GENETIC STUDIES OF YIELDING CAPACITY AND ADAPTABILITY IN CROP PLANTS.

3. Further Observations on the Effects of an Earliness Gene, *E*, in the Genetic Background of a Rice Variety, Taichung 65

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In our earlier paper (Tsai and Oka 1965), we reported variations in agronomic characters of isogenic early strains of Taichung 65. They carry an earliness gene, *E*, (Tsai and Oka 1966), and are maturing about ten days earlier than Taichung 65 (abridged as T.65). When the standard dose of fertilizers was applied, they gave in the first and second crpos at Taichung about 95% and 90% of the grain yield of T.65, respectively. But they showed a narrow adaptive latitude to the amount of fertilizers as compared with T.65, giving a low yield in no-fertilizer as well as in doubly fertilized plots.

To estmate the effects of the *E* gene in more detail, we compared the early strains with T.65 with regard to character development, temperature responses and grain yield at different locations. In yield trials, we are indbeted to the District Agricultural Improvement Stations of the Taiwan Provincial Government for their kind cooperation.

Materials and Methods

Two early isogenic lines, A3 and B96, were compared with a strain of T.65 that was used as the recurrent parent in back-crosses in order to obtain early lines. The donor parent used was Tatong-tasilai (an early variety from northern China) for A3, and Bozu 5 (an early variety from northern Japan) for B96. As mentioned in our previous paper, the early lines are selections from B_7F_2 populations. In this study, corresponding early lines from $B_{10}F_2$ populations ($A3_{10}$ and $B96_{10}$) were also observed. The cultural method and

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experimental conditions at Taichung were the same as those described in our previous papers.

Experiments in District Agricultural Improvement Stations (in 1965 and 1966) were conducted according to their standard cultural schemes, which did not differ much from ours, though the fertilizer level ranged from 50–40–60 to 100–60–100 NPK (kg/ha). In addition, the growth pattern of organs were observed at Misima, Japan, in 1967. Two-week seedlings (seeded on May 7) were transplanted to a concrete bed, with a single plant per hill, spaced at 25 cm×25 cm. The fertilizers applied were 100–60–60 NPK, the ratio of basic to top dressing being 4:6 for N. Three plants were weekly sampled from each plot and were recorded regarding the size of various organs.

Results

1. Differences between two early isogenic lines, A3 and B96

The early lines may carry a chromosome segment of the donor parent in which the *E* gene is borne, or the *E* gene-block. They may then have, in addition to *E*, different genes affecting their growth, deriving from Tatong-tsailai or from Bozu 5. The *E* genes from different origin may also differ as to effect, though they are at the same locus.

A3 was a few days earlier than B96, and generally showed more pronounced effects of *E* on various characters, as shown in Table 1 and other tables of this paper. To estimate how the differences between A3 and B96 may be accounted for, they were compared with corresponding early lines, $A3_{10}$ and $B96_{10}$. The four strains were seeded at six different dates in the 1967 first crop-season at Taichung. The results are given in Table 1, which shows that the difference in heading date between $A3_{10}$ and $B96_{10}$ was slightly smaller than between A3 and B96. Variance analysis of the data showed that the difference between A3 and $A3_{10}$ was significant, but that between B96 and $B96_{10}$ was not. It seems that in A3, the three additional back-crosses to T.65 have removed a gene or genes linked with *E* exaggerating the effect of *E*. But the difference between $A3_{10}$ and $B96_{10}$ was still highly significant. We can not neglect the possibility that the *E* gene from Tatong-tsailai (in A3) and that from Bozu 5 (in B96) are "isoalleles" with similar effects.

2. Effects of the E gene-block on organ development

It was concluded from repeated observations that *E* did not influence tillering and growth of leaves before flower initiation, as shown in Fig. 1. The dates of flower initiation in the early lines and T.65 were observed by the method given by Matsushima (1966, chapter 6), classifying the tillers into an early-developing (main stem and first to third tillers) and a late-developing

Table 1. *Comparison of heading dates between isogenic lines derived from B_7 and B_{10} generations (Mean for 3 replications, each plot consisting of 10 plants)*

