GENETIC STUDIES OF YIELDING CAPACITY AND ADAPTABILITY IN CROP PLANTS

4. Effects of an earliness gene, m_b, in the genetic background of a rice variety, Taichung 65

KUO-HAI TSAI[1] and HIKO-ICHI OKA[2]

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Abstract

From crossing experiments between isogenic early lines of Taichung 65, an earliness gene, m_b, was found, which was considered allelic with m_2. In the first crop season in which the temperatures at the time of floral initiation were about 20°–22°C, this gene moved up floral initiation by about five days. Under higher temperatures (28°–29°C) of the second crop season, it did not promote heading alone, but exaggerated the heading-promoting effect of E_a (from Tatong-tsailai) and E_b (from Bozu 5, allelic with the former). This pattern of gene action is similar to that formerly found for M_1 and m_2. The epistatic effect of m_b on E_a was apparently more pronounced than that on E_b, though E_a and E_b are isoalleles acting similarly without m_b. Further, in the first crop season, m_b tended to be dominant when E_b was absent, but was recessive when E_b coexisted. The effects of m_b on organ development were observed in comparison with those of E_b.

Introduction

In our previous paper (Tsai and Oka 1965), we reported the effects of an earliness gene, E, in the isogenic genetic background of Taichung 65. This gene was present in two isogenic early lines, A3 and B96, which were obtained from recurrent back-crossing of Taichung 65 (abbreviated as T65) with different donor parents, a Northern Chinese variety Tatong-tsailai (abbreviated

(1) Department of Agronomy, Chung-Hsing University, Taichung, Taiwan, Republic of China.
(2) National Institute of Genetics, Misima, 411 Japan.

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as Ttg) and a Northern Japanese variety Bozu 5, respectively. The *E* gene from Ttg, designated as E_a in this paper, had a slightly stronger effect in promoting heading than that from Bozu 5, E_b (Tsai and Oka 1968). In addition, we found from Ttg crosses two independent genes exaggerating the effect of E_a, M_1 and m_2. Their epistatic relation to E_a differed according to the crop season (Tsai and Oka 1966).

Our further genic analysis demonstrated that in Bozu 5 crosses was involved a gene similar to m_2, that was denoted by m_b. This paper deals with its detection and observation of its interaction with E_a and E_b in the isogenic genetic background of Taichung 65.

Materials and Methods

The rice strains used for crossing experiments are isogenic lines of Taichung 65 (T65), which were obtained from back-crosses repeated more than seven times. They are: A3 (carrying E_a from Ttg, derived from B_7), B96 (carrying E_b from Bozu 5, from B_7 and B_{14}), B172 (carrying m_b, from B_7), B20 (an early line obtained from B96×B172), and A24 (an early line obtained from A3×B172).

The plants were grown in the first and second crop seasons of 1965 to 1969 at Chung-Hsing University, Taichung. The seeding dates for the first crop were between middle January and early February, and that for the second crop was early July. Two to three week seedlings were transplanted to experimental plots dressed with 8–5–4 NPK (g/m^2), with a single plant per hill spaced at 25 cm×25 cm. For details, the reader may refer to previous papers of this series.

The date at which the first panicle emerged was recorded as the heading date for each plant. For a part of the plants, to examine the effect of genes on growth, the length of panicle, first to fifth internode (from the top), and the first to third leaf blades and leaf sheaths were measured at one week interval, starting from the time of floral initiation. To estimate this time, the growing meristems were sectioned and the developmental stage was determined by comparing the observed figure with Matsushima's (1966, p. 62–72) scheme in order to judge the time of occurrence of his first stage.

Results

1. *Detection of gene* m_b

As mentioned, B172 is an isogenic line a few days earlier than T65 in the first crop season; B96 is an isogenic line with E_b, heading about nine days earlier than T65. Data for their F_2 populations, recorded in the 1968 first and 1967 second crop seasons, are given in Table 1. The F_1 plants of B172×B96 produced panicles earlier than both parents (Table 2), and the F_2 showed a transgressive type of segregation. A fixed early F_3 line, B20, was obtained from an F_2 segregant which showed the earliest heading date. The F_2 of B172×B20 then segregated into 3 B20 and 1 B172 types, and the F_3 lines showed a ratio of 1 early: 2 segregating: 1 late (Table 1). The F_2 of T65×B172 gave a continuous range of heading dates, which could be judged to be due to a 1:2:1 type of segregation. The F_2 of T65×B20 gave an F_2 distribution similar to that of B96×B172 (Table 1).

