PHOTOPERIOD RESPONSE IN RICE
(*ORYZA SATIVA* L.)

I. EFFECTS ON INFLORESCENCE INITIATION AND EMERGENCE

By M. F. CHANDRARATNA

Department of Agriculture, Ceylon

(With 3 figures in the text)

Although photoperiod effects in rice have been extensively studied, the information available is surprisingly meagre. The quantitative nature of the response in this plant has been insufficiently stressed in previous work. Conflicting conclusions have been drawn from comparisons of single photoperiods with the fluid 'control' provided by natural day. The construction of response curves covering an adequately extensive range of photoperiods is an essential preliminary to the analysis of varietal behaviour. The response picture remains incomplete unless the range includes the photoperiod that exercises the maximum effect. Moreover, it is clear that any estimate of the photoperiod sensitivity of a variety must relate to the gradient of its response curve. The concept of photoperiod sensitivity has not hitherto been precisely defined, although the existence of marked differences in varietal sensitivity is generally realized, and the recognition of period-fixed and season-fixed forms is based on these differences.

Analogy with results obtained with other species suggests that the various stages leading from inflorescence initiation to maturity in rice may differ in their photoperiod requirements. Published work has been largely confined to the gross effect of day length on heading or blooming, and the study of dissected primordia which is necessary for resolving component effects has been conspicuously neglected. Wagenaar (1952) provides an excellent review of the literature that has accumulated on photoperiodism in rice. The work reported herein includes (*a*) the construction of response curves, and the calculation from them of parameters that permit the characterization of differences in varietal reaction, and (*b*) the separation of photoperiod effects on the initiation and the further development of inflorescence primordia.

MATERIALS AND METHODS

Eight pure lines, from Burma, Ceylon, India and Indonesia, formed the subject of the present study, and are listed in Table 1.

All the varieties except *Baok*, a *bulu* variety from Indonesia, belonged to the *indica* group; the *bulus* are believed to be *japonicas*.

In most instances, photoperiod induction commenced on the 21st day after germination, and continued till panicle emergence. A range of photoperiods was secured by the

daily transfer of plants in pots into a dark room at successive intervals. All pots were brought daily into the open at 6 a.m. Long photoperiods were provided by supplementary illumination of an intensity of 6 f.c. at plant height, delivered by incandescent lamps. The experiments were conducted at the Royal Botanic Gardens, Peradeniya, in 1952 and 1953.

Records were taken on the main culms, of lengths of dissected inflorescence primordia from initiation onwards, and of dates of inflorescence emergence (extrusion of the inflorescence tip above the flag leaf). Primordium measurements relate to random samples, and heading records to all the plants in the pots.

CURVES OF PHOTOPERIOD RESPONSE

The pure lines for which curves relating the photoperiod to heading have been constructed are listed in column 1 of Table 2. In the instance of all varieties for which a sufficiently extensive range of photoperiods was used, the curves exhibited a minimum,

Table 1

Nane of pure line	Country of origin	Photoperiod reaction
1. MYAC 104	Burma	Season-fixed
2. Heenati	Ceylon	Period-fixed
3. Vellai Ilankalayan 28061	Ceylon	Period-fixed
4. Devaredderi 26081	Ceylon	Period-fixed
5. Kohumawi B–11	Ceylon	Season-fixed
6. BR–4	India	Season-fixed
7. Ptb–16	India	Season-fixed
8. Baok	Indonesia	Period-fixed

beyond which extension or reduction of the photoperiod delayed heading. Mortality of plants was often high at photoperiods of 6 and 16 hr. It was also evident that the same type of curve could not be fitted over the whole of an extensive range. Data outside the range 8–14 hr. have not been considered in this paper.

The response of the highly sensitive varieties exhibited marked negative skewness, and the untransformed data did not lend themselves to simple curve fitting. It was, however, realized that only the part of the photoperiod spectrum corresponding to natural day was of practical interest to breeders and agronomists, and fitting was confined, in the instance of highly sensitive varieties, to the arm of the parabola that included the range of variation in natural day.

