# Studies on the Photoperiodism in the Genus *Oryza*

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A large amount of work on photoperiodism in rice from different view points has been reported by the investigators of many rice growing countries. The literature on the photoperiodism in rice was surveyed by many workers. However, most of investigations have been limited to the cultivated, *O. sativa*, and a few related species.

The object of the present investigation was to study the ontogenetic development and the differentiation of photoperiodic responses and to investigate their intra- and inter-specific variations within the genus *Oryza*. More than 600 strains belonging to 25 species, including 2 cultivated and 23 wild species, were used.

Photoperiodic sensitivity can be determined by classifying the strains into "sensitive" and "insensitive" on the basis of their short day responses, and by more exactly measuring their photoperiodic sensitivity.

## Classification of the strains into "sensitive" and "insensitive" on the basis of short day response

Strains which showed accelerated heading under the short day condition ($12^h l+12^h d$) were considered to be sensitive while those which did not show any acceleration to be insensitive. In section *Sativae*, the frequency of photoperiodically sensitive strains was 77% in cultivated rice, 99% in *Perennis* group, 81% in *Minuta* group and 63% in *Latifolia* group. It was 0% in *Granulatae* section and 89% in *Coarctatae* section. Only one *Rhynchoryza* strain was studied and it was proved to be insensitive (Table 1).

Of the two cultivated species, *O. sativa* contained more insensitive strains than *O. glaberrima*. The difference may be due to the longer history of cultivation and consequently wider distribution of the former. The geographical distribution of sensitive and insensitive strains of cultivated rice was interpreted in terms of their adaptation to agronomic requirements as well as to natural conditions. Almost all strains of *Perennis* group were sensitive. This indicates that this putative progenitor of cultivated rice must have been photoperiodically sensitive. *O. officinalis* showed an extremely high frequency of insensitive strains. Two tetraploid groups, *Minuta* and *Latifolia*, both of which contained C genome of *O. officinalis*, also showed higher frequencies of insensitive strains than the *Perennis* group. These facts indicate that genome C has a tendency to suppress photoperiodic sensitivity.

Some species were monotypic containing either only sensitive or only insensitive strains, while others were heterogeneous. The former have in general a small distribution area or have been geographically or ecologically isolated from other species. These factors seem to be responsible for a limited intraspecific differentiation in photoperiodic response. In both cultivated and wild species, great majority were photoperiodically sensitive. This indicates that the sensitive strains are, in general, favored under natural as well as artificial selection. Some sensitive strains were found in the equatorial region, where photoperiodic sensitivity seems to have no significance. They were, therefore, assumed to have originated

**Table 1. Materials used, species names, native habitats and photoperiodic responses**

| Species | No. of strains | | | Ratio of sensitive to total strains % | Habitat |
|---|---|---|---|---|---|
| | Total | Sensitive1) | Insensitive2) | | |
| Section *Sativae* | | | | | |
| *O. sativa* | 152 | 108 | 44 | 71. 1 | Asia, Africa and America |
| *O. glaberrima* | 75 | 66 | 9 | 88. 0 | Africa |
| *O.* s. f. *spontanea* | 151 | 151 | 0 | 99. 3 | Asia |
| *O. perennis* | 64 | 62 | 2 | | Asia and America |
| *O. barthii* | 31 | 31 | 0 | | Africa |
| *O. cubensis* | 3 | 3 | 0 | | America |
| *O. breviligulata* | 39 | 39 | 0 | | Africa |
| *O. stapfii* | 5 | 5 | 0 | | Africa |
| *O. australiensis* | 3 | 3 | 0 | 100. 0 | Australia |
| *O. officinalis* | 20 | 6 | 14 | 30. 0 | Asia |
| *O. minuta* | 15 | 11 | 4 | 80. 9 | Asia |
| *O. malampuzhaensis* | 2 | 2 | 0 | | Asia |
| *O. eichingeri* | 3 | 3 | 0 | | Africa |
| *O. punctata* | 1 | 1 | 0 | | Africa |
| *O. latifolia* | 21 | 13 | 8 | 63. 0 | America |
| *O. alta* | 4 | 2 | 2 | | America |
| *O. grandiglumis* | 2 | 2 | 0 | | America |
| Section *Granulatae* | | | | | |
| *O. granulata* | 4 | 0 | 4 | 0. 0 | Asia |
| *O. meyeriana* | 2 | 0 | 2 | | Asia |
| *O. abromeitiana* | 1 | 0 | 1 | | Asia |
| Section *Coarctatae* | | | | | |
| *O. ridleyi* | 4 | 1 | 0 | 88. 8 | Asia |
| *O. longiglumis* | 11 | 11 | 0 | | Asia |
| *O. coarctata* | 1 | 1 | 0 | | Asia |
| *O. brachyantha* | 2 | 0 | 2 | | Africa |
| Section *Rhynchoryza* | | | | | |
| *O. subulata* | 1 | 0 | 1 | 0. 0 | America |
| Total cultivated | 227 | 174 | 53 | 76. 7 | |
| Total wild | 390 | 350 | 40 | 89. 7 | |
| Total total | 617 | 524 | 93 | 84. 9 | |

1) Strains, whose heading date observed under short day condition was by more than 20 days earlier than that observed under natural condition.

