THE FLOWERING RESPONSE OF THE RICE PLANT TO PHOTOPERIOD

a review of the literature

Fourth Edition

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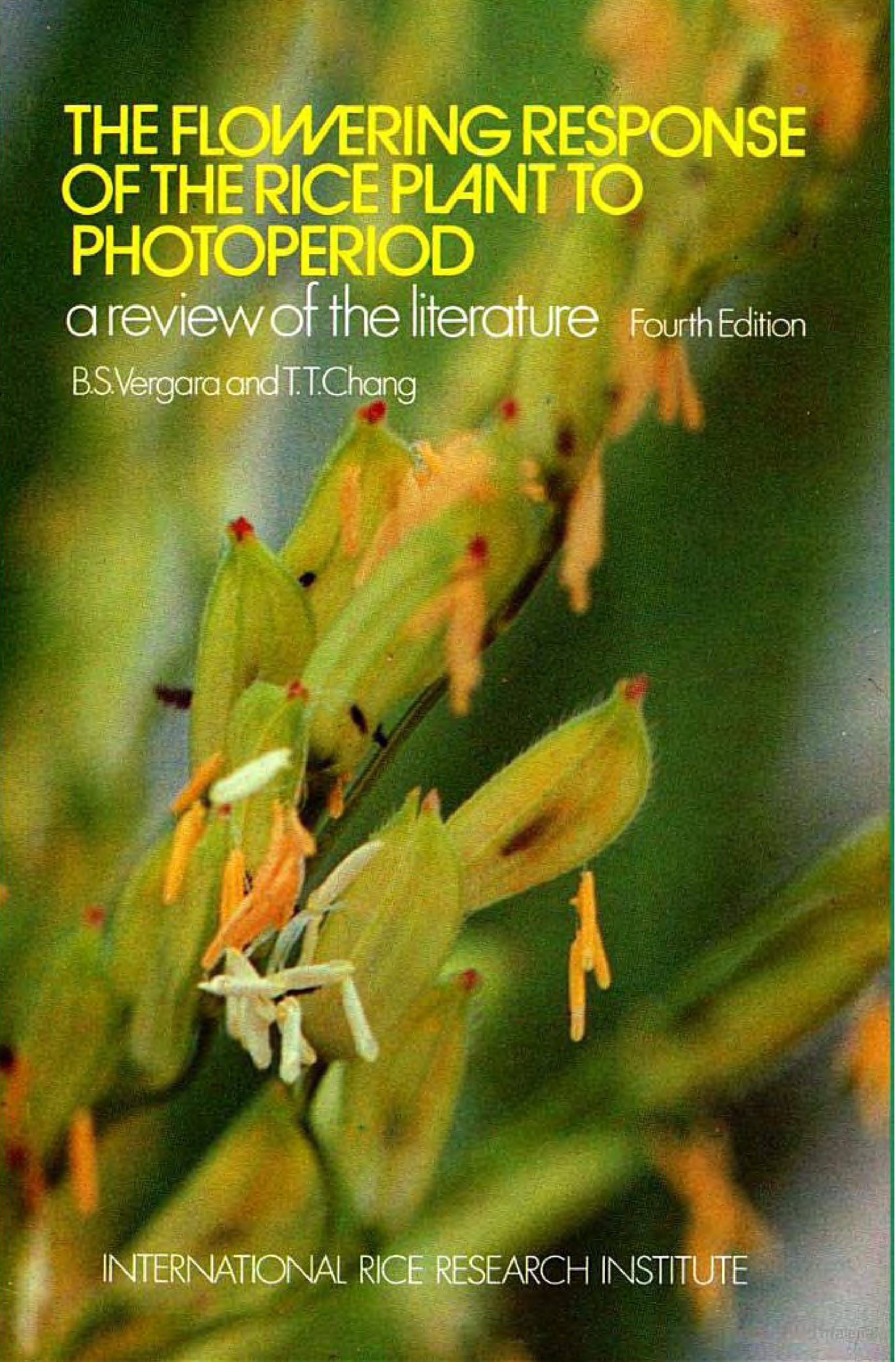

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The Flowering Response of the Rice Plant to Photoperiod

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Foreword

This review, first published in 1969, has been an important reference in understanding the rice plant. It has had a small but continuing demand. Many new reports on the flowering response of the rice plant have been published since the first edition. More than 100 publications were included in the third edition; this edition includes another 103 publications. For ease of reading, numbers have been used to cite the references.

This review was prepared with the cooperation of the IRRI Library Staff and the technical assistance of Mr. Romeo M. Visperas, and edited by Ms. Emerita P. Cervantes.

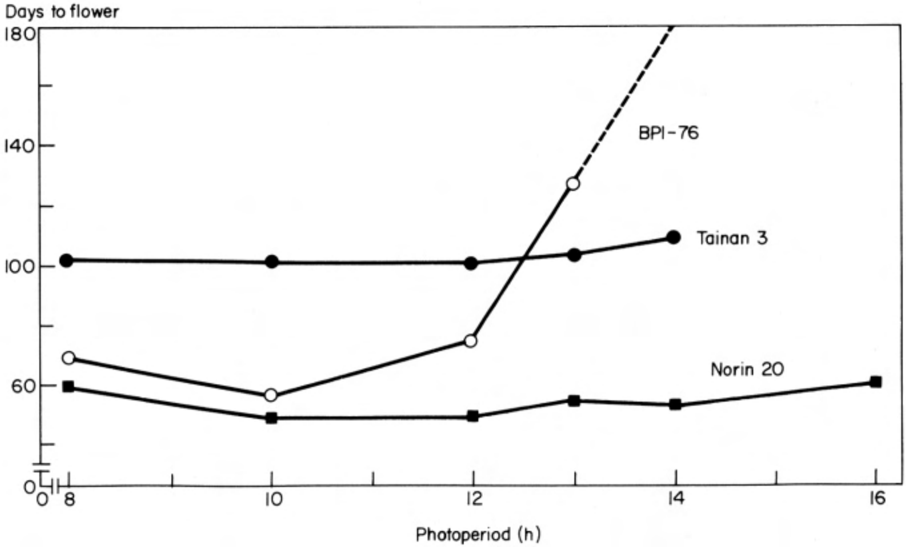
M. S. Swaminathan
Director General

Introduction

Photoperiod influences several aspects of plant growth. Some of its effects on rices have been reviewed by Best (24), Gwinner (111), Katayama (192), Morinaga (316), Sircar (439), and Wagenaar (534). This review is primarily concerned with the effect of photoperiod on the flowering of the rice plant. It includes more than 500 papers on the photoperiodism of rice, most of which are available at the International Rice Research Institute library. Several contributions in Japanese have been translated into English and also are available at the International Rice Research Institute library. A bibliography is given at the end of this review; not all papers listed were cited in this review but were nevertheless included as future references for interested workers.

Rice as a short-day plant

Rice is sensitive to photoperiod — long-day treatments can prevent or considerably delay its flowering. Rice cultivars exhibit a wide range of variation in their degree of sensitivity to photoperiod (87, 254, 319, 357, 531, 563). Figure 1 shows these variations, ranging from the very sensitive to the nearly insensitive.



1. Response curves of three representative types of rice cultivars.

Most of the wild species of *Oryza* and many of the primitive cultivated rices (*O. sativa* L.) are photoperiod sensitive and may be classified as short-day plants. Most papers agree on such a classification, and therefore in this review, rice will be considered as a short-day plant. It also will be classified into photoperiod-sensitive and photoperiod-insensitive types, the latter showing a low response or a slight delay in flowering with an increase in photoperiod. The present tendency is to select photoperiod-insensitive cultivars so that most of the cultivated rices may eventually become photoperiod-insensitive ones. These improved, early maturing cultivars may fit into the multiple cropping system characteristic of progressive agriculture.

There have been reports of cultivars whose flowering is delayed by short-day treatments and hence are considered long-day plants (1, 98, 99, 239, 254, 276, 277, 279, 283, 284, 287, 291, 303, 398,443,444, 488). Heenati, for instance, is often referred to in the literature as a long-day plant (1). Short photoperiods have delayed its flowering by 10 d, but this delay is relatively short and may be the result of nonphotoperiodic factors, such as low light intensity or relatively high temperature. The delay caused by short-day treatments ranged from 7 to 12 d in the Charnock and Panbira cultivars using an 8-h photoperiod (443), about 9 d in B. 76 (303), and 13 d in T. N. 32 and T. A. 64 (287). Many of the reported long-day and intermediate cultivars were found to be short-day cultivars in subsequent testing (522).

The apparent long-day reaction of Heenati resulted from using photoperiods shorter than the optimum, which delayed flowering (34). Some rices may have been classified as long-day plants because inadequate facilities were used in testing the photoperiod reaction. The range of photoperiods used has been limited, usually involving only two treatments. In some instances, the classification was based on field reaction to different planting dates (98). Short-day-treated plants were often compared with plants grown under natural day lengths (291, 303, 304). The difference and changes in temperature and the photoperiods used have made it difficult to interpret the data intelligently.

As will be discussed later, many photoperiod response curves show that photoperiods longer or shorter than the optimum delay the flowering of photoperiod-sensitive cultivars (34, 513).

Photoperiod response differs markedly among rices; this also explains the diversity of the results reported on the photoperiodism of the rice plant (see Appendix). However, more than 400 cultivars have been critically tested at IRRI (l59, 160, 161, 162, 163, 164, 166, 167, 168, 169, 170), and not one so far has shown a long-day response.

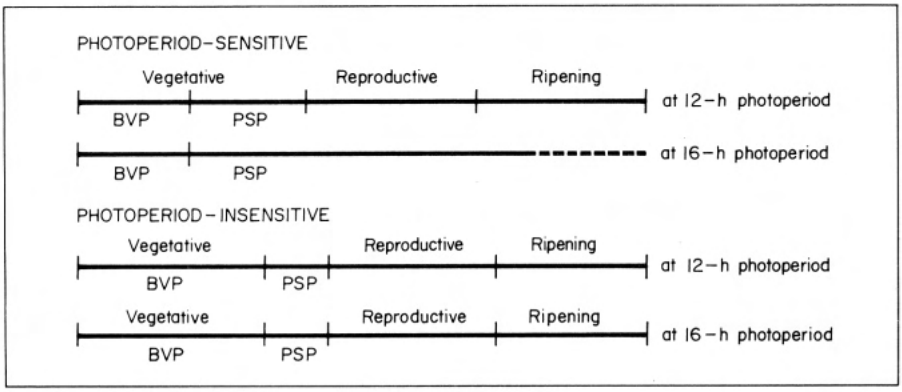
Growth phases

The growth of the rice plant can be divided into three stages: 1) the vegetative growth phase, from germination to panicle initiation; 2) the reproductive phase, from panicle initiation to flowering; and 3) the ripening phase, from flowering to full development of grain. In the tropics, the reproductive phase is about 35 d while the ripening phase ranges from 30 to 35 d. Both phases are relatively constant, although low temperatures have been known to prolong them and high temperatures to shorten them. The ripening phase may be prolonged to as much as 60 d. However, it is the vegetative growth phase whose duration generally varies greatly and which largely determines the growth duration of a cultivar, especially in the tropics.

