GENETICS OF PHOTOPERIOD SENSITIVITY IN RICE

BY M. FERNANDO CHANDRARATNA

Department of Agriculture, Peradeniya, Ceylon

(With Two Text-figures)

(Received 2 June 1954)

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:

\[
\frac{d^2y}{dx^2} = 2c.
\]

The parameters \( 2c \), \( -b/2c \) and \( a - b^2/4c \) thus provide estimates of photoperiod sensi-
tivity, 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
Genetics of photoperiod sensitivity in rice

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 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, auricule-junctura and pericarp.

Records made in 1952–3 indicate the pattern of day-length change at Batalagoda (latitude 7° 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

<table>
<thead>
<tr>
<th>Cross</th>
<th>Sowing date</th>
<th>Sensitive parent</th>
<th>Vellai Ilankalayan 28061</th>
<th>$F_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>MYAC 104 × Vellai Ilankalayan 28061</td>
<td>7 December 1951</td>
<td>92 ± 0.88</td>
<td>101 ± 1.84</td>
<td>86 ± 2.46</td>
</tr>
<tr>
<td>MLYC 401 × Vellai Ilankalayan 28061</td>
<td>20 December 1951</td>
<td>95 ± 1.92</td>
<td>92 ± 0.93</td>
<td>76 ± 0.88</td>
</tr>
<tr>
<td>GEB 24 × Vellai Ilankalayan 28061</td>
<td>7 December 1951</td>
<td>99 ± 1.57</td>
<td>101 ± 1.38</td>
<td>86 ± 3.51</td>
</tr>
</tbody>
</table>

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 $\chi^2$ 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
Genetics of photoperiod sensitivity in rice

The individual families composing the 1952 F₉ of MYAC 104 and MLYC 401 crosses provide estimates of the heterogeneity χ²; 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 parent MLYC 401 and Vellai Hallakalanay 28061, F₁ and F₉. The F₁ shows dominance of sensitivity, and possesses a variance comparable with that of the parents. The F₉ 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; χ² 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 F₁ in the south-west monsoon**

<table>
<thead>
<tr>
<th>Cross</th>
<th>Sowing date</th>
<th>Sensitive parent</th>
<th>Vellai Hallakanay 28061</th>
<th>F₁</th>
</tr>
</thead>
<tbody>
<tr>
<td>MYAC 104 × Vellai Hallakanay 28061</td>
<td>1 May 1952</td>
<td>161 ± 0.12</td>
<td>106 ± 0.15</td>
<td>144 ± 0.83</td>
</tr>
<tr>
<td>MLYC 401 × Vellai Hallakanay 28061</td>
<td>1 May 1952</td>
<td>164 ± 2.29</td>
<td>105 ± 2.45</td>
<td>169 ± 2.70</td>
</tr>
<tr>
<td>MLYC 401 × Vellai Hallakanay 28061</td>
<td>24 April 1953</td>
<td>166 ± 0.12</td>
<td>108 ± 0.17</td>
<td>160 ± 0.30</td>
</tr>
<tr>
<td>HMC 12 × Vellai Hallakanay 28061</td>
<td>10 April 1952</td>
<td>182 ± 0.69</td>
<td>—</td>
<td>166 ± 0.47</td>
</tr>
<tr>
<td>GEB 24 × Vellai Hallakanay 28061</td>
<td>1 April 1952</td>
<td>180 ± 0.66</td>
<td>—</td>
<td>166 ± 0.90</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Sensitive parent</th>
<th>F₉ family</th>
<th>Sensitive (Se)</th>
<th>Insensitive (se)</th>
<th>Total</th>
<th>3:1 ratio</th>
<th>Heterogeneity</th>
</tr>
</thead>
<tbody>
<tr>
<td>MYAC 104</td>
<td>1952 (1)</td>
<td>47</td>
<td>13</td>
<td>60</td>
<td>0-2556</td>
<td>0-7-0-5</td>
</tr>
<tr>
<td>1952 (2)</td>
<td>44</td>
<td>22</td>
<td>66</td>
<td>90</td>
<td>0-014</td>
<td>0-5-0-99</td>
</tr>
<tr>
<td>Total</td>
<td>159</td>
<td>37</td>
<td>216</td>
<td>60</td>
<td>0-0889</td>
<td>0-5-0-3</td>
</tr>
<tr>
<td>MLYC 401</td>
<td>1952 (1)</td>
<td>232</td>
<td>66</td>
<td>298</td>
<td>3-0858</td>
<td>0-0-0-05</td>
</tr>
<tr>
<td>1952 (2)</td>
<td>266</td>
<td>98</td>
<td>364</td>
<td>60</td>
<td>1-0301</td>
<td>0-0-3</td>
</tr>
<tr>
<td>Total</td>
<td>666</td>
<td>166</td>
<td>832</td>
<td>60</td>
<td>0-0531</td>
<td>0-8-0-7</td>
</tr>
<tr>
<td>1953 (1)</td>
<td>743</td>
<td>245</td>
<td>988</td>
<td>60</td>
<td>0-3673</td>
<td>0-7-0-5</td>
</tr>
<tr>
<td>HMC 12</td>
<td>1952 (1)</td>
<td>166</td>
<td>71</td>
<td>236</td>
<td>3-3955</td>
<td>0-1-0-05</td>
</tr>
<tr>
<td>GEB 24</td>
<td>1952 (1)</td>
<td>310</td>
<td>83</td>
<td>393</td>
<td>3-4300</td>
<td>0-1-0-05</td>
</tr>
</tbody>
</table>

The constitution of Vellai Hallakanay 28061 is Ap Ap Pr Pr. The F₉ 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.

