

GENETICS OF PHOTOPERIOD SENSITIVITY IN RICE

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(With Two Text-figures)

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INTRODUCTION

Published investigations of the inheritance of earliness in rice (*Oryza sativa* L.) have not attempted a separation of the factors that affect photoperiod response, and it does not appear to have been generally realized that records of flowering time are merely isolated points in the curve relating anthesis to the photoperiod. Appreciation of the nature of photoperiod response is an essential preliminary to the genetic analysis of earliness.

Rice differs from most cereals in the quantitative nature of its response to the photoperiod. The germination-heading interval drops to a minimum value at a photoperiod characteristic of the variety (Chandraratna, 1952, 1954). Extension or shortening of the photoperiod beyond this optimum value delays heading. Second-degree polynomials of the form $y = a + bx + cx^2$, where y is the germination-heading interval in days and x is the photoperiod in hours, provide satisfactory fits to curves relating the flowering date of a rice variety to the photoperiod.

The germination-heading interval reaches a minimum value when the first differential coefficient is zero. As $dy/dx = b + 2cx = 0$, the optimum photoperiod has the value $-b/2c$.

The germination-heading interval corresponding to this optimum photoperiod may be designated the minimum heading duration, and can be shown by substituting $x = -b/2c$ in the equation, $y = a + bx + cx^2$, to have the value $a - b^2/4c$.

The best estimate of photoperiod sensitivity, which must be related to the rate of change of slope of the parabola, is furnished by the second differential coefficient:

$$d^2y/dx^2 = 2c.$$

The parameters $2c$, $-b/2c$ and $a - b^2/4c$ thus provide estimates of photoperiod sensitivity, the optimum photoperiod and the minimum heading duration. The age expression of a rice variety can accordingly be resolved into these three measurable components, the genetics of each of which can be the subject of separate study. The present paper concerns only the inheritance of photoperiod sensitivity.

Data relating to a range of photoperiods would be necessary for evaluating the statistic, $2c$. Such data can be possible only in the instance of the parental and F_1 generations. Each individual in an F_2 population is unique, and there is no feasible method of securing the subjection of each F_2 segregate to a photoperiod range. If, however, the parents selected for study differ strikingly only in photoperiod sensitivity, and possess comparable optimum photoperiods and minimum heading durations, the use of suitable day lengths would permit the separation of sensitive and day-neutral segregates. The method employed in the investigation reported herein consisted in growing parental, F_1 and later generations

together in the south-west monsoon, during which the prevailing long days permitted marked expression of photoperiod sensitivity.

MATERIAL AND METHODS

Information relating to the five pure lines used as parents in the present investigation is given in Table 1.

Vellai Ilankalayan 28061 is the only pure line relatively insensitive to the photoperiod, and was one parent in all crosses. Sufficient data for fitting curves that related heading time to the photoperiod were available only in the instance of Vellai Ilankalayan 28061 and MYAC 104; second-degree polynomials fitted in the photoperiod range 8–12 hr., and derived statistics are presented in Table 2.

Estimates of photoperiod sensitivity for Vellai Ilankalayan 28061 and MYAC 104 are 3.9 and 7.3 respectively. MLYC 401, HMC 12 and GEB 24 possess sensitivity values

Table 1. *Descriptions of pure line parents*

Pure line	Country of origin	Photoperiod reaction	Apiculus colour	Stigma colour	Auricle-junctura colour	Pericarp colour
Vellai Ilankalayan 28061	Ceylon	Relatively insensitive	Purple	Purple	Colourless	Red
MYAC 104	Burma	Markedly sensitive	Colourless	Colourless	Colourless	White
MLYC 401	Burma	Markedly sensitive	Colourless	Colourless	Colourless	White
HMC 12	Burma	Markedly sensitive	Colourless	Colourless	Colourless	White
GEB 24	India	Markedly sensitive	Colourless	Colourless	Colourless	White