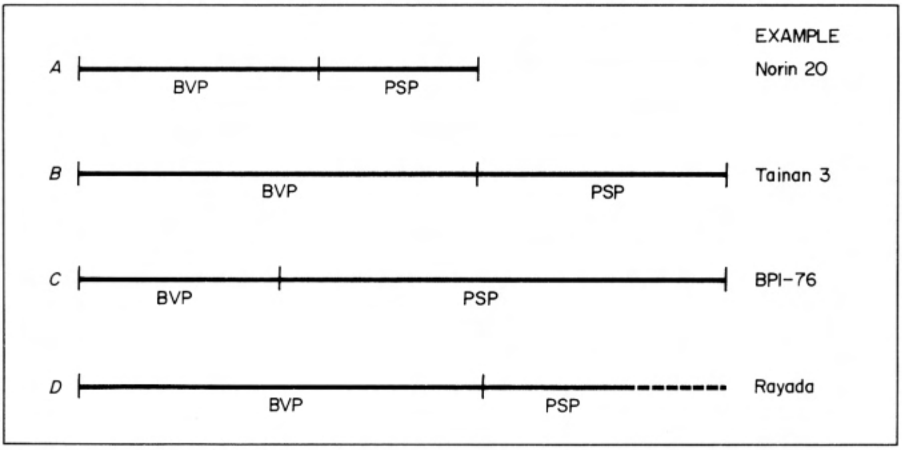
The vegetative growth phase can be further divided into the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP). The BVP refers to the juvenile growth stage of the plant, which is not affected by photoperiod. It is only after the BVP has been completed that the plant is able to show its response to the photoperiodic stimulus for flowering — this is the PSP of the plant.

Figure 2 shows the growth phases and the typical response of a photoperiod-sensitive rice and a photoperiod-insensitive rice.

Based on the BVP and PSP, varietal response to photoperiod can be classified into four types as shown in Figure 3 (105, 526).



2. Growth phases and typical responses of a photoperiod-sensitive rice and a photoperiod-insensitive rice. BVP = basic vegetative phase, PSP = photoperiod-sensitive phase.



3. Four types of varietal response to photoperiod. BVP = basic vegetative phase, PSP = photoperiod-sensitive phase.

The BVP and PSP are two separable growth phases controlled by different genes. Although some tropical cultivars may be classified as the D type having both long BVP and long PSP, most were probably eliminated during domestication since they would have had an unusually long growth period and could be planted only within a narrow range of dates. Such cultivars were found in Bangladesh and are known as Rayadas (105). The four types shown in Figure 3 were classified under one temperature condition. Norin 20 (Type A) has a short BVP. When grown in the tropics, however, it has a much shorter BVP than when grown in the temperate areas (Fig. 1). In classifying cultivars based on BVP, most of those from the low latitudes were found to have long BVP's (531, 532).

Basic vegetative phase

At the early growth stages, the rice plant is photoperiod insensitive so that the photoinductive treatments are usually started when the plants are 10-63 d old (13, 90, 142, 175, 186, 213, 230, 232, 273, 304, 316, 401, 512, 531). Because of this insensitivity to photoperiod, the early growth stage has been termed the basic vegetative phase; it is also referred to as the juvenile growth stage of the insensitive phase of the plant.

Suenaga recognized the BVP as early as 1936. He measured it by taking the duration of the vegetative growth phase at optimum day length. The BVP also has been measured by subtracting 35 d from the growth duration (sowing to flowering) of plants grown at the optimum photoperiod (526). This assumes that the period from panicle initiation to flowering is about 35 d. Anema (13) modified the determination of the BVP by subtracting 35 d and the minimum number of photoinductive cycles needed for panicle initiation from the heading date. The resulting BVP values are smaller but this complex method would mean determining the minimum number of photoinductive cycles needed for each cultivar.

The range of BVP reported in the literature has varied from 10 to 85 d (105, 175, 266, 273, 326, 381, 383, 401, 407, 445, 512). In an F_2 population, BVP's of more than 100 d were reported (249), but a BVP of this length has not been found in conventional rice cultivars. It is possible that such characters are eliminated during cultivar selection. The appendix shows the range of the BVP of the cultivars tested at IRRI. The indica cultivars generally have longer BVP (583).

Other workers have reported or measured BVP in terms of leaf number (93, 215, 340, 413, 551, 575). The minimum number of leaves can be less than five. The need for determining the BVP of a rice cultivar before using it as an experimental plant material is obvious but is frequently overlooked especially in the study of the inheritance of photoperiod sensitivity.

Several experiments showed that short-day treatments of seedlings accelerated heading (393, 401, 437, 438, 445) or delayed it (16, 273, 284, 287, 296, 426, 443, 447, 551). The results indicate the possible effect of photoperiod while the plant is in its early growth stage and the possible existence of a very short BVP. On the other hand, long-day treatments of seedlings have been reported to induce earliness in flowering (418, 427). These varied and conflicting results may have been caused by nonspecific factors. A good example is seedling vigor, which is known to affect the flowering date, especially in the weakly photoperiod-sensitive cultivars.

The degree of sensitivity of rice plants has been reported to increase with age (142, 190, 195, 202, 205, 347, 512). The increase in leaf area accompanying advancement in age does not explain this increase in sensitivity (413).

An increase in sensitivity with age up to 28 d and then a decrease in sensitivity with older plants (35- to 42-d-old plants) has been reported (296). The delay probably resulted from the setback from delayed transplanting and not from plant age because the plants were already 63 d old when transplanted, with some already flowering. The *optimum age of responsiveness* is probably the result of growth-limiting factors, such as space and nutrients and delayed transplanting.

Katayama (202) indicated that the BVP, or aging effect, probably resulted from small leaf area and (or) low metabolic activity and (or) lack of a specific metabolic pattern in young plants. The substance causing response to short-day conditions is produced in too small a quantity to affect morphogenesis at the growing point, but increases gradually with increasing age. Studying this aspect, Suge (460) found that the growth inhibitors in the plant were greatly reduced as the plant grew. However, it is not known whether these inhibitory substances are essentially involved in the sensitivity of the plant to photoperiod. In some instances, the apparent low sensitivity of the younger plants may be a matter of completing the BVP. If the photoinductive cycles were given before the BVP of the plants had been completed, the effective photoinductive cycles would be less and the resulting response of the plants would be smaller.

The transition from the BVP to the PSP is not well known; it could be abrupt or it could involve a gradual buildup. Using several cultivars, Best (26) found that the insensitive phase (BVP) changed to the fully sensitive phase (PSP) within a week.

The following are possible explanations for the existence of the BVP (26):

1) The first leaves formed are completely insensitive to photoperiod.
2) The first leaves formed have very low sensitivity that they do not reach an adequate level of induction to evoke floral initiation before the more sensitive leaves formed at higher nodes have reached this stage.
3) The first leaves formed do not attain the induced stage before the (early) senescence of these leaves.
4) The total leaf area required before the plant can react by floral initiation to the inductive photoperiod is so large that it is reached only at a relatively late stage of plant development.
5) The growing point of the young plant is unable to react to the floral stimulus or the stimulus cannot reach the growing point.

Photoperiod-sensitive phase

The PSP or the *eliminable phase* (186) is the growth stage indicative of the rice plant's sensitivity to photoperiod. In photoperiod-sensitive cultivars, the PSP determines the rice plant’s sensitivity.

The PSP of photoperiod-insensitive cultivars ranges from 0 to 30 d while that of sensitive cultivars lasts from 31 d or longer. Under continually long photoperiods, some cultivars have been reported to remain vegetative even after 12 yr of growth (234).

The PSP is usually determined by subtracting the minimum growth duration from the maximum growth duration of a cultivar (526). Because many cultivars remain vegetative for a long period if grown under long-day conditions, experiments are usually terminated after 200 d and the PSP of the cultivar is given the value of 200+. Besides measuring the PSP, there are many other ways — to be discussed later — of determining a cultivar's sensitivity to photoperiod.

A rice cultivar's response to photoperiod may be measured by the length of the PSP, which in turn is determined by both the critical and optimum photoperiods of the cultivar.

Because these two terms have been used interchangeably and in many ways, the following definitions will be adopted herein. Optimum photoperiod is the day length at which the duration from sowing to flowering is at a minimum (34). Critical photoperiod is the longest photoperiod at which the plant will flower or the photoperiod beyond which it cannot flower.

Figure 1 shows that BPI-76 has an optimum photoperiod of 10 h and a critical photoperiod of 13 h. Tainan 3 has an optimum photoperiod of 12 h but no critical photoperiod because it flowered under all photoperiods.

The critical photoperiod determines whether a cultivar will flower when planted at the usual time at a certain latitude, while the optimum photoperiod determines whether it will flower within a reasonable time if planted during a period with longer days than would normally occur during the growing season.

With BPI-76, if the optimum photoperiod is 10 h and the delay under photoperiods longer than 10 h is great, one would expect the flowering of this cultivar to be greatly delayed when planted in the northern latitudes where the photoperiod during the growing season is about 14 h. If the critical photoperiod is 12 h, flowering will occur very late at high latitudes, and if flowering does occur, the crop will not mature in time because frost will kill it.

A cultivar with a long optimum photoperiod or no critical photoperiod would have wider adaptability — it could be planted at any latitude and in any season, provided it is not too sensitive to temperature.

Optimum photoperiod

The optimum photoperiod differs with cultivars although many workers have observed it to be 8-10 h (39, 116, 135, 142, 311, 362, 371, 393, 512). Using intermediate photoperiods of less than and more than 10 h may reveal more important information. But this will require facilities in which a maximum of 15-min difference in photoperiods can be accurately obtained. There are also indications that the optimum photoperiod increases with increase in temperature (394).

Njoku (335) did not find any optimum photoperiod in the varieties he studied. The photoperiod he used was as short as 9 h, well below the range of natural day lengths.

Cultivars with optimum photoperiods longer than 10 h have also been reported (26, 90, 320, 322, 362, 568). The less sensitivity to photoperiod, the longer is the optimum photoperiod (116, 311). However, others found no correlation between the optimum photoperiod and the photoperiod sensitivity of the many cultivars they tested (572).

A photoperiod longer or shorter than the optimum has been shown to delay flowering, the delay depending upon the cultivar's sensitivity (311, 316, 319, 371, 393, 459, 513, 568).

The term supraoptimum photoperiod has been used when the photoperiod is shorter than the optimum. Panicle initiation in plants receiving a photoperiod as low as 4 h has been reported (140). No flowering has resulted under a 2-h light period (140). Plants receiving 8-h light and varying dark periods from 16 to 64 h showed inhibited shoot apex conversion (219). This was ascribed to inadequacy of carbon compounds for synthesis of requisite quantity of flowering hormone.

The *turning point* mentioned by Yu and Yao (568) is similar to the optimum photoperiod, but the photoperiod values they reported were larger because these were not the photoperiods at which growth is shortest but the photoperiods at which the first long-day effect is manifested.

Critical photoperiod

Scripchinsky (417), reviewing the literature on rice, indicated that the rice plants have a "critical length of day for flowering." Later studies showed the presence of a critical photoperiod ranging from 12 to 14 h (175, 209, 244, 354, 478, 490, 500, 553). The critical photoperiods determined under controlled photoperiod rooms were almost the same as the day length from sunrise to sunset at 30 d before flowering under natural conditions (499).

The lower the latitude of origin of a cultivar or strain, the shorter is its critical photoperiod (196, 356).

