing. The panicle length in the former paper was taken from the largest panicle of each plant, but the length of main rachis in the present paper is the average value of all panicles per plant. It should be noticed that in Sakai & Suzuki's paper, the difference between panicle lengths of control and X-rayed population was quite small in comparison with other characters.

It may thus be concluded that X-ray induced mutation is likely to cause a reduction in the means of those characters which are most closely related to plant vigour, while the changes induced in other characters are not necessarily unidirectional.

5. CONCLUSION

It has been found that development of main rachis, basal internode, and rachillas in rice panicles is pleiotropically controlled by the same set of genes. Let the set of genes responsible for the development of the main rachis be of primary importance for panicle formation, the fourth rachilla counted from the base is found to be strongly governed by this gene set, but the lower rachillas are only partly controlled by it, and partly possibly by independent genes. The basal internode is also partly governed by the gene-set responsible for the main rachis formation.

Developmental relationships among these characters indicates that the main rachis and the fourth rachilla are developmentally closely related, but the lower rachillas are more independent.

The above conclusions have been drawn from the estimation of parameters for pleiotropic gene effect on the one hand, and from studies on genetic correlations of developmental instabilities, on the other.

SUMMARY

By comparing genetic correlations between an X-rayed and a control population of rice, parameters for the strength of pleiotropic effects of quantitative genes have been estimated. It is evident that the gene-set which is responsible for main rachis formation and is therefore of primary importance for panicle formation, is pleiotropically controlling the development of rachillas and basal internode. It is found that the pleiotropic control over the development of higher rachillas is very powerful but less strong over the lower ones and basal internode.

Developmental relationships among these characters have also been investigated by measuring the genetic correlations between their developmental instabilities. The basis of our inference is the hypothesis that if two characters which are found to be pleiotropically controlled by the same set of genes take their own developmental paths from a very early stage, they will show only slight correlation between their developmental instabilities. If, on the contrary, they are taking the same developmental path and their differentiation sets in late, the correlation coefficient will be high.

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