PRELIMINARY REPORT ON THE INHERITANCE OF CLUSTERING HABIT OF SPIKELETS IN RICE PLANT[1)]

—Genetical Studies on Rice Plant, XXXIV.—

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Introduction

This is one of a series of reports on the scrutinying genic analysis of a morphological character called clustering habit or clustered spikelets which is met with some exotic rice varieties. In these varieties the spikelets are clustered on the tips of the primary and secondary branches of a panicle, two to five or even more spikelets occurring close together. In this panicle, however, the rest of the spikelets usually remain solitary, thus the degree of expressivity of this character is not so high.

With respect to the character expression in individual plants, continuous variations are to be seen in the extracted clustered types from the hybrid progenies of crosses involving clustered varieties as one of the cross parents. In this connection, this character is being studied quantitatively by the writers and detailed examinations are in progress, of which yielding results will be taken up in further reports.

However, although the character expression varied greatly making the assortment among several phenotypes with clustering habit far from simple, the line of demarcation set up between "clustered (irrespective of the degree of clustering" vs. "not-clustered" is one of a dependable criteria for identifying the presence of this character. In this line of thought, crosses between varieties with clustered spikelets and with normal spikelets were studied by such workers as RAMIAH (1930), PARTHASARATHY (1935), JODON (1940, 1947), NAGAO, TAKAHASHI and MORIMURA (1964), and from the evidence so far available at that time, it has been estimated that the clustering and non-

1) Contribution from The Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

clustering may be taken to form a simple pair of allelomorphs, "clustering" being partially dominant.

Recently the writers made several crosses and similar results were obtained. Thus it is most probable that the clustered form would appear to be governed by a single major gene, although it appears likely that the additive action of several alleles contributes to the degree of the character expression.

In the present report, by way of introduction of the following reports, description is focussed on the action of the said major gene and its linkage relationships with several marker genes of which linkage groups are known.

Before going further the writers wish to express their appreciation to Dr. S. NAGAO, Prof. Emeritus of Hokkaido University, to Dr. K. SAKAI of the National Institute of Genetics, and to Mr. T. KINOSHITA of the Plant Breeding Institute, Hokkaido University, for their guidance and aid in many ways.

TABLE 1. List of materials used.

Stock No.	Source	Genotype concerned
A- 5	Akage variety	C^{Br} *A Pr Rc Rd I-Bf*$^+$
A- 43	Hokkaimochi-1-goh variety	C^+ A^+ *wx*
A- 58	Kokushokutoh variety	C^B *A wx*
A- 60	Kurikaramochi variety	C^{Bp} *A wx*
H- 45	'45-226-1 : 178-1-2	C^+ *A lg*
H-115	'54-144-1 : 319-12-1	C^{Bp} *A* Pl^W
N- 44	an extracted genotype from A-31×A-96	C^+ *A wx*
N- 45	" A-28×A-77	C^{Bp} *A Pl*
(Fl-chl)	NAGAMATSU's stock, chlorina	*chl*
(Fl-dp)	" , depressed palea	dp_1
(Fl-ws)	" , white stripe	*ws*
L- 7	JODON's stock, black-leaf-spot	*blm*
L- 8	" , virescent	*v*
L-11	" , white hull	*Wh*
L-16	" , *Pl-Pp*-clustered	*Cl* Pl^W
L-28	" , clustered	*Cl*
(Cl-4)	a clustered form bred true from JODON's cluster×Japanese normal variety	*Cl*
(Cl-7)	"	*Cl*

In the parentheses are tentative designations.

Materials and Methods

Exotic varieties and their extracted strains or lines of which character expressions are the object of the present studies are given in Table 1, together with Japanese tester varieties or strains used in the present cross experiments. In this table, the expression of the clustering habit in L–16 and L–28 is similar to each other.

The majority of F_1 hybrids from crosses between these exotic varieties and the Japanese tester varieties showed a high fertility of more than 90% and 80% in their pollen and seed setting percentages, respectively. In order to examine the detailed inheritance mode, the writers made observations of the hybrid populations and strains up to F_6 generation; however, in the present report, because of its brevity, the greater part of the description will be centered on F_1, F_2 and F_3. The plants were cultured both in frame bed placed in a green house and in an ordinary paddy field outdoors.

