GENETIC STUDIES OF YIELDING CAPACITY AND ADAPTABILITY IN CROP PLANTS

2. Analysis of Genes Controlling Heading Time in Taichung 65 and Other Rice Varieties

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The inheritance of the growth period in rice has been studied by Nomura and Yamazaki (1925), Yamaguchi (1931), Ramiah (1933), Fuke (1954), Syakudo and coworkers (1954, etc.) and others. Early workers reported the role of a few genes in their varietal hybrids, those conditioning earliness being mostly dominant. Ramiah and later workers pointed out, as reviewed by Chang (1964), that epistatic interaction and pleiotropic effects of genes might be involved in the inheritance. However, on account of the complexity of segregation patterns, the effects of individual genes could not be clearly distinguished. It is also difficult to compare genes postulated by one author with those of the other authors.

In rice, the growing duration of a variety depends largely on the time of flower initiation, as the period from flower initiation to heading does not differ much among varieties. Flower initiation is controlled not only by the inherent vegetative period of the genotype, but also by daylength and temperature, and the modes of response to these outer conditions are genotypically determined. As regards the inheritance of photoperiodic response, a dominant gene linked with the apiculus coloration gene *Ap* (possibly synonimous with *C*) was described by Chandraratna (1955). Other workers (Fuke 1954b, I. R. R. I. 1964, etc.) also reported that photoperiodic sensitivity was completely or partly dominant. Since earliness in the basic vegetative period is dominant but that due to insensitivity to photoperiod is recessive, earliness genes may be either dominant or recessive according to the parentage, as set forth by Nagai (1958, pp. 327–337). The existence of genes conditioning temperature response was suggested by Fuke (1954a), though their effects were not analyzed.

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In the previous paper of this series (Tsai and Oka 1965), the writers have dealt with isogenic lines of Taichung 65, which carry an earliness gene derived from a Northern Chinese variety, Tatong-tsailai, and from a Northern Japanese variety, Bozu 5. Apparently, these varieties may differ from Taichung 65 not only in the particular earliness gene but also in many other genes controlling flower initiation. We have attempted an analysis of those genes. In this paper are reported the results of the genic analysis of Taichung 65×Tatong-tsai-lai and a few other crosses.

Materials and Methods

Genetically pure strains of Taichung 65, Tatong-tsailai, A3, Taichung 180 and Kissin, all belonging to the Japonica type, were used for crossing experiments. Taichun 65 (abridged as T.65) is a representative Ponlai variety of Taiwan, selected from a cross of two Japanese varieties, Kameji×Shinriki. Its growing duration (seeding—heading) ranges from about 110 days (first crop, seeded in early February) to about 80 days (second crop, seeded in early July). Tatong-tsailai (Ttg) has an about 75 (first crop) to 50 (second crop) days growing period; it is the earliest of our varietal collection from various Asian countries. A3 is an isogenic line of T.65 with an earliness gene derived from Ttg. Taichung 180 is an early Ponlai variety selected from Awned Asahi, a native variety of Japan. These varieties are insensitive to photoperiod, so that their growing duration in a given condition may be considered as determined by their basic vegetative period and temperature response. Kissin is a selection from a cross of Japanese varieties, Kibiho and Shinriki, and is sensitive to photoperiod.

The materials were grown in the first and second crop-seasons in the experimental field of Chung-Hsing University, Taichung, by the standard method of rice culture in Taiwan (the reader may refer to our previous paper, Tsai and Oka 1965). The date of emergence of the first panicle from a plant was recorded as the heading date of the plant, and recording was made on a single plant basis.

Results of Observations

1. Biometrical analysis of Taichung 65×Tatong-tsailai hybrid.

The F_1 hybrid of T.65×Ttg was about 25 days earlier than T.65, and about 10 days later than Ttg, the earliness being incompletely dominant. The F_2 population exhibited a continuous range of heading date, as shown in Fig. 1. The mode of frequency distribution suggested a 3 early to 1 late ratio, but plants showing the same maturity as the parents were rare. In the first crop-season of 1962, the F_2 (divided into 4 plots, each consisting of 30

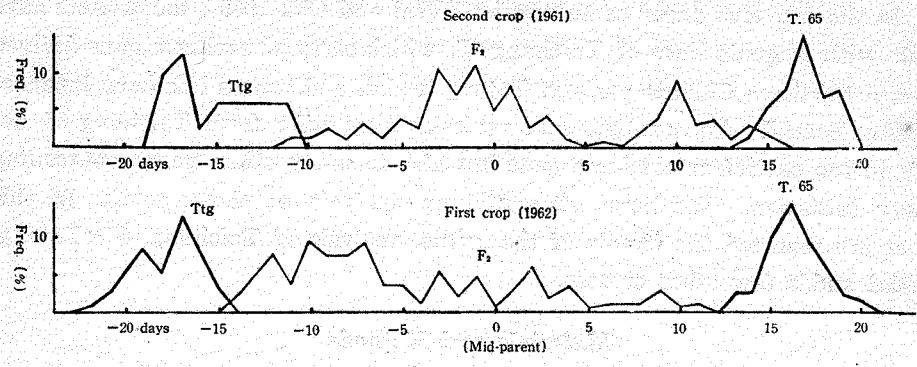

Fig. 1. Distribution of heading date in the F_2 of T.65 × Ttg.

