GENETIC STUDIES OF YIELDING CAPACITY AND ADAPTABILITY IN CROP PLANTS

1. Characters of Isogenic Lines in Rice

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Introduction

Taichung 65 is a representative Ponlai (or Horai, Japonica) rice variety of Taiwan, selected from a hybrid between two Japanese varieties, Kameji and Shinriki. This photoperiod-insensitive variety is adapted for growing in both first (January-June) and the second (July-October) crop seasons under different environmental conditions. It also has a wide regional adaptability and can be grown in various tropical and sub-tropical countries of the world. If cultivated intensively, it gives a high yield.

We have attempted to develop isogenic lines of this variety with single gene differences by back-crossing. The genotype of an established variety may be regarded as a balanced entity. When a gene is replaced by its allele, the whole adaptive balance might be affected. Knowledge in this respect may serve as a basis for studying problems related to mutation and adaptation in crop plants. This paper deals with character variations of the presumably isogenic lines grown under different conditions.

Materials and Methods

In the back-crossing experiment, a pure strain of Taichung 65 was used as the recurrent parent (used as the maternal parent at least once), and three different varieties each possessing a certain gene were employed as the donor parents. They are Kinoshita-mochi (glutinous, from Japan), Tatong-tsailai

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(early, from North China) and Bozu 5 (early, from Japan), all belonging to the Japonica type and insensitive to photoperiod. Back-crossing was repeated seven times, and a number of glutinous or early-maturing homozygous lines were selected from the B_7F_2 populations. As those lines appeared to be homogeneous, a few of them were selected for comparison with the recurrent parent.

The materials were grown in the experimental field of Chung-Hsing University, Taichung, according to the standard method of rice culture in Taiwan. Seeds were pre-soaked for germination in early January (for the 1st crop) and in early July (for the 2nd crop). Seedlings were raised in nursery-beds for about 35 days (1st crop), and for 20 days (2nd crop). The seedlings were transplanted and spaced at 25 cm×25 cm, with three plants per hill. The standard mixture of fertilizers applied consisted of ammonium sulfate, calcium superphosphate and potassium sulfate, the dosage being N 80, P_2O_5 50 and K_2O 40 kg/ha. P and K fertilizers and one half of the ammonium sulfate were applied as basic dressing. The other half of ammonium sulfate was divided into two parts, and they were applied at the time of the first and second weeding, which were made about 10 and 18 days after transplanting, respectively. For most experiments, the randomized block design with three replications was adopted. A plot was 5 m^2 or larger. Measurements were taken on grain yield, heading date and other agronomic characters.

Results of Experiments

1. *Glutinous isogenic lines*

As previously reported by Tsai (1961), 22 glutinous and 22 non-glutinous B_7F_3 lines, tested in 1958, were found to be homogeneous in grain yield and other agronomic characters. Then, in the following two years, three glutinous lines were compared with two of their non-glutinous sibs and the recurrent strain of Taichung 65, in 6×6 latin-square experiments. They showed no significant differences in grain yield and other characters (Table 1). They may be regarded as "isogenic lines" of Taichung 65.

Table 1. *Grain yield and plant height of glutinous and non-glutinous isogenic lines of Taichung 65.*
(Average for 1959 and 1960)

Endosperm character	Grain yield (kg/ha)		Plant height (cm)	
	1st crop	2nd crop	1st crop	2nd crop
Glutinous	5,648	5,426	111.6	107.6
Non-glutinous	5,528	5,540	111.9	108.3

Glutinous rice varieties are generally lower yielders than nonglutinous ones. It is believed that the glutinous gene, producing amylopectin instead of amylose and amylopectin, directly affects yield (Morinaga 1943). However, our results indicate that the glutinous gene in the genetic background of Taichung 65 did not affect yielding capacity. It was also found that rice cakes made from our glutinous lines were of the same eating quality as those made from commercial glutinous rice, though the ratio of amylose and amylopectin was not determined. Thus, isogenic glutinous varieties may be obtained simply by allele replacement.

It is well known that in hybrids between non-glutinous and glutinous varieties, the segregation ratios are often modified due to certation in favor of the non-glutinous pollen grains. In the F_1 hybrid between Taichung 65 and its glutinous isogenic strain, the certation effect was apparently weaker than that in other varietal crosses, as shown in Table 2. It seems that the usually observed decrease of glutinous segregants ascribed to certation might be due not only to the delaying effect of the glutinous gene on pollen-tube growth, bnt also to other modifying genes which magnify the effect.