Table 1. *Distribution of heading date in F_2 populations between isogenic early lines*

Population	May 6	8	10	12	14	16	18	20	22	24	26	28	30	June 1	3	5	7	No. of plants
1st crop, 1968:																		
T65											2	7	9	16	16	18	4	72
B96						14	31	40	33	19	19	5						161
B172									1	7	20	19	20	6	5			78
B20	1	9	31	64	54	24	14	2										199
F_2:																		
B96×B172				6	11	15	23	23	16	12	12	10	11	9	6			154
T65×B172								1		13	16	27	43	31	16	5	3	155
B172×B20		4	12	32	33	24	4	5	13	10	8	3	4	2				154
					114						40					$x^2=0.078$		(3:1)
T65×B20			1	2	8	22	19	19	18	14	12	12	11	14	1	1	1	155
F_3:			Early				Segregating				Late							Lines
B172×B20			34				66				35							135
																$x^2=0.066$		(1:2:1)

Population	Sep. 2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	Oct. 2	4	No. of plants
2nd crop, 1967:																		
T65										3	16	9	4	4	4	5		45
B96						6	10	8	12	7	1							44
B172											3	2	7	7	21	2		42
B20		4	10	14	7	4	2											41
F_2:																		
B96×B172		1	3	17	41	56	44	26	16	25	12	8	11	11	12	5	1	289
T65×B172									5	18	31	45	39	60	50	16	11	275
B172×B20	1	5	14	48	70	50	20	12	3	4	9	12	7	10	18	10	3	296
					223									73		$x^2=0.019$		(3:1)
T65×B20		2	5	16	39	58	42	28	18	28	12	7	12	10	13	4	2	296

These experimental results indicate that B172 carries an incompletely dominant earliness gene independent of E_b. It is denoted by m_b, and its allele present in T65 by $+_{m_b}$ (simply by + in the tables), as it seems to be a modifying gene exaggerating the effect of E_b as will be explained below.

2. Epistatic relation between E_b and m_b

As mentioned above, the genotypes of B172 and B20 may be considered to be $e\ m_b$ and $E_b\ m_b$, respectively. Their heading dates in the first and second crop seasons, as compared with those of T65 ($e\ +_{m_b}$) and B96 ($E_b\ +_{m_b}$), are given in the upper part of Table 2. The table shows that m_b alone (without E_b) speeds up heading by about five days in the first crop season, but in the second crop season it does not promote heading by itself only. But when m_b coexists with E_b, heading is promoted by about two weeks in similar manner in both the first and the second crop seasons, enhancing the heading promoting effect of E_b epistatically. In other words, m_b acts as an earliness gene in the first crop season, but as a modifier exaggerating the effect of E_b in

Table 2. *Effects in homo- and heterozygotic states of genes E_b and m_b on heading date*

Line	Genotype	No. of days to heading (compared with that of T65)	
		1st crop	2nd crop
(Average for 5 years, 1965–69)			
T65	e/e +/+	0 (=120.7)	0 (=83.0)
B96	E_b/E_b +/+	− 8.6	− 9.0
B172	e/e m_b/m_b	− 5.2	+ 1.3**
B20	E_b/E_b m_b/m_b	− 18.7	− 15.6
Standard error		0.48	0.58
F_1: Compared with mid-parental heading dates of respective crosses (1967 data)			
T65×B172	e/e $+/m_b$	−2.5 (−0.59)*	−0.1**
B96×B20	E_b/E_b $+/m_b$	+1.5 (+0.60)	−1.7 (−0.42)
T65×B96	E_b/e +/+	−6.5 (−0.94)	−4.5 (−1.46)
B20×B172	E_b/e m_b/m_b	−5.7 (−0.92)	−7.6 (−1.00)
T65×B20	E_b/e $+/m_b$	−2.6 (−0.24)	−1.9 (−0.27)
B172×B96	E_b/e $+/m_b$	−3.3***	−7.8***
Standard error		0.76	0.91