The critical period is influenced by temperature (566) and lengthens as the plant becomes older (212).

The PSP of a cultivar is probably a measure of the combined effect of photoperiod on its optimum photoperiod and critical photoperiod. The shorter the critical photoperiod, the longer is the PSP. Short optimum photoperiod is also associated with long PSP.

Photoinductive cycles

A photoperiodic cycle that induces the initiation of flowers on plants is called a photoinductive cycle. A 10-h photoperiod alternating with a 14-h dark period is one possible photoinductive cycle of a short-day rice cultivar.

The minimum number of photoinductive cycles necessary to initiate the panicle primordium of a rice plant varies from 4 to 24. This required minimum number varies not only with cultivar, but also with the photoperiod being used (13, 21, 26, 142, 195, 292, 338, 344, 408, 449, 500, 527, 529). The number of photoinductive cycles necessary increases with photoperiod length (190, 195, 203, 204, 527). According to Katayama (190), the minimum number increases proportionally with the photoperiod used, although others (527) failed to obtain a proportional increase using a different cultivar. Katayama (190) found that the minimum number was lower in cultivars from higher latitudes than in those from lower latitudes.

Suge (463) showed that different numbers of photoinductive cycles produced different amounts of floral stimulus. He also found that Gibberellin A_3 reduced the minimum number of photoinductive cycles necessary to induce flowering. However, gibberellin alone did not induce flowering under noninductive photoperiods.

That a certain number of photoinductive cycles is required to induce flowering suggests that the stimulus produced by the treatment is cumulative and that flower induction occurs when the stimulus has reached a certain threshold level (205, 206, 208).

Photoinductive cycles interrupted by noninductive cycles can negate to different degrees the effect of the photoinductive cycles (200, 206, 345).

There are also indications that emergence of the panicle from the flag leaf sheath is a process separate from panicle initiation. For example, internode elongation, after the panicle has been initiated, proceeds more rapidly at shorter than at longer photoperiods (26, 37, 67, 135, 425, 451, 512, 529), and earliness is further induced if the treatment is prolonged until flowering (33, 438, 498). It is possible, however, that panicle initiation and exsertion are separate processes, but certainly the latter proceeds only after the panicle has been formed. The effect of photoperiod on exsertion may be on fuller development of the panicle, hence indirectly affecting elongation of the first internode or exsertion of the panicle. Plants subjected to insufficient photoinductive cycles sometimes form panicles but no emergence occurs (see Table 1) (92, 122, 344, 512, 526). A difference of two photoinductive cycles could make the difference between exsertion or nonexsertion of the panicle.

Several workers, however, have reported that photoperiod has only a slight effect on culm elongation and panicle emergence (85, 116, 338, 473); but the cultivars used (85, 338, 473) were generally weakly photoperiodic because the differences between the control and the treated plants were relatively small (16 d at most). In another instance, the treatment was started at a later stage — 20 d before the standard heading time — at which time the plants had received sufficient photoperiodic stimulus for panicle initiation and emergence (1 16). In another experiment, long photoperiods had no effect on the terminal bud that had reached the stage of *differentiation of secondary branch primordia* (345).

Reversals from a reproductive to a vegetative phase have been reported (54, 342). In some instances, however, the panicle is initiated and differentiated but

Table 1. Response of 30-d-old BPI-76 seedlings given different numbers of 10-h photoinductive cycles.

Cycles (no.)	Days from sowing to panicle initiation	Days from sowing to panicle emergence
8	*	**
10	47	**
12	47	88
Continuous	46	**66**

*No panicle initiation 200 d after treament. **No panicle emeregence 200 d after treament does not emerge (526). The unexserted panicle ceases to grow, and instead the terminal growth is dominated by a shoot from a node below the panicle. Such a situation is not a true reversal of the growing point. In more recent histological studies, incomplete short-day treatment changed the bract primordium into a leaf primordium, a true reversal of some parts of the growing point (346).

Reception of the photoperiodic stimulus and translocation

The photoperiodic stimulus may be received by the leaves of the rice plant (24). The leaf sheaths can receive the stimulus as shown by removing the leaf blades and subjecting the plant to photoinductive treatments (26, 142, 481). More photoinductive cycles were needed to induce flowering when the leaf blades were removed (142). Defoliated plants responded to light interruption given during dark periods as well as the intact plants (142). In one cultivar, the culm received the photoperiodid stimulus (26). Evidently, the leaf most receptive to the stimulus is the youngest fully formed leaf (263). The first leaves, up to the sixth leaf, are either insensitive or have low sensitivity to photoperiod (26). It is difficult to study this aspect of leaf sensitivity because grafting experiments with the rice plant are difficult.

Removing the leaves at regular intervals after the end of the photoinductive cycles showed that the floral stimulus moves gradually from the leaves to the terminal bud (142, 464). The translocation of the stimulus depends on temperature. It was also reported that the rate of translocation of the stimulus is the same regardless of the number of photoinductive cycles received by the plant (463).

The question of stimulus movement from one tiller to another has also attracted the attention of several workers. When a plant was divided and half was kept under a 24-h photoperiod and the other half under an 8-h photoperiod, the half subjected to the short-day treatment flowered while that under long-day treatment remained vegetative (230, 232). The results indicate that the stimulus is not transmitted from one tiller to another. This finding has been substantiated by other workers using different cultivars and methods (263, 408, 521).

Manuel and Velasco (263) concluded that the stimulus that induces flowering can be conserved in the stubble and later transferred to the ratoon but not to a neighboring tiller of the same age as the donor. Sasamura (413), however, reported that the floral stimulus goes from the main culm to its tillers.

The irregularities observed in photoperiod-sensitive cultivars when planted during the off-season, for example, the high number of nonflowering tillers, have been attributed to the effect of the photoinductive cycles received by the plant and their nontranslocation to the succeeding tillers formed (521).

Light intensity and quality

The light intensities used to prevent or delay flowering varied from 1 to more than 200 lx. Incandescent, tungsten, as well as fluorescent bulbs have been used (69, 143, 310, 396, 484, 489, 503, 538, 565, 570, 577). The brighter the illumination, the stronger the retarding effect.

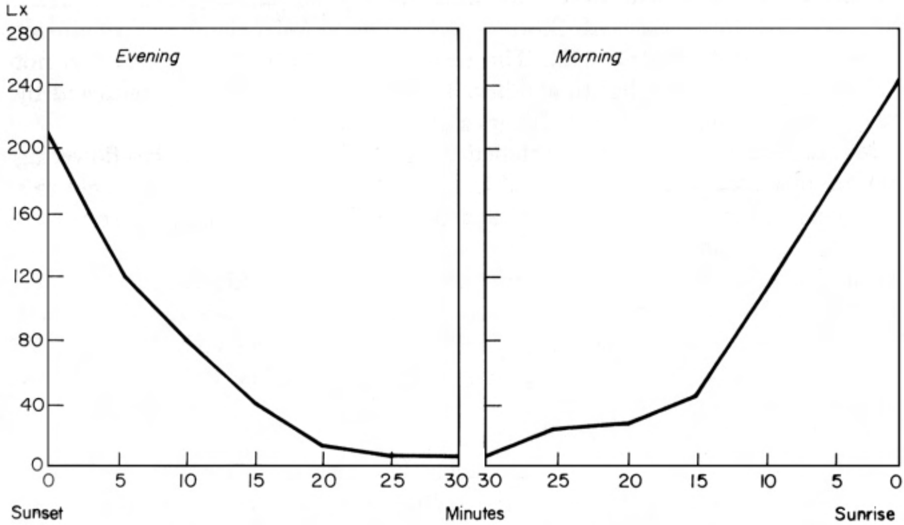
Delay in flowering with light intensities varying from 10 to 100 lx and even at 1 lx (310, 484) has been reported (538, 565, 589).

Extending the day length using light intensities of less than 200 lx during the first or last 3 h of the 12-h dark period did not prevent flowering (478). In another experiment, 2-h illumination at 15 lx before a 9-h dark period showed some inhibiting effect and 1-h illumination at 500 lx incandescent light before a 9-h dark period inhibited flowering (143).

In correlating laboratory studies with field studies, the natural photoperiod used is usually based on the sunrise-to-sunset duration. Such measurements are unsatisfactory in assessing periods of effective light because very low light intensities have been known to effect photoperiod responses in some experiments. Civil twilight in the morning can generally delay flowering but civil twilight in the evening may or may not delay flowering (143, 196, 205, 502). Civil twilight ends when the light intensity is about 4 lx. Twilight, of course, varies with localities and within the year. The critical light that results in delayed flowering is around 5 lx and sometimes 10 lx, depending on variety and other factors (174). Twilight intensity also varies and may be higher in the morning than in the afternoon (Fig. 4). Katayama (196) attributes the greater effectiveness of the morning twilight to higher intensity. Cloudy weather affects twilight duration.

Takimoto and Ikeda (478), however, concluded that the photoperiodically effective day length is equal to the astronomical day length (sunrise to sunset) because twilight (less than 200 lx) had little effect on photoperiodic induction in their experiment. Wormer (538) showed that low light intensities for 6 h (10-100 lx) given after a 12-h daylight can delay flowering.

Farmers have complained that their rice plants did not flower regularly because of the electric lights installed along their fields (552). One incident has been reported in which the light from a flame of waste natural gas prevented normal



4. Change of light intensity during civil twilight (after Katayama [196]).

flowering in rice. The effect of light was noticeable up to about 270 m from the flare (22).

Although light from incandescent bulbs is generally used for photoperiod studies, other colors have been tried in rice. The blue-violet part of the spectrum has been shown to retard flowering (260) as has infrared light (323). The delay in flowering caused by green light is very slight, only 4-5 d later than natural day length (234). Green has, therefore, been used in light traps for the moth. Red light is the most effective in delaying flowering, while blue showed some effect only at high intensities and in the most photoperiod-sensitive cultivars (26, 146, 153, 503).

The phytochrome pigment is generally regarded as the system that interacts with photoperiod or with different light qualities, such as red, far-red, and blue. Such pigment has been studied in rice coleoptile by Pjon and Furuya (378, 379).

For panicle initiation, rice needs a high light intensity during the light period. The inhibition caused by low-intensity light during the light period can be overcome effectively by exposing the plant to high-intensity light immediately before or after the inductive dark period (140, 145). This phenomenon is similar to that reported in other short-day plants and is evidently a carbohydrate requirement. This requirement would explain why a 2-h light period followed by 22-h dark period did not induce flowering (140). Ikeda (145) reported, however, that plants growing in low-intensity light during the photoinductive period but briefly exposed to high-intensity light before the inductive dark period had floral induction, suggesting that light requirement for floral induction of rice is not entirely concerned with photosynthesis.

In the flowering response of the rice cultivars to photoperiod, red light given during the dark period inhibited flowering (136, 146, 148, 411, 442). The effect of red light increased with intensity. Red light, as low as 10 $\mu W/cm^2$ given for 3 h or 290 $\mu Wc/cm^2$ for 15 min in the middle of the dark period, inhibited flowering (146, 148, 149). Red light was most effective in inhibiting panicle initiation when given in the middle of the dark period (150). With red light, the period of exposure needed to inhibit floral development was shorter than with white light (146).