Seeding date	From B_7 A3	From B_7 B96	From B_7 B96-A3	From B_{10} $A3_{10}$	From B_{10} $B96_{10}$	From B_{10} B96-A3	(B96-A3)-($B96_{10}$-$A3_{10}$)
Jan. 5	May 1.0	5.3	4.3	May 3.1	6.4	3.3	1.0
15	2.8	4.4	1.6	2.3	6 0	3.7	−2.1
25	2.8	5.1	2.3	4.3	6.5	2.2	0.1
Feb. 4	5.0	9.1	4.1	4.9	8.6	3.7	0.4
15	16.2	18.3	2.1	18.0	19.7	1.7	0.4
25	25.9	29.9	4.0	27.3	29.7	2.4	1.6
Mean	8.95	12.02	3.07	9.98	12.82	2.83	0.23
Dif. 5%[1)]			0.85			0.88	1.22

Variation due to:	D. F.	A3·$A3_{10}$	B96:$B96_{10}$	A3:B96	$A3_{10}$:$A96_{10}$	Expectation (line fixed)
Replication	2	8.30**	2.78	5.55*	5.27	
Line	1	9.31**	5.44	85.25**	72.53**	$\sigma_e^2+3\sigma_{ls}^2+18\ \sigma_l^2$
Seeding date	5	611.01**	596.17**	604.75**	602.23**	$\sigma_e^2+6\sigma_s^2$
Interaction	5	1.69	1.27	2.12	1.02	$\sigma_e^2+3\sigma_{ls}^2$
Error	22	1.15	1.31	1.43	1.54	σ_e^2
σ_l^2(for line)		0.42	0.23	4.62	3.94	

1) Difference significant at 5% level.
* Significant at 5%, level, ** at 1% level.

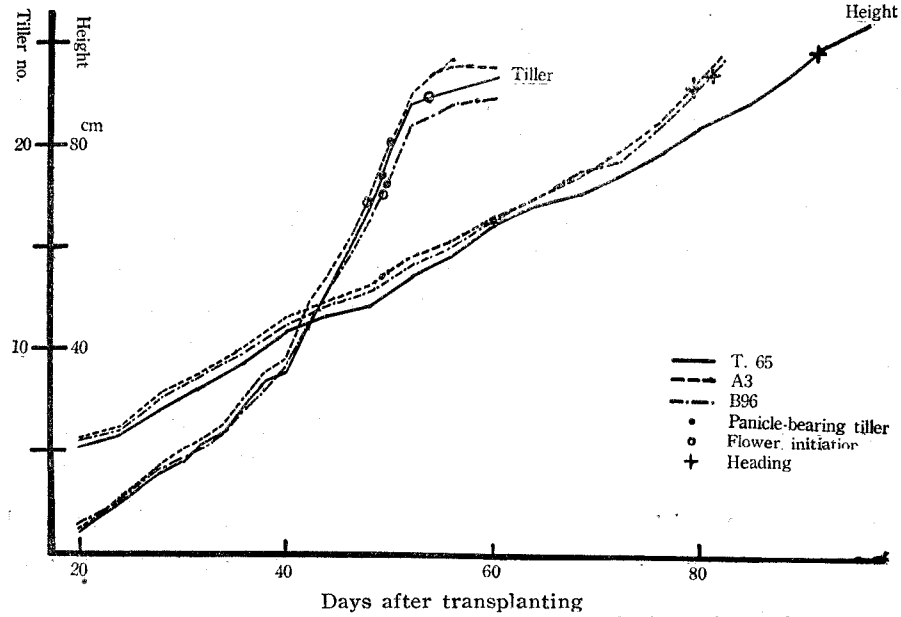

Fig. 1. Tillering and longitudinal growth in early isogenic strains and T. 65 (1965 1st crop, Taichung)

(last three panicle-bearing tillers) groups. The mean measurements recorded at Taichung for three years are given in Table 2. A3 and B96 initiated flower primordia 6 to 10 days earlier than T.65, and the period from flower initiation to heading was about 3 days shorter than that of T.65. The ripenning process after heading did not differ. The early lines were then 7 to 11 days earlier maturing than T. 65.

