

AN INDUCED MUTANT OF RICE SHOWING ABNORMAL DEVELOPMENT OF INNER GLUMES⁽¹⁾

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It is generally found in rice that lemma and palea develop to the same length tightly closing the floret. From the X-rayed progeny of a rice variety, however, a mutant strains was obtained which broke this developmental rule at a certain frequency. Crossing experiments were made in order to observe the expression of this particular character in hybrids.

Records of Observations

Seeds of a pure line of rice belonging to a native variety of Taiwan (Pei-ku; Ac. No. 108; Indica type) were X-rayed at a dosage of about 12,000 r. In the X_2 population, together with various other mutants, a plant was found with imperfectly developed inner glumes, apparently shorter than the outer glumes. They were easily split longitudinally, while the tip of the outer glumes was slightly bent inside. A sketch of such a spikelet is given in Fig. 1.

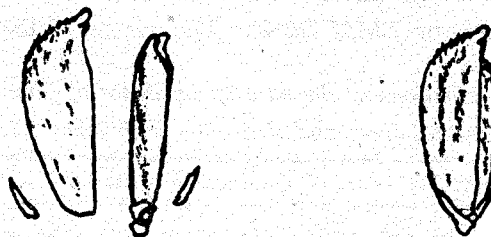


Fig. 1. Spikelets of the mutant with underdeveloped inner-glumes.

A line was then raised from selfed seeds of the X_2 plants. There, it was found that this character did not appear in all spikelets of a panicle; the spikelets could be distinguished into normal and abnormal ones, though in the latter the degree of abnormality varied. The rate of occurrence of abnormal spikelets also varied among the plants of X_3 line. Two plants, one with a high and the other with a medium rate (called *as-1* and *as-2*, respectively), were

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selected, and were propagated until the fifth generation by repeated self-fertilization from a single plant.

The two lines showed no other recognizable change in characters than the abnormal development of glumes, except that their plant height was by about 5% smaller than that of the control. Possibly due to incomplete closing of glumes, the abnormal spikelets were for a greater part sterile.

The sixth-generation lines, raised in the experimental field of the National Institute of Genetics, Misima, were investigated regarding the rate of incidence of abnormal spikelets, taking three panicles per plant. The mean percentages for *as-1* and *as-2* were $79.8 \pm 3.2\%$ and $23.6 \pm 4.8\%$ (standard deviations showing those on a single plant basis), respectively. Variance analysis of the data (transformed into $\sin^{-1}\sqrt{\%}$) showed that the variance among plants within line was insignificant if compared with the variance of panicles. We can then confirm that the two lines have become homozygous for the character under consideration, though they have different rates of incidence possibly due to their difference in genetic background, which might have resulted from selection after irradiation.

The two lines were crossed with pure lines of several different varieties. All the F_1 plants showed normal spikelets. The F_2 's segregated into plants with different percentages of incidence of abnormal spikelets, as shown in Table 1. The data in the table show that about $\frac{1}{4}$ of the F_2 plants had abnormal spikelets, while the rate of incidence in those plants was generally lower than in the parental lines and varied in a wide range. Estimating from the results of variance analysis mentioned already, a difference in the percentage of incidence between two randomly taken plants could be significant if it was larger than 9.5% (*as-1*) or 13.4% (*as-2*). The range of the percentages found

Table 1. Distributions of the rate of incidence of abnormal spikelets in parental lines and their F_2 's with other strains.

Parent or cross	Incidence rate of abnormal spikelets (%)										No. of plants		Mean ¹ rate (%)		
	0	0.1 -2.4	2.5 -9.5	9.6 -20.6	20.7 -34.6	34.7 -50.0	50.1 -65.5	65.6 -79.4	79.5 -90.4	9	10	Normal		Abn.	
<i>as-1</i>											9	10		19	79.8
F_2 , <i>as-1</i> × 104	31	1	1	2	4								31	8	18.0
F_2 , <i>as-1</i> × 160	29		1	7	2								29	10	15.4
F_2 , <i>as-1</i> × 563	18		5										18	5	6.5
<i>as-2</i>				6	11	3								20	23.6
F_2 , <i>as-2</i> × 108	86	17	9	5	2								86	33	5.3
<i>as-2</i> × 451	49	8	5	1									49	14	4.3

¹ Mean incidence rate in plants with abnormal spikelets. 104 & 160: Indica, from Taiwan, 563: Japonica, from Japan, 451: Indica, from India, 108: The original strain.

among the F_2 plants may then be considered to be due to segregation in the genetic background.