χ² 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 χ² value for independence of 1.263 (P = 0.3-0.2). In the instance of all four crosses, P from the χ² 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 $F_4$ 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 ± 2.21 derived from the pooled data for the MLYC 401 cross appears to be the best estimate of the recombination percentage.

![Graph](image)

Fig. 2. Frequency distributions for number of days to heading in parents, $F_1$, and $F_2$ of the MLYC 401 x Velia Hankanlayan 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; $\chi^2$ 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-junctura colour in the $F_2$ of the MYAC 104 cross, $\chi^2$ 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 $2.4 \pm 2.0$.

**Relation of tiller number of photoperiod sensitivity**

Frequency distribution of tiller numbers in $Se$ and $se$ phenotypes in the $F_2$ of the Vellai Ilankalayan 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 Ilankalayan 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 $3$ late : $1$ 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

<table>
<thead>
<tr>
<th>Sensitive parent</th>
<th>Linkage group</th>
<th>Linkage phase</th>
<th>Factor pair</th>
<th>( Y )</th>
<th>( y )</th>
<th>( Y^2 )</th>
<th>( P )</th>
<th>( Se )</th>
<th>( se )</th>
<th>Total</th>
<th>( \chi^2 ) for independence</th>
<th>( P )</th>
<th>( % ) for recombination</th>
</tr>
</thead>
<tbody>
<tr>
<td>MYAC 104</td>
<td>1</td>
<td>( R )</td>
<td>( Ap ) ap</td>
<td>0.305</td>
<td>0.7-0.5</td>
<td>112</td>
<td>47</td>
<td>54</td>
<td>3</td>
<td>216</td>
<td>13.835</td>
<td>&lt;0.001</td>
<td>23-9±0.35</td>
</tr>
<tr>
<td>MLYC 401, 1952</td>
<td>1</td>
<td>( R )</td>
<td>( Ap ) ap</td>
<td>2.299</td>
<td>0.2-0.1</td>
<td>470</td>
<td>106</td>
<td>211</td>
<td>5</td>
<td>882</td>
<td>62.701</td>
<td>&lt;0.001</td>
<td>16-3±0.36</td>
</tr>
<tr>
<td>MLYC 401, 1953</td>
<td>1</td>
<td>( R )</td>
<td>( Ap ) ap</td>
<td>0.049</td>
<td>0.9-0.8</td>
<td>501</td>
<td>242</td>
<td>237</td>
<td>8</td>
<td>988</td>
<td>83.951</td>
<td>&lt;0.001</td>
<td>17-9±0.38</td>
</tr>
<tr>
<td>MLYC 401, total</td>
<td>HMC 12</td>
<td>( R )</td>
<td>( Ap ) ap</td>
<td>0.776</td>
<td>0.5-0.3</td>
<td>971</td>
<td>438</td>
<td>448</td>
<td>13</td>
<td>1870</td>
<td>146.458</td>
<td>&lt;0.001</td>
<td>17-3±0.22</td>
</tr>
<tr>
<td>GEB 24</td>
<td></td>
<td>( R )</td>
<td>( Ap ) ap</td>
<td>0.814</td>
<td>0.5-0.3</td>
<td>115</td>
<td>50</td>
<td>65</td>
<td>3</td>
<td>238</td>
<td>21.160</td>
<td>&lt;0.001</td>
<td>21±6±0.16</td>
</tr>
<tr>
<td>MYAC 104</td>
<td>1</td>
<td>( R )</td>
<td>( Au ) au</td>
<td>2.298</td>
<td>0.2-0.1</td>
<td>47</td>
<td>112</td>
<td>33</td>
<td>24</td>
<td>216</td>
<td>14.446</td>
<td>&lt;0.001</td>
<td>21±6±0.77</td>
</tr>
<tr>
<td>MLYC 401</td>
<td>IV</td>
<td>( R )</td>
<td>( Pr ) pr</td>
<td>3.138</td>
<td>0.1-0.05</td>
<td>380</td>
<td>101</td>
<td>154</td>
<td>53</td>
<td>697</td>
<td>1.283</td>
<td>0.3-0.2</td>
<td>2-4±2-0</td>
</tr>
</tbody>
</table>

\( Ap \) ap

| MYAC 104         | 1            | \( C \)       | \( Au \) au | 79   | 87   | 106  | 1    | 2     | 1     | 216  | 34±249            | <0.001 | 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 \( F_2 \)

<table>
<thead>
<tr>
<th>Sensitive parent</th>
<th>Phenotype</th>
<th>Frequencies of plants with tillers numbering</th>
<th>Total nos. of plants</th>
<th>Mean tiller no. per plant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0-4</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>MYAC 104</td>
<td>se</td>
<td>3</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Se</td>
<td>22</td>
<td>23</td>
<td>29</td>
</tr>
<tr>
<td>MLYC 401</td>
<td>se</td>
<td>9</td>
<td>19</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Se</td>
<td>1</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>HMC 12</td>
<td>se</td>
<td>3</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Se</td>
<td>11</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>GEB 24</td>
<td>se</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Se</td>
<td>1</td>
<td>6</td>
<td>10</td>
</tr>
</tbody>
</table>

Genetics of photoperiod sensitivity in rice
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 S'p 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, segregates, of a regression of tiller number onto 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.

I am deeply grateful to Messrs J. J. Niles and H. Weeraratne for their painstaking assistance.

References