Experimental Results

1. Segregation modes

As a first step of the present examination, crosses were made among varieties with clustered spikelets. Their F_1s were clustered with equal outward appearance, and their F_2s were similar to their predecessors, involving no conspicuous segregant or variant. Thus it is evident that these parental varieties possess, at least, a basically identical major gene for the clustering habit.

In crosses between the varieties with spikelets of clustering and of normal arrangement, their F_1's panicles bore many point of resemblance to the clustered parents, but the peripheral spikelets appeared mostly in twos, indicating that the F_1 approximates to the mid-parent. The F_2 gave three groups of plants—"clustered, intermediate, and normal", the intermediate class covering a large part of the interparental range. Though the intermediate formes may occur, it is possible to include them in the clustered group, and a 3 : 1 ratio of clustered arrangement to normal solitary arrangement was obtained, of which the actual data are shown in Table 2.

Thus the writers obtained the results comparable to those of JODON and others, and it was confirmed that the clustering habit basically was under the control of a single partially dominant allele, of which gene symbol was designated as *Cl*.

As to an example of pedigree culture in F_3, Table 3 is presented, where

TABLE 2. Major genic segregation of clustering habit in F_1 and F_2.

Cross combination	Phenotype of F_1	Segregation mode in F_2 (3 : 1)			d.f.	χ^2	p
		Clustered	Normal	Total			
N-44× L-28	clustered but approximates to mid-parent	93	27	120	1	0.400	0.7-0.5
A-43× L-16	〃	150	36	186	1	3.160	0.1-0.05
〃 × 〃	〃	194	51	245	1	2.286	0.2-0.1
N-44× 〃	〃	432	165	597	1	2.216	0.2-0.1
〃 × 〃	〃	91	35	126	1	0.518	0.5-0.3
〃 × 〃	〃	224	86	310	1	1.242	0.3-0.2
N-45× 〃	〃	124	28	152	1	3.508	0.1-0.05
〃 × 〃	〃	27	8	35	1	0.032	0.9-0.8
〃 × 〃	〃	86	18	104	1	3.281	0.1-0.05

TABLE 3. F_3 segregation of clustering habit.

Degree of clustering in F_2	Segregation or distribution in F_3				
	C_1	C_2	C_3	C_4	Total
C_1 (similar to clustered parent)	11	4			15
	10	1			11
	13				13
	13	4			17
	3	6	4	3	16
	23	2			25
	9	8			17
C_2[1]		20	5		25
C_3 (more likes F_1)		1	6	2	9
		1	4	1	6
		5	13	6	24
		2	11		13
			11	3	14
C_4 (normal solitary arrangement)				23	23
				32	32
				11	11
				12	12
				12	12
				24	24
				1	1
				25	25

1) C_2 means "between the clustered parent and the F_1".

the total number of 20 F_2 plants from one cross combination was carried into F_3. With regard to the degree of character expression, the F_2 phenotypes consist of C_1 (similar to the clustered parent), C_2 (between the clustered parent and the F_1), C_3 (more likes the F_1) and C_4 (normal). The result shown in this table is illustrative of a type of inheritance associated with modifying genes—or polygenes—governing the degree of clustering. Thus, at present, it is probable to assume that the clustering habit is oliogenic, appearing to be conditioned by an additive action of the polygenes under the coexistence with a single major gene.

2. Linkage

The first case of linkage between *Cl* and a marker gene was reported by JODON (1940), in which a recombination percentage of 35 has been obtained with a virescent gene, *v*, of the 1st linkage group. This group includes such genes as *C* (anthocyanin chromogen) and *wx* (waxy endosperm). Therefore the writers made examination of joint segregations in F_2 of three types of crosses: between *Cl* and *C*, between *Cl* and *wx*, and between *C* and *wx*. The data are given in Table 4. As seen in this table, the average recombi-

TABLE 4. Recombination values postulated from joint segregation in F_2s from crosses involving genes, *Cl*, *wx* and *C*.