Table 2. *Mid-tillering, flower initiation and heading dates of early isogenic lines, as shown by the difference from those for T.65 (Mean for 4 experiments in 1965 to 1967 at Taichung)*

Crop season	Strain	Mid-tiller*	Flower initiation		Fl. initiation to heading		Heading		Maturity
			(a)	(b)	(a)	(b)	(a)	(b)	
1st (seeded Jan. 31)	T.65	Apr 6.1	Apr 16.1	20.2	40.0 days	38.9	May 26.0	29.1	June 22
	A3	−0.3	−9.5	−9.7	34.5	36.1	−14.9	−11.7	−10.8
	B96	0.2	−6.4	−7.4	36.0	37.5	−10.3	− 8.9	− 7.0
2nd (seeded July 7)	T.65	Aug 17.4	Aug 26.1	27.9	37.7	36.2	Oct 2.8	3.1	Oct 31
	A3	0.7	−6.9	−6.4	33.9	33.5	−10.7	− 9.1	−10.5
	B96	−0.1	−6.1	−6.0	32.6	32.5	−11.1	− 9.6	−10.0

* The time at which tiller number reaches ½ of the maximum number, estimated by fitting the data to the logistic function.
(a) Mean for the main stem and first three tillers.
(b) Mean for the last three panicle-bearing tillers.

The promotion of flower initiation seems to shorten various organs that develop after flower initiation, namely, the panicle, internodes and upper leaves. As shown in Table 3, the proportion of shortening differed aoccrding to the organs. The fifth and fourth internodes (from the top) were strongly shortened, while the panicle and upper internodes were not much shorter. This brought about an "upper-elongation" type, which was found among mutant strains of rice by Morishima and Oka (in press).

The longitudinal growth rates of panicle, internodes and upper leaves in T.65, A3 and B96 were observed at Misima. As also given in Table 3, the final lengths of organs at Misima showed a similar pattern of between-line differences as found at Taichung, though the shortening of organs in early lines was smaller than at Taichung.

The growth rates of these organs were calculated by fitting the measurements (taken at one week interval) to the logistic function, $y=A\ (1+ae^{-bt})^{-1}$, or $\log_e\left(\frac{A}{y}-1\right)=\log_e a-bt$, where y is the size of an organ at time t, A is the final size, and b stands for growth rate. Using this formula, the time at which y reaches $_1/_2A$ ($t_{1/2}$) is given by $\log_e a/b$, and the actual growth rate (dy/dt) at $t_{1/2}$ is given by $\frac{1}{4}\ b\ A$. The number of days needed for an organ

Table 3. *Organ sizes at maturity of early isogenic lines, shown in per cent of the values for T.65*

Organ	1st crop, Taichng			2nd crop, Taichung			Misima (1967)		
	T.65	σ	A3 B96	T.65	σ	A3 B96	T.65	σ	A3 B96
Length,	cm		% %	cm		% %	cm		% %
Panicle	21.5±0.32		92 99	20.1±0.31		93 98	21.8±0.33		97 101
Internode,									
1st	42.4±0.87		91 98	37.9±0.85		97 100	46.2±0.53		97 94
2nd	21.5±0.50		101 100	21.4±0.47		98 96	25.2±0.30		91 94
3rd	13.9±0.54		92 95	12.9±0.57		94 85	16.6±0.50		91 100
4th	8.1±0.54		48 61	6.6±0.42		70 59	12.0±0.66		76 94
5th	1.6±0.22		34 38	1.4±0.15		63 50	4.8±0.61		50 83
Leaf sheath,									
1st	30.4±0.33		93 100	29.4±0.40		95 98	33.2±0.57		98 99
2nd	24.3±0.48		93 102	23.7±0.38		96 97	26.8±0.31		98 98
3rd	24.0±0.25		91 96	22.8±0.28		94 96	26.9±0.56		98 99
Leaf blade,									
1st	32.0±1.00		86 95	29.1±1.04		90 95	32.4±0.67		97 98
2nd	41.4±1.08		90 95	37.9±1.05		95 97	43.9±0.57		96 98
3rd	41.3±0.97		90 92	39.7±0.85		96 96	50.6±0.45		98 101
Leaf width,	mm			mm			mm		
1st	14.2±0.30		96 98	13.1±0.32		98 102	13.9±0.28		100 103
2nd	11.4±0.31		90 90	10.5±0.27		97 98	13.1±0.25		95 96
3rd	9.7±0.27		83 93	9.2±0.26		88 92	12.9±0.34		90 91
Spikelet no. p. panicle	115.7±3.84		97 98	126.1±3.31		93 86	128.0±3.74		99 100
Panicle no. p. plant	18.3±1.32		102 96	12.5±0.73		101 92	11.8±0.42		93 95
Spikelet,	mm			mm			mm		
length	7.17		101 100	7.20		101 103	6.99		100 102
width	3.29		95 99	3.32		98 100	3.55		98 99
100 grain	g			g			g		
weight	2.32		104 102	2.55		100 105	2.57		100 102

