INHERITANCE OF THE OPTIMUM PHOTOPERIOD AND CRITICAL PHOTOPERIOD IN TROPICAL RICES

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Abstract

The inheritance of the optimum photoperiod and of the critical photoperiod in strongly photoperiod-sensitive genotypes was analyzed. Six crosses involving four sensitive parents of tropical origin produced all photoperiod-sensitive F_1 hybrids. The degree of dominance varied among different crosses. Data obtained from a 4-parent half-diallel set and from F_2 progenies of a sensitive × sensitive of BPI-76 × Raminad Strain 3 cross showed that a short optimum photoperiod is dominant to a long one. Similarly, a short critical photoperiod is dominant over a long one. Each of the two components appears to be controlled by a single gene and probably modifying genes. A genetic association between a short critical photoperiod and a short optimum photoperiod was detected in the F_2 population. This combination would result in a long photoperiod-sensitive phase in strongly sensitive genotypes when grown under a long-day treatment.

Estimates on the basic vegetative phase obtained in the half-diallel set confirm earlier findings that a short b. v. p. is dominant to a long one. The degree of dominance varied among F_1 hybrids. Dominant alleles controlling a short b. v. p. exceeded recessive alleles in frequency.

A strongly photoperiod-sensitive genotype representative of the tropical rices contains a very short basic vegetative phase, a short critical photoperiod, a short optimum photoperiod.

Introduction

The vegetative growth duration of rice (*Oryza sativa* L.) is a complex and variable trait. Under natural environments with different or changing photoperiods, the variation in heading date becomes greater when the genotypes concerned are photoperiod-sensitive. Numerous studies have been conducted concerning the flowering response of rice varietes to photoperiod (cf. Vergara

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et. al. 1969). However, the diverse array of interpretations did not provide complete information on the breeding behavior of different genotypes, particularly when planting in non-identical seasons or latitudes.

The growth duration of a rice plant can be divided into three stages: vegetative growth, reproductive, and ripening phases. Since the reproductive and ripening phases are relatively constant in duration, it is the vegetative growth phase that largely determines the total growth duration of a plant. By subjecting primary tillers of a rice plant to different photoperiods, the findings described in a recent study (Chang et. al. 1969) have demonstrated the feasibility of separating and reconstituting the vegetative growth duration (from germination to panicle initiation) into two major components, the basic vegetative phase (b. v. p.) and the photoperiod-sensitive phase (p. s. p.). The above two components have contributed much to the understanding of the flowering behavior in rice (Chang et. al. 1969).

Among photoperiod-sensitive varieties, the variation in the photoperiod response is determined by two major components: (1) the critical photoperiod beyond which flowering is greatly delayed or totally suppressed, and (2) the optimum photoperiod at which the duration from seeding to heading is minimum (Chandraratna 1954). The critical photoperiod is similar to the "turning point" of Yu and Yao (1962) and has been studied in detail by a number of investigators (cf. Vergara, et. al. 1969). Determinations on the optimum photoperiod in temperate and tropical rices are available in literature (Chandraratna 1964; Vergara, et. al. 1969). However, genetic bases of the phenomena have not been elucidated.

The objectives of this investigation are to study the inheritance of the two components (optimum photoperiod and critical photoperiod) of photoperiod sensitivity in tropical rices and to elucidate the genetic relationship among the basic vegetative phase, the optimum photoperiod and the critical photoperiod.

Materials and Methods

Four tropical varieties which showed high photoperiod-sensitivity were chosen as parents to produce a set of non-reciprocal hybrids. These varieties are designated as follows:

Varieties	Photoperiod sensitivity	Critical photoperiod in hours and minutes	Optimum Photoperiod in hours and minutes	Basic vegetative phase (days)	Country of origin
BPI-76	high	13:00	10:07	21	Philippines
Raminad Strain 3	high	12:30	9:16	39	Burma
Siam 29	high	13:00	9:59	28	Malaysia
Podiwi-A (8)	high	13:00	9:59	32	Ceylon

The four parents and six F_1 populations of the half-diallel set with two replications were tested in a completely randomized design. The plants were exposed to 10-hour natural light in the greenhouse and then transferred to darkrooms with photoperiod treatments of 10, 11, 12, 13, 14, and 16 hours of light up to 200 days of culture. The number of plants per pot was four. Forty plants were provided for each F_1 hybrid and parent respectively under different photoperiod treatments. The experiments were conducted in two replicates. In the long-day treatments, artificial light of 400 lux at pot level was administered. The temperatures in the photoperiod chambers were maintained at 21°C at night while day temperatures in the greenhouse at The International Rice Research Institute (Los Baños, Philippines) ranged from 25°C to 35°C. Heading date was recorded on the first emerging panicle of each plant.