Gene pair	Cross combination	Joint segregation ratio	N(F_2)	d.f.	χ^2	*p*	R.C.V. (%)
Cl-wx		(3 : 1) (3 : 1)		3	4.77	0.2-0.1	41.0
Cl-C	N-44× L-16	(3 : 1) (3 : 1)	126	3	5.27	0.2-0.1	39.0
wx-C		(3 : 1) (3 : 1)		3	17.81	<0.001	35.0
Cl-wx		(3 : 1) (3 : 1)		3	3.05	0.5-0.3	45.0
Cl-C	N-44× L-16	(3 : 1) (3 : 1)	209	3	7.96	0.1-0.05	39.0
wx-C		(3 : 1) (3 : 1)		3	31.49	<0.001	24.5
Cl-wx		(3 : 1) (3 : 1)		3	0.41	0.7-0.5	49.0
Cl-C	N-44× L-28	(3 : 1) (3 : 1)	120	3	2.37	0.2-0.1	40.5
wx-C		(3 : 1) (3 : 1)		3	11.79	<0.01	29.5
Cl-C	A-43× L-16	(3 : 1) (9 : 7)	186	3	3.43	0.1-0.05	44.0
Cl-C	" × "	(3 : 1) (9 : 7)	245	3	4.01	0.05-0.02	41.0
Cl-C	N-44× L-16	(3 : 1) (3 : 1)	597	3	18.47	<0.001	39.0
Cl-C	H-45× L-16	(3 : 1) (3 : 1)	152	3	12.85	<0.01	33.0

TABLE 5. Homogeneity test on F_2 data of crosses, N-44×L-16 and N-44×L-28, involving three gene pairs of *Cl–wx*, *Cl–C* and *C–wx*.

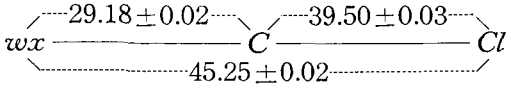
	Cl	*wx*	d.f.	I.T.	d.f.
D	0.612	0.163	1	2.762	3
H	0.383	3.490	2	5.471	6
T	0.995	3.653	3	8.233	9

	Cl	*C*	d.f.	I.T.	d.f.
D	0.612	0.122	1	12.841	3
H	0.383	1.735	2	2.396	6
T	0.995	1.857	3	15.237	9

	C	*wx*	d.f.	I.T.	d.f.
D	0.122	0.163	1	51.164	3
H	1.735	3.490	2	9.930	6
T	1.857	3.653	3	61.094	9

D: deviation, H: homogeneity, T: Total, I.T.: interation test (joint segregation)

nation value between *Cl* and *wx* is 42.3%, though varying from 41.0% to 49.0% in three cross combinations. The recombination value between *Cl* and *C* is 39.5%, though a considerable variation from 33.0% to 44.0% is presented in seven crosses examined. As to linkage intensities of *C* with *wx*, an average recombination value of 29.2%, varying from 24.5% to 35.0%, was calculated from three cross combinations. With regard to these linkages, *Cl–wx*, *Cl–C*, and *C–wx*, a homogeneity test, viz. interaction test of the joint segregations, was also made. This is shown in Table 5. The data presented in Tables 4 and 5 may be an indication of the gene sequence given below.



This estimate shows fair agreement with the previous estimate formed by JODON (1948, 1957), who, in addition to this, identified a gene in this group, viz. those relating to a heading-date locus, *Lf*. NAGAMATSU and OHMURA (1962) announced that genes which are responsible for such characters as the

white striped leaf (*ws*) and the depressed palea (dp_1) may also be assigned in this group. And then, a gene for magnolia-black-leaf-spot, bl_m, the finding of which is credited to JODON, is suggested, by NAGAO and the writers (1964), to be inserted in this group.

For further verification of these announcements, examination of joint segregations involving the following gene pairs was carried out.

i) *Cl–C*, *Cl–wx*, *Cl–ws*, *Cl–v*
ii) *C–wx*, *C–*dp_1, *C–v*, *C–*bl_m
iii) *ws–wx*, *ws–C*, *ws–*bl_m
iv) *wx–v*, *wx–*bl_m

The actual segregation patterns in F_2s are shown in Table 6. Scrutiny of the individual recombination value leads to the following linkage estimates

TABLE 6. F_2 segregation modes and recombination values of linked genes, *Cl*, *C*, *ws*, *wx*, dp_1, *v* and bl_m, estimated to belong to the 1st linkage group.