The inhibiting effect of red light has also been shown in experiments involving red and far-red lights. Far-red after red nullifies the delaying effect of red light and promotes flowering (411). Far-red before a 9- or 10-h dark period promotes flowering and this effect can be reversed by red light (146, 149, 152). Far-red enhances flowering whereas blue retards flowering (185). Far-red after the critical dark period can shorten the critical dark period as well as reduce the minimum number of inductive cycles required (145).

Interruption of the dark period

Sensitive strains of rice respond to light interruption (26, 69, 218, 232, 260, 323, 449, 570, 577). Light given in the middle of the dark period delayed the flowering of the sensitive cultivar Shuan-chiang (570). The light intensity used was 1001x and the duration varied from a flash to as long as 15 min. The degree of delay was greater in the light interruption of a 12-h dark period (12 light and 12 dark) than of a 16-h dark period (8 light and 16 dark) (577). Interrupting the light period with darkness did not accelerate flowering.

The earlier the interposition of the light during the dark period, the greater was the delay (449). The findings show that the flowering response of the plant is determined by the longest dark period.

Days from photoinductive treatment to flowering

The literature indicates that the number of days from panicle initiation to flowering is about 35. Many workers have reported that the difference among cultivars is small (7, 407, 511, 551). Others found that the number of days from panicle initiation to flowering ranges from 10 to 241 d (425). It seems obvious, however, that 10 d is too short for the full development of a panicle.

Flowering may be delayed by long photoperiods after panicle initiation (176, 524). But if the plants are given photoinductive cycles beyond the minimum requirement, the subsequent photoperiods have very little effect on flowering and elongation (501, 524). Auxin application can nullify the delaying effect of long photoperiods (176).

Under natural day length, the number of days from the first-bract differentiation stage to flowering varied from 27 to 46 d, depending upon the cultivar and time of sowing (14, 270).

Reports vary on the number of days from the start of the photoinductive treatment to flowering. Misra (285) reported 37 d in 30-, 40-, 50-, 60-, and 70-d-old plants of the cultivar T.36 using a 10-h photoperiod.

Fuke (93) noted that the plants flowered about 28 d after treatment. The number of days from photoinductive treatment to flowering depends upon the photoperiod being used. Panicle initiation and flowering were earlier under the 10-h than under the 11- and 12-h photoperiods (527).

Using 168 F_2 plants, those treated under the 10-h photoperiod took 30-47 d to flower, or a mean of 35.8 d (Li, unpublished data. For practical purposes, an estimate of 35 d should be workable. Thus, to obtain the BVP or the time of panicle initiation, 35 d can be subtracted from the minimum growth duration of the cultivar.

In studying the effect of photoperiod on the flowering of the rice plant, the most fundamental consideration is panicle initiation because it marks the actual change from the vegetative to the reproductive phase. Instead of using this as a basis, however, most studies use the flowering date, which is only a projection of the variations of the date of panicle initiation. To a certain extent, several factors can affect the stage from panicle initiation to emergence. In some instances, panicle initiation can occur without the subsequent emergence. The panicle primordium is aborted and a vegetative shoot may dominate the growing tip (527).

A methodological question might therefore arise regarding accuracy of the experiments based on flowering date. The practicality of the method, however, far outweighs the need for extreme accuracy.

Biochemical changes during photoinduction

Very little work has been done on the chemical changes occurring during photoinduction and panicle development in rice. An increase in the rate of respiration of rice shoot apices with each photoinductive cycle given to the eighth day, followed by a gradual decline in rate, has been reported (293). The peak of the respiration rate almost coincides with the minimum photoinductive cycles needed by the rice plant at 8 h of photoperiod. The results suggest that the photoperiodic mechanism in the flowering of rice involves a respiratory shift. This corroborates the findings of Elliot and Leopold (86) who used other plant species.

The changes in carbohydrate and nitrogen content of rice plants subjected to short days were also studied by Misra and Mishra (299). Unfortunately, the difference in heading between treated and control plants was only 4 d. Khan and Misra (222) reported an increase in sugar and nitrogen content of the leaves when subjected to photoinductive cycles.

Photoinduction increases the gibberellic acid activity, although the value is low (461). This immediate rice, visible after three photoinductive cycles, returns to a level lower than that of the original.

The rice plant is difficult to use for studies on biochemical changes during reproduction. Perhaps it is best to leave this type of study to other short-day plants.

Effect of temperature on the flowering response to photoperiod

The flowering of the rice plant is mainly controlled by two ecological factors — day length and temperature — which are often interrelated. The plant may respond to temperature and photoperiod simultaneously, but the degree would vary according to the cultivar. Cultivars have been classified based on these two factors (248, 356, 530). Temperature affects both the photoperiod-sensitive and photoperiod-insensitive cultivars. Generally, high temperature accelerates and low temperature delays heading (5, 6, 90, 126, 186, 307, 339, 340, 370, 376, 409, 410, 439, 456, 531). Some reports, however, have shown that high temperature delays flowering (15, 18,394).

The acceleration of the photoperiod response by high temperature is an overall effect, but it does not indicate the specific effects on the different stages leading to flowering. The effect of temperature on the BVP, photoinductive period, panicle differentiation and development, and critical photoperiod has not been fully studied.

Uekuri (506, 507) studied the effect of low temperature during the BVP and found a definite delay in attaining the PSP. The degree of extension of the BVP by low temperature varied with the cultivars used. The growing point of the shoot is the receptive organ for the low-temperature effect, not the leaf blades (506). Ahn (5) reported that high temperature reduced the BVP but had very little effect on the PSP.

As early as 1931, Fuke had considered the effect of temperature during the photoinductive period. He used snow to lower the darkroom temperature, but the 5-10°C decrease had little effect on heading. Temperatures above 20°C to 29°C accelerate panicle initiation (24, 341). Vergara and Lilis (524) showed that the vegetative primordium was converted to reproductive primordium at the same time or at the same morphological stage regardless of temperature (21-32°C).

Haniu et a1 (1 15) found similar results. These results contradict those reported by Noguchi and Kamata (341) and Best (24). Temperatures below 15°C inhibited initiation and bud development (156). Floral induction, however, is possible at 15°C (341) but not at 12 or 40ºC (115). Because many test plants died in the growing process, 15° C is assumed to be near the lowest limit for rice growth (341). The optimum temperature reported for photoinduction is 30º C (1 15). The question still remains as to whether a critical temperature for photoinduction exists.

The optimum temperature for photoinduction may vary depending upon the photoperiod being used. The optimum temperature tended to be higher under a longer photoperiod and vice versa (24, 364). Putting it another way, at a certain temperature each cultivar has its own optimum day length under which it flowers at the earliest date (459, 572).

Detailed microscopic studies of the development of the panicle primordium have shown that high temperature accelerates panicle development (260). The critical temperature for young panicle differentiation has been reported to be 18ºC (555). Best (24) has also shown that panicle development, especially in its later stages, is accelerated at high temperatures (35–37ºC). On the other hand, low temperature markedly retards panicle primordium development, and, below 25ºC, the panicle may not emerge completely from the flag leaf sheath (24). A night temperature of 24.4ºC was found more favorable than 29 and 35° C in accelerating the flowering of the Elon-elon cultivar (263). High night temperature accelerates flowering (220). This was attributed to increased production of florigen during the dark period. This may not be the case and dissecting plants after photoinductive treatments may reveal if it was an acceleration in panicle development and exsertion rather than in panicle initiation. Others have found that the acceleration in flowering with high temperature is the result of acceleration in panicle exsertion, which, in turn, is the result of shorter leafing interval (524). Obviously, caution should be taken in determining the time of panicle initiation by observing the heading date because the exact date of panicle initiation cannot be determined by this method.

Measurements and methods of testing photoperiod sensitivity

Most studies on the photoperiodism of the rice plant have been considered from two standpoints, namely, classification of the cultivar into photoperiod-sensitive and photoperiod-insensitive types and measurement of the degree of sensitivity. The classification may be relatively easy, but the measurement is rather complex (195). As a result, several methods of measuring photoperiod sensitivity have been developed.

Studies on the measurement of photoperiod sensitivity are usually based on the reduction in the number of days as a result of short-day treatment (1 16, 195, 205, 327, 329, 357, 553, 574). Other methods were more specific; they measured the optimum photoperiod (40), critical photoperiod (351), or the gradient of the response curve (34, 192, 247) as the basis of sensitivity.

Hara (116) was the first to measure photoperiod sensitivity using the formula: X

= T – Y/Y X 100, where Y is the number of days required to head under standard conditions and T is the number of days required under an 8-h photoperiod. Several similar formulas have been used by other workers. The percentage or index obtained from such formulas, however, does not clearly define photoperiod sensitivity. The results usually apply only to the area where the rice was tested since the natural day length is usually used as the control.

Chandraratna (37, 40) used second-degree polynomials to compute the minimum heading duration and optimum photoperiod; this method involved using at least three photoperiods. He showed that cultivars differ in both characters.

Oka (352) and Katayama (192, 201) measured the critical photoperiod and the degree of sensitivity of several cultivars using different methods and formulas and came up with their preferred method of measurement. Both workers used the natural day length as a basis for computation and assumed that flowering occurs 30 d after photoinduction.

Best (25) and Li (249), using a method similar to Chandraratna's (34, 37, 40), measured sensitivity based on response curves obtained by plotting the time from sowing to floral initiation on the ordinate and the photoperiod used on the abscissa. The method, however, requires a wide range of photoperiods. Li (249) also studied photoperiod sensitivity in terms of the BVP and the PSP. The BVP was obtained in plants grown under 10 h of light, and the PSP (which is a measure of sensitivity) by subtracting the growth duration under the 10-h photoperiod from that under the 16-h photoperiod. The PSP values obtained show the possible maximum range in growth duration as a result of extending the photoperiod.

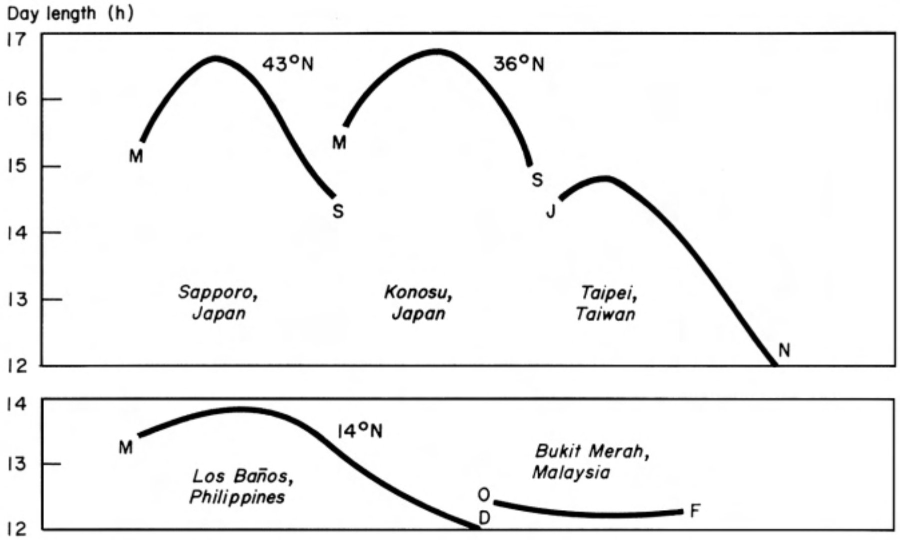
The photoperiodic characteristics of a rice plant have been described by Stewart (458) who used a different criterion based on 1) basic vegetative period in terms of degree-days (based on temperature accumulation), 2) photoinduction period in degree-days or degree-minutes (using accumulated night length), and 3) panicle development period in degree-days (based on temperature accumulation). Tests under field conditions were analyzed by this method and predictions were made on the response of the cultivar sown in different months.