plants), 100 F_3 lines (each consisting of 15 plants) and the parental strains (divided into 4 plots, each consisting of 15 plants) were observed in a randomized block expeiment with two replications, and the data were analyzed by Mather's (1949) method. The hybrid populations of T.65×A3 were also investigated in parallel. The results of analysis on heading date are given in Table 1.

Table 1. *Values of variance components of heading date estimated by Mather's method for T.65×Ttg and T.65×A3 (First crop, 1962).*

Item	T.65 × Ttg					T.65 × A3				
	Observed			Expected,		Observed			Expected,	
	I	II	Aver.	Excluded	$\bar{V}_{F3}$ Included	I	II	Aver.	Excluded	$\bar{V}_{F3}$ Included
V_{F2}	44.93	40.85	42.89	42.36	41.27	18.43	15.12	16.77	16.75	16.03
$V_{\bar{F}3}$	33.17	37.00	35.08	34.05	34.06	9.28	12.69	10.99	10.94	10.94
$W_{F2/F3}$	31.78	32.67	32.23	33.79	33.79	10.21	12.53	11.37	11.44	11.44
$\bar{V}_{F3}$	21.24	19.05	20.15	(20.15)	22.41	8.08	6.66	7.37	(7.37)	8.86
E_1	4.13	4.13	4.13	4.64	3.55	4.05	2.74	3.40	2.41	1.68
E_2	1.50	0.83	1.17	2.23	2.24	1.14	0.66	0.90	0.96	0.96
Sum of squares of deviations				29.01	44.09				17.93	27.38
D				59.69** ± 4.67					17.05** ± 3.67	
H				31.52 ±14.94					23.28 ±11.75	
K_1				4.45					1.03	
K_2				1.76					0.76	
Variance due to:	d. f.									
Linkage	1			15.08*					9.44*	
Interaction	1			19.67*					9.55	
Error	6			1.56					1.33	

** Significant at 1% level, * at 5% level.

The data in the table show that the observed values of variance components are generally consistent with the expected values. The T.65×A3 cross involves only one genic difference, since A3 is an isogenic line of T.65 carrying an earliness gene derived from Ttg (Tsai and Oka 1965). The values of K_1 and K_2 estimated for this cross, being approximately 1.0, also prove this. The relatively large value of H variance may be regarded as indicating the dominance of the earliness gene over its recessive allele. This gene pair is symboled as *E/e*.

The difference in the values of variance components between the two crosses may be considered as due to the effects of other genes than *E/e*. As regards the additive genetic variance, D, about 30% of that released from T.65×Ttg seems to be due to the effect of *E/e*, while the remaining portion may be attributed to the other genes. In T.65×Ttg, the values of K_1 and K_2 indicate that two to four effective factors might be concerned. The larger value of K_1 than that of K_2 suggests that all genes conditioning earliness are carried by Ttg, and all for late maturity by T.65.

A linkage test by Mather's method showed that in both crosses, the variances due to linkage and residual interaction were significant. These variances are indicative of heterogeneity of genetic variances in different segregating populations, which may also result from sampling deviation or from an inadequate scaling. A test of scaling showed that the conventional number of days could be used. Since the T.65×A3 cross involves only a single genic difference, the linkage and interaction variances found from this cross seem to be due to some bias in sampling of F_3 lines from the F_2 population. Subtracting them from the corresponding variances obtained from T.65×Ttg, the residuals may be a rough estimate of linkage and interaction variances in the latter cross. It may then be inferred that in T.65×Ttg, interaction variance can be relatively large. In view of sampling deviations easily involved in experimental hybrid populations, however, it seems difficult to estimate precisely the effects of various genes by a biometrical method of this type. The only conclusion from the above computation may be that several genes with some epistatic effect might be involved in the T.65×Ttg hybrid.

2. Analysis of modifying genes controlling maturity.

For analysing genes controlling maturity of the T.65×Ttg hybrid, we selected a number of seemingly homozygous F_4—F_6 lines from the initial cross and crossed them again with T.65, so as to observe various segregating populations in a relatively uniform genetic background. The heading dates of those selected lines and their F_1 hybrids with T.65 are shown in Fig. 2. The F_1 hybrids of very early lines generally showed an incomplete dominance for

earliness, in the same manner as did T.65×Ttg. This suggests that some genes for earliness would be incompletely dominant or recessive.