2) Strains, whose heading was not accelerated more than by 10 days by short day treatment.

in higher latitudes and migrated to the equator.

## Aging effect

In order to investigate the change in photoperiodic sensitivity during the life history of the rice plants, they were treated at different ages by applying several short day conditions for various periods. Plants became respondent to short day condition only when they reached a certain age; short day treatment before that age was entirely ineffective. Sensitivity to the treatment increased with the age, reaching to

**Table 2. Heading dates of Kyoto Asahi treated under different short day conditions; heading dates of treated plants are expressed by the difference (in days) from those of respective control plots**

| Plot | Day length | Treatments (days) | Plant age | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 |
| Control | — | — | 86 | 93 | 101 | 111 | 117 | 124 | 125 | 135 |
| L-1 | $14^h00^m$ | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| -2 | ,, | 6 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| -3 | ,, | 9 | 1 | 0 | 0 | 0 | 0 | 6 | 3 | 3 |
| -4 | ,, | 12 | 1 | 0 | 0 | 1 | 7 | 9 | 3 | 6 |
| -5 | ,, | 15 | 0 | 1 | 2 | 4 | 5 | 5 | 6 | 6 |
| 5 % l. s. d. | — | — | 2. 3 | 1. 9 | 1. 2 | 1. 5 | 1. 2 | 2. 1 | 1. 5 | 1. 6 |
| Min. No.* | — | — | — | — | 13. 8 | 12. 5 | 9. 5 | 6. 7 | 7. 5 | 7. 6 |
| M-1 | $13^h00^m$ | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 |
| -2 | ,, | 6 | 0 | 0 | 12 | 25 | 20 | 19 | 10 | 6 |
| -3 | ,, | 9 | 0 | 1 | 25 | 27 | 20 | 20 | 10 | 10 |
| -4 | ,, | 12 | 0 | 2 | 22 | 29 | 20 | 20 | 14 | 14 |
| -5 | ,, | 15 | 2 | 15 | 24 | 30 | 18 | 24 | 13 | 13 |
| 5 % l. s. d. | — | — | 0. 0 | 3. 2 | 1. 5 | 1. 9 | 0. 0 | 0. 8 | 2. 0 | 1. 2 |
| Min. No.* | — | — | 12. 0 | 12. 3 | 3. 4 | 3. 2 | 3. 0 | 3. 1 | 3. 0 | 3. 6 |
| S-1 | $12^h00^m$ | 3 | 0 | 2 | 0 | 0 | 1 | 6 | 3 | 3 |
| -2 | ,, | 6 | 0 | 1 | 20 | 27 | 20 | 22 | 12 | 12 |
| -3 | ,, | 9 | 8 | 20 | 30 | 31 | 29 | 25 | 14 | 15 |
| -4 | ,, | 12 | 7 | 25 | 32 | 32 | 28 | 25 | 15 | 16 |
| -5 | ,, | 15 | 9 | 26 | 33 | 33 | 22 | 25 | 17 | 17 |
| 5 % l. s. d. | — | — | 0. 4 | 3. 9 | 1. 4 | 1. 6 | 2. 5 | 1. 0 | 2. 1 | 1. 1 |
| Min. No.* | — | — | 6. 2 | 6. 5 | 3. 2 | 3. 1 | 3. 7 | 0. 5 | 2. 1 | 2. 1 |

* Estimated minimum number of short day treatments required for flower induction. The estimation for 70 days old plant treated under $14^h00^m$ day length, for example, was made as follows: Min. No. of days $=6+\frac{2.1-1}{5}\times 3=6.7$

a plateau at a certain age (Table 2). The ontogenetic development of sensitivity was due to the effect of age and was termed *"aging effect"*. When plants at a specific age were treated by a specific short day length, a certain number of repeated treatments were required for flower initiation. This fact indicates that a stimulus produced by repeated treatments is cumulative and flower induction can take place only when it has reached a certain threshold. This was termed *"threshold effect"*. A greater acceleration of heading took place, when plants were treated by a shorter day length than the critical one. This fact suggests that the shorter is the day or the longer is the treatment repeated, the greater is the stimulation produced. Stimulation above the threshold value has apparently a *"dosage effect"* on acceleration of heading.