Table 2. *Second-degree polynomials and derived statistics*

Pure line	Curve of response ($y = a + bx + cx^2$)	Photoperiod sensitivity (2c)	Optimum photo-period (hr.)		Minimum heading duration (days)	
			Observed	Calculated ($-b/2c$)	Observed	Calculated ($a - b^2/4c$)
Vellai Ilankalayan 28061	$y = 258.5 - 36.99x + 1.968x^2$	3.9	10.0	9.4	84.6	84.7
MYAC 104	$y = 470.4 - 77.11x + 3.692x^2$	7.3	10.5–11.0	10.5	67.0	67.8

comparable to that of MYAC 104, and approximate in their values of the minimum heading duration even closer to Vellai Ilankalayan 28061 than does MYAC 104. The optimum photoperiod in the instance of all the pure lines was within the range 9.5–11.0 hr. Vellai Ilankalayan 28061 crosses with the other four pure lines would accordingly appear to provide suitable material for the genetic analysis of photoperiod sensitivity.

Parents, F_1 and later generations were grown simultaneously in replicated, randomized blocks at the Central Rice Research Station, Batalagoda. In the south-west monsoon, 1953, each of the five randomized blocks contained the following:

- 200 plants of each parent,
- 10 F_1 plants,
- 200 F_2 plants.

Plant numbers in previous seasons were much smaller and varied with the cross. Records included heading (extrusion of panicle tip of main culm above flag leaf), tiller number and colour of apiculus, auricle-junctura and pericarp.

Records made in 1952–3 indicate the pattern of day-length change at Batalagoda (latitude $7^\circ 28'$). Day length dropped to a minimum value of 11 hr. 43 min. on 22 December.

Days commenced lengthening rapidly in early February, and reached a maximum of 12 hr. 32 min. on 22 June. Rapid shortening of days began towards the end of July. Day-length differences, which in a 12-month period do not exceed 49 min., exercise a profound influence on the initiation and further development of inflorescence primordia in rice.

The south-west and north-east monsoons proper commence in May and December respectively. It is, however, customary to regard the intermonsoonal periods immediately preceding them as part of the respective monsoons. The north-east monsoon covers a period of short days, and the behaviour of varieties in this season provides rough indications of genetic differences in the minimum heading duration. The genetic analysis of sensitivity is based on heading records of parental and filial generations in the south-west monsoon, which is a season of long days.

RESULTS

North-east monsoon season

Mean germination-heading intervals in the north-east monsoon, 1951, of the parents, Vellai Ilankalayan 28061, MLYC 401, MYAC 104 and GEB 24, and of the F_1 of crosses with Vellai Ilankalayan 28061 are given in Table 3. MYAC 104 was slightly but significantly earlier than Vellai Ilankalayan 28061. The shorter minimum heading duration of MYAC 104 contributed to its greater earliness. Vellai Ilankalayan 28061 did not differ significantly in heading time from MLYC 401 and GEB 24; these three pure lines have approximately the same minimum heading duration. At least in the instance of these parents and of crosses between them, the age extension that occurs in the south-west monsoon may be considered almost purely a function of photoperiod sensitivity. Precise records are not available for HMC 12, but its behaviour closely resembles that of MLYC 401 and GEB 24.

Heterosis was manifested in this season, in a significant increase in earliness in the F_1 of all crosses.

Table 3. *Germination-heading intervals of parents and F_1 in the north-east monsoon*

Cross	Sowing date	Mean no. of days to heading		
		Sensitive parent	Vellai Ilankalayan 28061	F_1
MYAC 104 × Vellai Ilankalayan 28061	7 December 1951	92 ± 0.88	101 ± 1.84	86 ± 2.46
MLYC 401 × Vellai Ilankalayan 28061	20 December 1951	95 ± 1.92	92 ± 0.93	76 ± 0.88
GEB 24 × Vellai Ilankalayan 28061	7 December 1951	99 ± 1.57	101 ± 1.38	86 ± 3.51

South-west monsoon season

Table 4 represents the mean germination-heading intervals in the south-west monsoon, of four parents and of the F_1 of crosses with Vellai Ilankalayan 28061. The F_1 showed dominance of sensitivity. Except in the instance of the 1952 data for the MLYC 401 cross, dominance was partial.