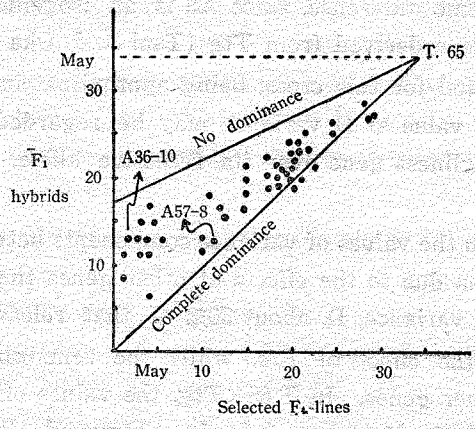

Fig. 2. Scatter diagram showing the heading dates of F_1 hybrids as compared with those of parental lines.

A57–8 is one of such selected lines, about 24 days (first crop) to 19 days (second crop) earlier than T.65. As will be mentioned later, the effects of genes differ between the first and second crop-seasons. In the following genic analysis, data from the second crop experiments are mainly used. When A57–8 was crossed with T.65, the F_1 plants showed approximately the same heading date as A57–8. The F_2 and F_3 distributions of heading date are shown in Table 2. The table shows that 20 F_3 lines from relatively late F_2 segregants were of T.65 type, while those from earlier F_2 segregants were either similar to A3 (5 lines) or to A57–8 (8 lines), excepting those supposedly heterozygous (48 lines in total).

It was also found that the F_1 of A57–8×A3 was as early as A57–8, and the F_2 plants varied continuously from A57–8 to A3 types, the latter comprising about one fourth of the total number. Further, a progeny line (R15–3) derived from T.65×A57–8, showing approximately the same heading date as T.65, was crossed with A3. The F_1 was as early as A57–8, and the F_2 ranged from A57–8 to T.65 types.

These facts may be accounted for by assuming that A57–8 has the same earliness gene *E* as has A3, and a dominant gene exaggerating the effect of *E*. The latter is symboled by M_1. As shown in Table 2, the observed numbers of F_3 lines in different maturity classes fitted the 9 : 3 : 4 ratio, indicating that M_1/m_1 would be independent of *E/e*. It may then be assumed that A57–8 has the genotype $E\ M_1$, A3 has $E\ m_1$, R15–3 has $e\ M_1$ and T.65 has $e\ m_1$, and that M_1 accelerates flower initiation only when *E* is present, so that $e\ M_1$ plants show the same heading date as T.65. This statement, howeve, does not mean

that A57-8 differs from T.65 only in the possession of E and M_1. As they are not isogenic, some other genes with smaller effects may also be involved in their hybrid.

Table 2. *Distributions of heading date in the F_2 and F_3 populations of T.65×A57-8 (Second crop, 1964).*

Plot	Assumed F_2 genotype	Sep. 10	12	14	16	18	20	22	24	26	28	30	Oct. 2	4	6	No. of plants	No. of lines	
T.65	eem_1m_1							1	6	31	28	8	1	1		76		
A57-8	EEM_1M_1	4	8	27	11	7	4									61		
F_1	EeM_1m_1			6												6		
F_2			3	39	70	53	24	15	27	25	14	7				277		
F_3 lines	EEM_1M_1	1	6	47	53	33	8									148	8	
	EeM_1M_1		7	16	30	27	26	3	5	20	17	4				155	8	
	EEM_1m_1	6	24	48	52	37	12	9	15	6						209	12	50
	EeM_1m_1		12	48	86	74	49	46	37	24	22	9	4	2		413	22	
	EEm_1m_1				13	21	24	27	9	4						98	5	
	Eem_1m_1				11	18	33	21	9	9	6	2	4	1		114	6	11
	eeM_1M_1																	
	eeM_1m_1						3	44	79	106	98	39	16	5	2	392	20	
	eem_1m_1																	
A3×A57-8 F_1	EEM_1m_1		5	2												7		
A3	EEm_1m_1					1	5	41	6	1	1					55		

Expected F_2 ratio (9 : 3 : 4) = 45.56 : 15.19 : 20.25
No. of corresponding F_3 lines = 50 : 11 : 20
$X^2 = 1.59$ $(0.50 > P > 0.30)$

Further, A36-10 is a homozygous early line selected from the same original cross, T.65×Ttg, and is nearly as early as Ttg. The F_1 hybrid of T.65×A36-10 showed incomplete dominance for earliness, the heading being 17 days earlier than that of T.65 and 16 days later than that of A36-10 (second crop, 1963). The F_2 and F_3 distributions of heading date are given in Table 3. The frequencies of F_3 lines with similar heading dates as those of A36-10, A57-8, A3 and T.65 suggest that A36-10 might have, in addition to E and M_1, some other either earliness genes. It was found that the F_1 A3×A36-10 had the same heading date as the F_1 of T.65×A36-10, and the F_2 plants varied in a continuous range from A36-10 to A3 types, as shown in Table 4. When certain early homozygous lines (M4-1, etc.) selected from T.65×A36-10 were crossed with A3, the F_1 hybrids also showed the same haading date as the above-mentioned, and the F_2 segregation appeared to represent a 1 early (M4 type) : 2 medium : 1 late (A3 type) ratio or a 1 early : 3 late ratio,