In Japan, the flowering response is evaluated using the floral stages (135, 463). The Japanese workers have used the scale of 0-7, based mainly on the length of the developing panicle. This destructive measurement is more accurate than the usual days from sowing to flowering or treatment to flowering.

The choice of the most appropriate method of testing and describing the response to photoperiod depends upon the purpose of the experiment and the available facilities. From the physiological standpoint, however, controlled photoperiod and temperature are desired because of their advantages over natural photoperiods and temperatures.

Date-of-planting experiments

Day length changes rhythmically within a year and varies depending upon the latitude. The amount of change in day length during the rice cropping season differs from one latitude to another (Fig. 5). Even in locations at the same latitude the day length during the cropping season may differ because the planting dates



5. Day length changes during the cropping season at various locations in Asia.

may differ greatly depending mostly on the rainfall pattern at each location.

At northern latitudes (Sapporo, 43° N, and Konosu, 36° N) day length increases and then decreases during the cropping season (Fig. 5). At lower latitudes (Taipei, 25°N, and Los Baños, 14°N) day length decreases during the main growing season. Near the equator (Bukit Merah, 5°N) there is little change. These differences in day length during the growing season may account for the wide range of photoperiod response of rice cultivars. A rice cultivar that must have less than 12 h o daylight to flower will obviously flower too late at the northern latitudes because frost will set in before harvest.

In the northern hemisphere, the longest days are in June and the shortest are in December. Taking these into account, the photoperiod response of the rice cultivars can be tested to a limited extent by planting the cultivars at a certain location at different dates. Maximum differences in growth duration can be obtained in the May and November plantings if temperatures are not too low for growth. If a rice's growth duration changes more than 30 d, agronomists usually consider it photoperiod sensitive or a seasonal cultivar. As Best (24) has pointed out, this criterion is not specific enough for research on photoperiodism, and caution should be taken in evaluating the data obtained. These phenological data, however, are important to breeders in selecting ecotypes.

This method of testing sensitivity to photoperiod has been followed in Australia (245), Brazil (l03, 579), China (44, 356, 582), India (98, 99, 101, 214, 220, 295, 298, 423), Indonesia (467), Japan (533, 548), Korea (247, 466), Malaysia (74, 77, 244), Philippines (91, 512), Russia (452), Senegal (66), Sierra Leone (68, 536), Sri Lanka (112, 259, 402), Thailand (381), Trinidad (325), and United States of America (177, 180).

These experiments strongly confirm the existence of wide cultivar differences in the effect of planting date on flowering date.

Many of the results obtained from this type of testing, however, are not applicable to identical cultivars grown at different latitudes. A cultivar can be insensitive to day length in Malaysia but sensitive in Taiwan. Results of field tests at a certain latitude are, therefore, not always applicable at another latitude. Some published papers on the use of this testing method failed to mention latitude or the place where the tests were conducted.

Under natural conditions very small differences in day length can affect the rice plant. In Malacca (Malaysia), the difference between the maximum and the minimum day lengths is only 14 min and yet the cultivar Siam 29 takes 329 d to flower when planted in January and only 161 d when planted in September (76).

Another instance showing the sensitivity of the rice plant to small differences in day length was reported in a date-of-planting experiment in Malaysia (244). There was a difference of as much as 156 d in the growth duration of photoperiod-sensitive cultivars when planted in the same month but in different years (Table 2). This presumably resulted from differences in weather during the critical periods. Cloudy weather early or late in the day shortens the twilight hour, thus shortening the day length.

Toriyama et al (490) tested rice cultivars involving not only monthly planting but also sowing at different latitudes (Sri Lanka, Taiwan, and Japan). This gives a better idea of the photoperiodic response of the cultivars but involves much work and cooperation.

Ecology and photoperiodism

Rice can be grown over a wide range of environmental conditions, from the equator to about 53° N latitude, leading to the differentiation and establishment of various ecotypes and forms. The great diversity in photoperiod sensitivity from one latitude to another or within a latitude probably indicates that the rice cultivars predominantly cultivated in each area are those that have been selected on the basis of local adaptability (that is, adaptability to the temperature of the rice-growing season, day length, and duration of the growing season) to assure the full development of the plant and the best possible balance between vegetative and reproductive growth (423, 530, 532, 584, 585).

Table 2. Growth duration (days from sowing to flowering) of photo. period-sensitive cultivars when planted in January 1962 and 1963 at several localities in Malaysia (244).

Cultivar	Locality	Jan 1962	Jan 1963	Difference
Engkatek	Telok Chengai	136	292	156
	Kota Bahru	146	243	97
	Kuala Lumpur	134	97	37
Subang	Bukit Merah	270	224	46
Intan 117	Kuala Lumpur	171	138	33
	Kota Bahru	276	176	100

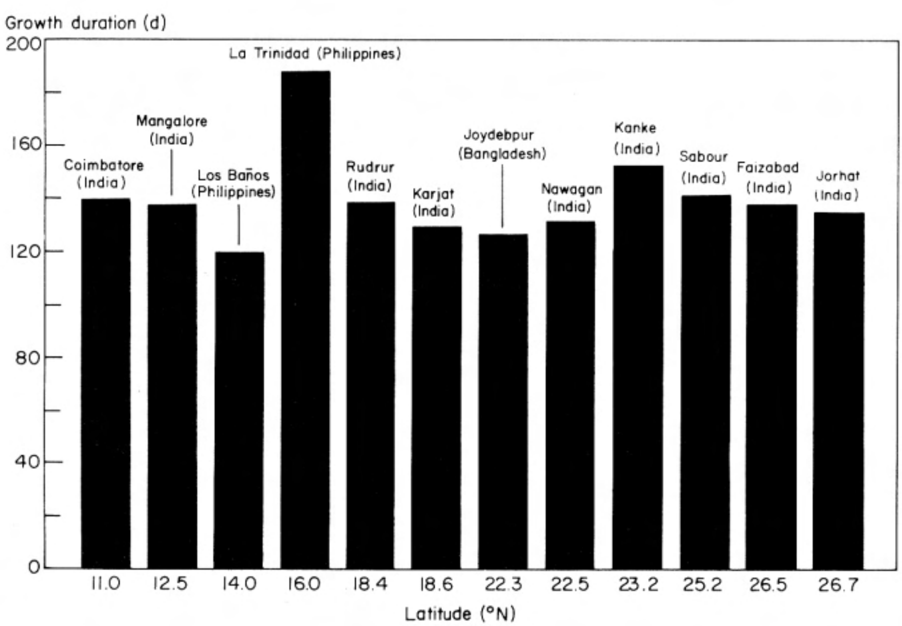
A major problem in studying the ecology of the rice plant, especially in reference to photoperiodism, is that cultivars in farmers' fields keep changing. For example, Hara reported in 1930 that Japanese cultivars were more sensitive than the cultivars from mainland China and Taiwan. He concluded that the lower the latitude of the region of the native habitat, the less sensitive were the cultivars there. Wada (531), using 134 cultivars, showed contrasting results — the cultivars from the northern region of Japan had lower photoperiod sensitivity than those from the southern region.

Recent papers, however, generally agree that among the photoperiod-sensitive cultivars, the lower the latitude ofdistribution, the higher the sensitivity (351, 352, 356, 531, 583).

The cultivars in the tropics or lower latitudes are usually late maturing (long growth duration). Many studies show that the *late* cultivars are more sensitive to photoperiod than the *early* ones (116, 248, 357, 511, 563, 583).

In the tropics, where rice can be grown any time of the year provided there is sufficient water, photoperiod sensitivity presents certain problems. During the off-season, when the day length during the early growth stage is increasing, the sensitive cultivars are uneconomical to use because they take a very long time to produce any grain. For wider adaptability, cultivars should have low photoperiod sensitivity (53, 70) and thus have little differences in growth duration when planted at different times of the year or at varying latitudes.

Insensitive cultivars have been successfully grown at different latitudes where rice is used as a crop (45, 351, 352, 511, 532, 568. This indicates that it should not

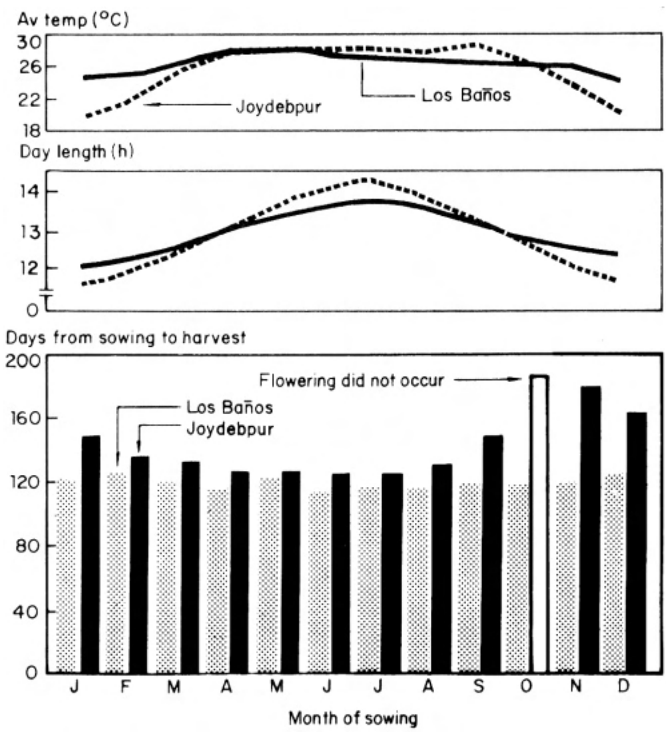


6. Growth duration of IR8 planted in June or July at 12 sites in Asia. La Trinidad and Kanke are high-altitude areas (52).

be difficult to introduce new photoperiod-insensitive cultivars to different rice-growing areas or to culture them year-round in the tropics. The plant breeders, as the varieties coming out indicate, are developing more photoperiod-insensitive cultivars.

Extensive testing in various rice-growing areas of the world has established the wide adaptability of photoperiod-insensitive cultivars. In general, the longer the BVP the less variation ingrowth duration and the stronger the PSP the greater the variation in growth duration (581). The wide adaptability and the stable growth duration of IR8, a photoperiod-insensitive cultivar, are indicated by the data furnished by cooperators in various parts of the world. IR8's growth duration varied within a range of 20 d at latitudes from 11° to 27°N except at high altitudes where low temperatures prevailed during part of the growing season (Fig. 6).

A more illuminating example of the effect of temperature comes from monthly planting at Los Baños, Philippines, and at Joydebpur, Bangladesh (Fig. 7). A comparison between the monthly mean temperatures and mean photoperiods shows that the more variable heading pattern at Joydebpur is more closely associated with temperature rather than with the prevailing photoperiod. The effect of low temperature on the improved tropical cultivars becomes more obvious in photoperiod-insensitive cultivars.