Gene concerned	Cross combination	Joint segregation ratio	F_2 segregation mode					χ^2	p	R.C.V. (%)	Phase
			AB	Ab	aB	ab	Total				
C–wx	A-58×L-8	(9:7) (3:1)	65	20	54	9	148	3.96	0.2	33.0	r
	L-8×A-60	(3:1) (3:1)	189	76	110	2	377	44.50	0.001	15.0	»
	» × »	(3:1) (3:1)	114	44	43	3	204	8.91	0.02	27.5	»
	» ×A-58	(3:1) (3:1)	179	70	60	2	311	18.13	0.001	20.0	»
	A-58×L-7	(3:1) (3:1)	185	73	67	9	334	8.82	0.02	35.5	»
	Fl-ws×A-58	(3:1) (3:1)	34	22	12	1	69	9.56	0.02	24.0	»
	A-58×L-7	(3:1) (3:1)	32	42	44	1	169	18.59	0.001	14.5	»
	Total of the above 4 crosses						1464			24.0	
C–dp_1	Fl-dp×A-58	(3:1) (3:1)	210	26	26	56	318	109.00	0.001	18.0	c
C–v	L-8×Cl-7	(9:7) (3:1)	110	39	85	25	259	0.63	0.80	46.0	r
	A-58×L-8	(9:7) (3:1)	69	16	50	14	149	3.38	0.30	46.0	c
	L-8×A-60	(3:1) (3:1)	126	35	32	11	204	3.64	0.80	47.0	»
	A-58×L-8	(3:1) (3:1)	129	48	33	17	227	3.41	0.30	46.5	»
	L-8×H-115	(3:1) (3:1)	105	42	29	15	191	3.21	0.30	46.5	»
	Total of the above 3 crosses						622			46.5	
C–bl_m	A-58×L-7	(3:1) (3:1)	100	24	36	9	169	2.94	0.30	49.5	c
	Cl-7× »	(3:1) (3:1)	67	27	22	10	126	1.38	0.70	48.5	»
	Total of the above 2 crosses						295			49.0	»

TABLE 6. (continuous)

ws-wx	Fl-ws×A-58	(3:1) (3:1)	31	21	15	2	69	8.67	0.02	30.0	r
ws-C	Fl-ws×A-58	(3:1) (3:1)	146	25	31	40	242	56.98	0.001	24.0	c
	" × "	(3:1) (3:1)	45	6	5	4	60	9.69	0.02	26.5	"
	" × "	(3:1) (3:1)	48	6	10	7	71	53.02	0.001	27.5	"
	" ×Cl-7	(3:1) (3:1)	45	25	2	18	90	17.76	0.001	17.0	"
	Total of the above 4 crosses						463			25.5	
ws-bl$_m$	Fl-ws×L-7	(3:1) (3:1)	64	24	17	6	111	1.35	0.70	49.5	r
	" × "		156	38	38	10	242	7.03	0.05	51.5	"
	Total of the above 2 crosses						353			50.0	
wx-v	A-58×L-8	(3:1) (3:1)	95	24	24	5	148	4.61	0.20	48.0	r
	" × "	(3:1) (3:1)	140	57	43	17	257	2.42	0.30	50.0	"
	" × "	(3:1) (3:1)	102	35	21	11	169	2.57	0.30	56.0	"
	" × "	(3:1) (3:1)	90	36	28	8	162	1.77	0.50	45.5	"
	L-8×A-58	(3:1) (3:1)	186	53	57	15	311	2.23	0.50	49.0	"
	" ×A-60	(3:1) (3:1)	121	34	39	8	202	2.60	0.30	46.0	"
	Total of the above 6 crosses						1249			49.0	
wx-bl$_m$	L-7×Cl-7	(3:1) (3:1)	94	27	37	6	164	3.52	0.30	42.0	r
	A-58×L-7	(3:1) (3:1)	102	24	34	9	169	1.13	0.70	52.0	"
	Total of the above 2 crosses						333			47.5	
Cl-C	A-43×L-16	(3:1) (3:1)	58	13	15	4	90	2.64	0.30	48.0	c
	Cl-7×L-8	(3:1) (3:1)	144	30	39	17	230	6.52	0.05	40.0	"
	Total of the above 2 crosses						320			41.5	
	Fl-ws×Cl-7	(3:1) (9:7)	41	29	6	14	90	5.53	0.10	26.0	c
	Cl-7×L-7	(3:1) (9:7)	66	38	7	15	126	10.00	0.01	25.0	"
	L-28×A-5	(3:1) (9:7)	79	46	18	29	172	26.89	0.001	14.0	"
	Cl-4× "	(3:1) (9:7)	87	60	30	25	202	18.96	0.001	46.0	"
	Total of the above 4 crosses						590			34.0	
Cl-wx	N-44×Cl-7	(3:1) (3:1)	168	47	57	23	295	2.46	0.30	45.0	c
	Fl-chl× "	(3:1) (3:1)	89	32	25	6	152	2.29	0.50	44.5	r
Cl-ws	Fl-ws×Cl-7	(3:1) (3:1)	60	10	10	10	90	10.74	0.01	27.5	c
Cl-v	L-8×Cl-7	(3:1) (3:1)	124	40	48	11	223	1.63	0.50	55.0	c
	" × "	(3:1) (3:1)	158	48	37	16	259	3.80	0.20	45.5	"
	Total of the above 2 crosses						482			50.0	