σ Standard doviation for 10 plant means, average for three lines.
Taichung data: Mean for 3 experiments in 1965 to 1967.

to grow from 1/10 to 9/10 of fhe final size ($t_{9/10}-t_{1/10}$) was also computed. The results are given in Table 4, which shows that the *E* gene-block increased the growth rates of panicles and upper internodes, and shortened their growth duration ($t_{9/10}-t_{1/10}$). In contrast, it reduced the growth rates of lower internodes and upper leaves, extending their growth duration.

In general, the fifth internode (from the top) starts elongation immediately after flower initiation. Its $t_{1/10}$ days for T.65, A3 and B96 were estimated to

Table 4. *Parameters of growth curves for organ elongation, as compared between early isogenic lines and T.65 (Misima 1967)*

Organ	$t_{1/2}$ date			dy/dt at $t_{1/2}$ (cm/day)			No. of days, $t_{9/10}-t_{1/10}$		
	T.65	A3	B96	T.65	A3	B96	T.65	A3	B96
	July								
5th internode	29.3	22.7	24.2	0.16	0.07	0.04	31.3	32.4	35.4
1st leaf blade	27.9	25.1	24.8	4.10	2.82	3.80	8.7	12.2	9.2
2nd leaf sheath	28.9	25.4	26.0	5.12	2.84	3.40	5.8	10.1	9.4
	Aug.	July							
4th internode	6.0	30.1	29.0	0.40	0.44	0.70	33.2	21.4	16.1
		July	Aug.						
1st leaf sheath	3.3	29.9	1.3	4.84	3.81	3.54	7.6	9.3	10.1
Panicle	6.2	1.4	4.4	1.51	1.69	1.87	15.9	13.1	12.8
3rd internode	9.9	1.9	5.2	1.27	1.24	1.19	15.3	13.3	15.4
2nd internode	16.8	8.7	12.9	1.73	1.91	1.86	16.0	13.2	14.2
1st internode	18.4	10.2	13.3	4.78	5.15	5.03	10.6	9.8	9.4

be July 13.7, 6.5 and 6.5, respectively. The *E* gene thus seems to have moved up flower initiation by about 7 days, in the same manner as at Taichung. Then follows, as reported by Seko *et al.* (1957), the elongation of the first leaf blade, second leaf sheath and fourth internode. Some seven days after this, the simultaneous elongation of the panicle, first leaf sheath, and third internode takes place. Finally, the first and second internodes elongate resulting in heading. These are diagrammatically shown for T.65 and A3 in Fig. 2.