The diallel-cross analysis of Hayman (1954a, 1954b) and Jones (1965) and the second-degree polynomial forms used by Chandraratna (1954) to estimate photoperiod sensitivity were employed in this study. For this experiment, the following assumptions were made:

1. Parental homozygosity,
2. Normal diploid segregation,
3. No maternal effect,
4. No multiple alleles,
5. No linkage, and
6. No non-allelic gene interaction (that is, no epistasis)

The optimum photoperiod is defined as the daylength at which the minimum number of days from sowing to flowering is obtained. Critical photoperiod is the daylength beyond which no flowering occurs. In some sensitive genotypes, it was determined by dissecting the plants for signs of panicle initiations at the termination of the photperiod treatment (200 days). The basic vegetative phase (b. v. p.) was estimated by subtracting 35 days from the duration between seeding and panicle emergence (IRRI, 1967).

The cross of Ramiand Strain 3 and BPI-76 was selected for a genetic analysis of the optimum photoperiod and of the critical photoperiod. Previous studies (Vergara et. al. 1969) at the IRRI have shown that the two varieties differed appreciably in the optimum photoperiod and critical photoperiod. The two parents, F_1 plants, and a population of F_2 plants were initially grown in pots under 24-hour photoperiod until the time of treatment. About 50 days after transplanting, when the seedings had developed 6 to 8 tillers, each plant was divided into six parts of one to two tillers. Each part was planted in a separate pot. To reduce the number of pots required, parts of four distinct F_2 plants were planted in the same pot. Finally, there were six groups of pots

and each group contained a plant part of each F_2 line. The tillers were allowed to grow for another 35 days at 24-hour photoperiod before the treatments were started. Each set of pots were subjected to the following photoperiod: 8, 10, 12, 12½, 13, and 13½ hours. One hundred and sixty-three F_2 plants were included in the study. The recording of heading date was terminated on 160th day, after the start of the photoperiod treatments. In a number of F_2 plants which gave differences in flowering date greater than 50 days between two successive photoperiods, the shorter photoperiod was considered as the critical photoperiod.

The optimum photoperiod of individual plants was calculated using Chandraratna's second degree polynomial function $\frac{-b}{2c}$ where X is the photoperiod and Y the number of days from treatment to heading. The calculations of the optimum photoperiod used in the present experiment were based on 8, 10, 12. 12, ½, 13 and 13½ hours up to the critical photoperiod of the individual plant.

Results

1. *Half-diallel set*

The responses (to six photoperiods) of the four parents and six F_1 populations in the half-diallel cross are illustrated in Figure 1. The estimates of optimum photoperiod and of minimum heading duration (equivalent to the basic vegetative phase plus 35 days for the panicle formation phase) are enumerated in Table 1.

The second-degree polynomial formula provided estimates of the optimum photoperiod and photoperiod sensitivity from four photoperiods spaced one hour apart from one another (Table 1). The estimated optimum photoperiod of Raminad Strain 3 was 9 hours and 16 minutes; those of the other three parents were approximately 10 hours. The value of optimum photoperiod in Raminad Strain 3 array indicated that the F_1 plants of BPI-76 × Raminad Strain 3 and Raminad Strain 3 × Siam 29 crosses showed a partial dominance of the short optimum photoperiod of Raminad Strain 3. In the F_1 plants of Raminad Strain 3 × Podiwi-A (8), the complete dominance of a short optimum photoperiod was indicated. It clearly showed that a short optimum photoperiod is dominant to a long optimum photoperiod.

The four parents did not differ widely in their critical photoperiods. All parents and F_1 hybrids failed to initiate panicles beyond the 12-hour daylength (Fig. 1). Therefore, the one-hour difference between successive treatments was not practical in classifying the F_1 hybrids into distinct classes.

All four parents belonged to the short b. v. p. group, ranging from 21 days in BPI-76 to 39 in Raminad Strain 3. The F_1 hybrids ranged from 22 to 42