The F_2 segregations in the season are illustrated in Fig. 1. The frequency distributions are bimodal in all four crosses; earlier, day-neutral segregants are recognizably distinct from the later sensitive segregants. The numbers in the two categories are given in Table 5. The values of χ^2 in column 6 indicate that in every F_2 , an acceptable fit to a ratio of 3 sensitives : 1 day-neutral was obtained; P uniformly exceeds 0.05. Data for

individual families composing the 1952 F_2 of MYAC 104 and MLYC 401 crosses provide estimates of the heterogeneity χ^2 ; the values of 1.9259 ($P=0.5-0.3$) and 4.0674 ($P=0.2-0.1$) justify pooling of data. Photoperiod sensitivity appears to be determined by a single gene pair for which the symbols *Se se* have been proposed (Chandraratna, 1953).

Fig. 2 illustrates the frequency distributions in the 1953 season, of the parents, MLYC 401 and Vellai Ilankalayan 28061, F_1 and F_2 . The F_1 shows dominance of sensitivity, and possesses a variance comparable with that of the parents. The F_2 has a strikingly larger variance and is conspicuously bimodal. The sensitive and day-neutral segregates number 743 and 245 respectively. The fit to a 3:1 ratio is almost perfect; χ^2 has the value 0.0216 ($P=0.9-0.8$).

Linkage relations of the *Se* locus

Marker genes for only two linkage groups were identifiable in the experimental material; genes for colour of apiculus (*Ap ap*) and pericarp (*Pr pr*) occur in groups I and IV respectively (Jodon, 1948). All the sensitive parents possess the genotype *ap ap pr pr*.

Table 4. Germination-heading intervals of parents and F_1 in the south-west monsoon

Cross	Sowing date	Mean no. of days to heading		
		Sensitive parent	Vellai Ilankalayan 28061	F_1
MYAC 104 × Vellai Ilankalayan 28061	1 May 1952	161 ± 0.13	106 ± 0.15	144 ± 0.38
MLYC 401 × Vellai Ilankalayan 28061	1 May 1952	164 ± 2.29	105 ± 2.65	169 ± 1.87
MLYC 401 × Vellai Ilankalayan 28061	24 April 1953	166 ± 0.12	108 ± 0.17	149 ± 0.51
HMC 12 × Vellai Ilankalayan 28061	10 April 1952	182 ± 0.59	—	166 ± 3.47
GEB 24 × Vellai Ilankalayan 28061	1 April 1952	180 ± 0.66	—	168 ± 3.90

Table 5. Summary of ratios for factor pair for photoperiod sensitivity

Sensitive parent	F_2 family	No. of plants			3:1 ratio		Heterogeneity	
		Sensitive (<i>Se</i>)	Insensitive (<i>se</i>)	Total	χ^2	P	χ^2	P
MYAC 104	1952 (1)	47	13	60	0.3556	0.7-0.5	1.9259	0.5-0.3
	1952 (2)	44	22	66	2.4444	0.2-0.1		
	1952 (3)	68	22	90	0.0148	0.95-0.90		
	Total	159	57	216	0.8889	0.5-0.3		
MLYC 401	1952 (1)	232	66	298	3.0885	0.1-0.05	4.0674	0.2-0.1
	1952 (2)	266	98	364	1.2931	0.3-0.2		
	1952 (3)	168	58	226	0.0531	0.8-0.7		
	Total	666	216	882	0.3673	0.7-0.5		
HMC 12	1953 (1)	743	245	988	0.0216	0.9-0.8		
HMC 12	1952 (1)	165	71	236	3.3955	0.1-0.05		
GEB 24	1952 (1)	310	83	393	3.4830	0.1-0.05		

The constitution of Vellai Ilankalayan 28061 is *Ap Ap Pr Pr*. The F_2 segregations given in Table 6 show good fit to a 3:1 ratio for both factor pairs, except in the instance of apiculus colour in the GEB 24 cross, where a serious and inexplicable deficiency of *Ap* phenotypes is recorded.