among the genes mentioned above.

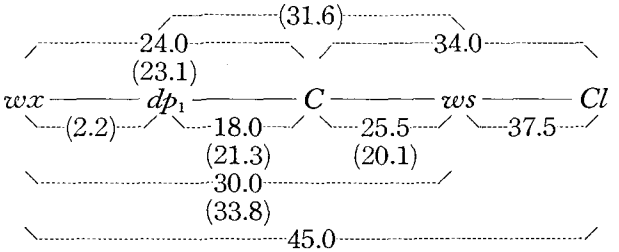
i) *Cl–C* (34.0%), *Cl–wx* (45.0%), *Cl–ws* (27.5%), *Cl–v* (50.0%)

ii) *C–wx* (24.0%), *C–dp*$_1$ (18.0%), *C–v* (49.5%), *C–bl*$_m$ (49.0%)

iii) *ws–wx* (30.0%), *ws–C* (25.5%), *ws–bl*$_m$ (50.0%)

iv) *wx–v* (49.0%), *wx–bl*$_m$ (47.5%)

Therefore, based on these estimates, the following gene sequence would become to be most probable.



In this diagram the parenthesized numerals are the linkage magnitudes reported by NAGAMATSU and OHMURA (1962). As shown in the diagram the writers' estimates are fairly similar to those of NAGAMATSU *et al.*

An additional gene, *chl* (chlorina), possibly is assigned to this group, by adapting three linkage estimates: between *chl* and *C*, between *chl* and *Cl*, and between *chl* and *wx*, with recombination values of 34.5%, 33.0% and 39.5%, respectively. Since the estimate of the percentage recombination of *chl* with *wx* was 24.0%, *chl* might be located on the opposite side of *wx* and *C*, putting *Cl* in the center. The F_2 segregations on these linkages are presented in Table 7; however, due to lack of sufficient data, the location of

TABLE 7. F_2 segregation modes and recombination values of gene pairs, *chl–C*, *chl–Cl*, *wx–chl* and *chl–bl*$_m$

Gene concerned	Cross combination	Joint segregation ratio	F_2 segregation mode					χ^2	p	R.C.V. (%)	Phase
			AB	Ab	aB	ab	Total				
chl–C	Fl-chl×L-7	(3:1) (3:1)	23	30	16	6	75	6.96	0.05	33.0	r
chl–Cl	Fl-chl×L-7	(3:1) (3:1)	124	32	23	13	92	7.59	0.05	39.5	r
wx–chl	Fl-chl×A-58	(3:1) (3:1)	61	17	18	1	97	5.07	0.10	28.5	r
	" ×Cl-7	(3:1) (3:1)	86	28	34	4	152	4.29	0.20	36.0	"
	Total of the above 2 crosses						248			34.5	
chl–bl$_m$	Fl-chl×L-7	(3:1) (3:1)	41	17	14	6	78	0.86	0.80	50.0	r

chl is not so definit.

