LINKAGE RELATIONS OF ANOTHER INDUCED DWARFNESS GENE d_{31} [1] GENIC ANALYSIS IN RICE IX

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The dwarfness gene d_9 carried by rice strain D-155-8 was first reported by Hsieh (1962) and later renamed d_{31} by Chang and Jodon (1963), in view of the necessity of conforming to gene symbolization. This strain is a radiation-induced dwarf mutant from Taichung no. 155. It is about 70 cm in height at maturity, the leaves being narrow and dark green. The dwarfness gene d_{31} has been known to be linked with the ligulelessness gene *lg* with 19.3±3.97 percent of recombination value (Hsieh 1962), which is located on linkage group II of Nagao and Takahashi (1952, 1960). In the cross of D-155-8 with other strains, linkages were found between d_{31} and genes of phenol staining and narrow leaf blade. The experimental results are presented in this paper.

Materials and Methods

Nine strains of the *japonica* type, one strain of the *indica* type and two strains from the USA were used as the materials. The parents used and their pertinent characters are listed in Table 1. The F_1 plants were obtained in 1963-1965, and the F_2 populations with random samples of about 300 plants of each cross were planted in the field the following crop season. Some characteristics of individual plants, such as narrow leaf, ligulelessness, laziness, and brittle culm were observed during the growing stage, but characteristics such as dwarfness, clustered spikelets and phenol staining were investigated at maturity or after harvesting.

The test of goodness of fit of each segregating characteristic to the expected segregation ratio and independency between two characteristics was made by

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Table 1. *List of strains used and their sources, concened characteristics and putative genic constiution.*

Strains	Local name	Characteristics	Putative genic constitution	Sources
K-1	Mutant from Taichung no. 65	Narrow leaf, dwarfness	*nal*	Taiwan (*japonica*)
D-155-8	Dwarf mutant from Taichung no. 155	Dwarfness, narrow leaf	d_{31}, *nal*	Taiwan (*japonica*)
IG-65-2	Isogenic line of Taichung no. 65	Phenol positive staining	*Ph*	Taiwan (*japonica*)
P167	Pai-kan-tao	Ligulelessness	*lg*	Taiwan (*japonica*)
T201	Pai-mei-fen	Phenol positive staining	*Ph*	Taiwan (*indica*)
A-28	Nagao's strains	Dwarfness	d_6	Japan (*japonica*)
A-58	Nagao's strains	Dwarfness	d_6	Japan (*japonica*)
H-45	Nagao's strains	Ligulelessness	*lg*	Japan (*japonica*)
H-79	Nagao's strains	Dwarfness, liguleless-ness lazy, brittle	d_2, *lg*, *la*	Japan (*japonica*)
J301	Yoshino no. 1			Japan (*japonica*)
7102	Jodon's strains	Clustered spikelet	*Cl*	U. S. A.
7245	Jodon's strains	Dwarfness	*d*	U. S. A.

the chi-square test. Moreover, when more than two crosses possessed the same pertinent characteristics, a test of heterogeneity was conducted before pooling the data.

The recombination value between two genes was calculated either by the products methods of Immer (1930) or by the maximum likelihood method.

In this paper the gene symbols recommended by the Rice Genetics and Cytogenetics Symposium held at the International Research Institute and compiled by Dr. T. T. Chang (1963) were used.

Results

1. Genes of dwarfness and other characteristics

When the dwarf strain D-155-8 was crossed with each of nine normal strains, the F_2s invariably showed a good fit to a 3:1 ratio. The pooled numbers of normal and dwarf plants in the F_2s of 9 crosses were 1619 and 515 and also fit very well to a 3:1 ratio. A few plants with heights intermediate between those of their parents were also found in some crosses, but mostly could be classified as the tall parental type.

The segregation of narrow leaf was also studied with the F_2s of 9 crosses;

all of the data gave a good fit to a ratio of 3 normal and 1 narrow leaf, showing that narrow leaf is controlled by a single recessive gene. It was found further from the present data that phenol staining and clustered spikelets were each controlled by a single dominant gene *Ph* and *Cl*, while brittle culm, ligulelessness, and laziness are each controlled by a single recessive gene of *bc*, *lg* and *la*, respectively. These results were consistent with those reported by the previous workers (Nagao and Takahashi 1959, Hsieh *et al.* 1950).