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, were fitted into the data, and are given in column 3 of Table 2. The curves for Vellai Ilankalayan 28061 and MYAC 104 are plotted in Fig. 1.

The germination-heading interval drops to a minimum value when $dy/dx = 0$; this minimum value may be called the *minimum heading duration*, and the photoperiod corresponding to it, the *optimum photoperiod*. As $dy/dx = b + 2cx = 0$, the optimum photoperiod has the value, $-b/2c$.

The minimum flowering duration is obtained by substituting $x = -b/2c$ in the equation, $y = a + bx + cx^2$, and assumes the value, $a - b^2/4c$.

As the coefficient of x tends to zero, the minimum heading duration approximates a.

Change in the magnitude of *a* alters the minimum heading duration without affecting either sensitivity or the optimum photoperiod.

If sensitivity is related to the rate of change of curvature of the second-degree polynomial, the second differential coefficient provides the best estimate of sensitivity:

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

Estimates of sensitivity, the optimum photoperiod and the minimum heading duration are thus furnished by the parameters, $2c$, $-b/2c$ and $a-b^2/4c$ respectively. Statistics calculated from the fitted curves are given in columns 4, 6 and 8 of Table 2.
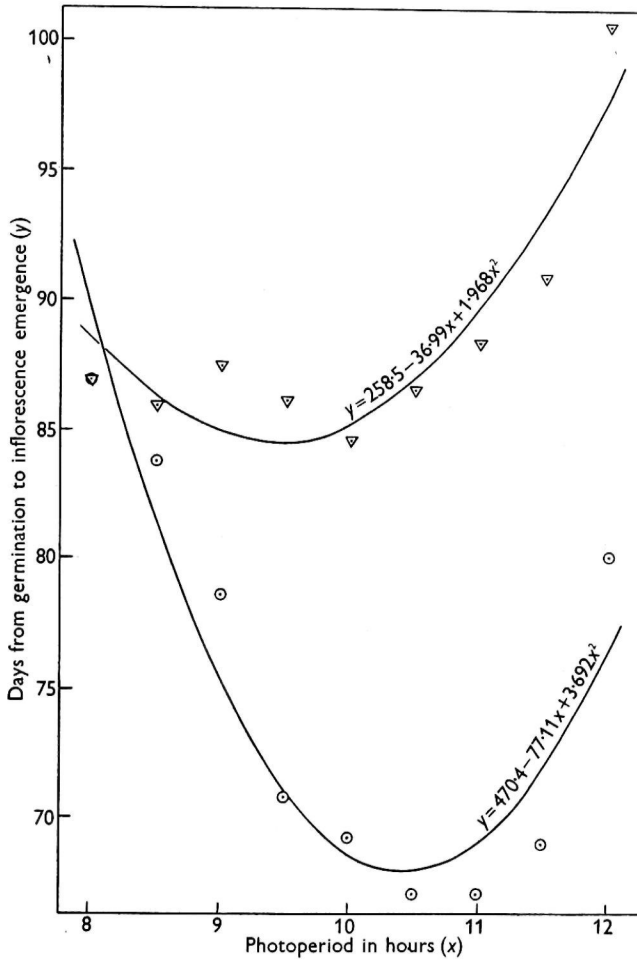

Fig. 1. Photoperiod effect on inflorescence emergence. ⊙, MYAC 104; ▽, *Vellai Ilankalayan* 28061.

Varieties show striking differences in sensitivity. Values range from 1·1 for *Heenati* to 42·9 for Ptb-16. Varieties normally regarded as period-fixed, e.g. *Vellai Ilankalayan* 28061, *Devaredderi* 26081 and *Baok*, have sensitivity values not exceeding 4·8.

The agreement of calculated values of the optimum photoperiod and of the minimum heading duration with the observed values is close. The observed values of the optimum photoperiod in all varieties except *Heenati* approximate 10·0–10·5 hr.