It is needless to mention that both linked inheritance data and independent inheritance data are indispensable to identify a linkage group to which the gene belongs. Tests of independence of *Cl* with other respective markers in some linkage groups, other than the 1st group, were made. Table 8 shows a part of the results studied in this respect. Here, it is pointed out that *Cl* appears to be independent from those markers as *Pr* (purple lemma and palea, the 2nd group), *Pl* (purple leaf, the 2nd group), *lg* (liguleless, the 2nd group), *Rc* (brown pericarp, the 4th group), *I-Bf* (inhibitor of brown forrows, the 5th group) and *sp* (short panicle, the 8th group).

TABLE 8. Recombination values of *Cl* with known linkage markers other than those of the first linkage group.

Linkage group	Marker gene	Cross combination	Joint segregation ratio	N(F_2)	χ^2	p	R.C.V. (%)	Phase
2nd	*Pr*	L-28×A-5	(3 : 1) (3 : 1)	308	0.51	0.90	48.0	c
	Pl	A-43×L-16	(3 : 1) (9 : 7)	73	0.86	0.80	49.0	"
	"	N-44× "	(3 : 1) (3 : 1)	225	2.74	0.30	50.5	"
	lg	H-45× "	(3 : 1) (3 : 1)	104	4.17	0.20	45.0	"
	"	" × "	(3 : 1) (3 : 1)	152	4.12	0.20	46.0	"
	Total of the above 2 crosses						45.5	
4th	*Rc*	Cl-4×A-5	(3 : 1) (3 : 1)	202	2.30	0.50	47.0	r
	"	L-28× "	(3 : 1) (3 : 1)	172	1.31	0.70	49.5	"
	"	" × "	(3 : 1) (3 : 1)	308	2.95	0.30	45.0	"
	Total of the above 3 crosses			682			47.5	
5th	*I-Bf*	L-28×A-5	(3 : 1) (3 : 1)	139	1.14	0.70	51.0	c
8th	*sp*	Fl-dp×Cl-7	(3 : 1) (3 : 1)	100	1.62	0.50	45.5	c
	"	Fl-chl× "	(3 : 1) (3 : 1)	192	3.98	0.20	41.0	"
	"	Fl-ws× "	(3 : 1) (3 : 1)	88	2.87	0.30	59.0	"
	"	" × "	(3 : 1) (3 : 1)	46	0.92	0.80	49.0	"
	Total of the above 4 crosses			426			46.5	"

As to the location of bl_m, NAGAO and the writers (1964) have suggested a possibility of the gene order of *wx-C-*bl_m. In the present examination, however, no possitive datum was obtained to support this.

Conclusion and Summary

1. Clustered spikelets or clustering habit of a rice panicle mean a clumped arrangement of the spikelets on the peripheral part of the rice panicle.

2. It is most probable that this character is essentially governed by a single partially dominant allele. At the same time, it appears likely that the additive or modifying action of several genes contributes to the degree of character expression.

3. The causal major gene, of which the gene symbol is *Cl*, is assigned its position on the 1st linkage group, in the sequence of *wx* (waxy or glutinous endosperm)—dp_1 (depressed palea)—*C* (anthocyanin chromogen)—*ws* (white striped leaf)—*Cl*, which is nearly in accord with the previous estimation proposed by JODON, NAGAMATSU and OHMURA.

4. Genes for chlorina, *chl*, and the magnolia-black-leaf-spot, bl_m, appear to be another members of this linkage group, indicating this possible order of genes: *wx–C–chl* and *wx–C–*bl_m respectively.

5. Due to lack of sufficient data, joint mapping of these three, *wx–*dp_1*–C–ws–Cl*, *wx–C–chl*, and *wx–C–*bl_m is not successful yet.

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