2. The narrow leaf gene in strains D-155-8 and K-1

Leaves of both strains D-155-8 and K-1 are narrow and dark green. In order to know whether the narrow leaf gene carried by these two strains are the same or different from each other, crosses with two of the liguleless strains were made. It was found that narrow leaves appeared in both F_1 and F_2 plants of all the crosses. The results of the heterogeneity test given in Table 2, indicate further that the deviation between the chi-square value of the total data and that of the pooled data is 0.804, P value between 0.30 and 0.50. This shows that the data are homogeneous. It is then possible that the narrow leaf gene in both strains is the same. Since the narrow leaf gene, *nal*, carried by strain D-155-8 is linked with lignleless gene, *lg*, as it will be mentioned later. the same linkage relationship between *nal*, carried by K-1 and *lg* is to be expected. The data in Tables 2 and 3 confirmed this assumption.

Table 2. *Heterogeneity test for narrow leaf gene carried by strains D-155:8 and K-1.*

Crosses	Combined characters				Total	χ^2	P. value
	Lg Nal	Lg nal	lg Nal	lg nal			
D-155-8 × P167	145	77	77	1	300	33.471	0.01
D-155-8 × H-45	122	53	64	1	240	22.462	0.01
K-1 × P167	163	69	67	0	299	25.900	0.01
K-1 × H-45	160	65	64	0	289	23.843	0.01
Pooled Data	590	264	272	2	1,128	104.872	0.01
Total χ^2						105.676	
Deviation						0.804	0.30-0.50

3. Linkages between the narrow leaf gene and other mutant genes.

Various combinations of characteristics, such as ligulelessness and brittle culm; ligulelessness and laziness; narrow leaf and brittle culm; narrow leaf and laziness; brittle culm and laziness; dwarfness (d_{31}) and clustered spikelets; and clustered spikelets and narrow leaf were tested in order to determine the independence of the characteristics from one another. The chi-square values from the test of independence of the two characteristics in the pairs given

above ranged from 0.03 to 2.761 (P=0.90–0.08) showing that there were no linkage relations between the genes concerned.

On the other hand, some of the data in Table 3 were pooled after the the heterogeneity test. For instance, the heterogeneity test for the data of combined characteristics between ligulelessness and narrow leaf gave only 0.695 of the chi-square value of deviation (P=0.95–0.98), suggesting that the data could be pooled. However, the P-value for the test of independence between these two characteristics is less than one percent. It is then suggested that the genes of ligulelessness, *lg*, and narrow leaf, *nal*, are linked. The recombination value between genes *lg* and *nal* was estimated to be 19.12±1.38 percent in the repulsion phase as shown in Table 3.

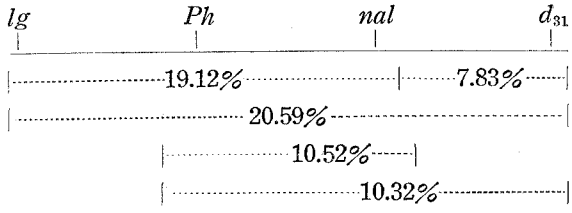
Table 3. *Linked genes and their segregation modes in the F_2 of crosses between strain D-155-8 and other strains*

Characters concerned	F_1 genotype	Crosses	Combined characters				Total	Linkage phase	Recombination values	P
			AB	Ab	aB	ab				
Dwarfness-narrow leaf (3:1)(3:1)	$\frac{D_{31}\text{-}Nal}{d_{31}\text{-}nal}$	D-155-8xJ301 D-155-8xA-28 D-155-8xA-58 D-155-8x7102 D-155-8x7245	994	45	51	261	1354	C	7.83±0.52	0.30–0.20
Ligulelessness-narrow leaf (3:1)(3:1)	$\frac{lg\text{-}Nal}{Lg\text{-}nal}$	D-155-8xP167 D-155-8xH-45 D-155-8xH-79 K-1 xP167 K-1 xH-45	894	429	411	9	1743	R	19.12±1.38	0.50–0.30
Dwarfness-ligulelessness (3:1)(3:1)	$\frac{d_{31}\text{-}Lg}{D_{31}\text{-}lg}$	D-155-8xP167 D-155-8xH-79 K-1 xP167	453	230	213	3	899	R	20.59±1.87	0.20–0.10
Dwarfness-phenol reaction (3:1)(3:1)	$\frac{D_{31}\text{-}Ph}{d_{31}\text{-}ph}$	IG-65-2 x D-155-8	220	17	11	50	298	C	10.32±1.27	0.50–0.30
Narrow leaf-phenol reaction (3:1)(3:1)	$\frac{nal\text{-}ph}{Nal\text{-}Ph}$	D-155-8xT201 IG-65-2x D-155-8	495	33	33	124	685	C	10.52±0.84	0.70–0.50