7. Mean monthly temperatures and day length in relation to the growth duration of IR8 at Los Baños, Philippines, and Joydebpur, Bangladesh (52)

Sensitivity to photoperiod of rice cultivars in the deep water areas is an important characteristic for survival (104, 520). The floating rice cultivars are highly photoperiod sensitive. They are planted early in the season when the soil can still be worked and without danger of submerging the young seedlings. Flowering occurs when the floodwater peaks or starts receding. If the cultivar flowers when the floodwater is still rising, it would mean the complete loss of the crop if the panicles are submerged. Elongation ability ceases after panicle emergence. Harvesting is usually done when the floodwaters have receded. The maturity of floating rice cultivars coincides with the receding of the annual floodwaters which may be 150–270 d after sowing. Such a long growth duration requires a photoperiod-sensitive cultivar. So far, there is no known tropical cultivar that has a long growth duration and is not sensitive to photoperiod.

Photoperiod sensitivity may work as a safety mechanism when precise planting dates are not followed and environmental conditions such as water level cannot be effectively controlled. If the date of sowing or transplanting is delayed because of insufficient rainfall, a photoperiod-sensitive cultivar may still mature at its usual time (352, 382). Plants are not seriously damaged if left in the seedbed for prolonged periods because the growth duration of the main crop is sufficiently long for the plants to adjust. Thus, land preparation and transplanting can be staggered (382).

Maturation of the crop at the same time. as with photoperiod-sensitive cultivars planted at different dates, may reduce rat and insect damage in any one field. Also, harvesting and drying are simplified.

If the soil is not sufficiently fertile, a photoperiod-sensitive cultivar will continue its compelled vegetative growth until the short days come. This would give the plant enough time to reach a reasonable plant weight and accumulate enough carbohydrates before flowering (528). Thus, a photoperiod-sensitive cultivar generally may be more resistant to unfavorable conditions. Long-growth-duration cultivars (essentially photoperiod sensitive) are least affected by strong soil reduction (549).

Most upland rice cultivars have short growth duration and are photoperiod-insensitive (11, 12). However, in areas where the rainfall pattern is bimodal, as in northern Thailand, the cultivars are of medium growth duration and are photoperiod-sensitive — possibly another indication of the greater specific adaptability of long-growth-duration cultivars to adverse conditions.

The sensitivity to photoperiod of wild species has also been studied in relation to their ecological distribution. Most of the wild rice materials tested were sensitive (191, 201, 205, 209, 353). They suggested that this sensitivity favors the wild rice plants and is perhaps essential to their survival.

Terminology used in describing photoperiod sensitivity

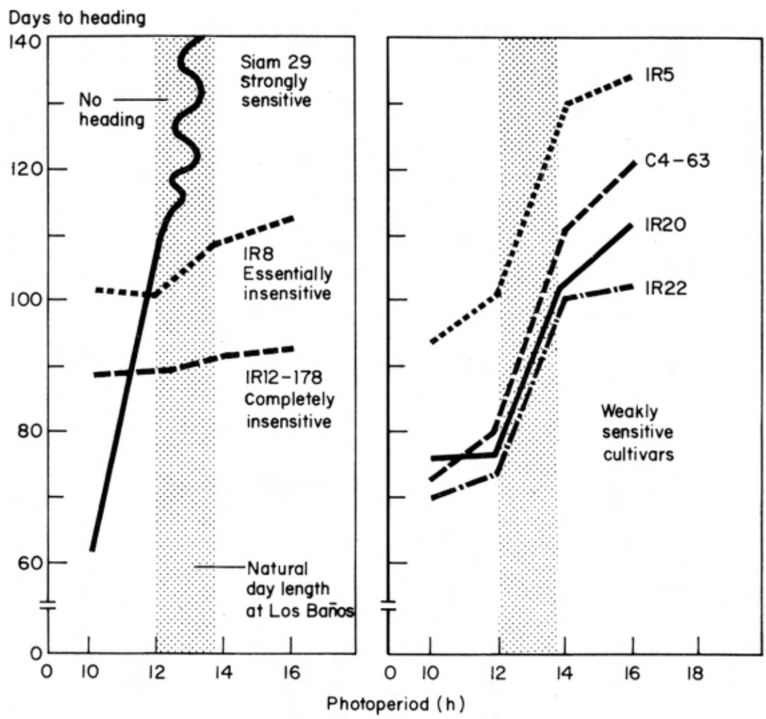
There is confusion in the terms used to describe the response of the rice plant to day length (515). Often, the terms used for growth duration are also used for response to photoperiod (see Table 3). As early as 1912, Kikkawa pointed out that

Table 3. Some terms used in describing the growth duration and day length response of rice cultivars.

Terms	References
Response to day lengths:	
date fixed vs period fixed	33
season fixed vs period fixed	37
season bound vs period bound	214, 511
timely fixed vs periodically fixed	308
short-day plant vs long-day plant	1, 99, 336
sensitive vs indifferent	3
sensitive vs insensitive	68, 352, 353
sensitive vs less sensitive	21, 98, 449, 538
short-day plant vs indifferent plant	563
strongly photoperiodic vs weakly photoperiodic	511
photoperiodic sensitive vs photoperiodic insensitive	195, 352
photosensitive vs photononsensitive	339
day length sensitive vs day length nonsensitive	574
Growth duration:	
early, medium, and late	91, 276, 277, 281
long-aged vs short-aged	259
early flowering vs late flowering	158
late maturing vs early maturing	3, 230, 374
Season of planting:	
aman vs non-aman	427
yala vs maha	112
winter vs summer	444
main-season vs off-season	Malaysia, Indonesia, and Thailand
first crop vs second crop	China
wet vs dry season	Philippines
aus, aman, boro, rabi, kharif	Bangladesh, India

it is meaningless to classify the rice cultivars of the world into such groups as early, medium, late, aus, or aman. He said, however, that this classification is useful in districts where the climates are similar. The use of the terms *photoperiod-sensitive* and photoperiod-nonsensitive in reporting the flowering response of a rice cultivar to changes in day length has been suggested (515). *Weakly photoperiod-sensitive* is sometimes used in place of *photoperiod-nonsensitive* because the existence of a completely photoperiod-nonsensitive cultivar is difficult to prove. *Weakly photoperiod-sensitive* is also used to describe cultivars whose flowering is delayed by as many as 70 d by long photoperiods. However, those types can be planted any month of the year in the tropics and can be expected to flower within the crop season.

The terms *short-day plant* and *long-day* plant are not satisfactory because most rice cultivars today are short-day plants. *Sensitive* and *insensitive, sensitive* and *indifferent,* and *sensitive* and *less sensitive* are ambiguous terms. Because the response being described is a response to light period and not only to light, the terms *photosensitive* and *photononsensitive* are inappropriate.



8. Effect of four photoperiod treatments on the seeding-to-heading period of seven rice cultivars.

Chang and Vergara (51, 52, 53) classified rice cultivars into four types using the length of the BVP and PSP as criteria (Fig. 8). Their classification was based on duration of plants grown in the greenhouse. Under this classification, the Japanese varieties, such as Fujisaka 5 and Norin 20 (Appendix), do not fall under any category because they have a short BVP and short PSP. Also, at least four photoperiods (10, 12, 14, and 16 h) are needed to classify the cultivars.

A more practical grouping could be as follows (using also the length of the BVP and PSP).

1. Photoperiod nonsensitive — very short PSP (less than 30 d) and BVP varying from short to long.
2. Weakly photoperiod-sensitive — marked increase in growth duration when photoperiod is longer than 12 h; PSP may exceed 30 d, but flowering occurs under any long photoperiod.
3. Strongly photoperiod sensitive - sharp increase in growth duration with increase in photoperiod; no flowering beyond critical photoperiod; BVP usually short (not more than 40 d).

Cultivars tested under only two photoperiods, such as 10 and 14 h, can also be classified according to these groupings (1 1). Agronomists and farmers would tend to use these groupings.

Inheritance of vegetative growth duration

The inheritance of the duration from seeding to heading in cultivated rices has been studied by many research workers, but the findings have resulted in diverse interpretations. Three categories of genetic postulates were generally offered: 1) monogenic or digenic control of heading date, with earliness dominant to lateness; 2) monogenic or digenic control of flowering date, with lateness being a dominant trait; and 3) multiple-factor inheritance in which the F_2 population showed a continuous and often unimodal distribution and in which the same population might produce a bimodal distribution when grown in a different season (44, 509). In experiments where photoperiod sensitivity was recognized, delayed flowering under a long photoperiod was generally inherited as a monogenic or digenic dominant trait (38, 242, 406, 424, 567). In several crosses involving distantly related parents, sensitivity to photoperiod appeared to be a recessive trait (242, 406). The continuous and transgressive segregation in several F_2 populations involving photoperiod-insensitive parents was ascribed to multiple genes, which indicated dominance of earliness (41, 95, 96, 97, 333, 389, 469, 554). However, in crosses among varieties in Yunnan Province in China, photoperiod sensitivity appeared to be a recessive trait in some F_1 hybrids (252).

Some of the divergent interpretations just mentioned resulted partly from failure to recognize the composite nature of the vegetative growth period from seeding to panicle primordium initiation, partly from failure to control the interaction of the environmental factors (mainly photoperiod and air temperatures) and the different genes controlling the vegetative growth period, or from failure to relate the phenotypic expression with the prevailing environment.

Recent studies at IRRI (48, 161, 162, 163, 164, 165, 167, 168, 249) have demonstrated physiologically and genetically the feasibility of partitioning the vegetative growth duration into the BVP and the PSP under two or more photoperiods. When vegetative tillers from a pureline parent or hybrid progeny are separated and grown to represent duplicate samples of the same genotype, the concurrent determination of BVP (under a 10-h photoperiod) and of PSP (under a 16-h photoperiod) on the same plant becomes practical. This procedure also makes it possible to elucidate the relationship between genes controlling the two physiologic phases.

Using this experimental approach, the F_1 and F_2 progenies from nine sensitive × insensitive crosses produced clear-cut segregation for both phases. The F_1 and F_2 data showed that 1) strong photoperiod sensitivity is controlled by one *(Se)* or two (Se_1 and Se_2) dominant genes, producing F_2 ratios of 3:l or 15:l; 2) the F_2 variation in BVP can be attributed to two or more genes (Ef_1, Ef_2...) of cumulative but unequal effect, with a short BVP dominant to a long one; 3) the *Se* genes are epistatic to the *Ef* genes under a long photoperiod; and 4) an association between photoperiod sensitivity and a short BVP is indicated in a number of F_2 plants (48) and in two isogenic lines of Japanese × Malaysian parents (558). In two crosses each involving a semidwarf, the semidwarf parent appears to carry a recessive inhibitor for sensitivity (*i-Se*), producing an F_2 ratio of 9 sensitive to 7 insensitive. These gene in two sensitive cultivars and these, gene in another appear to belong to multiple allelic series. Transgressive segregation for BVP was observed in most of the crosses at both ends of the F_2 distribution curve (48).

In crosses where insensitive cultivars were analyzed, the dominant nature of a short BVP was also observed. The F_2 variation in BVP could be ascribed to several cumulative genes of equal or unequal effect. The polygenic-additive pattern of inheritance is indicated in one cross where two insensitive parents differed little in BVP (48, 251). A short BVP appears to be associated with photoperiod sensitivity (559).