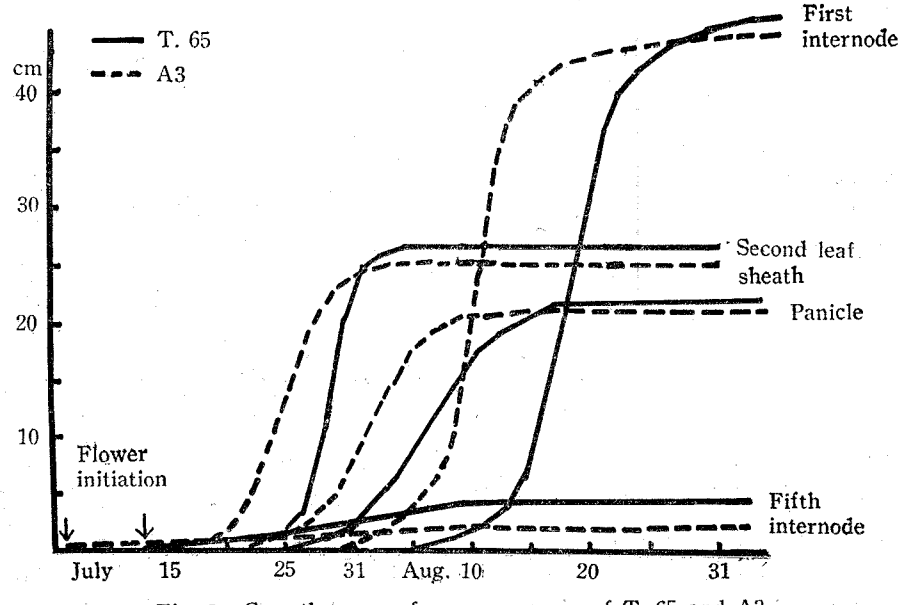

Fig. 2. Growth curves for some organs of T. 65 and A3

The number of days from the aboove-estimated flower-initiation time to panicle-elongation time as shown by $t_1/_2$ was 23.5 for T.65, 25.9 for A3, and 28.9 for B96, while the number of days from the $t_1/_2$ day for panicle to that for the first internode (heading time) was 12.2 for T.65, 7.8 for A3, and 9.0 for B96. Thus, the *E* gene-block does not seem to shorten the time from flower initiation to panicle elongation (time for panicle differentiation), but shortens the time from panicle elongation to heading. It seems that the direct effect of the gene block is to move up flower initiation, to retard the elongation of lower internodes and upper leaves, and to accelerate the elongation of panicle and upper internodes.

3. Temperature responses as affected by the E gene-block

The three strains, T.65, A3 and B96, were repeatedly grown 9 times at Taichung, being seeded at one month interval from December 10, 1962 to August 10, 1963, and were recorded as to heading date and other characters. Since the strains are insensitive to photoperiod, and as will be demonstrated later, the variations in number of days to heading found from this experiment may be attributed to temperature differences. Adding to the data those from three additional experiments in 1962, the temperature responses of the strains were computed as follows:

The period from germination to heading of a plant was conventionally divided into four parts, *i.e.*, 1) vegetative period (from seeding to the formation of panicle-bearing tillers), 2) flower initiation period (from the first bract to secondary rachila differentiation, ca. 10 days), 3) panicle growth period (10 days after the above), and 4) heading period (10 days before and after heading), and the average temperatures of these four periods (x_1, x_2, x_3 and x_4, respectively) were computed in each strain for respective seeding dates. The temperatures ranged from 20.6C (x_1, December 10 seeding) to 28.2C (x_3, June 11 seeding). Assuming that the number of days to heading depends upon the temperatures of the first three period, the standard partial regressions of the number of days to heading (y) on x_1, x_2 and x_3 were computed by the method given by Snedecor (1957, pp. 413–446).

As shown in Table 5, the early lines, A3 and B96, were found to have lower response to the temperatures of vegetative period (x_1) and higher response to the temperatures of flower-initiation period (x_2) and of panicle-growth period (x_3) than T.65. As x_3 did not seem to play an important role, recomputation was made neglecting it, resulting in the same between-line differences as above-mentioned. The partial variances of days to heading due to these regressions, as shown by R^2, were high enough to show that the number of days to heading was primarily controlled by temperatures. Most of the differences in regression coefficient between the three strains did not

exceed the 5% level of significance. But the similarity between A3 and B96 may support the above conclusion.

Table 5. *Standard partial regressions of the number of days to heading on mean temperatures of different growth periods, as compared between early isogenic lines and T.65 (Taichung 1962-3)*

Strain	$b_{yx1\cdot23}$	$b_{yx2\cdot13}$	$b_{yx3\cdot12}$	R^2	$b_{yx1\cdot2}$	$b_{yx2\,1}$	R^2	Temp. constant*			
								x_1	x_2	x_3	R^2
T.65	−.52	−.44	.03	.88	−.55	−.40	.88	−.69	−.87	.08	.95
A3	.15	−.99	−.22	.97	−.17	−.80	.93	−.43	−.93	−.30	.95
B96	.08	−.96	−.12	.95	.08	−1.04	.94	−.52	−.90	−.15	.96

* Partial regression coefficients from logarithmic data, not standardized.

When the data for temperatures and days to heading are both converted into logarithms, the regression coefficients then obtained may be regarded as "temperature constants", which measure the effect of temperatures on growth by linear regression. This transformation reduced deviations from regression, bringing about higher R^2 values than those from the original data. In terms of "temperature constants", it was also found that the early lines had lower response to x_1 and higher response to x_2 than T.65 (Table 5). It seems that the promoting effect on flower initiation of the *E* gene-block is intensified when temperature rises in that stage, and this makes the temperatures in earlier stages less influential concerning the days to heading.