Table 3. *Distributions of heading date in the F_2 and F_3 populations of T.65×A36-10 (Second crop, 1964).*

Plot	Assumed F_2 genotype	Aug. 25	28	31	Sep. 3	6	9	12	15	18	21	24	27	30	Oct. 3	6	No. of plants	No. of lines	
T.65	$eem_1m_1+_2+_2$										1	11	31	27	12	8	90		
A36-10	$EEM_1M_1m_2m_2$	13	54	15	3												85		
F_1	$EeM_1m_1+_2m_2$							3									3		
F_2		1	8	8	7	7	4	25	64	31	10	16	25	10	1		217		
F_3 lines:																			
	$EEM_1M_1m_2m_2$		6	3	1												10	1	
	$EEM_1m_1m_2m_2$	3	6	13	11	4											37	2	10
	$EeM_1M_1m_2m_2$	1	6	10	11	3	2						2	5			40	2	
	$EeM_1m_1m_2m_2$		5	11	16	21	11	1				4	13	17	1		100	5	
	$EEm_1m_1m_2m_2$			1	2	4	2										9	1	3
	$Eem_1m_1m_2m_2$			2	8	10	11						7	2			40	2	
	$EEM_1M_1+_2m_2$	2	8				4	12	10	7	4	1					48	3	31
	$EEM_1m_1+_2m_2$	2	8	4	6	4	7	7	11	4	3						56	3	
	$EeM_1M_1+_2m_2$		4	6	6	7	1	2	33	31	16	8	13	5	2		134	8	
	$EeM_1m_1+_2m_2$		11	10	12	6	19	21	81	41	17	15	40	26	3	2	304	17	
	$EEM_1M_1+_2+_2$							4	21	14	1						40	2	
	$EEM_1m_1+_2+_2$							3	11	18	11	3	2				48	3	15
	$EeM_1M_1+_2+_2$								27	25	11	3	6	1			73	4	
	$EeM_1m_1+_2+_2$							1	17	39	19	11	18	10	3		118	6	
	$EEm_1m_1+_2m_2$				4	1		1	6	7	1						20	1	5
	$Eem_1m_1+_2m_2$				1	4	3	13	17	17	4	8	9	1	2		79	4	
	$EEm_1m_1+_2+_2$								1	11	21	4	1				38	2	4
	$Eem_1m_1+_2+_2$								1	21	7	2	3	2	1		37	2	
	Others with *ee*										11	65	149	117	22	11	375	20	
F_1: A3×A36-10	$EEM_1m_1+_2m_2$					1	1	2	1								5		
A3	$EEm_1m_1+_2+_2$								1	16	32	9	2				60		

Expected F_2 ratio 9 : 3 : 18 : 9 : 6 : 3 : 16) = 12.38 : 4.13 : 24.75 : 12.38 : 8.25 : 4.13 : 22.00

No. of corresponding F_3 lines = 10 : 3 : 31 : 15 : 5 : 4 : 20

$X^2 = 4.36$ $(0.75 > P > 0.50)$

as also shown in Table 4. The early segregants of M4 type were found to breed true. These facts indicate, as assumed from the results of comparison of many F_1 hybrids (Fig. 2), that A36-10 has an additional earliness gene which is recessive or has no dominance. It is given the symbol m_2.

Table 4. *Distributions of heading date in the F_2's of A3×A36-10 and A3×M4-1 (First crop, 1965).*

Plot	Apr. 20	23	26	29	May 2	5	8	11	14	17	No. of plants
A3							2	21	5	2	30
A36-10	13	11	3	1							28
F_1				1							1
F_2	3	13	20	10	13	28	32	21	9	1	150
A3								12	15		27
M4-1		1	27	1							29
F_1				1							1
F_2			20	8	1	20	46	36	18	1	150

The pattern of segregation in Table 3 may be accounted for by assuming that m_2 is independent of E and M_1, and that it exerts a heading-promoting effect only when E is present, in the same manner as does M_1. The genotypes of the relevant strains may then be assumed as follows:

A36-10 (=Ttg)	—EM_1m_2	M 4-1	—Em_1m_2
A57-8	—EM_1+_2	A 3	—Em_1+_2
T.65	—em_1+_2	M24-4	—eM_1m_2

A number of F_3 lines showing the same heading date as T.65 were selected from T.65×A36-10. One of them, M24-4, was considered to have the genotype eM_1m_2, because, when it was crossed with A3, the F_1 showed the same heading date as the F_1 of A3×A36-10, and the F_2 showed a wide-range distribution similar to that of T.65×A36-10, about 3/16 being as early as A36-10. In the same manner, the genotypes of M36 and other six lines were found to be eM_1+_2, and that of M34-12 to be em_1m_2. These facts support the above assumption of genes.