Table 2. *Response curves and derived statistics*

Pure line (1)	Range of photoperiods (hr.) (2)	Curve of response ($y = a + bx + cx^2$) (3)	Photo-period sensitivity ($2c$) (4)	Optimum photoperiod (hr.) Observed (5)	Optimum photoperiod (hr.) Calculated ($-b/2c$) (6)	Minimum heading duration (days) Observed (7)	Minimum heading duration (days) Calculated ($a - b^2/4c$) (8)
Heenati	8·0–13·5	$y = 134\cdot5 - 11\cdot79x + 0\cdot5284x^2$	1·1	12·5	11·2	67·7	68·7
Vellai Ilankalayan 28061	8·0–12·0	$y = 258\cdot5 - 36\cdot99x + 1\cdot9681x^2$	3·9	10·0	9·4	84·6	84·7
Devaredderi 26081	8·0–12·0	$y = 358\cdot0 - 52\cdot21x + 2\cdot4061x^2$	4·8	10·5	10·8	72·7	74·8
Baok	10·0–13·0	$y = 322\cdot3 - 46\cdot21x + 2\cdot4281x^2$	4·8	10·5	9·5	103·0	102·4
MYAC 104	8·0–12·0	$y = 470\cdot4 - 77\cdot11x + 3\cdot6921x^2$	7·3	10·5–11·0	10·5	67·0	67·8
BR–4	10·0–12·5	$y = 722\cdot0 - 121\cdot2\,x + 5\cdot7201x^2$	11·4	10·0	10·6	80·8	80·0
Kohumavi B–11	10·0–12·0	$y = 1992 - 363\cdot4\,x + 17\cdot20x^2$	34·4	10·5	10·6	76·3	72·5
Ptb–16	10·0–12·0	$y = 2298 - 438\cdot3\,x + 21\cdot46x^2$	42·9	10·0	10·2	60·7	60·0

Table 3. *Effect of the photoperiod on inflorescence initiation and emergence*

Photoperiod (hr.)	Mean number of days from sowing to Inflorescence initiation in series A	Mean number of days from sowing to Total emergence in series A	Mean number of days from sowing to Total emergence in series B
6	63·0±7·9	95·0±9·7	78·8±8·9
7	59·0±7·7	84·4±9·2	78·2±8·8
8	52·8±7·3	78·2±8·8	76·6±8·8
9	50·6±7·1	72·5±8·4	76·0±8·7
10	48·2±6·9	72·4±8·5	74·8±8·6
11	51·8±7·2	83·6±9·1	78·2±8·8
12	∞	∞	82·6±9·1
13	∞	∞	87·8±9·4

The high value of the minimum heading duration in *Baok* is exceptional. All the other varieties tested have relatively low values. The most sensitive variety, Ptb-16, has also the shortest minimum heading duration.

INITIATION AND FURTHER DEVELOPMENT OF INFLORESCENCE PRIMORDIA

In experiments set down in 1952, plants of the pure line, *Kohumawi*-B11, received the following series of treatments:

Series A. Subjected from the time of appearance of the first foliage leaf until the completion of blooming to photoperiods ranging from 6 to 13 hr.