In plant height, the temperatures before and after heading (x_4) were taken into account, in addition to x_1, x_2 and x_3, and partial regressions were computed. As shown in Table 6, the lower were the temperatures of vegetative period (x_1), and the higher were the temperatures in other periods, the higher were the plants. These temperature responses appeared to be more pronounced in the early lines than in T.65. In panicle number per plant, as also shown in Table 6, it appeared that the lower were the temperatures in vegetative period (x_1) and the higher were the temperatures in flower-initiation period (x_2), the more panicles were produced. Early lines showed this tendency more strongly than T.65. Though the *E* gene does not affect tillering, it may modify the temperature response of panicle number, as a result of its promoting effect on flower initiation intensified by rising temperatures. But the partial variances of plant height or panicle number due to the regressions on temperatures were about one half of the total variance. These characters may be to a considerable extent affected by other climatic conditions than temperature.

In general, the changing pattern of temperatures from low in the early to high in later stages is favorable for the development of organs (Oka 1959).

The *E* gene-block seems to intensify such an effect of rising temperatures on the growth of plants.

Table 6. *Standard partial regressions of plant height and panicle number per plant on mean temperatures of different growth periods, as compared between early isogenic lines and T.56 (Taichung 1962–3)*

Strain	Plant height					Panicle number		
	$b_{yx1\cdot234}$	$b_{yx2\cdot134}$	$b_{yx3\cdot124}$	$b_{yx4\cdot123}$	R^2	$b_{yx1\cdot2}$	$b_{yx2\cdot1}$	R^2
T.65	−1.27	.71	.15	.20	.54	−2.03	1.59	.48
A3	−2.16	1.39	.76	.37	.35	−2.66	3.08	.44
B96	−2.84	2.35	.38	.42	.57	−3.83	3.54	.56

4. Grain yield of early isogenic lines at different locdtions

Experiments at Taichung showed that the grain yield of A3 and B96 was relatively low in the second crop (Tsai and Oka 1965). To estimate their yielding capacity in different environments, they were tested at seven District Agricultural Improvement Stations for two years, together with T.65 and seven early Ponlai varieties newly selected from hybrids by the Stations. As shown in Table 7, the results proved that in the northern region of Taiwan, *i.e.*, Taipei, Lotung and Hsingchu, where the second crop often fails on account of the early advent of winter rains, early lines produced higher second-crop yields than T.65. Our previous conclusion that the early lines were inferior in the second crop was correct only in the southern region of Taiwan.

Table 7. *Yield records at seven District Agricultural Improvement Stations in Taiwan (kg/10a)*

Location	1965 1st crop			1965 2nd crop			1966 1st crop			1966 2nd crop		
	T.65	A3	B96	T.65	A3	B96	T.65	A3	B96	T.65	A3	B96
Taipei	438	283	374	238	331	352						
Lotung	431	364	323	360	356	303	394	387	331	324	369	364
Hsingchu	479	465	486	365	399	412	379	253	319	437	466	451
Hwaleng	248	259	296	288	258	251	397	174	131	328	239	282
Taichung	534	550	581	220	242	307	325	312	293	351	345	346
Chiayi	616	534	582	485	445	481	587	353	531	488	393	436
Taitung	352	286	327	412	272	309	413	285	395	517	444	466
Mean	442	392	424	338	329	345	416	294	333	408	376	391

The varietal mean yields at the seven locations are given in Table 8. B96 showed a yielding capacity comparable to commercial early varieties. The variability of yield due to location and year was estimated by Finlay and

Wilkinson's (1963) method, computing for each variety the regression of yields on location means. The results are also given in Table 8, which shows that in yield stability our early isogenic lines were not inferior to other commercial early varieties.