It may be concluded from these experimental results that when T.65 and Ttg are crossed, Ttg has an earliness gene E and at least two independent modifiers, M_1 and m_2, and that both M_1 and m_2 accelerate flower initiation when E interacts. Different genotypes may be arranged in the order of earliness as follows:

EM_1m_2 (Ttg and A36-10) > Em_1m_2 (M4-1) > EM_1+_2 (A57-8) > Em_1+_2 (A3) > eM_1m_2 (M24-4) = em_1m_2 (M34-12) = eM_1+_2 (M36, etc.) = em_1+_2 (T.65)

As will be mentioned later, however, this relation holds true only in the second crop-season.

3. Comparison between observed and expected disirtbutions.

Basing on the above results of genic analysis, the F_2 distribution of heading date was computed assuming that the environmental variation in each maturity group follows a normal distribution whose standard deviation is represented by that for the parental strains. The observed distribution was then compared with the expected one. The results for T.65×A57–8 are given in Table 5. As the table shows, a chi-square test proved that the observed distriution fitted the expected one, though the expected numbers for both early and late extremity classes exceeded the observed numbers. This test may serve as a proof for the correctness of the assumed gene constitution.

Table 5. *Comparision of observed and expected distributions of heading date for the F_2 of T.65×A57–8.*

Genotype	Freq.	Mean	Sep. 11	14	17	20	23	26	29	No. of plants
EEM_1M_1, EEM_1m_1, EeM_1M_1, EeM_1m_1	9/16	Sep. 15.2 (A57-8)	6.7	82.9	63.4	2.8				155.8
EEm_1m_1, Eem_1m_1	3/16	21.6 (A3)			1.2	23.5	25.5	1.7		51.9
eeM_1M_1, eeM_1u_1, eem_1m_1	4/16	26.4 (T.65)				0.1	7.7	44.7	16.8	69.3
Expected distribution			6.7	82.9	64.6	26.4	33.2	46.4	16.8	277.0
Observed distribution			3	84	78	32	34	33	13	277
x^2			2.04	0.01	2.78	1.19	0.02	3.87	0.86	10.77 ($0.10 > P > 0.05$)

$\sigma = 1.57$ was assumed from the parental distributions.

A similar attempt was made with the data for T.65×A36–10. However, the observed F_2 distribution did not fit the expected one in certain classes; at both early and late extremities, the expected frequencies were too high, while they were too low in some intermediate classes. The observed and expected distributions had almost the same mean value, but the former had a larger variance (99.2) than the latter (66.2). This suggests that some genes with modifying effects on E, M_1 and m_2 might be involved in the cross. As their individual effects do not seem to be analyzable from the results of these crossing experiments, they are regarded as polygenes.

As already mentioned, A36-10 is as early as Ttg. Comparing between T.65×A36-10 and T.65×Ttg the values of genetic variances estimated in a comparable condition, it was found that the former cross had larger values than the latter ($_HV_{F_2}$=67.19 and $_HV_{\bar{F}_3}$=44.01 for T.65×A36-10. $_HV_{F_2}$=43.26 and $_HV_{\bar{F}_3}$=37.84 for T.65×Ttg. Estimation in 1964, first crop). Since A36-10 is a homozygous line derived from T.65×Ttg, it cannot have more genic differences from T.65 than Ttg would have. If the segregating genes other than *E*, M_1 and m_2 are additive in effect, the genetic variance released from T.65×A36-10 cannot be larger than that from T.65×Ttg. It may then be suggested that polygenes segregating in the present cross would on the whole tend to paralyze the effects of major genes, in such a manner as delaying the heading of early lines and accelerating the heading of late lines. The discrepancy between observed and expected F_2 variances found in T.65×A36-10, the former being smaller than the latter, may be accounted for in the same manner. If polygenes exert such a paralyzing or buffering on phenotypes determined by major genes, the frequencies of segregants at both extremities of a distribution will be lowered and the distribution will become more continuous in appearance than expected from an additive model. This situation is often found in the data of this study (e. g., Fig. 1) as well as in other papers on quantitative characters.

4. Seasonal difference in genic effect.

The genic analysis mentioned above is based on the data from second-crop experiments. It was found that the F_2 population of T.65×Ttg, grown in the second crop-season, contained a few segregants with the same heading date as that of T.65, but when grown in the first crop, no such segregants appeared (Fig. 1). It is possible that the buffering action of polygenes, postulated in the previous chapter, is intensified in the first crop-season. In the same manner, about 25% of the F_2 plants of T.65×A36-10 were of T.65 type in the second crop, but only about 10% showed the same heading behavior as T.65 in the first crop. The mean heading date of this F_2 population was in the first crop by 1.4 days earlier, but in the second crop by 4.0 days later than the mid-parental value. This suggests that in addition to the possible seassonal difference in polygenic action, some of the major genes controlling flower initiation exert different effects in the first and second crop-seasons.