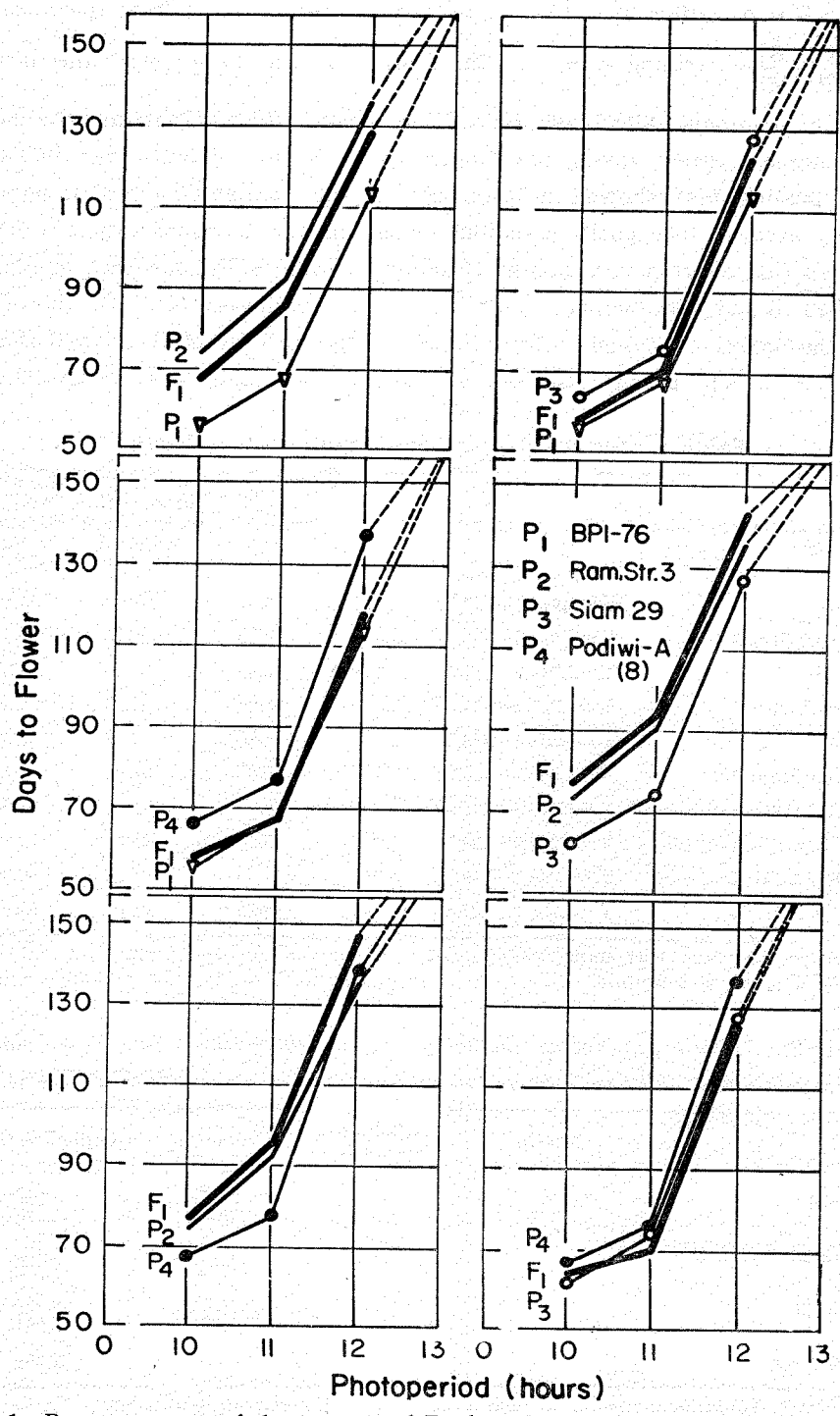


Fig. 1. Response curves of the parents and F_1 plants grown under different photoperiods. The dotted line indicates that no panicle was exserted at the end of the 200-day experiment.

days in b. v. p. (Table 2). The scaling value was obtained from the formula $h_p = \frac{\overline{F_1} - \overline{MP}}{\overline{P} - \overline{MP}}$ (Griffing 1950). In the scaling test, h_p is potence value in the degree of dominance effect, and $\overline{MP}$, $\overline{P}$ are mean of two parents and the mean of the highest parent among two comparative parents, respectively. in Table 2, the scaling test showed a difference in the dominance effect of parent-progeny arrays. The positive scaling values in the Raminad Strain 3 array indicated that short b. v. p. parent (Raminad Strain 3) is partially dominant over BPI-76 and overdominant over Siam 29 and Podiwi-A (8). On the other hand, the negative scaling values found in the BPI–76 array showed that a very short b. v. p. parent (BPI–76) is partially dominant over Siam 29 and

Table 1. *Curves of photoperiod response in F_1 plants.*

Parents and F_1 hybrids	Curve of response*	Photoperiod sensitivity (2c)	Optimum photoperiod in hours and minutes (-b/2c)	Minimum heading duration in days ($a-b^2/4c$)
BPI-76	$Y=1{,}847.5-354.3X+17.5X^2$	35.00	10:07	54.19
Raminad Str. 3	$Y=1{,}152.6-223.4X+11.6X^2$	23.10	9:16	72.41
Siam 29	$Y=1{,}575.9-303.4X+15.2X^2$	30.40	9:59	62.33
Podiwi-A (8)	$Y=1{,}345.4-261.8X+13.4X^2$	26.75	9:59	64.30
BPI-76 × Ram. Str. 3	$Y=1{,}306.4-253.2X+12.9X^2$	25.86	9:47	66.94
BPI-76 × Siam 29	$Y=1{,}923.2-366.5X+18.0X^3$	36.00	10:11	57.17
BPI-76 × Podiwi-A (8)	$Y=1{,}920.3-366.6X+18.0X^2$	36.05	10:10	56.01
Ram. Str. 3 × Siam 29	$Y=992.9-194.5X+10.3X^2$	20.56	9:28	72.70
Ram.Str.3 × Podiwi-A(8)	$Y=755.2-153.1X+8.5X^2$	17.00	9:01	66.00
Siam 29 × Podiwi-A(8)	$Y=1{,}758.7-335.9X+16.6X^2$	33.25	10:06	62.02