Table 2. *Segregation ratios for glutinous endosperm.*

Cross	No. of grains		Ratio	x^2 from the 3:1 ratio
	Non-gluti.	Gluti.		
Isogenic: Non-glu. × Gluti.	657	208	3.16:1	0.420
Taichung 65 ×: Taichung-mochi 46	958	242	3.96:1	14.952
Kinoshita-mochi	976	231	4.23:1	22.116
Hung-chio-chiu (indica)	879	228	3.89:1	11.448

2. *Breeding of early isogenic lines of Taichung 65*

Twenty seven B_7F_3 lines with the earliness gene or genes of Tatong-tsailai (group A), and seven with that of Bozu 5 (group B) were tested in 1959 and 1960 in simple-lattice experiments with four replications. These lines were about eight days earlier than Taichung 65, and had the same plant type. But they were to some extent heterogeneous in yielding capacity. A few lines giving high yields were then selected from both groups for further experimentation. Mean measurements on yield and other characters for two early lines, A3 and B96, are given in Table 3. They are called "early isogenic lines" of Taichung 65.

The two early lines did not differ significantly in all measured characters. As shown in Table 3, both were eight days earlier (ca. 6% in the first crop and 10% in the second crop) than Taichung 65, and also had shorter straw, shorter panicles, and fewer spikelets per panicle. Their 1000 grain weight did not differ from that of Taichung 65 in the first crop, but was somewhat lower in the second crop. They had as high a fertility as Taichung 65 in most cases. Their panicle number per hill was the same as that of the control, or slightly, but insignificantly, larger. In the first crop, the early lines gave yields slightly lower than Taichung 65, the differences being in most cases statistically insignificant. In the second crop, their yields were significantly lower, though the difference was in some cases (for instance, in 1961) due to typhoon damage suffered at the heading stage. Thus, the early lines tended to be better adapted to the first than to the second crop.

In Taiwan, early varieties generally give lower grain yield than late ones. Earlier varieties than Taichung 65 are generally low yielders. The early isogenic lines of Taichung 65 however gave the same yield as Taichung 150 (3 days earlier than Taichung 65) and a higher yield than Taichung 180 (11 days earlier), which are both commercial varieties. The rate of decrease in yield per day due to the shortening of growing period was 0.9% (1st crop) to 2.2% (2nd crop), for the early isogenic lines 1.3% to 4.4%, for Taichung 150 and 1.7% to 2.1%, for Taichung 180 when compared with Taichung 65.

Table 3. *Grain yield and other characters of early isogenic lines of Taichung 65. (Average for 1960–62)*

Strain	No. of days seed.-head.		Grain yield (kg/ha)				(in %)	
	1st crop	2nd crop	1st crop		2nd crop		1st crop	2nd crop
			1961	1962	1960	1962		
Taichung 65	122	79	5,284	6,571	4,832	3,915	100	100
Isogenic, Early A3	114	71	5,105	5,856	4,040	2,896	92.9	79.0
Early B96	115	71	5,035	6,144	4,120	3,301	94.4	84.8
Taichung 150	119	76	—	6,309	—	3,397	96.0	86.5
Taichung 180	112	67	—	5,490	—	2,944	83.5	75.2

Strain	Plant height (cm)		Panicle length (cm)		Panicle no./hill	
	1st	2nd	1st	2nd	1st	2nd
Taichung 65	112.1	110.4	20.7	20.7	18.5	15.7
Isogenic, Early A3	101.0	104.3	18.4	19.2	19.6	15.5
Early B96	105.2	106.9	19.1	18.9	21.0	16.6
Taichung 150	110.8	111.7	19.4	19.0	19.0	17.6
Taichung 180	97.9	97.5	17.8	17.5	19.0	16.8

Strain	Grain no./pancile		1000 grain weight (gm)	
	1st	2nd	1st	2nd
Taichung 65	99.6	91.7	29.2	28.0
Isogenic, Early A3	90.8	86.4	28.6	24.5
Early B96	86.1	89.5	28.9	24.4
Taichung 150	95.1	78.0	28.4	26.3
Taichung 180	85.0	80.3	28.2	24.5

In addition to these, lines about three days earlier than Taichung 65 were obtained from the B_7F_3 populations. They had the same character measurements and grain yield as Taichung 65.