When a short day treatment was given for a limited number of days, a certain day length shorter than the *"critical"* one was required for flower induction. The *"critical"* day length is dependent upon the number of repetitions of the treatment and, therefore, was called *"partial critical day length"*. When the treatment is repeated longer enough, the partial critical day length approaches the ultimate day length, *i.e.*, the critical day length. It has been shown that aging of plants has three-fold effects. First, the minimum number of short day treatments required for induction is smaller for old plants than for young ones. Secondly, dosage effect is dependent upon plant age; photoperiodic stimulation above the threshold causes in general a greater acceleration of heading in old plants than in young ones. And thridly, the partial critical day length is also dependent upon the age, being shorter at a young age than at an old age (Fig. 1).

Different rice strains responded differently to short day treatments according to the aging effect. The difference is mainly attributable

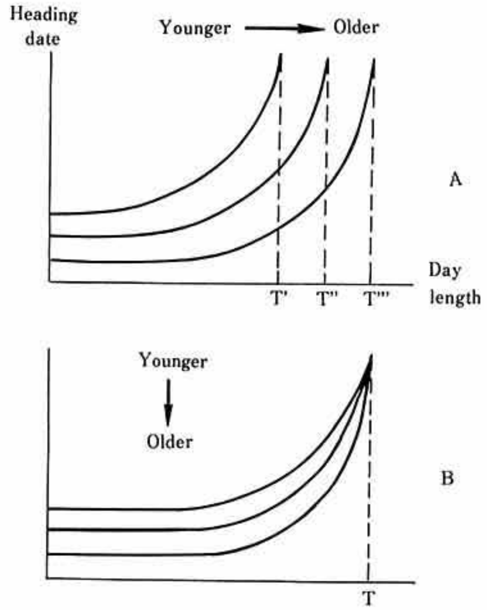

Fig. 1. Schematic representation of the relationships between plant age and day length in respect of heading date.
A : When short day treatment is limited to a certain period.
B : When short day treatment is given indefinitely.

to different patterns of the ontogenetic development of photoperiodic sensitivity. Moreover, responses to three sub-factors mentioned above differed significantly among strains, and some species-specific-behaviours were found. In general, cultivated species was more sensitive than the wild species. The minimum number of days of short day treatment, necessary to initiate flower buds, increased in the order of *O. sativa*, *O. glaberrima*, *O. sativa* var. *spontanea*, *O. perennis*, *O. breviligulata* and *O. barthii*. The number of days shortened by the number of repetitions of the same short day length increased in the order of *O. sativa*, *O. sativa* var. *spontanea*, *O. glaberrima* and *O. perennis*.

## Critical day length

The critical day length was estimated from the day length at the time of flower bud formation that occurs 30 days prior to heading. It was found that the lower was the latitude of their distribtuion area, the shorter was the critical day length. The critical day length, the heading date in other words, of photoperiodically sensitive strains was mainly determined by the latitude of their respective native places, regardless of the species. Concerning wild species, correlation coefficient between critical day length and latitude was +0.5274 for all wild strains and +0.5778 when Assamese strains and *O. longiglumis* from New Guinea were excluded. These differed distinctly from the others. Apparently, photoperiodic adaptation to their native places was primarily important in the differentiation of wild strains. A linear regression of critical day length ($T$) in minutes on latitude of native place ($L$) in latitudinal degrees was as follows; $T=3.548L+19.272$. This indicates that the critical day length of a wild strain becomes 3.548 minutes longer, when its native place is shifted by one degree northward in the northern hemisphere (or southward in the southern hemisphere).

A similar correlation was also found in the cultivated rice. The correlation coefficient was +0.5264 for all cultivated starains, +0.6737 for strains of *O. sativa* and +0.6230 for those of *O. glaberrima*. The linear regression of critical day length ($T$) on latitude of native place ($L$) for all cultivated strains was shown as follows; $T=2.563L+26.064$. This indicates that the critical day length of a cultivated strain becomes 2.563 minutes longer, when its native place is shifted by one degree northward in the northern hemisphere (or southward in the southern hemisphere).

Dependence of the critical day length upon the latitude of the native place was similar in cultivated and wild rice. This indicates that a diversity of photoperiodic responses has been similarly preserved under cultivated as well as wild conditions.