These findings provide a workable basis to collate the action of genes controlling the two phases and the effect of the prevailing environment. With such genetic information, it is feasible to reconcile some of the seemingly divergent findings in previous genetic studies when both the genetic constitution of the parents and the prevailing environment are considered.

Although the findings provided clarification on the genes controlling the two component phases of vegetative growth duration and on the interaction among genes, the discrete action of the *Se* and *Ef* genes observed under constant photoperiods was not readily detected under a changing photoperiod in the field. The interaction of different genes with the changing photoperiod under field conditions could explain some of the loss in discreteness of genetic information which was obtained under controlled photoperiods. However, the genetic variables involved could conceivably be attributed to the optimum and the critical photoperiods. Preliminary studies at IRRI (161, 162) have indicated a distinct segregation of the two components of photoperiod response. A short optimum photoperiod appears to be dominant to a long one. A short critical photoperiod also appears to be dominant to a long one in the F_1 hybrids. An association between a short optimum and a short critical photoperiod was indicated in one F_2 sample (250). Further studies are needed to elucidate the genetic control of the optimum photoperiod and critical photoperiod which undoubtedly give complexity to the expression of different genotypes when grown in different environmental conditions.

Weakly photoperiod-sensitive cultivars which will flower between 10 and 16 h of day length but which may vary by as much as 60 d in the vegetative growth period have been identified at IRRI (166, 167) and in Japan (237, 238, 242). Such progenies were also obtained from strongly sensitive × insensitive crosses (97).

Inheritance of the weakly sensitive response appears to be rather complex. The F_1 performance indicated the partial dominance of the weak response in one cross and the reverse in the other two crosses. The F_2 distributions of the PSP were continuous; these included a larger proportion of short-PSP plants than of long-PSP plants. Transgressive segregation for long-PSP plants was indicated in all the crosses studied and a few strongly sensitive progenies were obtained in one cross (168, 258).

In crosses between strongly sensitive cultivars and weakly sensitive cultivars, the strong photoperiod response of Latisail was expressed as a monogenic dominant to the weak response in Peta (a progeny derived from Tjina × Latisail). However, a few insensitive plants were found in the F_2 population. In Latisail × Sukanandi, the strong response was dominant over the weak response in both the F_1 and F_2 generations. But the segregation for PSP appeared to be more complex and could involve more than one gene (Chang and Hung, unpublished). These findings indicate the complex nature of the weak photoperiod response especially in crosses involving the weak and strongly sensitive parents.

The interaction between thermo-sensitive genes and BVP and/or photoperiod-sensitive alleles is another area which warrants detailed investigation under controlled environments (50).

Because it takes at least two crop seasons in the tropics to determine photoperiod sensitivity under field conditions, observations were made on morphological and physiological characters that might be closely correlated with photoperiod sensitivity.

One of the six alleles involved in photoperiod sensitivity is linked with one of the complementary loci for apiculus color (96). In a different study, photoperiod sensitivity and anthocyanin pigmentation in the apiculus were not correlated (492). Photoperiod sensitivity has been reported to be linked with auricle color (41), seed dormancy (32, 42), and tillering capacity (41).

In several Japanese varieties a gene-complex C and 3 major E genes controlled maturity as well as culm height, panicle length, panicle weight, and grain length (211, 472). From isogenic lines derived from Taichung 65, the gene (E) controlling early maturity was found to be a complex locus, consisting of 4 isoalleles. Moreover, two isoalleles of an independent m gene modified the expression of the E isoalleles in different crop seasons (494).

Problems in the study of the rice plant's photoperiodism

Coolhaas and Wormer (67) gave the following reasons for the failure to gather enough information on photoperiodism of the rice plant despite the voluminous research on the subject since 1923 (272): 1) failure to carefully dissect the plants during growth and development, 2) the use of the *normal* and *natural* day lengths as *control,* when it is not a control treatment at all, and 3) no distinction is made between the photoperiodic and photosynthetic action of light.

In some experiments reported, the treated plants were grown under poor cultural conditions compared with the control, and therefore the results of the experiments are doubtful.

Chandraratna (37) and Best (24) also believe that the conflicting conclusions have been the result of comparisons of a single photoperiod with the fluid *control* provided by natural day. They indicated that constructing a response curve covering an adequately wide range of photoperiods is an essential preliminary to the analysis of cultivar behavior. The location of the optimum photoperiod is necessary for interpreting the quantitative response,

Best (24) gave additional reasons for the many conflicting statements in the literature, among them, the tendency to overlook the influence of nonspecific factors on the photoperiodic induction since the quantitative aspect of the photoperiodic response has only rarely been recognized in interpreting experimental data.

One of the most important nonspecific factors is temperature, whose effect on photoperiod response is usually taken for granted.

The use of different cultivars in the experiments on photoperiod makes generalizations hazardous. Also, most of the experiments reported did not involve controlled conditions. The conflicting results may actually be the result of the cited factors.

There is also the problem of selecting the proper term(s) for describing the response to photoperiod or classifying the plant according to its response. Such terms should be standardized.

The effect of photoperiod on the so-called photoperiod-nonsensitive cultivars needs intensive study. More and more cultivars of this type are being developed and yet the quantitative and qualitative effects of photoperiod on these cultivars are hardly known except that the growth duration seems generally unaffected by photoperiod.

Summary

The following general statements may be drawn from the important contributions:

1. Rice is a short-day plant. Almost all cultivars mature in a shorter time under a short photoperiod (about 10 h) than under a long one (14 h), but the degree of sensitivity varies greatly among cultivars.
2. Younger leaves are more receptive to the photoperiodic stimulus than older leaves. Leaf sheaths may also receive the stimulus.
3. The photoperiodic stimulus is not translocated from one tiller to another tiller of the same plant.
4. The minimum number of photoinductive cycles necessary to initiate the panicle primordium varies from 5 to 24. The number differs not only with cultivars but also with the photoperiod being used.
5. The response of the rice plant to photoperiod is governed by the length of the longest continuous dark period. Very short light periods (3–15 min) during the dark period may markedly affect the time of heading in some cultivars.
6. For supplementary illumination or light breaks, the red spectrum is the most effective.
7. Cultivars that are very sensitive to photoperiod may react to very low light intensities (1-100 lx). Twilight may contribute significantly to the length of the photoperiod under natural day length.
8. Besides panicle initiation, the developmental processes between initiation and anthesis may also be affected by the prevailing photoperiod.
9. The duration of the BVP ranges from 10 to 60 d, while the PSP can be extended to as long as 12 yr (actually recorded). For the photoperiod-sensitive cultivars, the optimum photoperiod is about 10 h, while the critical photoperiod ranges from 12 to 14 h.
10. The BVP, PSP, critical photoperiod, and optimum photoperiod differ among cultivars. Variations in each of these components are largely responsible for the intervarietal variation in flowering response to photoperiod.
11. High photoperiod sensitivity is controlled by one or two dominant genes while the BVP is controlled by two or three genes of cumulative but unequal effect. The short BVP is dominant to a long one.

Appendix

Photoperiodic reaction of rice cultivars and promising IRRI breeding lines.

Variety	Country	Photoperiod[a] 10	12	14	16	PSP[b]	BVP[c]	Date of test[d]
Acheh	Malaysia	93	116	168	–	80	58	Jul 1962
Aeb 368 Rip P Type	India	74	87	94	*	200+	39	Jul 1982
Ahgabyeo	Korea	–	47	92	93	46	12	Feb 1979
Ahgudo	Korea	–	49	93	**	61	14	Feb 1979
Ahgukdo	Korea	–	42	91	94	52	7	Feb 1979
Akulu	West Africa	76	130	*	*	200+	41	Jul 1982
Allorio	Portugal	62	63	71	75	13	27	Nov 1972
Apostol	Philippines	56	77	–	*	200+	21	Feb 1978
Arborio	Italy	73	68	76	82	14	33	Nov 1972
ARC5955	India	73	78	88	–	15	38	Jul 1975
Azmil	Philippines	90	–	98	–	8	55	Mar 1974
Azucena	Philippines	81	90	–	108	27	46	Feb 1978
B76	India	69	72	86	91	22	34	Dec 1966
B5319A1-7-2-1	USA	–	79	81	94	15	44	Aug 1966
Bahia	Spain	62	61	90	92	31	26	Nov 1972
Baishbish	Bangladesh	54	120	*	–	200+	19	Jul 1975
Balilla	Italy	61	59	86	91	32	24	Nov 1972
Banih Hirang 1	Indonesia	67	132	–	*	200+	32	Dec 1981
Banih Hirang 2	Indonesia	69	129	–	*	200+	34	Dec 1981
Banih Pekat 1	Indonesia	66	129	–	*	200+	31	Dec 1981
Banih Tayan 1	Indonesia	58	118	–	*	200+	23	Dec 1981
Baok	Indonesia	126	122	147	163	41	87	Dec 1966
Basmati 370	Pakistan	81	94	121	145	64	46	Jul 1967
Bayar Kuning	Indonesia	60	128	–	*	200+	25	Dec 1981
Bayar Kuning 1	Indonesia	58	117	–	*	200+	23	Dec 1981
Bayar Kuning 2	Indonesia	60	117	–	*	200+	25	Dec 1981
BE3	Burma	54	123	–	*	200+	19	Feb 1978
Belle Patna	USA	–	66	81	96	30	31	Aug 1966
Bengawan	Philippines	79	119	133	139	60	44	Aug 1963
BG66-1	Sri Lanka	78	79	–	109	31	43	Feb 1974
BG90-2		70	80	108	–	38	35	May 1976
Bibit Delapan I	Indonesia	60	125	–	*	200+	25	Dec 1981
Biji Nangka	Indonesia	59	128	–	*	200+	24	Dec 1981
Bilis/Banih Hirang 1	Indonesia	53	121	–	*	200+	18	Dec 1981
Binato	Philippines	69	76	–	95	26	34	Feb 1966
Binicol	Philippines	79	102	–	*	200+	44	Feb 1978
Binocane	Philippines	92	104	–	120	28	57	Feb 1978
Bir-me-fen	China	73	77	99	120	47	38	May 1963
Birpak	India	74	74	*	*	200+	39	Jul 1982
BKN6517-9-2	Thailand	90	90	138	144	54	55	Mar 1973
BKN6517-63-4	Thailand	97	100	146	159	62	62	Mar 1973
BKN6652-249-1	Thailand	69	84	–	114	45	34	Feb 1974
BKN6809-74-40	Thailand	66	79	–	100	34	31	Feb 1974
Blue Bonnet 50	USA	80	109	114	–	34	45	Jan 1963
BM5	Malaysia	64	80	119	121	57	29	May 1964
BP176 (NS)	Philippines	70	85	114	110	44	35	May 1964
BP176-1	Philippines	73	84	109	115	42	38	Jul 1967
BPI76 (S)	Philippines	52	77	*	*	200+	17	May 1963
BPI121-407	Philippines	80	106	100	108	28	45	Mar 1972