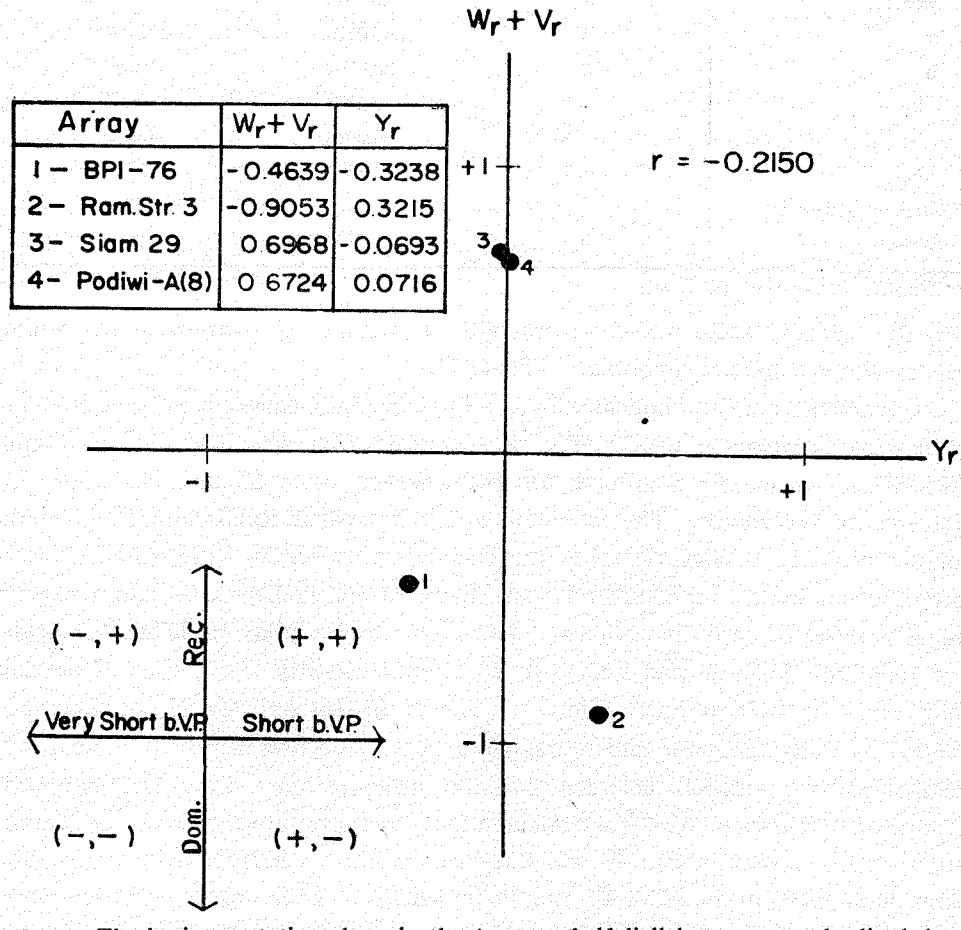
* Curve of response was used second-degree polynomials of the form $Y=a+bx+cx^2$, where Y is the sowing-to-heading interval in days, and X is the photoperiod in hours.

Table 2. *Mean b. v. p. values (days) of parents (underlined) and F_1 hybrids and dominance value of hybrids (in parenthesis) in 4×4 half-diallel cross.*

Male array / Female array	BPI-76	Raminad Strain 3	Siam 29	Podiwi-A (8)
BPI-76	<u>21.375</u>	36.625 (0.268)	22.750 (-0.607)	21.830 (-0.916)
Raminad Strain 3		<u>39.125</u>	42.125 (1.558)	41.125 (1.582)
Siam 29			<u>28.375</u>	29.750 (-0.291)
Podiwi-A (8)				<u>32.250</u>

Class of dominance: $h_p=0$, no dominance; $h_p=\pm1$, complete dominance; $-1<h_p<0$, incomplete negative dominance; $0<h_p<+1$, incomplete positive dominance; $h_p>1$, positive overdominance.

complete dominant over Podiwi-A (8). The F_1 hybrids of Siam 29×Podiwi-A (8) showed a low degree of partial dominance of a very short b. v. p. Both of two parents (BPI-76 and Raminad Strain 3) had an excess of dominant alleles but different in their direction and magnitude (Fig. 2).