χ^2 tests indicate (a) independent assortment of the factor pairs *Se se* and *Pr pr*, and (b) linkage of *Se se* with *Ap ap*. The joint segregation of *Se se* and *Pr pr* in the MLYC 401 cross has a χ^2 value for independence of 1.263 ($P=0.3-0.2$). In the instance of all four crosses, P from the χ^2 for independence in the joint segregation of *Se se* and *Ap ap* is uniformly below 0.001. Recombination percentages for linkage between *Se* and *ap* loci

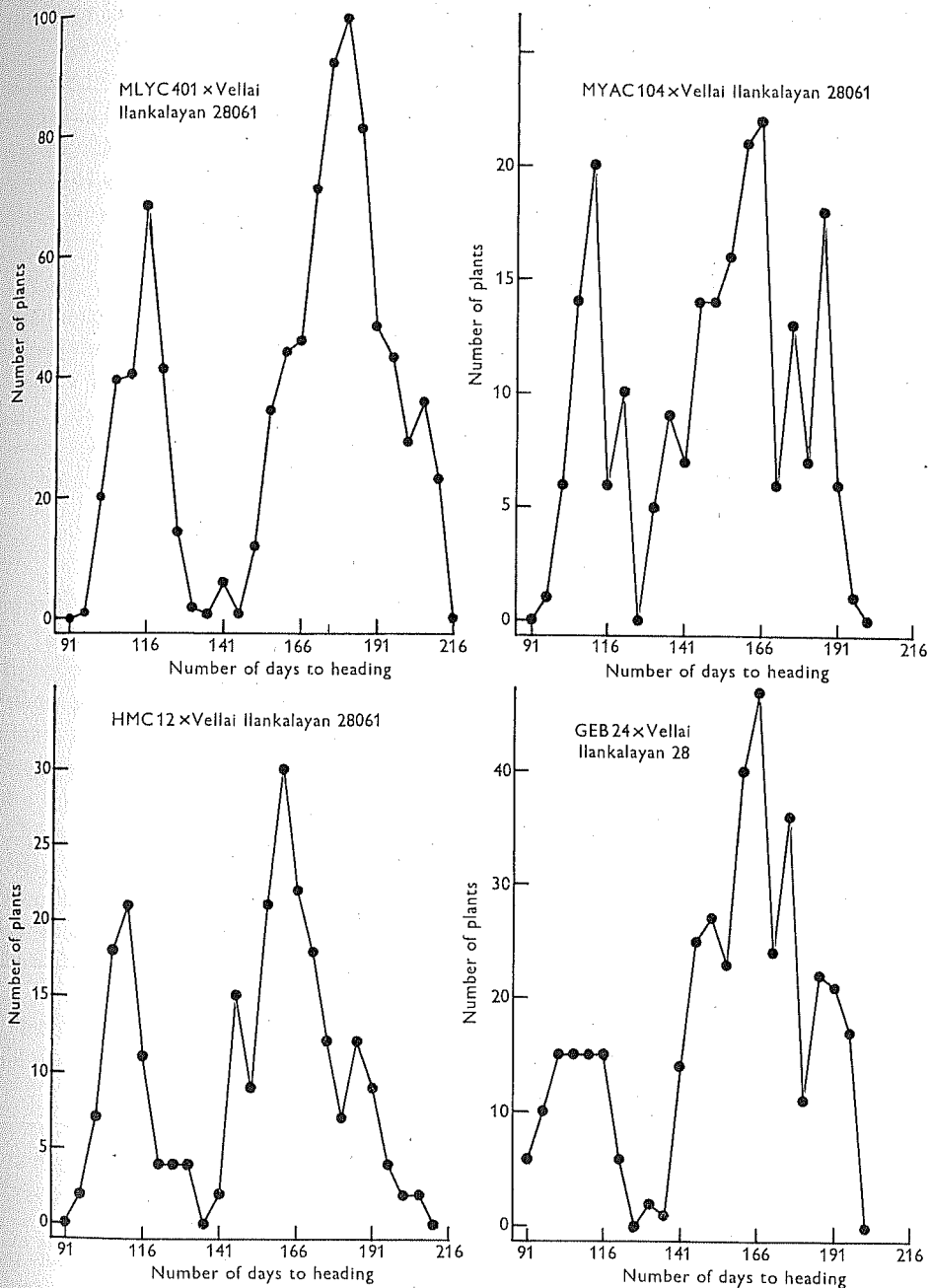


Fig. 1. Frequency distributions for number of days to heading in P_2 of crosses grown in the south-west monsoon, 1952.

have been calculated by the product formula (Immer, 1930) and range in value from 16.3 ± 3.26 to 23.9 ± 6.35 . The differences are not significant. The value of 17.3 ± 2.23 derived from the pooled data for the MLYC 401 cross appears to be the best estimate of the recombination percentage.