* Falconer's $d/a=\frac{\bar{F}_1-\frac{1}{2}(\bar{P}_1+\bar{P}_2)}{\frac{1}{2}(\bar{P}_1-\bar{P}_2)}$ (1960)

** m_b does not exert effect without E_b.

*** Transgressive segregation in F_2.

Minus signs show earliness as compared with controls, and plus signs show lateness.

the second crop season. This pattern of gene action is essentially the same as previously found for the other two genes, M_1 and m_2, which were found from Ttg crosses (Tsai and Oka 1966).

Data for the dominance of m_b in the two different crop seasons, as conditioned by the presence or absence of E_b, are given in the lower part of Table 2. In the first crop season, when E_b is absent, m_b is dominant (promotes heading) over $+_{mb}$, but when E_b is present m_b is recessive. The degree of dominance (given in parenthesis in Table 2) is about 0.6 in both positive (promoting heading, without E_b) and negative (retarding heading, with E_b) directions.

In the second crop season in which m_b alone in homozygous state does not exert effect, in heterozygous state without E_b it appears to be also null. Coexisting with E_b, m_b acts as an incompletely dominant gene promoting heading. Thus, the dominance relation of m_b differs not only according to the crop seasons, but also due to the presence or absence of E_b.

The data in Table 2 also show that E_b is a completely dominant earliness gene as described before (Tsai and Oka 1965).

3. *Epistatic relation between E_a and m_b*

To know whether m_b is allelic or not with anyone of the three modifying gene found from Ttg crosses, M_1, m_2 and m_3 (a gene similar to m_2, unpublished), lines carrying these genes in different combinations were crossed with B20 (E_b m_b). When line M70 which appeared to have E_a m_2 (derived from T65× Ttg×A3×A3) was crossed with B20, as shown in Table 3, the F_1 plants had a heading date intermediate between the parents, and the F_2 showed a segregation pattern presumably representing a 1:2:1 ratio. In contrast, crosses of B20 with lines having M_1 or m_3 all gave transgressive types of F_2 seg-

Table 3. *Comparison between m_b and m_2 and differential epistatic effects of E_a and E_b on m_b*

Line	Sep. 28	30	Oct. 1	3	5	7	9	11	13	15	17	19	No. of plants
					(1967 data)								
B20 ($E_b m_b$)					4	3	14	18	7	3			49
M70 ($E_a m_2$)	2	28	12	2									44
F_1			2	2	1								5
F_2	2	6	20	36	47	21	7	3	2	2			146
					(1969 data)								
B20 ($E_b m_b$)									1	2	5	2	10
A24 ($E_a m_b$)				1	4	3	1	2					11

regation. This suggests that m_b may be allelic with m_2.

From the cross between B172 ($e\ m_b$) and A3 ($E_a\ +_{mb}$), a fixed F_3 line showing an earlier heading date than both parents, A24, was obtained which had $E_a\ m_b$. Its heading date in the second crop season was, as shown in the lower part of Table 3, by about ten days earlier than that of B20 ($E_b\ m_b$). As mentioned, A24 and B20 are isogenic.

The earliness genes, E_a from Ttg and E_b from Bozu 5, are allelic (Tsai and Oka 1965). As already mentioned, E_a had a slightly stronger effect than E_b when no modifier coexisted (Tsai and Oka 1968). However, as shown above, m_b exerted an apparently more pronounced epistatic effect with E_a than with E_b. The effect of m_b on E_b in the second crop season was estimated to promote heading by 6.6 (=15.6−9.0, in Table 2) days, while its effect on E_a was to promote heading by more than 16 days. The F_2 segregation for heading date due to E_a/E_b and m_2/m_b, shown in Table 3, may be attributed rather to E_a/E_b than to m_2/m_b. This indicates that E_a from Ttg and E_b from Bozu 5 are isoalleles as defined by Allard (1964, p. 468), differing in the mode of epistatic effect with m_b.