Array	W_r+V_r	Y_r
1 – BPI-76	-0.4639	-0.3238
2 – Ram.Str. 3	-0.9053	0.3215
3 – Siam 29	0.6968	-0.0693
4 – Podiwi-A(8)	0.6724	0.0716

Fig. 2. The basic vegetative phase in the 4-parent half-diallel cross; standardized dev., Y_r and $W_r + Y_r$ graph.

The analysis of variance of the half-diallel cross is shown in Table 3. Source of variation "a" is due to genetical variation among the parent lines; "b", to the dominant alleles in the heterozygous conditions; "b_1", to mean dominance effect in the F_1 progenies; "b_2", to the equality of gene distribution of frequency; "b_3" residual dominant effect. Analysis of variance of the half-diallel cross indicates that (1) the parents differed in b. v. p. at the 1-percent level, largely due to additive variance (effect of a), and (2) a highly significant dominance effect was also present (effect of b), but the parents also differed in the number and direction of dominant genes being carried (effect of b_2,

Table 3. *Analysis of b. v. p. in F_1 plants of 4×4 half-diallel cross.*

Source of Variation	Degree of Freedom	Mean Squares	Variance Ratio
Total	19		
Block	1	0.8000	
a	3	309.0724	175.08**
b	6	29.8752	16.92**
b_1	1	7.5350	4.27
b_2	3	55.8040	31.61**
b_3	2	2.1522	1.22
Sum of a and b	9		
Error	9	1.7653	

** Significant at the 1% level.

Fig. 2). Hence, some showed complete dominance or overdominance while others showed partial dominance (Table 2).

Covariance analysis indicated by the Y_r (parental measurement) and W_r+V_r (order of dominance) graph (Fig. 2) suggests that Raminad Strain 3 and BPI-76 carried mostly dominant alleles, whereas Siam 29 and Podiwi-A (8) had mostly recessives. The dominant genes present in Raminad Strain 3 were mostly positiive in direction, i. e. short in b. v. p., whereas BPI-76 had largely negative dominants for shorter b. v. p. Siam 29 and Podiwi-A (8) had a nearly equal number of recessive alleles. The result was similar to Table 2 indicating that both Siam 29 and Podiwi-A (8) show a slightly low degree of partial dominance in their arrays. Thus, the b. v. p. in this half-diallel set was controlled by both dominant and recessive genes. The low negative correlation coefficient ($r= -0.2150$) between parental measurements (Y_r) and parental orders of dominance (W_r+V_r) indicated that equal proportions of the dominant genes were present in BPI-76 and Raminad Strain 3 whereas unequal proportions were present in Siam 29 and Podiwi-A (8). Thus, when averaged over all loci showing dominance a shorter b. v. p. showed partial dominance to a short b. v. p. over all loci.

2. Parents, F_1 and F_2 Populations

In another experiment, in which BPI-76, Raminad Strain 3 and their F_1, F_2 hybrids were grown under six photoperiods (8, 10, 12, 12½, 13 and 12½). In this experiment, the days to flower (Fig. 3) were taken from the start of the photoperiods treatment to flowering as mentioned in Materials and Methods (i. e. after 85 days long-day treatment). The critical photoperiod of the parents and F_1 plants are shown in Fig. 3. Raminad Strain 3 indicated a critical photoperiod at about 12 hours and 30 minutes, BPI-76 at 13 hours, and the F_1 plants at 12 hours and 30 minutes.

The critical photoperiod of F_2 plants ranged between 12 and 13½ hours. On this basis, the F_2 plants were classified into four types of critical photoperiod: 12, 12½, 13 and 13½ hours. Following the difference between parents, the first two types could be considered as short, and the other two as long. The classification of F_2 plants on this basis is given in Table 4. The ratio of short long types is 122:41 which does not differ significantly from a 3:1 ratio.