3. *Crossing experiments with early isogenic lines and Taichung 65*

When the early isogenic lines were crossed with the original strain of Taichung 65, a 3:1 ratio, earliness being dominant, was found in the F_2. As the above-mentioned comparisons between the early and original strains have shown, all early F_2 segregants had smaller measurements in plant height and other characters than the late ones. This indicated that the early lines differ from Taichung 65 monogenically in the gene for maturity while the gene (and/or genes closely linked with it) reduces the magnitude of other characters, which are inter-related physiologically in the developmental process. Genetic and environmental correlations between those characters were estimated from variances and covariances of the parental strains and the F_2 population. As given in Table 4, it was found that growing period, plant height, panicle length, and grain number per panicle were genetically correlated, in so far as the second crop experiment was concerned. This also indicates the pleiotropic effects of the earliness gene on other characters. It seems that the pattern of pleiotropic effects differs between the first and second crop seasons. This point is now under observation.

The two selected early lines, one (A3) having the earliness gene of Tatong-tsailai and other (B96) with that of Bozu 5, were then crossed with each other. The F_1 showed the same heading date as both parents and the F_2 had approximately the same variation range as the parents (Table 5). As already mentioned, the two lines have the same measurements of other characters. It may then be inferred that the earliness genes of the donor parents, Tatong-tsailai and Bozu 5, are located at the same locus and have almost the same effect. Tatong-tsailai is a variety from North China, while Bozu 5 is from Hokkaido, Japan. When grown in Taichung, the former reaches heading at about 40 days after germination (2nd crop), and is about 15 days earlier than the latter. Their difference might be due mainly to modifiers acting on the earliness gene.

Table 4. *Genetic and environmental correlations estimated from F_2 populations between early isogenic lines and original strain.* (*2nd crop, 1961*)

Character	Taichung 65×Early A3		Taichung 65×Early B96	
	Genetic	Environ.	Genetic	Environ.
Heading date-				
Plant height	0.75	-0.13	0.62	0.01
Panicle length	1.03	0.05	1.12	-0.07
Grain no./panicle	1.07	-0.18	1.04	-0.24*
Panicle no./plant	0.02	-0.07	-0.35	-0.06
Plant height-				
Panicle length	0.97	-0.19	1.03	-0.04
Grain no./panicle	0.92	-0.06	1.09	0.01
Panicle no./plant	0.27	0.18	0.89	0.30*
Panicle length-				
Grain no./panicle	1.00	0.65**	1.01	0.77**
Panicle no./plant	0.12	-0.18	0.43	-0.02
Grain no./panicle-				
Panicle no./plant	0.22	-0.11	0.60	-0.09

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

Table 5. *Distributions of heading date in F_2 populations between the original and two early isogenic lines.* (*1961*)

Strain	Sep. 14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Oct. 1	No. of plants
Taichung 65											2	7	9	16	6	8	1	1	50
Early A3	3	10	21	13	2														49
Early B96		3	10	13	15	7	1												49
F_2:																			
Taichung 65×																			
A3	9	19	35	34	8	3						16	14	3	1	1	1		144
B96		8	21	27	25	10	8	2	1	3	5	15	14	7	1	1			148

Between two early isogenic lines. (*1963*)

Strain	May 17	18	19	20	21	22	23	24	25	26	No. of plants
Early A3	1	6		5	9	9	2	2			34
Early B96	1	2		5	6	5	2	2		1	24
F_2	1	3	15	9	17	29	17	6	2		98

It was found, however, that when seeded in September, the two early lines had different growing periods; A3 was significantly earlier than B96. It may be that the earliness genes, or closely linked genes, from the two donor parents differ in the mode of temperature response. This problem, and the presumable difference in modifiers between the two donor parents are now under further study.

4. *Responses to growing conditions of early isogenic lines*

As the two early lines had almost the same character measurements, their average measurements were used for looking into how they may be compared with Taichung 65 in response to growing conditions. Their differences from Taichung 65 may be, as mentioned above, mainly ascribed to the action of the earliness gene under discussion.