As already mentioned, a number of F_3 lines showing in the second crop the same heading date as T.65 were selected from T.65×A36-10. Their genotypes were thought to be eM_1m_2 (M24-4) or eM_1+_2 (M36 and others). The heading dates of these and other strains in the first and second crop-seasons are given in Table 6. The table shows that the strains with *e* and M_1, which show in the second crop the same heading date as T.65, are in the

first crop significantly earlier. This implies that the earliness modifier M_1, which intensifies the effect of E in the second crop, can promote heading in the first crop without E. The other modifier, m_2, also seems to have such a season-dependent effect to some extent.

Table 6. *Growing duration of strains with different genotypes in the first and second crop-seasons, as shown by the number of days earlier than T.65.*

Strain	Genotype	First crop					Second crop				
		1962	1963	1964	1965	Aver.	1962	1963	1964	1965	Aver.
		Seeded on Feb.: Jan.					Seeded on July:				
		12	25	6	23		11	19	9	3	
A3	Em_1+_2	8.4	11.4	8.9	11.6	10.1	7.5	11.8	9.3	7.3	9.0
A57-8	EM_1+_2		23.0	26.3	21.5	23.6		22.3	17.9	17.7	19.3
M4-1	Em_1m_2				26.1	26.1			29.8	27.3	28.6
A36-10	EM_1m_2		31.6	35.4	29.3	32.1	30.2	33.7	32.9	28.9	31.4
Ttg	EM_1m_2	31.9	34.7	35.4	31.3	33.3	27.9	35.0	31.2	31.7	31.5
M24-4	eM_1m_2			8.4	7.2	7.8			2.4	-0.5	0.9
M36*	eM_1+_2			6.9		6.9			-0.1		-0.1
M34-12	em_1m_2				5.9	5.9				-0.4	-0.4
T.65**	em_1+_2	111.5	98.0	114.3	119.0	110.7	80.2	84.3	81.7	83.3	82.4

* Average for M36, M39, M44, M52, M84, M86 and M93 is shown.
** Actual number of days to heading is shown. It was taken as zero.

It is known that all the strains under obervation are insensitive to photoperiod. The major factor responsible for the seasonal change in the genic effect may then be considered to be temperature; in the first crop-season weekly average temperatures for the period from tillering to flower initiation are 19° to 23°C, while those in the second crop are 26° to 28°C. It may be inferred that the action of the earliness modifiers differs according to temperature.

From the data in Table 6, the heading-promoting effect of various earliness genes in the first and second crop-seasons may be estimated as follows:

	No. of days earlier than T.65	
	Second crop	First crop
E	9.0	10.1
E and M_1	17.0	23.8
E and m_2	28.6	26.1
E, M_1 and m_2	31.4	32.7
M_1	0.1	6.9
m_2	0	5.9

M_1 and m_2	0.9	7.2
M_1 (with E)	8.0	13.5
m_2 (with E)	19.6	16.0

For estimating seasonal changes in dominance effect of the major earliness genes, the heading dates of F_1 hybrids with different gene combinations in the first and second crop-seasons were compared. E as well as M_1 were almost completely dominant over their recessive alleles in both the first and second crop-seasons, but the dominance relation between m_2 and $+_2$ seemed to differ according to season. m_2 was slightly dominant in the first crop, but tended to be recessive in the second crop.

*5. Distribution of the earliness gene **E** in different varieties.*

For finding out genes controlling photoperiodic response, T.65 was crossed with a photo-sensitive variety, Kissin, which was about two weeks earlier than T.65 in both the first and second crop-seasons. The F_1 hybrid showed the same heading date as Kissin in both seasons. The F_2 showed different patterns of frequency distribution according to the growing season, as shown in Table 7. In the second crop-season where day-length gets short, early F_2 segregants were Kissin types and the late ones T.65 types, though the distribution was continuous. It may be inferred from the data in the table that the early plants carry a dominant gene conditioning photoperiodic sensitivity, and a major part of the F_2 variation is due to segregation for this allele. The same would be the case with the first-crop experiment. However, when the F_2 plants were seeded in May and grew under long-day condition, plants earlier than Kissin as well as those later than T.65 were found. From their frequencies, the major genic differences between the two varieties may be considered as follows:

P: A photoperiodic sensitivity gene, dominant over its non-sensitivity allel, *p*.

E_2: An earliness gene controlling basic vegetative period, dominant over its late maturity allele, e_2, and independent of *P*.