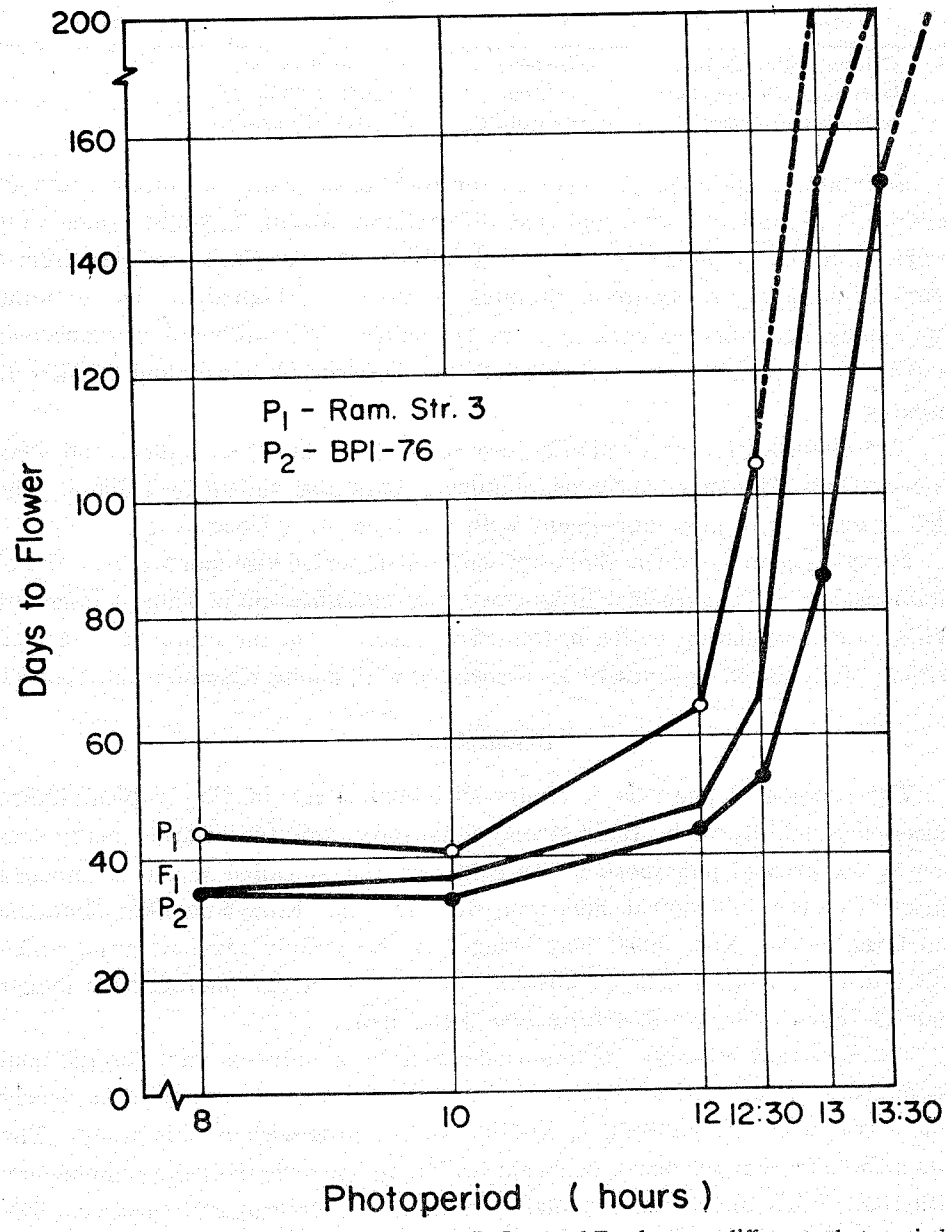


Fig. 3. Response curve of Raminad Str. 3, BPI-76 and F_1 plants to different photoperiods.

Table 4. *Two-way classification of F_2 plants with respect to critical photoperiod and optimum photoperiod in the cross of BPI-76 × Raminad Strain 3*

Critical photoperiod	Optimum photoperiod (days)		
	Short	Long	Total
Short	119	3	122
Long	5	36	41
Total	124	39	163

Critical photoperiod:	$\chi^2=0.0020$	P=0.98−0.95 (3:1)
Optimum photoperiod:	$\chi^2=0.1003$	P=0.80−0.70 (3:1)
Independence test:	$\chi^2=119.6734$	P < 0.01 (linkage)

Estimats of optimum photoperiod for BPI-76, as mentioned in the previous section, is around 10 hours, and that of Raminad Strain 3, slightly under 9½ hours. For the F_2 population, the distribution of 163 plants ranging from 8 hours 15 minutes to 9 hours 45 minutes is given in Figure 4. The dividing line among F_2 plants appears to be at 9½ hours. The optimum photoperiods of the five F_1 plants were estimated to be between 9 hours and 9 hours 15 minutes.

The classification of F_2 plants into short (9½ hours or under) and long (longer than 9½ hours) optimum photoperiods is also shown in Table 4. The high P value is in good agreement with a 3 (short): 1 (long) ratio.

Many F_2 plants with a short optimum photoperiod also had a short critical photoperiod. Chi-square test of the two-way classification in Table 4 indicates evidence of association between the two classes. On the other hand, a long critical photoperiod appears to be associated with a long optimum photoperiod.

Discussion

The component analysis of photoperiod sensitivity in the tropical indica varieties is facilitated by their strong sensitivity and the clearcut manifestation of the critical photoperiod. In contrast, the so-called sensitive japonica varieties of the subtropical and temperate regions (Kuriyama 1965, Asakuma and Kaneda 1967, Kudo 1968) may belong to the weakly sensitive type which will flower at a much delayed interval when grown under photoperiods longer than 13 hours (Vergara and Lilis 1967, IRRI 1967).