The other characteristics in Table 3 were treated in the same way in the course of calculations. Linkage was found between genes of dwarfness and narrow leaf and the recombination value was calculated to be 7.83±0.52% in the coupling phase. The dwarfness gene d_{31} was also found to be linked with the ligulelessness gene with a 20.59±1.87% recombination value in the repulsion phase. In addition to these, the dwarfness gene, d_{31}, and the phenol staining gene, *Ph*, and narrow leaf gene, *nal*, and phenol staining gene, *Ph*, were each

linked with the recombination values of 10.32±1.27% and 10.52±0.8%, respectively.

The loci of the genes above-mentioned on chromosome II may be putatively arranged as follows:



Discussions

The narrow leaf in strain D-155-8 had been considered to be the pleiotropic effect of dwarfness gene d_{31}, since most of the dwarf segregations in F_2 between D-155-8 and other strains showed the narrow and dark green leaves (Hsieh and Yen 1966). In the present study, however, recombination between narrow leaf gene *nal* and d_{31} was found with a 7.8±0.52% recombination value. It is then clear that the narrow leaf characteristic is controlled by a single recessive gene. This is consistent with the report of Mohamed *et al.* (1960). Not many data on linkage relation between *nal* and other genes has been reported to date. In the present study we found linkage between *nal* and the genes of ligulelessness (*lg*), phenol staining (*Ph*) and dwarfness (d_{31}). The 20.59±1.899% recombination value between d_{31} and *lg* found in the present study is in agreement with the earlier report by Hsieh (1962).

According to Nagao and Takahashi (1960), six genes, i. e. d_2 (Ebisu dwarf), d_3 (tillering dwarf), *Pl* (Purple leaf blade), *lg*, *Ph* and *Pr* (Purple hull) were involved in their linkage group II. Hsieh and Chang (1962) added one purple pericarp gene *Pb* (*pl*), and stigma color gene Ps_1 to this group. In the present study the narrow leaf gene *nal* and d_{31} are further added to this group. With these genes, the linkage relations in group II can be analyzed more intensively.

In the present study the narrow leaf gene *nal* carried by strain D-155-8 was found to be identical with that carried by strain K-1. Since these two mutants were obtained from different varieties through different irradiations. It seems that the same gene mutations occur relatively easily in the irradiated materials. This is an interesting problem to be noticed.

Summary

A radiation induced dwarf mutant strain D-155-8 was crossed to eleven strains of rice and the linkage relations between dwarfness (d_{31}), narrow leaf (*nal*) and other characteristics were studied. The narrow leaf gene (*nal*) was

found to be linked with d_{31} with a 7.38±0.52% recombination value. The ligulelessness gene *lg* and *nal* were linked with a 19.12±1.38% recombiuation value. Further, *nal* and *Ph* were linked with 10.52±0.84% recombination value. No linkages between brittle culm (*bc*) and clustered spikelets (*Cl*) and other genes were found. Further, the narrow leaf gene, *nal*, carried by D-155-8 was found to be identical with that carried by strain K-1.

稻之遺傳因子分析

第九報 另一突變矮稻之遺傳因子 d_{31} 與其他性狀之連鎖

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利用放射線誘變之矮稻系統 D-155-8 與其他11系統遺傳因子標識稻或保存品種間什交。由親本及什交後代植株中分析此矮性因子（d_{31}），與細葉因子（*nal*），無葉舌因子（*lg*），石炭酸反應因子（*Ph*），以及其他許多因子間的關係。此 D-155-8 之矮性因子，作者以前曾訂爲 d_9，後統一改訂爲 d_{31}。經分析結果，發現無葉舌（Ligulelessness）與脆性（brittle culm），無葉舌與向地性（laziness），細葉（narrow leaf）與脆性和矮性（d_{31}）與簇粒（Clustered spikelets）等因子之間相互獨立。但矮性因子（d_{31}）與無葉舌因子間却有 20.59±1.87%之連鎖值。另外 d_{31} 與 *Ph* 以及 *nal* 與 *Ph* 間分別有 10.32±1.27%與10.52±0.84%之連鎖值。

此外亦討論到同一因子支配 D-155-8 之細葉性狀與 K-1 之細葉性狀的可能性。

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