As mentioned already, the two strains with abnormal spikelets have been derived from the same original strain. It is found in Table 1 that the F_2 between *as-2* and the original strain produced plants with as low an incidence as its F_2 with another variety, 451. This suggests that the rate of incidence of abnormal spikelets is sensitive to the genetic background. It may then be concluded that the abnormal spikelet is due to a recessive gene, while the expression of the gene is easily modified by the genetic background.

Discussion

The above-mentioned experimental results suggest the following two points: First, rice might have genes which control the developmental symmetry of the outer and inner glumes. Secondly, the rate of expression or penetrance of those genes depends on a modifier system or the genetic background.

As to the first problem, the writer knows no previous reports of such an abnormal development of glumes as described in this paper, in rice nor in other cereals. The hooded or trifurcate awns in barley may however be regarded as a similar case. It is known that the expression of the hooded character is controlled by a specific modifier system (Takahashi and Hayashi 1956). X-ray induced mutants of barley showing abnormal awns have been reported by Gustafsson (1947), Yamaguchi (1959), etc. Also in these cases, the degree of expression was found to vary among spikelets of the same panicle. These facts suggest that the development of spikelets of cereals is controlled by a particular genic system, and if it mutates, the developmental process is disturbed. However, the expression of those mutant genes may be in itself unstable and subjected to the effect of other modifying genes.

Regarding modifiers controlling the phenotypic expression of a particular gene, we find many examples in genetic literature. It is known that modifiers control not only the phenotypes of homozygotes, but also dominance; dominance may be a result of natural selection for modifiers which make heterozygotes similar to the wild type (Fisher's dominance theory). Then, natural selection for modifiers may make homozygotes either similar to, or distinguished from, the wild type. Newly created genes of major effect are mostly disadvantageous in homozygous combination. But readjustment of the genotype by natural selection may enable the species to utilize the new genes for its evolution.

An example of this relation in cultivated plants was given by Takahashi *et al.* (1961); barley varieties homozygous for a dwarf gene *uzu* are of economical importance in south-western Japan owing to the high tillering ability and nitrogen response. However, the *uzu* gene, if stripped of the modifiers,

was merely a dwarf gene of disadvantageous effect. By putting it in different genetic backgrounds, the above authors found that *uzu* homozygotes were displaying a spectrum of performance. A similar case with dwarf rice would probably be found if commercial varieties such as Taichung-Tsailai no. 1 were examined in the same way.

The abnormal glume development dealt with in this paper is apparently a disadvantageous character. However, its expression was unstable and could be easily buffered by the genetic background. This suggests that a modifier system which masks the disadvantageous effect can be established rapidly, so that the mutant gene is not necessarily eliminated from the population.

Irradiating crop plants, we find many undesirable mutants which may potentially be of some use in combination with other genes. The above considerations will lead us to the view that such unfavorable mutants can be utilized for breeding purposes if a proper modifier system is established. For evaluating and selecting newly created genes, it will be necessary to cross mutant strains with other genotypes so as to test the genes in different genetic backgrounds, and to let them have an opportunity of being tested by natural selection which may build up modifier systems for them.

Summary

A mutant strain of rice having the inner glumes shorter than the outer ones was found among the X-rayed progeny of a pure line. This character did not appear in all spikelets of a panicle, and its incidence was significantly lowered by hybridization with other varieties. It was pointed out that rice might have genes controlling the developmental symmetry of inner and outer glumes, but when those genes mutate, the expression would be unstable and easily modified by the genetic background. It was suggested further that modifiers might play an important role in determining the adaptability of newly created genes.

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