Series B. Subjected to a 10 hr. photoperiod until inflorescence initiation, and thereafter to photoperiods ranging from 6 to 13 hr.
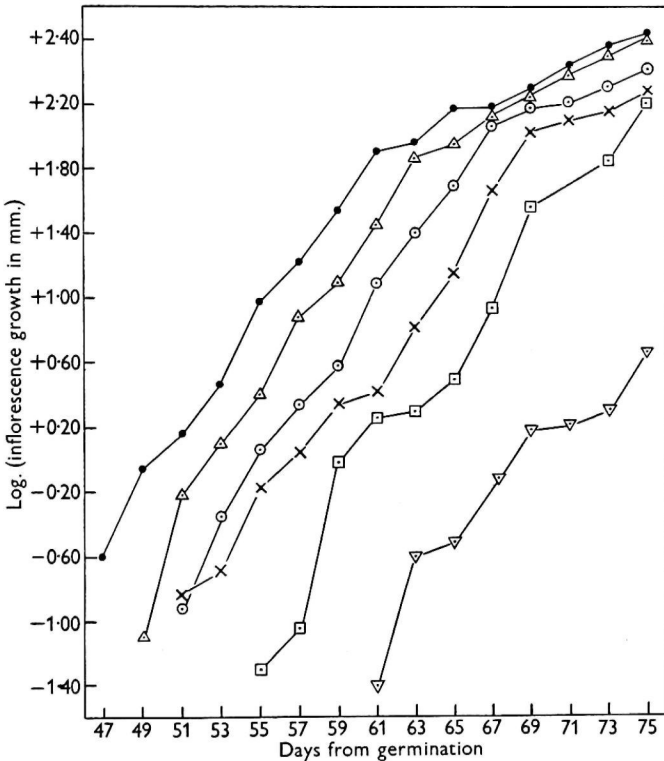

Fig. 2. Growth of inflorescence primordia at various photoperiods. ▽, 6 hr.;
⬜, 7 hr.; ⊙, 8 hr.; △, 9 hr.; ●, 10 hr.; ×, 11 hr.

Photoperiod induction in series A commenced in nursery pots and continued after the transplanting of 20-day seedlings. The second and third columns in Table 3 give the numbers of days to inflorescence initiation and emergence respectively in series A. The day-length effect on primordium formation is striking and parallels that on inflorescence emergence; the optimum photoperiod for both effects approximates 10 hr. No primordia were initiated during the currency of the experiment, in plants receiving 12 hr. and longer photoperiods.

In Fig. 2 the logarithms of primordium lengths for the various photoperiods are plotted against time. There are apparent deviations from exponential growth in the final stages.

The effects in series B are purely on the elongation of the inflorescence initials. In this series, subjection to the range of photoperiods commenced as soon as dissection revealed recognizable inflorescence primordia, i.e. 51 days after the sowing of germinated seed and 31 days after transplanting from nursery pots. The fourth column in Table 3 records the number of days to emergence of the total population in series B. The response resembles that of primordium initiation, but is not as striking. That the photoperiod effects on primordium elongation are real is shown in the variance analyses presented in

Table 4. *Analysis of variance of emergence percentages transformed to the inverse sine scale (series B)*

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Photoperiods	7	15,539·260	2,219·894	24·761***
Linear regression	1	4,589·869	4,589·869	51·195***
Deviations	6	10,949·391	1,824·898	20·355***
Error	32	2,868·916	89·654	—
Total	39	18,408·176	—	—

*** Significant at the 0·1 % point.

Summary of results

	Photoperiod in hours								Standard error
	6	7	8	9	10	11	12	13	
Degrees ($\theta = \sin^{-1}\sqrt{p}$)	60·3	60·9	77·4	79·9	80·7	71·6	31·7	27·5	±4·13
Percentages	75·4	76·3	95·2	96·9	97·4	90·0	27·7	21·3	

Table 5. *Analysis of variance of inflorescence lengths (series B)*

	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Photoperiods	7	305,427·775	43,632·539	9·587***
Linear regression	1	30,661·458	30,661·458	6·927*
Deviations	6	274,766·317	45,794·386	10·346***
Error	32	141,644·200	4,426·383	—
Total	39	447,071·975	—	—

* Significant at the 5 % point.
*** Significant at the 0·1 % point.

Summary of results

	Photoperiod in hours								Standard error
	6	7	8	9	10	11	12	13	
Mean inflorescence length in mm.	238	327	376	391	448	414	248	170	±29·7

Tables 4 and 5. Table 5 relates to inflorescence lengths in series B measured on the 75th day after sowing. Table 4 gives the variance analysis of inflorescence emergence percentages on the same date, transformed to the inverse sine scale ($\theta = \sin^{-1}\sqrt{p}$) appropriate to a binomial distribution. Photoperiod effects in both variance analyses assume significance at the 0·1 % point. The significance of the mean squares for deviations from regression in both analyses indicate that the regressions are curvilinear.