4. Effects on organ development of m_b and E_b

Comparing four isogenic lines carrying $e\ +_{mb}$ (T65), $E_b\ +_{mb}$ (B96), $e\ m_b$

Table 4. *Date of floral initiation as conditioned by genes E_b and m_b (difference in days from the date for T65, in 1967)*

Crop season	Line	Genotype	Midtiller*	Floral initiation	Days from fl. initia. to heading	Heading date	Maturity
1st	T65	e +	Apr. 23	a) May 3.0 b) May 5.9	39.6 39.1	June 11.6 June 14.0	July 10
	B172	$e\ m_b$	+ 2.5	a) − 4.3 b) + 0.8	− 1.9 − 4.0	− 6.2 − 3.2	− 7
	B96	E_b +	+ 1.3	a) − 4.8 b) − 4.6	− 3.5 − 2.7	− 8.3 − 7.3	− 9
	B20	$E_b\ m_b$	+ 1.0	a) − 13.4 b) − 13.5	− 10.1 − 3.3	− 23.5 − 16.8	− 18
2nd	T65	e +	Aug. 16	a) Aug. 25.6 b) Aug. 26.3	38.1 39.2	Oct. 2.7 Oct. 4.5	Nov. 2
	B172	$e\ m_b$	+ 3.0	a) + 2.2 b) + 3.0	+ 1.8 + 0.9	+ 4.0 + 3.9	0
	B96	E_b +	+ 3.0	a) − 5.3 b) − 2.0	− 3.2 − 5.4	− 8.0 − 7.4	− 14
	B20	$E_b\ m_b$	+ 2.6	a) − 14.4 b) − 8.2	− 9.7 − 7.3	− 24.1 − 15.5	− 24

* The time at which tiller number reaches 1/2 of the maximum number, estimated by fitting the data to a logistic function.
a) Mean for earliest heading four stems.
b) Mean for latest heading three stems.

(B172) and E_b m_b (B20), the effects of m_b and E_b on the development of various organs were investigated. The dates of floral initiation estimated in different lines are given in Table 4. In the first crop season, the promoting effect on floral initiation of E_b was by about five days and that of m_b by about four days. When they worked together, they promoted floral initiation by about 13 days. They also shortened the period from floral initiation to heading by a few days. In the second crop, m_b promoted floral initiation and shortened the period from floral initiation to heading only when E_b coexisted. Without E_b, m_b tended to retarding flower initiation and heading slightly.

The size or number of various organs measured at maturity in the four isogenic lines is given in Table 5. As formerly reported (Tsai and Oka 1968),

Table 5. *Measurements for various organs at maturity of isogenic early lines, in per cent of the values of T65 (in 1967)*

Organ	1st crop season				2nd crop season			
	T65	B172 m_b (%)	B96 E_b (%)	B20 E_bm_b (%)	T65	B172 m_b (%)	B96 E_b (%)	B20 E_bm_b (%)
Panicle (cm)	21.5±0.79	96	96	91	20.6±0.85	94	93	91
Internode (cm)								
1st	42.9±4.68	101	98	91	40.3±1.94	94	97	94
2nd	21.7±1.18	101	91	98	20.8±1.28	100	104	84
3rd	11.8±0.86	114	116	53	13.4±2.09	93	87	57
4th	8.7±1.39	71	55	12	5.9±1.79	98	70	26
5th	1.2±0.66	67	58	25	1.4±0.70	78	57	21
Leaf sheath (cm)								
1st	31.2±0.89	99	98	92	30.1±1.07	95	97	95
2nd	24.9±0.82	100	97	88	24.1±1.67	95	97	90
3rd	24.0±0.65	98	95	78	23.2±0.22	99	97	81
Leaf blade (cm)								
1st	32.7±3.79	95	88	87	29.8±3.59	88	89	92
2nd	40.2±3.06	105	99	91	38.9±4.16	99	96	89
3rd	41.1±2.29	99	95	76	40.7±2.66	102	96	76
Blade width (mm)								
1st	13.9±0.67	97	97	90	12.7±0.95	99	99	97
2nd	10.5±0.91	98	100	84	9.9±0.70	100	95	95
3rd	8.9±0.80	99	97	81	8.7±0.71	101	90	85
Spikelet no. per panicle	102±10.6	102	102	94	128±16.2	89	79	71
Panicle no. per plant	16.0±2.61	112	97	100	10.4±2.37	100	121	110
Spikelet (mm)								
length	7.23±0.08	102	102	103	7.36±0.08	102	101	102
width	3.36±0.06	100	95	96	3.35±0.04	101	98	98
1,000 grains (g)	27.2	99	94	94	24.6	95	104	116