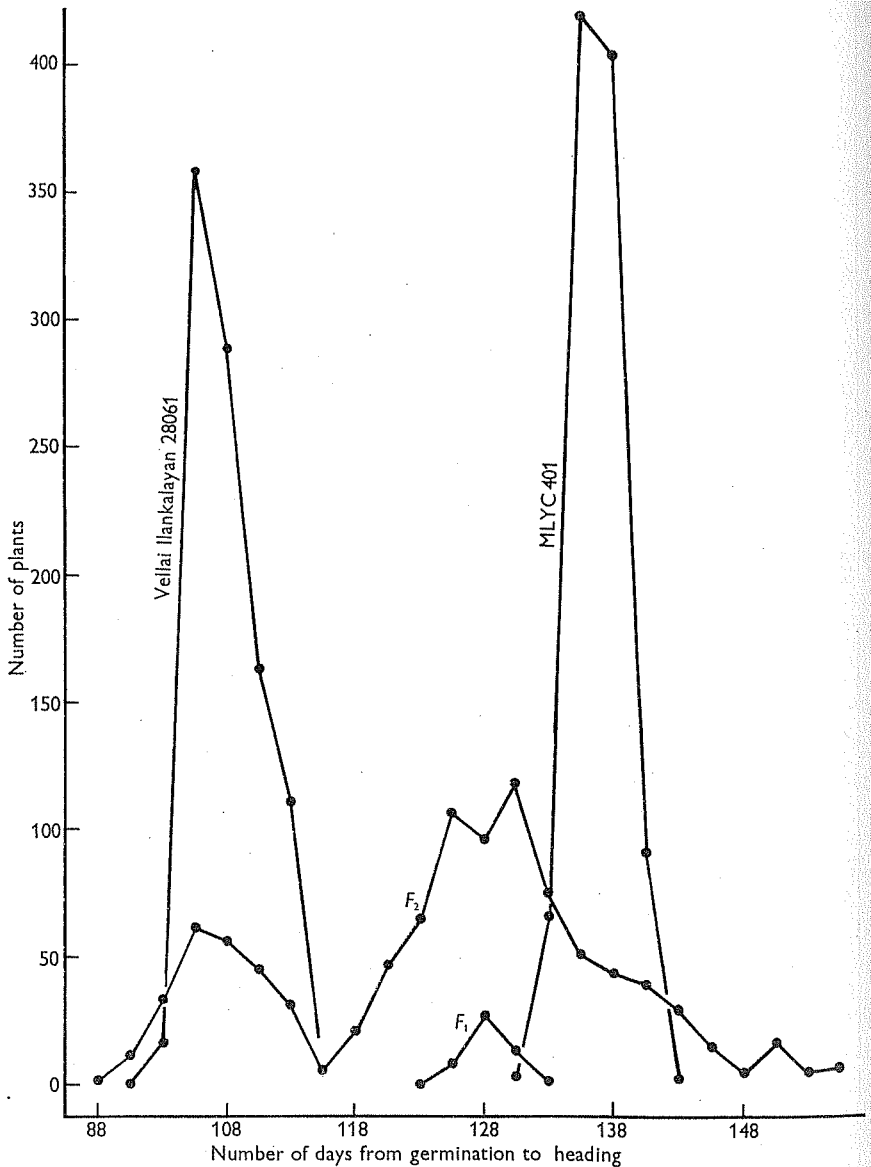


Fig. 2. Frequency distributions for number of days to heading in parents, F_1 and F_2 of the MLYC 401 \times Vellai Ilankalayan 28061 cross grown in the south-west monsoon, 1953.