Fertilizer response: Early varieties tend to have higher nitrogen response than late ones (c. f. Oka 1956). To investigate the effect of the earliness gene on fertilizer response, the early strains and the original one were compared at three levels of fertilizer application, namely, no fertilizer, standard (80–50–40) and double fertilizer (160–100–80). This experiment was carried out in the two crop seasons of 1961 to 1963, according to randomized complete blocks with three replications.

The average measurements of grain yield and other characters at different fertilizer levels (as per cent of those at the standard level) are given in Table 6. The data show that the original strain gave the highest yield in double-fertilizer plots, while the early lines yielded best in standard plots, and in no-fertilizer plots the yield of early lines was much lower than that of the original strain. This indicates that the early lines have a higher initial fertilizer response, but a lower tolerance to a heavy fertilization, than Taichung 65. In other words, the early lines had a narrow adaptive range to the amount of fertilizers applied. Variance analysis of the data showed that these differences between the early and the original genotypes were significant.

As to other characters, however, as shown in Table 6, differences in fertilizer response between the early and the original strain were not clearly recognized. Grain number per panicle seemed to behave in the same manner as grain yield. In panicle number per hill, which may be used as an index of fertilizer response (Oka 1956), the early lines had a higher response than the control in the first crop, but showed the same response in the second crop. It may be inferred that the early lines are more responsive to fertilizers than Taichung 65 in panicle production, but when too many panicles are produced, the spikelets are not fully filled with grains.

Response to plant number per hill: When hills are spaced at 25 cm × 25 cm, three seedlings per hill is generalized as an appropriate planting density. The

Table 6. *Fertilizer response of early isogenic lines.* (*Average for 1961–63*)

Character	Line	1st crop			2nd crop		
		No. ferti.	Standard	Double	No. ferti.	Standard	Double
Grain yield	Early	56.4	100	92.3	69.4	100	95.5
	T. 65	77.8	100	104.7	80.0	100	103.6
Plant height	Early	89.6	100	107.5	90.8	100	103.6
	T. 65	90.3	100	108.5	93.4	100	102.7
Panicle length	Early	93.4	100	102.4	96.6	100	102.1
	T. 65	95.5	100	104.6	99.7	100	100.1
Grain no./panicle	Early	87.0	100	101.8	97.3	100	95.6
	T. 65	94.3	100	114.1	102.4	100	95.0
Panicle no./hill	Early	66.2	100	122.3	65.4	100	119.1
	T. 65	67.0	100	114.2	65.8	100	119.8

Early: Average for A3 and B96.

manner in which grain yield and other characters were affected by single-plant-per-hill plantings, was investigated in the early strains and Taichung 65. Randomized block experiments with three replications were made in 1961 to 1962. As shown in Table 7, the early lines were found to exhibit a greater decrease in grain yield due to the single-plant planting than Taichung 65. This suggests that the early lines are adapted to dense planting, though they might have the same tillering capacity as Taichung 65.

Table 7. *Responses to plant number per hill and nursery-bed period of early isogenic lines.* (*Average for 1961–62*)

Character	Line	(Plant number per hill)				(Nursery-bed period)			
		1st crop		2nd crop		1st crop		2nd crop	
		1 plant	3 plants	1 plant	3 plants	30 days	50 days	20 days	25 days
Grain yield	Early	90.4	100	92.9	100	100	87.2	100	97.6
	T. 65	94.8	100	95.3	100	100	85.5	100	97.4
Panicle no./hill	Early	76.5	100	83.5	100	100	90.8	100	93.7
	T. 65	77.5	100	89.3	100	100	92.9	100	97.3

Early: Average for A3 and B96.

Response to nursery-bed period: Grain yield in Ponlai varieties generally tends to decrease as the nursery-bed period is extended. Experiments to compare this response between the early strains and Taichung 65 were repeated several times (30, 40 and 50 days for the first crop; 15, 20 and 25 days for the second crop), but the results fluctuated from experiment to experiment as an effect of other factors, and no definite conclusion could be drawn. It was observed however that the early lines had a higher rate of panicle number reduction due to the extension of nursery-bed period than Taichung 65.

Fertilizer level, planting density, and the nursery-bed period, constitute an important portion of the cultural condition of plants. The above experimental results seem to indicate that the optimum growing conditions for the early lines do not differ much from that for Taichung 65, but that the former are more sensitive to deviations from the optimum than the latter.