E_b reduced the length of various organs that develop after floral initiation, particularly of the fourth and fifth internodes. Working alone (without E_b), m_b also reduced the length of fourth and fifth internodes in the first crop season, and the fifth internode only in the second crop. When E_b and m_b worked together, they remarkably reduced the length of third to fifth internodes as well as of the second and third leaves; the panicle and first leaf were also shortened to some extent. In the second crop season, the two genes both tended to reduce spikelet number per panicle and to increase panicle number per plant.

From the measurements of organ length recorded at one week intervals, logistic equations were computed for individual organs that develop after

Table 6. *Parameters of growth curves for organ elongation, as compared between isogenic early lines and T65 (in 1969)*

Organ	No. of days from fl. initia. to $t_{1/2}$				No. of days from $t_{1/10}$ to $t_{9/10}$				dy/dt at $t_{1/2}$ (cm/day)			
	T65	B172	B96	B20	T65	B172	B96	B20	T65	B172	B96	B20
First crop season:												
Date of floral initiation	Apr. 23	18	13	7								
2nd leaf sheath	19	21	22	19	12	15	16	17	2.3	2.2	2.0	1.6
1st leaf blade	21	16	19	19	18	11	15	21	2.2	2.7	2.4	1.6
4th internode	22	26	24	17	30	25	23	18	0.2	0.2	0.3	0.1
1st leaf sheath	21	22	26	22	10	11	11	10	3.8	3.0	3.4	3.2
Panicle	25	26	27	23	9	11	12	9	3.0	2.2	2.2	2.6
3rd internode	28	31	31	27	15	18	16	10	1.0	0.8	0.8	1.0
2nd internode	35	35	36	34	10	11	10	8	2.5	2.3	2.5	2.6
1st internode	35	36	36	34	9	8	9	11	5.4	6.4	5.8	3.9
Second crop season:												
Date of floral initiation	Aug. 31	31	25	7								
2nd leaf sheath	21	17	17	16	22	13	12	15	1.2	2.1	2.5	1.7
1st leaf blade	21	18	17	16	23	7	11	18	1.4	5.1	2.9	1.9
4th internode	21	22	23	20	22	24	24	36	0.4	0.3	0.3	0.1
1st leaf sheath	27	22	22	21	17	9	7	9	2.5	5.7	5.1	3.7
Panicle	26	25	21	21	12	12	8	10	1.4	1.9	1.0	2.4
3rd internode	28	29	27	27	20	16	19	17	0.7	0.8	0.8	0.7
2nd internode	37	37	32	29	14	16	10	13	1.4	1.4	2.0	1.7
1st internode	39	37	30	33	12	13	9	11	3.6	3.3	4.0	3.8

$t_{1/2}$, $t_{1/10}$ and $t_{9/10}$: The time at which the size of a given organ reaches 1/2, 1/10 and 9/10 of the final size, respectively.

dy/dt: Growth rate in cm/day.

floral initiation, in the same manner as reported for A3 and B96 (Tsai and Oka 1968). The results are given in Table 6, which shows that as previously found for E_a and E_b, m_b may increase or decrease the growth rate (dy/dt at $t_{1/2}$, at which the size of an organ reaches 1/2 of the final size) and growth duration (number of days from $t_{1/10}$ to $t_{9/10}$) of certain organs. It seems that in the first crop season m_b moves up the time of elongation of the first leaf blade and increases its growth rate, but reduces its growth duration. It also retarded elongation of the fourth internode. When E_b and m_b worked together, the growth duration as well as the growth rate of fourth internode were much reduced, while the second leaf sheath and first leaf blade had a prolonged growth duration.

In the second crop season, when E_b was absent, m_b moved up the elongation time and increased the growth rate of first leaf blade and first and second leaf sheaths, reducing their growth duration. Working together with E_b, m_b moved up further the elongation time of panicle, increasing its growth rate and reducing its growth duration. Thus, m_b seems to control primarily the time of floral initiation and consequently modifies the pattern of organ development in different ways between the first and second crop seasons.