Curves of primordium growth for photoperiods of 10 and 13 hr. in series B have been plotted in Fig. 3. Exponential curves have been fitted into the data up to the 65th day. Subsequent growth appears linear, and straight lines have been fitted. Measurements had unfortunately not been made on the 67th day which falls between the exponential and linear phases. The regression lines for the 10 hr. photoperiod are steeper in both the exponential and linear phases.
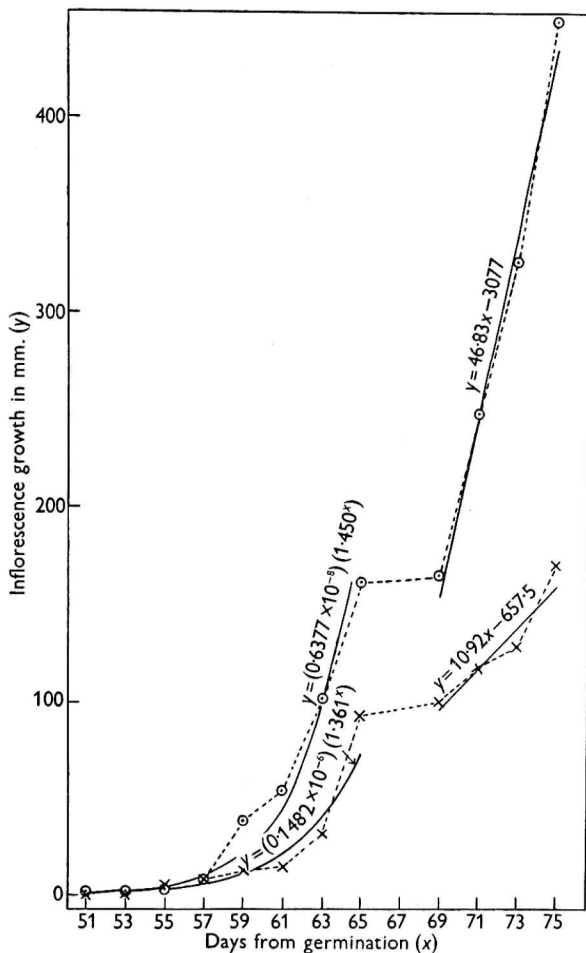

Fig. 3. Further growth of initiated inflorescence primordia. ⊙, 10 hr. photoperiod; ×, 13 hr. photoperiod.

DISCUSSION

The results presented herein reveal a common pattern of photoperiod response in rice varieties, notwithstanding the generally expressed view that 'all rice varieties do not react in the same way' (Wagenaar, 1952). If an adequate range of photoperiods is used, it should be possible to locate, in the instance of every variety that possesses appreciable sensitivity, an optimum photoperiod at which the heading duration assumes a minimum value; photoperiods longer and shorter than the optimum delay heading.

Rice varieties differ markedly in sensitivity, and, to a less extent, in the values of the

optimum photoperiod and of the minimum heading duration. The variation in both the optimum photoperiod and the minimum heading duration appear greater in the less sensitive varieties.

In natural day, the relatively insensitive varieties are, as a rule, early, and the sensitive varieties late. At the optimum photoperiod, these age differences narrow and often vanish; the sensitive varieties tested have shown at least as short a minimum heading duration as the relatively insensitive varieties.

Much of the confusion that characterizes previous work on photoperiodism in rice derives from the failure to apply methods appropriate to a factor that is quantitative in action. The location of the optimum photoperiod is necessary for the interpretation of quantitative response of the type exhibited by rice varieties. Kuilman (1937) claimed that the Indonesian *tjerehs* were short-day plants, and the *bulus*, long-day plants. The logical limit of the definition implicit in Kuilman's classification would be a claim that any variety exhibits long-day behaviour at photoperiods shorter than the optimum. The differential response of *bulus* and *tjerehs* that Kuilman noted, and the comparable differences between summer and winter rices of Bengal, reported by Sircar & Ghosh (1947), apparently result from varietal differences in the optimum photoperiod. Tests over an adequate range would probably show that some of the Indonesian *bulus* and the summer rices of Bengal have a high optimum photoperiod. It should, however, be mentioned that in *Baok*, the only *bulu* variety included in the present studies, an optimum photoperiod of 10·5 hr. has been observed.