The genotypes of T.65 and Kissin would then be $p\ e_2$ and $P\ E_2$, respectively. They show the same heading time when seeded in May. Segregants earlier than Kissin appearing in May seeding would have $p\ E_2$, and those later than T.65 would have $P\ e_2$. The segregation ratio in May seeding is then expected to be 3 early : 10 medium : 3 late, and the observed frequency distribution gave a good fit to the expected distribution. An F_3 line (D53-3), possibly having the genotype $p\ E_2$, was selected from the cross, and wes crossed with A3 which would have $p\ E$. As shown in Table 7, the F_2 plants did not segregate in such a wide range as in T.65×Kissin. The F_2 distribution somewhat exceeding the range of the parental distributions may be regarded as

Table 7. *Distributions of the number of days to heading in the F_2 populatins of T.65×Kissin and other crosses.*

Plot (genotype)	Date seeded	No. of days to heading																	No. of plants
		66	69	72	75	78	81	84	87	90	93	96	99	102	105	108	111	114	
T. 65 (pe)	Feb. 13 (1963)														2	23	24	5	54
Kissin (PE)	Feb. 13 (1963)										24	30							54
F_1	Feb. 13 (1963)										7	10	1						18
F_2	Feb. 13 (1963)										15	29	27	15	9	5	3		103
T. 65	May 25 (1964)							2	10	10	11								33
Kissin	May 25 (1964)							26	23	7	4								60
F_2	May 25 (1964)			1	8	12	2	23	23	24	5	16	4						118
T. 65	July 8 (1963)						5	23	8	7									43
Kissin	July 8 (1963)	11	6	8	4														29
F_1	July 8 (1963)	14	11	6	1														32
F_2	July 8 (1963)	8	31	44	21	28	13	10	3										158
D53-3 (pE)	July 6 (1965)	10	15	4	5														34
A3 (pE)	July 6 (1965)	6	14	4															24
F_2	July 6 (1965)	48	44	29	13	2													136
D53-3	July 6 (1965)	5	7	8	10	4	1												35
B96 (pE)	July 6 (1965)	5	22	2	2														31
F_2	July 6 (1965)	35	75	42	29	6	2												189
C48-1 (pE)	July 6 (1965)	7	9	6	3	3													28
B96	July 6 (1965)	14	6	6	3	1													30
F_2	July 6 (1965)	11	58	25	18	5													117

due to polygenic segregation. It may then be inferred that the earliness gene E_2 is located at the same locus as E, or E_2 is isoallelic with E.

It was found further that Taichung 180, originating from Awned Asahi, would have the same earliness gene E. From its cross with T.65, an early line C48-1 was selected, and was crossed with B96. B96 is an isogenic line of T.65 with an earliness gene from Bozu 5, which was found to be isoallelic with E (Tsai and Oka 1965). The F_2 of C48-1×B96 did not show a significant segregation, as also shown in Table 7. Therefore, C48-1 must have E. From these experiments, it may be pointed out that Tatong-tsailai (Ttg), Bozu 5, Awned Asahi, Taichung 180 and Kissin have the same earliness gene, E, in common.

Discussion

When confronted with phenotypically continuous genetic variations in a quantitative character, we employ a statistical method of analysis to estimate the values of various genetic parameters. We have no other means if the variation is really due to polygenes with minor individual effect. In many cases, however, genes with considerable individual effects are hidden behind continuous variation. Such genes would have epistatic as well as pleiotropic effects on different characters, while the whole picture of genic effects may differ according to environmental conditions. By statistical methods, heritability values may be easily estimated, but an analysis of genic interaction is harder to be achieved, as we have learned at the beginning of this study. On the other hand, it is a timeconsuming work to detect individual genes and estimate their effects from the results of various crossing experiments. In practice, an analysis of individual genes may be conducted to a limited extent.

From these considerations, we have attempted to analyze individual genes to a certain limit, treating the residual variations as polygenic portions. The method we mainly used was to select progeny lines with certain phenotypes from the initial cross and to cross them again with the parental strains. By repeating this procedure, the genetic background should become relatively uniform, and the effect of a particular gene could be detected. The gene constitution once assumed is then checked by crossing the progeny lines with one another.

Taichung 65 is a representative Ponlai variety with a medium growth period, while Tatong-tsailai is an extremely early variety. Our genic analysis proved that in respect to maturity these two varieties differ in at least three major genes, E, M_1 and m_2, in addition to polygenic differences. M_1 and m_2 appeared to be modifiers which promote flower initiation when E interacts.

This relation suggests a chain of reactions controlling flower initiation, as is often found in the process of pigment formation in plants.