The fact that strongly photoperiod-sensitive genotypes vary in the dual components of the critical photoperiod and the optimum photoperiod is clearly demonstrated by the parents, F_1 hybrids and F_2 progenies in this study. The data also show that the above genotypes differ in one or both of the components, with the critical photoperiod showing a higher degree of expressivity. The more significant role of the critical photoperiod in controlling the flowering

behavior under different photoperiods (or in different seasons at a given latitude, or in a given season at different latitudes) is supported by findings in other studies where controlled photoperiods were used (cf. Chandraratna 1964; Vergara, Chang and Lilis 1969). However, among the entire range of photoperiod-sensitive genotypes, the estimates of optimum photoperiod appear to vary more widely than the critical photoperiod. The full range of optimum photoperiod estimates reported in literature covers the interval between 8 hours and 12 hours 30 minutes (Suenaga 1936, Matsuo 1942, Chandraratna 1954). The average value appears to fall between 9 and 10 hours (cf. Vergara, Chang and Lilis 1969) which agrees with the estimates obtained in the half-diallel set (cf. Table 1). The critical photoperiod ranged from 12 to 14 hours in other studies (Vergara, Chang and Lilis 1969).

There is general agreement among rice workers that one (*Se*) or duplicate (Se_1 and Se_2) dominant genes and possibly a recessive inhibitor (*i–Se*) control the strongly photoperiod-sensitive reaction in indica varieties of tropical origin (Chandraratna 1955; Sen *et. al.* 1964, 1967; Chang, Li and Vergara 1969) and in indica varieties of subtropical or temperate origin (Yu and Yao 1957). However, the question of whether the *Se* gene(s) directly control the critical photoperiod component needs to be further studied.

The dominance of the short critical photoperiod over a long one is indicated by the F_1 hybrids of the BPI–76 × Raminad Strain 3 cross. Similarly, the dominant nature of a shorter optimum photoperiod is shown in Table 1. Comparison of parent-progeny arrays in the half-diallel set also indicates that a short optimum photoperiod was dominant to a long one. Howeveer, transgressive segregates for critical photoperiod and optimum photoperiod were detected in this cross (cf. Fig. 4). The above results suggested that in addition to the two postulated dominant genes which control a short critical photoperiod and a short optimum photoperiod, other alleles of a modifying nature may be involved. These also point to the complex nature of the photoperiod sensitive reaction.

A plant with short optimum photoperiod would result in a long photoperiod-sensitive phase when the genotype is grown under a long daylength. Workers in Japan also reported that a low degree of photoperiod sensitivity was associated with a long optimum photoperiod (Hara 1930, Miyabayashi 1944). However, in a study involving a diverse group of varieties, Yu and Yao (1967) found no distinct correlation between the optimum photoperiod and the degree of photoperiod sensitivity.

The genetic association between a short critical photoperiod and a short optimum photoperiod is indicated in this study. The plant with short optimum and short critical photoperiod appears to be representative of the strongly