Table 8. *Within-and between-plant variances of characters in early and original strains.* (*1963*)

Character	Line	Within-plant variance				Between-plant variance			
		No. ferti.		Standard		No. ferti.		Standard	
		1st	2nd	1st	2nd	1st	2nd	1st	2nd
Culm length	Early*	119.4	89.4	128.2	97.8	29.3	23.7	31.8	23.2
	T. 65	122.5	88.2	105.8	87.3	14.7	31.6	21.5	31.6
Panicle length	Early*	7.30	4.70	5.70	5.55	1.54	0.90	0.79	0.90
	T. 65	6.03	4.69	5.29	6.62	0.33	1.22	0.82	1.96
Grain no./panicle	Early*	963.1	503.2	933.8	630.0	150.1	88.4	156.2	116.6
	T. 65	705.5	626.0	697.5	773.8	52.7	159.9	114.0	239.1

* Average for A3 and B96.

Further, under the assumption that the uniformity of growth may be a measure of adaptability to a given environment, the early strains and Taichung 65 were compared regarding between-and within-plant (among-tillers) variances of three characters. As shown in Table 8, the early line tended to have larger between-plant variances than Taichung 65, particularly in the first crop, but no significant differences were found in the amount of within-plant variances.

Mix-planting of the early strains and Taichung 65 was also made to compare their relative competitive ability. When mix-planted with Taichung 65, the early lines showed a slight decrease in panicle number per plant, though the difference was insignificant. The earliness gene did not seem to affect competitive ability adversely.

Discussion

Back-cross derivatives carrying a particular gene may be compared with induced mutants. The major difference between them is that the former possess a gene of spontaneous origin which has long been maintained in a certain genetic background, while the latter carry a newly mutated gene. In this study two kinds of "isogenic" lines of Taichung 65 were examined, one with the glutinous gene and the other with an earliness gene. Repetition of back-crossing for seven times is not enough to produce completely isogenic strains. Our materials may be considered isogenic in the sense that they have practically the same genetic background. Similarly, induced mutants from a pure line may be regarded as another isogenic group.

Our results showed that the glutinous gene did not affect the yielding capacity of the original genotype. The enzymic reaction leading to the loss of a capacity for amylose production is not associated with a reduced grain yield. This suggests that the back-crossing method is useful for breeding essentially isogenic varieties with a modified character such as glutinous endosperm. In the same manner, a mutant with such a genic change, if selected, may be directly used. It may be questioned, however, why most glutinous rice varieties are low yielders if compared with nonglutinous ones.

In contrast, our early isogenic lines differed in many respects from the original strain, indicating that the replacement of a gene controlling the so-called yield characters involves changes related to the physiology and adaptation to environment of the original genotype. As mentioned in the introduction, Taichung 65 is a variety with wide seasonal as well as regional adaptabilities. It can give high yields in a diversity of environmental conditions though it requires intensive cultivation. It was also found that the early lines of this variety gave a high yield, when they were grown under good cultural conditions. This indicates that the original genotype allows a latitude not only for environmental variations but also for gene replacements, which leads to the following consideration. The early lines had a relatively narrow adaptive range to fertilizers and other cultural conditions in the present study. Also their yields were relatively low in the second crop which growed under high temperatures. It seems that the gene replacement diminished the potential latitude of the original genotype, resulting in a reduction of the adaptive range to environmental variations. The same result may be expected for genic changes towards larger grain number per panicle, grain size, etc. We may thus assume that an established genotype possesses a latitude which is reduced by genic changes.

The earliness gene used in this experiment simultaneously reduced plant height, panicle length, and grain number per panicle. It may possibly shorten internodes, panicle axes, and rachillae. However, the rates of reduction in these characters seemed to be lower than the rate of shortening of the growing period. It seems that the earliness gene accelerates the growth of various organs but stops their development early, and thus reduces the potential yielding capacity of the original genotype. It also reduces the adaptive range to environment. In the present experiment, the two early varieties used as the donor parents, appeared to involve the same earliness locus. This suggests that major earliness genes distributed in various *sativa* varieties are not numerous and that a survey of their allelic relationships may not be very troublesome if those controlling photoperiodic and temperature responses are excluded, though there might be a number of modifying genes controlling growth duration. It remains to be investigated whether other earliness genes, if found, have the same pleiotropic effects as above mentioned. Induced early mutants may also be examined from this viewpoint.