Table 8. *Varietal mean yield, mean number of days to heading and yield stability as shown by the regression on location means (b)*

Variety	1st crop				2nd crop			
	Growing* period	Mean yield	*b*	R^2	Growing* period	Mean yield	*b*	R^2
		kg/10a				kg/10a		
T.65	116	430	0.85	0.85	101	399	0.94	0.76
A3	107	352	0.81	0.67	90	366	0.99	0.82
B96	108	394	0.98	0.95	91	375	1.10	0.95
Hsinchu-line 274	111	459	1.10	0.95	95	386	1.16	0.87
Taipei-line early 11	109	434	0.95	0.94	91	370	1.12	0.80
Taipei-line early 18	107	436	1.14	0.98	87	342	0.90	0.83
Taichung-line early 88	108	360	1.21	0.81	91	357	0.86	0.72
Taitong-line early 138	109	438	1.02	0.81	93	378	1.16	0.90
Taitong-line early 150	111	426	0.92	0.94	94	368	0.62	0.70
Taitong-line 157	110	462	0.98	0.87	92	361	0.94	0.84
Taichung 180	108	408	0.81	0.97	90	346	0.99	0.90

* No. of days from transplanting to maturity

Discussion

Our early isogenic lines of T.65 have been selected from B_7F_2 populations. They may differ from T.65 in a chromosome segment carrying the *E* gene. According to Hanson's (1959) theoretical expectation, the segment would occupy about one seventh of the chromosome (in half length), and contain a number of genes tightly linked to constitute a linkage block. Breeders may consider the strains as practically isogenic.

The gene block of A3, derived from Tatong-tsailai, generally had stronger effect than that of B96 from Bozu 5, while the difference in effect was slightly reduced when three additional back-crosses with T.65 were made. Such a gradual reduction in the effect of a chromosome segment was observed by Harding and Allard (1965) in repeatedly selfed lines of lima bean. In that case, dealing with the difference in seed size between lines with colored and colorless beans, they considered the reduction of difference to be due to re-combination of linked genes. In our case, the difference in earliness between two early isogenic lines showed a reduction trend in the course of back-crosses. This suggests that *E* is linked with genes having a similar but smaller effect. It may be inferred that a locus comprises, as often found in micro-organisms,

a number of gene sites with similar effects, whose changes bring about a series of "isoalleles" (Stern and Shaeffer 1943; Komai 1950). Under this assumption, the *E* gene-block of A3 and that of B96 may be considered as "isoalleles".

The various effects of a gene on character development may be estimated from differences between isogenic lines, though pleiotropy and linkage can not be clearly distinguished. Qualset *et al.* (1965) reported investigations along this line, dealing with the effect of two gene loci controlling awn development on various agronomic characters in barley. The effects of the *E* gene-block so far found in the genetic background of T.65 may be listed as follows:

A. Growth period,
   1) from germination to flower initiation: shortened by ca. 7 days,
   2) from flower initiation to heading: shortened by ca. 3 days.
   3) panicle, from 1/10 to 9/10 in length: shortened by ca. 2 days,
   4) first and second internodes, from 1/10 to 9/10 in length: shortened by 1 to 2 days,
   5) fourth internode, from 1/10 to 9/10 in length: shortened by ca. 14 days,
   6) fifth internode, from 1/10 to 9/10 in length: extended by ca. 3 days,
   7) upper leaves, sheath and blade, from 1/10 to 9/10 in length: extended by a few days,
   8) from flower initiation to panicle elongation: extended slightly, and
   9) from panicle elongation to heading: shortened by ca. 3 days.

B. Growth rate,
   1) panicle: increased by ca. 10%,
   2) first and second internodes: increased by ca. 10%,
   3) third and fourth internodes: increased slightly,
   4) fifth internode: decreased by ca. 50%,
   5) upper leaves, blade and sheath: decreased by ca. 30%, and
   6) seedling growth and tillering: no effect.

C. Final size,
   1) panicle: ca. 95% of T.65,
   2) first internode: ca. 95% of T.65,
   3) second internode: ca. 100% of T.65,
   4) third internode: ca. 95% of T.65,
   5) fourth internode: ca. 55% of T.65,
   6) fifth internode: ca. 35% of T.65,
   7) upper leaves, sheath and blade: ca. 95% of T.65,
   8) leaf width: ca. 90% of T.65,
   9) spikelet number per panicle: ca. 95% of T.65,

10) panicle number per plant: ca 100% of T.65 (no effect), and
11) spikelet size and mean grain weight: ca. 100% of T.65 (no effect).

D. Response,
1) temperature: increase of temperature sensitivity in the period of flower initiation, and increase of beneficial effect of rising temperatures on growth,
2) nitrogen: reduction of the adaptive latitude (Tsai and Oka 1965), and
3) planting density: similar as above (Tsai and Oka 1965).