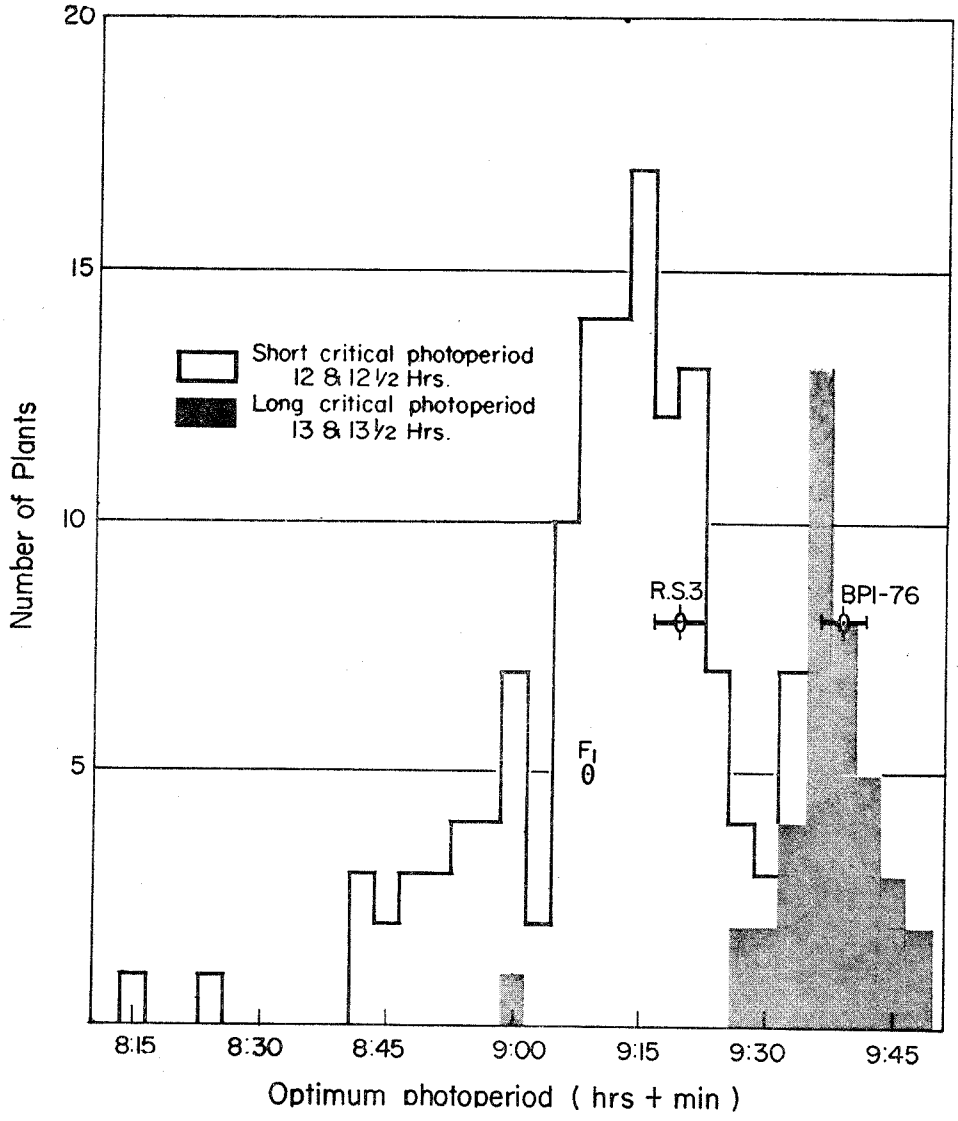


Fig. 4. Distribution and mean of parents, F_1 and F_2 plants by the length of the optimum photoperiod (hours and minutes) and critical photoperiod in the cross of Raminad Str. 3 × BPI-76.

sensitive genotypes. It is interesting to note that the above combination is common in varieties coming from the lower latitudes, whereas the long optimum-long critical combination is more prevalent among Japanese varieties (Oka, Lu and Tsai 1952; Katayama 1964; Kuriyama 1965; Kudo 1968).

The effect of high temperatures on lengthening the optimum photoperiod has been reported (Roberts and Carpenter 1965). Similarly, the critical photoperiod may be affected by temperature (Yoshida and Hanyu 1964). The

complicating effect of temperature on the components of vegetative growth duration was decreased in this study by the use of thermo-insensitive parents of tropical origin, by the control of night temperatures in the photoperiod chambers, and by the rather small variation in day temperatures at Los Baños.

Analysis of the half-diallel set shows that a very short basic vegetative phase is dominant to a short b. v. p. The genetical variation among parents is highly significant and the additive effects are due to parental variation. The degree of dominance varies among crosses. The analysis indicates that the alleles in the two parents (BPI-76 and Raminad Strain 3) are dominant to the other two parents (Podiwi-A (8) and Siam 29). The dominant alleles of BPI-76 and Raminad Strain 3 also differed in their direction and magnitude (cf. Fig. 2).

Estimates of the minimum heading duration in the half-diallel set were similar to those on the b. v. p. Again, dominance of a short duration is indicated in all crosses except Raminad Strain 3×Siam 29. These are in agreement with the b. v. p. data obtained from sensitive × insensitive crosses in another study (Chang, Li and Vergara 1969).

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熱帶地區水稻之適宜日照與臨界日照之遺傳

李 成 章

本文係利用水稻高度感光性品種研究適宜日照 (optimun photoperiod) 與臨界日照 (critical photoperiod) 之遺傳行爲。由來自不同熱帶地區國家之四種强感光性品種間雜交所得之六個組合中，其 F_1 均顯示高度感光性，且顯性之程度在不同組合中亦有變異存在。在 4×4 部份互交組合 (half-diallel cross) 之 F_1 及强感光性 × 强感光性之 F_2 (BPI-76 × Raminad Strain 3)，顯示出短適宜日照對長適宜日照呈顯性，同時，短臨界日照對長臨界日照亦呈顯性現象。該兩種成份均係由一對主效因子及影響因子 (modifying genes)所控制。在 F_2 植株中發現短臨界日照與短適宜日照間有高度之連鎖遺傳現象存在。且由上述結果顯示出高度感光性遺傳型者 (具有短適宜日照與短臨界日照者) 生長於長日照處理下則其感光期 (photoperiod sensitive phase) 愈長。

利用部份互交法分析結果，顯示出短基本營養生長期 (basic vegetative phase, b. v. p.) 對長 b. v. p. 呈顯性，此種結果再度證實筆者與其他共同學者 (Chang, Li and Vergara 1969) 之昔前解釋。在 F_1 雜種組合中其顯性程度亦有所變異。由短 b. v. p. 所控制之顯性對性因子之頻率比隱性對性因子爲高亦發現于本試驗中。

由本試驗結果得之，熱帶地區水稻之强感光性遺傳型均具有極短之基本營養生長期，短臨界日照與短適宜日照之特徵。

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