## Acceleration rate of the heating by short day treatments

The difference in photoperiodic sensitivity

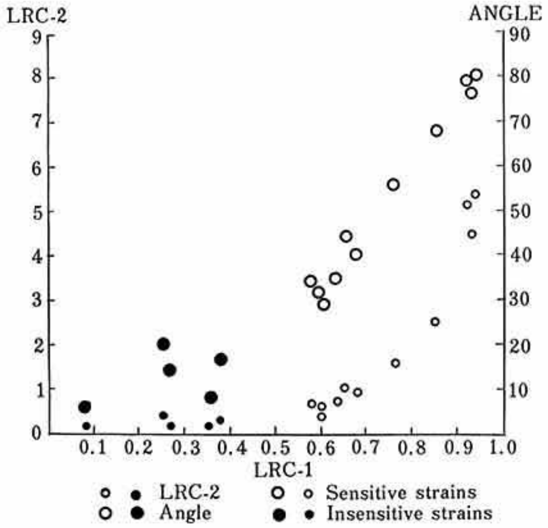

Fig. 2. Interrelation between the coefficients of linear regression of growing period on sowing time (LRC-1), those of growing period on day length at time of flower bud formation (LRC-2) and angles converted from the latter (Angle-LRC-2).

was analyzed from the third viewpoint, namely, from the differential acceleration of heading among various strains by a short day condition. Three different indices for the acceleration rate of heading were used and compared. These were (1) coefficient of the linear regression of growing period on sowing time (expressed by LRC-1), (2) coefficient of linear regression of growing period on day length at the time of flower bud formation (LRC-2), and (3) angle changed from the latter coefficient (Angle-LRC-2). Correspondence between the three indices was very good; all fitting well with the previous classification of strains into sensitive and insensitive (Fig. 2). The difference between the two groups was 0.5 for both LRC-1 and LRC-2 and 30° in Angle. LRC-1 indicates acceleration of heading (in number of days) by delaying the sowing by one day, while LRC-2 and Angle represent acceleration rate of heading by shortening the day length by one minute, the latter being biologically more significant than the former. LRC-2 was less suitable than Angle for differentiating sensitive from insensitive strains. For these reasons, Angle was thought to be the most recommendable among the three indices. Thus, with the help of this method, especially determination of Angle, it becomes possible to define the degree of sensitivity of various rice species. Using this index, the acceleration rate of heading was investigated with all the strains used. Their sensitivities were previously estimated as some being sensitive and the others being insensitive. This classification by Angle was in a complete agreement with the previous grouping by the other methods.

Regardless of the species, strains that have short critical day length showed in general greater sensitivity than those having long critical day length. From this behaviour, it was assumed that strains which could respond to a small change in day length had a selective advantage in low latitudes.

Boundary between the two groups was flexible for LRC-1, LRC-2 and the Angle according to the respective year and sowing time. Strains having large values in the indices used, showed, in general, the smaller flexibility than those having smaller values. In other words, the higher is the sensitivity, the smaller is the flexibility. No definite relationship was found between the taxonomic status and the flexibilty.

The minimum number of short days, degree and processes of acceleration rate with increase in short days, differed significantly among strains. Therefore, these factors can also be used as indices of photoperiodic sensitivity. Strains can be classified into several patterns as regard to responses upon the combinations of minimum number of short days or given day length, basing on the standard deviations at the 5% level.

## Effect of civil twilight

Effect of civil twilight on photoperiodic induction was investigated using four strains belonging to *O. sativa*, *O. glaberrima* and *O. perennis*.

In the neighborhood of the critical day

**Table 3. Factors affecting photoperiodic responses in the genus *Oryza***

- I. Classification of rice strains into "sensitive" and "insensitive" on the basis of short day response
- II. Measuring of photoperidic sensitivity on the basis of short day response
  - a) Aging effect......threshold effect
    dosage effect
    partial critical day length
  - b) Critical day length
  - c) Acceleration rate of the heading by short day treatments
  - d) Accumulation effect
  - e) Effect of decreasing degree of natural day length
  - f) Stability of the photoperiodic response
- III. Effect of civil twilight
- IV. Genetic constitution
- V. Evolutional relationship

length, morning civil twilight delayed heading of all the three species. This fact indicates that the morning twilight is accepted as light by the plants. On the other hand, evening civil twilight delayed heading of some strains but not of others. This indicates that some variations in responding to evening twilight occur in various strains.

## Conclusion

Several factors are accounted for different photoperiodic sensitivities in the genus *Oryza* found among various strains. The difference in the sensitivity was analyzed from the respective factor, and it has been found that these factors can be used as indices of photoperiodic sensitivity, with universal validity for most species and strains in the genus *Oryza* (Table 3).

It can be concluded that the adaptation to natural photoperiod has played an essential role in the existence of cultivated and wild species. Some articles become clear from the viewpoint of the physiological and evolutional relationships and phylogenetic differentiations of the genus *Oryza*.

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