Discussion

In this series of studies on earliness genes of rice, our method is basically developed for detecting genes of relatively small effect by isolating them in an isogenic genetic background and to observe their effects on growth pattern. In a segregating population between two given strains, such genes will bring about a continuous array of intergrades, which is usually subjected to biometrical methods of analysis. But we are not satisfied with the biometrical method as it can give us only a generalized picture. A gene controlling quantitative characters may have a particular mode of action and a particular epistatic relation with another gene. Though our method is time-consuming, we expect to learn to some extent the pattern of gene actions conditioning floral initiation and growth.

It is interesting to find that gene m_b is in the second crop season a modifier exaggerating the effect of E_a and E_b, while in the first crop season it promotes floral initiation and panicle development without the aid of E_b. This is consistent with the pattern found for M_1 and m_2 (Tsai and Oka 1966). In our previous work, the action of these two genes was estimated by using materials obtained after one or two back-crosses; in the present study, the action of m_b was estimated more precisely in a practically isogenic genetic background.

The difference in gene action between the two crop seasons may be due to a difference in temperature, since all plants studied are insensitive to photoperiod. The average temperatures around the time of floral initiation are in the first crop (early April) about 20°–22°C and in the second crop (middle August) 28°–29°C.

We also found that the dominance of m_b differed according to the presence or absence of E_b. When E_b was absent, m_b tended to be dominant, but when E_b was present, it was recessive. Such an epistatic change in dominance does not seem to have been reported before, to the knowledge of the present writers. This relation may also differ according to temperatures. Further, m_b had different epistatic relations with the two isoalleles, E_a and E_b. It may be suggested that the enzyme protein synthesized by m_b is activated by a delicately adjusted inducer-repressor system.

In the same manner as found for E_a and E_b (Tsai and Oka 1968), m_b produced a particular pattern of pleiotropic effects on character development, which differed between the first and second crop seasons. Possibly, the primary effect of m_b may be a promotion of floral initiation. It may then modify the developmental process changing the growth rate and growth duration of organs that develop after floral initiation and their time sequence. Under seasonally fluctuating environments, this gene may then modify the adaptability of the plants as formerly discussed for E_a and E_b (Tsai and Oka 1968).

作物生產能力及適應性之遺傳學的研究

4. 水稻早熟遺傳因子 m_b 在臺中65號遺傳的背景下之作用

蔡 國 海　岡 彥 一

稉稻早熟品種坊主5號具有早熟遺傳因子 E_b 與 m_b。E_b 與大同在來所攜之 E_a 爲相對因子，效應亦相似，而 m_b 與 m_2 (Tsai and Oka 1966) 亦爲相對因子。低溫條件之一期作時，m_b 與 m_2 同樣單獨可促進幼穗形成約5日，而在高溫條件之二期作時，與 E_a 或 E_b 共存時，其作用始能顯現，惟與前者共存時作用較著。一期作 m_b 單獨時顯示顯性，而 E_b 存在時顯示隱性。此外，採用過去研究 E_b 之效應的方法 (Tsai and Oka 1968)，曾分析 m_b 對各種器官之發育的效應。

Literature Cited

ALLARD, R. W. Principles of Plant Breeding. Wiley, New York, 1964.

FALCONER, D. S. Introduction to Quantitative Genetics. Ronald Press, New York, 1960.

MATSUSHIMA, S. Crop Science in Rice. Fuji Publ. Co., Tokyo, 1966.

TSAI, K. H. and H. I. OKA Genetic studies of yielding capacity and adaptability in crop plants, 1. Characters of isogenic lines in rice. Bot. Bull. Acad. Sinica **6**:19-31, 1965.

_______ and _______ Ditto, 2. Analysis of genes controlling heading time in Taichung 65 and other rice varieties. *Ibid.* **7**:54-70, 1966.

_______ and _______ Ditto, 3. Further observations on the effects of an earliness gene, *E*, in the genetic background of a rice variety, Taichung 65. *Ibid.* **9**:75-88, 1968.