It is interesting that under the high temperatures (26°–28°C) of the second crop, both M_1 and m_2 exert their effect only when E is present, but under lower temperatures (19°–23°C) of the first crop they can work without E. As already mentioned, since both Taichung 65 and Tatong-tsiliai are insensitive to photoperiod, these seasonal differences in genic action may be attributed to temperature differences. It seems that the action of these modifiers is twofold, one to exaggerate the effect of E in a complementary manner, and the other to promote directly flower initiation. The latter is limited to a low temperature condition and is hindered under high temperatures. As regards the former action—to exaggerate the effect of E, our data (Table 6) suggest that this action of M_1 is enhanced under relatively low temperatures, but that of m_2 is rather weakened under low temperatures. In view of these facts, M_1 and m_2 may be regarded as genes which promote flower initiation in a low-temperature condition, lowering the temperature response in respect to flower initiation.

The junior writer (Oka 1959) has shown that temperature response of the growing period can be partitioned into that of vegetative growth and that of flower initiation. The rates of acceleration of vegetative growth and of flower initiation due to 1°C rise, estimated by the junior writer as well as by Dr. S. C. Hsieh and Miss T. M. Chang of the Taiwan Agricultural Research Institute by the same method, are as follows:

	Rate of acceleration due to 1°C rise			
	Vegetative growth		Flower initiation	
	(Oka)	(Hsieh and Chang)	(Oka)	(Hsieh and Chang)
Taichung 65	2.6%	9.9%	4.3%	4.7%
Tatong-tsailai	6.3	2.9	0.8	2.6

The above comparison shows that Tatong-tsailai has a lower temperature response of flower initiation than Taichung 65. This seems to be due to the effects of the earliness modifiers carried by Tatong-tsailai.

In the present study, we have suggested that polygenes, whose individual effects could not be analyzed, would as a whole exert a buffering action, accelerating the heading of late-maturity genotypes and delaying the heading of early-maturity genotypes. It may be that a minor gene with a heading-promoting effect tends to be less active when it interacts with a certain earliness gene, and vice versa. Or, it may be that polygenes have a "canalizing effect", as postulated by Waddington (1952). Such a polygenic effect also seemed to be temperature-dependent, being enhanced by low temperatures.

On the other hand, the effect of the earliness gene E did not seem to be

much influenced by temperatures. This gene may be regarded as conditioning the so-called vegetative period. We have pointed out before (Tsai and Oka 1965) that in the genetic background of Taichung 65, *E* exerts pleiotropic effects not only on plant height and other characters but also on the pattern of responses to nitrogenous fertilizers and other growing conditions. It seems that an acceleration of flower initiation by this gene brings about various physiological changes which might be developmentally correlated. We do not know yet the effects of M_1 and m_2 on the development of characters. Their effects will be investigated after placing the genes in an isogenic genetic background.

We have found that the earliness gene *E* is distributed in various varieties of China and Japan. It might be one of basic genes setting up early varieties. The distribution of M_1 and m_2 remains unknown. Their locations in linkage groups are also unknown. Studies on these problems are still under way.

Summary

A representative Ponlai variety of Taiwan, Taichung 65, and an extremely early variety from Northern China, Tatong-tsailai, were compared regarding their differences in genes controlling the heading date; both varieties belong to the Japonica type and are insensitive to photoperiod. After a biometrical survey by Mather's method, genic analysis was made by selecting certain homozygous progeny lines from the original cross and crossing them with the parental strains or with one another, so that the effects of individual genes could be observed in a relatively uniform genetic background. In addition to the earliness gene, *E*, which was carried by our isogenic lines of Taichung 65, at least two modifiers promoting flower initiation, M_1 and m_2, were found to be involved. Under high temperatures of the second crop-season, they exert their effect only when *E* is present, but in lower temperature of the first crop, they promote flower initiation without *E*. They were considered to be genes lowering the temperature response in respect to flower initiation. It was found further that polygenes would exert a buffering action on the effect of major genes, accelerating the heading of late lines and delaying that of early lines. The earliness gene *E* was found to be distributed in various early varieties of the Japonica type, even in a photoperiod s nsitive variety, Kissin.

作物生產能力及適應性之遺傳學的研究

2. 水稻臺中65號及其他品種抽穗期之遺傳因子分析

蔡國海 岡彥一

粳稻不感光性品種臺中65號與大同在來間雜交組合之抽穗期經遺傳學的分析結果，發現華北極早熟稻大同在來除包含臺中65號 Isogenic 品系 (Tsai and Oka 1965)所攜之早熟性遺傳因子 E 外，至少還有促進抽穗期作用的兩修改遺傳因子 M_1 與 m_2 之存在。此等遺傳因子在一期作低溫條件 E 不存在時尙可促進抽穗期，惟二期作高溫條件下僅有 E 存在時其作用始能顯現。同時發現本雜交組合有促進晚熟系統或延遲早熟系統抽穗期作用之微效遺傳因子 (Polygenes)。

此外，粳稻早熟品種大同在來，坊主5號，臺中180號，以及日本感光性品種吉神皆含有早熟性遺傳因子E。

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