Complementary gene action for purple auricle and junctura was manifested only in the instance of the MYAC 104 cross. The purple pigment varies widely in expressivity and evanesces rapidly, and underestimation of coloured plants in F_2 may result. As is seen in Table 6, the F_2 for auricle-junctura colour gives acceptable fit to a 27:37 ratio and

genes at three loci, Au_1 , Au_2 and Au_3 , may be assumed. The joint segregation of auricle colour and photoperiod sensitivity indicates linkage of the *se* locus with one of the *Au* loci; χ^2 for independence has a value of 14.446 ($P < 0.01$). The estimate of the recombination percentage for this linkage, as it is based on repulsion data involving a character resulting from complementary gene action, is subject to high error and has not been recorded. The linkage appears, however, to be close.

In the joint segregation of apiculus and auricle-juntura colour in the F_2 of the MYAC 104 cross, χ^2 for independence is 34.249 ($P = 0.01$). The recombination percentage for linkage in the coupling phase of *Ap* with the *Au* locus in group I is 2.4 ± 2.0 .

Relation of tiller number of photoperiod sensitivity

Frequency distribution of tiller numbers in *Se* and *se* phenotypes in the F_2 of the Vellai Iankalayan 28061 crosses with MLYC 401, MYAC 104, HMC 12 and GEB 24 are presented in Table 7. In all crosses, the *Se* phenotypes possess a higher tiller number per plant. Values of *t* in the last column of the table indicate that the superiority is significant in every instance at the 0.1% point. In the GEB 24 cross, the *Se* phenotypes show a mean tiller number almost double that of the *se* phenotypes.

DISCUSSION

The south-west monsoon data relating to the Vellai Iankalayan 28061 crosses with the four photoperiod-sensitive pure lines, MLYC 401, MYAC 104, HMC 12 and GEB 24, satisfactorily fit the hypothesis that a single-gene substitution determines the expression of photoperiod sensitivity; sensitivity exhibits dominance in the F_1 , and a segregation of 3 sensitives : 1 day-neutral in the F_2 . In the north-east monsoon planting, the prevalence of near-optimum day lengths prevents the expression of the *Se* factor, and the F_1 exhibits not a dominance of lateness but a heterosis of earliness.

The wide variation in varietal sensitivity consists of differences in degree rather than in kind, and does not find a complete explanation in the hypothesis of a single-gene pair. 'Insensitive' varieties are in reality forms with low sensitivity, and 'sensitive' varieties vary widely in the expression of this character. The postulate of a series of multiple alleles at the *Se* locus appears necessary. The occurrence of modifiers at other loci is also likely.

There is evidence that minimum heading duration is polygenic (Chandraratna, unpublished). Information that has now become available on the genetic nature of photoperiod sensitivity and minimum heading duration would at least partly explain some of the conflicting conclusions of previous workers in regard to the inheritance of earliness in rice. F_2 data have often been of two types, viz. a ratio of 3 lates : 1 early (Nomura & Yamazaki, 1927; Jones, Adair, Beachell & Davis, 1935; Ramiah, 1933; Sethi, Sethi & Mehta, 1936), or a unimodal distribution of the form that characterizes a polygenic character (Ramiah, 1933; Sethi *et al.* 1938). The 3:1 ratios possibly resulted from the expression of genes at the *Se* locus, when the F_2 received long days. Unimodal F_2 distributions would have been obtained in instances where either (a) the two parents were both day neutral, or (b) the F_2 was subjected to day lengths approximating to the optimum. Conditions (a) and (b) would have permitted the expression of polygenes that determine minimum heading duration.