The characterization of varietal behaviour in terms of parameters derived from second-degree polynomials in the manner indicated in this paper permits the genetic analysis of photoperiod response. The estimates of sensitivity, minimum heading duration and the optimum photoperiod provided by the parameters $2c$, $a - b^2/4c$ and $-b/2c$ respectively are varietal characters amenable to separate study. Previous to the precise definition of sensitivity given in this paper, the writer had demonstrated that sensitivity in certain crosses is determined by a single gene pair in Jodon's Linkage Group I (Chandraratna, 1953). A series of multiple alleles at this locus or a series of modifiers may be postulated to explain varietal variation in sensitivity. Minimum heading duration is possibly polygenic. The nature of the optimum photoperiod is completely obscure, but it appears to show some measure of environmental variation.

The results obtained in the two series of photoperiod treatments with *Kohumawi* B-11 clearly indicate that the curve relating the photoperiod to heading integrates two separate and similar responses, viz. a striking effect on inflorescence initiation, and a less pronounced but significant effect on the subsequent growth of inflorescence initials. The effect noted in series A on the initiation of inflorescence primordia is of a magnitude that makes statistical analysis unnecessary. The curve relating primordium initiation to the photoperiod parallels the integrated curve for the total emergence effect, and has the same optimum, viz. 10 hr. As the photoperiod effect on further development of inflorescence primordia cumulates into the total effect, the integrated curve exhibits higher sensitivity than the curve for primordium initiation.

Variance analyses of data in series B demonstrate a significant photoperiod effect on the further growth of inflorescence primordia. The regressions of inflorescence growth and emergence on the photoperiod are curvilinear.

The growth of the inflorescence primordium is initially exponential and continues

to be so over a considerable period, but tends to become linear in the later stages. The deviation from exponential growth possibly occurs when vacuolation commences making a greater contribution to size increase than cell division. Parallel records of primordium length and cell dimensions would be illuminating.

Even in series A, the differences in regression coefficients for primordium elongation at the various photoperiods (Fig. 2) suggest the existence of a separate effect on the relative elongation rate. It may, however, be argued that the higher elongation rates at the near-optimum photoperiods inhere in the initiated primordia. An experiment in which induction of a range of photoperiods commences early and ceases at primordium initiation would be necessary to decide this issue.

Series B provides more critical evidence of photoperiod effects on the further development of initiated primordia. Apart from eliminating carry-over effects of pre-initiation induction, this series includes a wider range of photoperiods; in series A, photoperiods of 12 and 13 hr. produced no emergence and provided no data. In series B, the regression lines relating to the optimum photoperiod differ in slope from those for the 13 hr. photoperiod in both the exponential and linear phases. It is, however, evident that although the photoperiod influences primordium elongation, the contribution of this effect to final inflorescence emergence is extremely small in comparison with the contribution of the primordium initiation effect.

SUMMARY

Curves relating the inflorescence emergence to the photoperiod have been constructed for eight rice pure lines from Burma, Ceylon, Indonesia and India. Estimates of photoperiod sensitivity, minimum heading duration and the optimum photoperiod have been derived from parameters of second-degree polynomials fitted to these curves. The pure lines varied widely in sensitivity. Variation in the minimum heading duration and the optimum photoperiod was less marked.

In the instance of one pure line, viz. *Kohumawi* B-11, the gross photoperiod response has been resolved into component effects. Apart from the striking influence on the initiation of infloresence primordia, the photoperiod exercises a small but significant effect on their further development.

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