E. Yielding capacity,
1) mean yield: ca. 95% of T.65 if grown in favorable conditions in Taiwan,
2) seasonal adaptability: the same as T.65, but earliness is an adaptive character in the second crop in northern Taiwan.
3) yield stability: the same as T.65.

If examined in more detail, many more pleiotropic effects of the *E* gene-block may be enumerated. We may imagine that an impact on a certain phase of development gives rise to a series of changes in the outcome of development. Such might be the pleiotropic effects of a gene. Perhaps *E* has one primary effect, that is to promote flower initiation and the subsequent development of certain flower organs. The result may be increase or decrease of growth rate, growth duration and final size of various organs that develop after flower initiation.

The *E* gene was found to suppress the fifth internode that elongates immediately after flower initiation, to slow down the elongation of subsequently growing leaves, and to accelerate the elongation of panicle and upper internodes. We do not know why such sequential effects are brought about. Further, it is difficult to interpret why such a change in growth pattern results in a reduction of adaptive latitude to the amount of nitrogen applied. If we could look into the intrinsic nature of gene action and the developmental paths through which ripples provoked by a stone are transmitted, we would arrive at a solution of these questions. It may however be said that the whole pattern of genic effects is due to a particular modification of the developmental process caused by the gene.

Agronomically, the effect of the *E* gene-block may be regarded as reduction of so-called "lag-phase", or interphase between tillering and flower initiation. In general, the lag phase, that consumes time and nutrition, is not necessary for grain production when the plants are grown in good conditions (Kawano and Tanaka in press). But, in an unfavorable environment, it may serve as a safety mechanism to help the plants to restore normal growth after flower initiation. Plasticity in the early stage of growth may thus be combined

with stability in maturing. When the lag phase is removed, the plants will have a strong requirement for external conditions that are fitted to the developmental scheme prescribed by the genotype. If compared with long-term varieties, T.65 has quite a short lag-phase. But its elimination may bring about a sensitivity to unfavorable growing conditions such as too low or too high nutrient supply.

However, when tested by the standard cultural method, the early isogenic lines appeared to have seasonal and regional adaptabilities comparable to those of T.65. Also they were in both mean yield and yield stability comparble to early Ponlai varieties. If a more productive variety than T.65 were used as the recurrent parent in back-crosses, more productive early strains would be obtained. It may be suggested that early rice varieties may be obtained by the isogenic breeding method.

Summary

Taichung 65, a representative Ponlai rice variety, and its early isogenic lines, A3 and B96, were compared regarding the growth pattern of organs, temperature response and yielding capacity, to estimate the effects of the *E* gene-block carried by the isogenic lines. A comparison of lines derived from B_7 and B_{10} generations showed that the three additional back-crosses with T.65 slightly reduced the effect of the *E* gene-block on heading date. Perhaps *E* might be linked with genes exaggerating that effect. The primary effect of the *E* gene-block seemed to promote flower initiation and subsequent growth of certain flower organs. This resulted in increase or decrease of growth rate, growth duration and final size of various organs that develop after flower initiation. Further, it increased sensitivity of the plants to temperatures in the flower-initiation period. But the *E* gene did not seem to affect the seasonal and regional adaptabilities of the original genotype. In yielding capacity, the early lines were comparable to other early Ponlai varieties, and when grown in the northern regioh of Taiwan in the second crop, they gave better yield than T.65.

作物之生產能力及適應性遺傳學的研究

3. 水稻早熟遺傳因子在臺中 65 號遺傳的背景下 (genetic background) 之作用

蔡 國 海 岡 彥 一

臺中 65 號爲輪廻親本經連續回交 7 次育成之早熟 Isogenic 品系與原品種之間僅有 1 對早熟遺傳因子之差異 (Tsai and Oka 1965)。此等早熟品系 A3 與 B96 較其再經回交

3次育成的 B_{10} 品系，抽穗期稍爲提早。此可能由於 E gene-block 所含遺傳因子的作用所致。E gene-block 初步的作用係促進幼穗分化及其生長。對於幼穗分化後發生的器官之生長率，生長期間及成熟器官的大小，則產生不同的效應。此外，增加幼穗分化時期溫度反應之敏感性。惟E遺傳因子並不改變原遺傳型所具有的分蘖能力，及栽培季節與地域適應性。早熟品系在臺灣北部第二期作產量較臺中 65 號爲佳。

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