Table 6. F_2 data on the linkage of the *Se* and *ap* loci

Sensitive parent	Linkage group	Linkage phase	Factor pair		Yy		No. of plants in F_2				Total independence	P	Percentage recombination
			Y	y	χ^2 *	P	<i>Se</i>		<i>se</i>				
MYAC 104	1	R	<i>Ap</i>	<i>ap</i>	112	47	54	3	216	13,835	<0.001	23.9 ± 6.35	
MLYC 401, 1952	1	R	<i>Ap</i>	<i>ap</i>	470	196	211	5	882	62,791	<0.001	16.3 ± 3.26	
MLYC 401, 1953	1	R	<i>Ap</i>	<i>ap</i>	501	242	237	8	988	83,951	<0.001	17.9 ± 3.06	
MLYC 401, total			<i>Ap</i>	<i>ap</i>	971	438	448	13	1870	146,458	<0.001	17.3 ± 2.22	
HMC 12	1	R	<i>Ap</i>	<i>ap</i>	115	50	68	3	236	21,160	<0.001	21.2 ± 6.16	
GEB 24	1	R	<i>Ap</i>	<i>ap</i>	193	117	78	5	393	34,932	<0.001	21.6 ± 4.77	
MYAC 104	1	R	<i>Au</i>	<i>au</i>	47	112	33	24	216	14,446	<0.001	—	
MLYC 401	IV	R	<i>P+</i>	<i>pr</i>	389	101	154	53	697	1,263	0.3-0.2	—	
			<i>Ap</i>		<i>ap</i>								
			Y	y	Y	y	Y	y					
MYAC 104	1	C	<i>Au</i>	<i>au</i>	79	87	1	49	216	34,249	<0.01	2.4 ± 2.0	

* In *Au au*, fit to 27:37; in others, fit to 3:1.

Table 7. Association of tillering with photoperiod sensitivity in F_2

Sensitive parent	Phenotype	Frequencies of plants with tillers numbering																	Total nos. of plants	Mean tiller no. per plant	t
		0-4	5	6	7	8	9	10	11	12	13	14	15	16	17	>17					
MYAC 104	<i>se</i>	3	9	5	6	10	6	2	3	1	3	0	0	0	1	2	57	8.58 ± 0.388	8.62		
	<i>Se</i>	2	5	3	9	10	13	11	9	23	11	10	14	8	8	23	159	12.72 ± 0.288			
MLYC 401	<i>se</i>	22	23	29	49	29	20	16	11	5	7	2	1	2	—	—	216	7.52 ± 0.187	17.52		
	<i>Se</i>	9	19	23	36	58	59	78	72	74	63	40	43	19	25	48	666	11.32 ± 0.132			
HMC 12	<i>se</i>	1	6	10	8	16	14	7	1	3	3	1	0	1	—	—	71	8.30 ± 0.342	6.84		
	<i>Se</i>	—	3	1	12	15	23	29	21	17	15	6	4	4	6	9	165	11.24 ± 0.261			
GEB 24	<i>se</i>	11	5	11	15	11	7	4	6	4	3	0	1	—	—	—	82	7.91 ± 0.311	16.06		
	<i>Se</i>	2	1	3	10	18	17	23	19	30	27	33	18	23	61	310	13.95 ± 0.212				

Of the twelve possible linkage groups in rice, only seven may be said to have been established with any degree of certainty, viz. groups I, IV, V, VI, VII and VIII of Jodon (1948), and the *Sp* group of Nagao (1951). Jodon's Group I, to which I have assigned the *Se* locus, corresponds to the *gl* group of Nagao, and the latter's *C* locus appears to be the same as Jodon's *Ap*. The best estimate of the recombination percentage for linkage between *se* and *Ap* is 17.3 ± 2.23 . One of the three complementary genes for auricle-junctura colour shows close linkage with both *Ap* and *se*. The recombination percentage of this *Au* locus with *Ap* is 2.4 ± 2.0 . The gene order is either *Ap—Au—se* or *Au—Ap—se*.

The association with high tiller number per plant adds to the economic importance of the *Se* factor, and may account for its perpetuation under human selection. Tillering capacity determines ear number, which is a yield component. The absence either within the sensitive or the day-neutral group of F_2 segregates, of a regression of tiller number on heading duration, confirms the conclusion that the association of tillering with sensitivity is genetic and not physiological. Pleiomorphic effects of genes at the *Se* locus appear to contribute to differences in tillering capacity.

SUMMARY

A single-gene pair, designated *Se se*, determines the sensitivity of rice varieties to the photoperiod.

The *Se* locus occurs in group I, linked to *ap* with a recombination percentage of 17.3 ± 2.23 , and to one of the three complementary genes for auricle-junctura colour. The recombination percentage for the linkage of the *Au* gene in group I with *Ap* is 2.4 ± 2.0 .

The *Se* gene exercises a pleiomorphic effect on tillering capacity; *Se* phenotypes possess a higher tiller number.

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