Grain yield and the length of growing period are often found to be genetically negatively correlated in a hybrid population, or in a certain variety group. It is thought that the shorter the vegetative period, the less is the amount of carbohydrate assimilation. It is however known that about 2/3 of the starch accumulated in rice grains of Japanese varieties is due to assimilation after heading (Matsushima 1959 pp 171–8). Also under the conditions of intensive culture, the "lag-phase" of vegetative growth, if ever, may be eliminated without affecting grain yield. Historically saying, the advancement of rice yield achieved in Taiwan as well as in Japan is largely due to breeding of early varieties with a high yielding capacity, which are generally insensitive to photoperiod and have higher responses to fertilizers, early planting, and other improved cultural, conditions. (c. f. Ishizumi 1962). Within the limits of a given cultivation system, yield and growing period may be negatively correlated, but when growing conditions shift, yield per unit time can be improved. To improve early varieties, therefore, breeders should explore new growing conditions and simultaneously select genotypes adapted to the new environment. This is however a long-time effort.

To obtain an early variety for a given condition, we may use hybridization, mutation, or back-crossing. From the theory that genic replacement or change decreases the adaptive latitude of the original genotype, hybridization and careful selection seem to be the only way for obtaining an early genotype with an adequate adaptive latitude. In other words, an earliness gene will perform best in its particular genetic background. However, rice breeders have often experienced that selection of an early variety with a high yielding capacity is difficult. This is quite true for the second crop in Taiwan. Our early isogenic lines of Taichung 65 were, in terms of yield reduction per unit abbreviation of the growing period, better yielders than the established early varieties, Taichung 150 and Taichung 180. This indicates that if the original genotype has a wide adaptability, the mutation or gene replacement method can be favorably used. It may be safely used at least when the desired maturity is less than one week earlier than that of a given variety.

Summary

"Isogenic lines" of a Ponlai (Horai, Japonica) rice variety of Taiwan, Taichung 65, having the glutinous gene or an earliness gene, were obtained by repeated back-crossing (seven times). The glutinous lines had the same yielding capacity as Taichung 65, indicating that the glutinous gene itself does not reduce yield. In the F_1 hybrid with the original non-glutinous strain, certation in favor of non-glutinous pollen was not so pronounced as in ordinary varietal crosses.

The earliness gene in two isogenic lines, for which two early varieties (one from Japan and the other from North China), were used as the donor parents, was found to involve almost at the same locus. They were about eight days earlier than Taichung 65 in both the first and the second crop, and their grain yield was, when grown in a conventionary optimum condition, about 94% (1st crop) and 85% (2nd crop) of that of the original strain. The earliness gene pleiotropically reduced plant height, panicle length, and grain number per panicle in the second crop season. Further, the early lines showed higher sensitivity to fertilizer, planting density, and the duration of nursery-bed period than the original strain, suggesting that the adaptive latitude of the original genotype might have been diminished by the gene replacement. On the basis of these findings, the use of back-crossing and mutation-induction methods for variety improvement was discussed.

作物之生產能力及適應性遺傳學的研究

1. 水稻 Isogenic 系統之特性

蔡國海　岡彥一

以粳稻蓬萊種臺中 65 號爲輪廻親本，粳稻與糯米及早熟粳稻，行連續回交 7 次，育成臺中 65 號的糯米及早熟 Isogenic 新品系。糯米新品系產量與臺中 65 號相同，顯示糯性因子本身並無減低產量之作用，糯米品質亦佳。新品系與臺中 65 號間之雜種，亦少於粳糯性花粉之競爭授精現象。

華北及日本早熟品種爲一次親本，所育成之早熟臺中 65 號品系，早熟遺傳因子具有相同座位。早熟新品系在一、二期作均早熟約 8 日，產量在適宜栽培條件下，一期作可達臺中 65 號之 94%，二期作 85%。早熟新品系之稈長，穗長，及一穗粒數等略見低減，二期作早熟遺傳因子對其他農藝性狀具有多種效應外，對肥料，單株苗數及苗齡等栽培條件似亦較敏感，適應性較狹；早熟遺傳因子之更換似可能減少原有因子型所有的適應寬度。基於此種發現，對利用回交法及誘變法之育種曾加以討論。

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