Variety	Country	Photoperiod[a] 10	12	14	16	PSP[b]	BVP[c]	Date of test[d]
C4-63	Philippines	72	81	110	123	51	37	Jul 1967
C12	Philippines	72	98	112	107	40	37	Mar 1972
C18	Philippines	66	74	-	114	48	31	Feb 1966
C22	Philippines	69	106	105	106	87	34	Aug 1972
Calrose-76	USA	–	66	99	**	44+	31	Feb 1979
Carnaroli	Italy	77	70	78	91	21	35	Nov 1972
Carreon	Philippines	46	59	–	*	200+	11	Feb 1978
Cartuna	Indonesia	72	–	89	–	17	37	Mar 1974
CH10	India	76	78	80	85	9	41	Dec 1966
Chianung 242	China	102	94	98	–	8	59	Jan 1963
Chiclayo	Peru	55	54	*	*	200+	30	Mar 1973
Chingair	India	82	136	*	*	200+	47	Jul 1982
Chonbunok	Korea	59	59	65	117	58	24	Jan 1967
Chubu	Japan	–	58	88	**	52+	23	Feb 1978
Chung–Lin-Chun	China	45	64	168	–	123	10	Jul 1962
CN540	India	107	126	152	157	50	72	Dec 1982
Colombia 1	Colombia	98	–	101	–	3	63	Mar 1974
Consejala	Philippines	58	73	–	*	200+	23	Feb 1978
CP231	USA	84	87	90	95	11	49	Jan 1964
DA31	Bangladesh	49	52	67	110	61	14	Aug 1970
Dadajo	Korea	–	66	101	**	44	31	Feb 1979
Darun 1	Indonesia	64	114	–	*	200+	29	Dec 1981
Datakan	Philippines	82	90	108	101	26	47	Apr 1969
Dawley 4-2	Thailand	79	79	107	156	77	44	May 1963
Deepwater Type	India	86	110	*	*	200+	51	Jul 1982
Dhanya	India	82	118	*	*	200+	47	Jul 1982
Dharial	Bangladesh	64	63	79	83	20	28	Aug 1970
Donradao	Brazil	85	112	*	*	200+	50	Jul 1982
Dulai Aman	India	83	125	*	*	200+	48	Jul 1982
Dulai Baron	India	85	108	*	*	200+	50	Jul 1982
Dular	India	70	66	72	74	8	31	Aug 1970
Dwarf Biji/ Nangkalayang	Indonesia	63	136	–	*	200+	28	Dec 1981
E-425	West Africa	93	–	100	–	7	58	Mar 1974
Eal 20	Peru	55	59	*	*	200+	20	Mar 1973
Eal 60	Peru	55	62	*	*	200+	20	Mar 1973
Elon-elon	Philippines	56	71	–	*	200+	21	Feb 1978
Elon-elon	Philippines	58	70	185	138	127	23	Apr 1969
Engkatek	Malaysia	60	107	*	*	200+	25	May 1964
FB121	Philippines	50	73	*	*	200+	15	Aug 1963
FK-178A	Philippines	49	90	–	*	200+	14	Feb 1978
FMC4	Peru	65	76	*	*	200+	30	Mar 1973
FM L58	Peru	63	70	*	*	200+	28	Mar 1973
Fortuna	Philippines	107	110	106	108	4	71	Aug 1972
Fujisaka 5	Japan	67	64	71	–	7	29	Jul 1962
Geb 24	India	63	90	*	*	200+	28	Dec 1966
Girola	Spain	65	61	93	149	88	26	Nov 1972
Gowai 84	Bangladesh	60	126	*	–	200+	25	Jul 1975
Gow Ruang	Thailand	59	71	*	*	200+	24	May 1963
Guinangang	Philippines	80	116	–	*	200+	45	Feb 1978
Guinata	Philippines	84	91	–	109	25	49	Feb 1978
Gutak	India	104	107	112	112	8	69	Jul 1982
Guze	China	48	50	117	123	75	13	May 1963
Habiganj-II	Bangladesh	80	81	78	82	4	43	Aug 1970
Habiganj-IV	Bangladesh	68	71	73	85	17	33	Aug 1970
Habigani-VI	Bangladesh	78	78	77	80	3	42	Aug 1970

Variety	Country	Photoperiod [a]				PSP [b]	BVP [c]	Date of test [d]
		10	12	14	16			
Habiganj Aman1	Bangladesh	38	80	–	–	140+	3	Nov 1982
Habiganj Boro5	Bangladesh	92	92	–	–	5	51	Nov 1982
Habiganj DW 1	Bangladesh	41	92	*	–	200+	6	Jul 1975
Habiganj DW 2	Bangladesh	44	111	*	–	200+	9	Jul 1975
Habiganj DW 8	Bangladesh	78	135	*	–	200+	43	Jul 1975
Heenati 8963	Sri Lanka	75	77	91	112	37	40	Dec 1966
Heenati 8965	Sri Lanka	51	63	90	125	74	16	Dec 1966
Heenati 8976	Sri Lanka	73	86	165		200+	38	Dec 1966
IAC1246	Brazil	85	–	91	–	6	50	Mar 1974
I-Geo-Tze	China	81	85	–	95	14	46	Feb 1966
Inintiw Str. 107	Philippines	107	99	–	116	17	64	Feb 1978
Intan	Indonesia	78	102	–	145	67	43	Feb 1978
Intan	Philippines	77	90	136	149	72	42	May 1964
IR3-36-3	Philippines	–	82	125	140	58	47	Aug 1966
IR3-66	Philippines	–	90	106	112	22	55	Aug 1966
IR4-2	Philippines	–	83	93	102	19	48	Aug 1966
IR4-93-2	Philippines	–	99	135	150	51	64	Aug 1966
IR5	Philippines	93	101	130	134	41	58	Mar 1970
IR5-114-3 (Pankaj)	Philippines (India)	90	–	120	136	46	55	May 1971
IR5-177	Philippines	73	87	133	133	60	38	Jul 1967
IR5-192-1	Philippines	80	96	138	150	70	45	Jul 1967
IR5-264- 1	Philippines	74	88	142	143	69	39	Jul 1967
IR5-264-3	Philippines	74	90	134	142	68	39	Jul 1967
IR5-278 (Bahagia)	Philippines (Malaysia)	81	–	122	146	65	46	May 1971
IR6-53-2	Philippines	–	91	108	126	35	56	Aug 1966
IR6-156-2 (Mehran 691	Philippines (Pakistan)	104	–	108	126	22	69	May 1971
IR8	Philippines	101	100	109	112	12	65	Mar 1970
IR8-36	Philippines	–	91	102	111	20	56	Aug 1966
IR8-(40)	Philippines	74	76	93	112	38	39	Jul 1967
IR8-(68)	Philippines	88	86	104	118	32	51	Jul 1967
IR8-172-3	Philippines	79	92	136	149	70	44	Jul 1967
IR8-279-2	Philippines	69	85	131	141	72	34	Jul 1967
IR8-288-3	Philippines	85	92	–	107	22	50	Feb 1966
IR8-288-3-13E	Philippines	79	82	95	114	35	44	Jul 1967
IR8-288-3-16-1 (E)	Philippines	76	80	93	111	35	41	Jul 1967
IR8-288-3-17-1 (L)	Philippines	89	90	104	125	36	54	Jul 1967
IR8-288-3-VL-8 (L)	Philippines	88	91	102	124	36	53	Jul 1967
IR9-60	Philippines	80	86	92	89	12	45	Aug 1963
IR 11 -2224	Philippines	–	80	97	110	30	45	Aug 1966
IR11-288-3	Philippines	80	83	100	126	46	45	Jul 1967
IR11-452-1	Phllippines	–	89	112	123	34	54	Aug 1966
IR12-178	Philippines	89	89	–	91	2	54	Dec 1968
IR14-149-3	Philippines	–	102	112	130	28	67	Aug 1967
IR20	Philippines	76	76	103	112	36	41	Mar 1970
IR22	Philippines	69	73	101	102	33	34	Mar 1970
IR24	Philippines	95	–	95	110	15	60	May 1971
IR26	Philippines	93	85	99	–	14	50	May 1976
IR28	Philippines	74	68	76	–	8	33	May 1976
IR30	Philippines	70	70	82	–	12	35	May 1976
IR32	Philippines	84	95	133	–	49	49	May 1976

Variety	Country	Photoperiod [a]				PSP[b]	BVP[c]	Date of test [d]
		10	12	14	16			
IR34	Philippines	83	88	121	–	38	48	May 1976
IR36	Philippines	68	70	81	96	28	33	Oct 1982
IR39-14	Philippines	85	81	91	105	24	46	Jul 1967
IR39-19	Philippines	79	78	90	103	25	43	Jul 1967
IR42	Philippines	78	91	–	138	60	43	Feb 1978
IR52-18-2	Philippines	–	89	106	119	30	54	Aug 1966
IR81-105-2	Philippines	71	79	111	134	63	36	Mar 1970
IR84-3-4	Philippines	80	84	85	101	21	45	Jul 1967
IR95-42-11	Philippines	71	89	122	140	69	36	Jul 1967
IR95-42-13	Philippines	84	82	94	144	32	47	Oct 1969
IR127-2-2	Philippines	78	78	102	112	34	43	Jul 1967
IR127-70-3	Philippines	83	82	–	108	26	47	Dec 1968
IRl57-61-3	Philippines	94	96	116	138	44	59	Jul 1967
IR160-25-1 (CS2)	Philippines (Ivory Coast)	91	–	91	104	13	56	May 1971
IR160-27-4 (Sinaloa A68)	Philippines (Mexico)	93	–	105	113	20	58	May 1971
IR238-28-3	Philippines	81	77	89	97	20	42	Jul 1967
IR253-4 (RD-2)	Philippines (Thailand)	79	–	94	105	26	44	May 1971
IR253-16-1 (CS3)	Philippines (Ivory Coast)	79	77	97	104	27	42	Jul 1967
IR262-7-1 (CS1)	Philippines (Ivory Coast)	90	77	96	120	43	42	Mar 1972
IR262-43-8	Philippines	82	82	99	108	26	47	Oct 1979
IR272-4-1	Philippines	86	80	94	112	32	45	Mar 1972
IR332-2-10	Philippines	98	116	148	165	67	63	Mar 1970
IR410-1-16	Philippines	85	99	–	126	41	50	Dec 1968
IR441-2-50-2 (Huallaga)	Philippines (Peru)	83	90	119	128	45	48	Oct 1969
IR442-2-58	Philippines	88	93	113	120	32	53	Oct 1969
IR480-5-9	Philippines	104	74	91	117	43	39	Mar 1972
IR532-1-176 (Chandina)	Philippines (Bangladesh)	66	–	78	88	22	31	May 1971
IR532-1-218	Philippines	66	68	–	87	21	31	Dec 1968
IR578-181-3	Philippines	87	85	97	104	19	50	Oct 1969
IR579-48-1 (Nilo 11)	Philippines (El Salvador)	66	80	85	90	24	31	Mar 1972
IR589-54-2	Philippines	87	96	123	129	42	52	Oct 1969
IR589-66-2	Philippines	65	80	106	113	48	30	Oct 1969
IR627-1-31	Philippines	104	99	116	119	20	64	Oct 1969
IR627 -1 -35	Philippines	80	88	110	107	30	45	Apr 1969
IR658-32-22	Philippines	69	81	116	97	47	34	Apr 1969
IR661-1-140 (Mummai)	Philippines (Fiji)	97	91	107	114	23	56	Oct 1969
IR665-48	Philippines	82	84	102	102	20	47	Mar 1970
IR667-98 (Tongil)	Philippines (Korea)	77	–	84	96	19	42	May 1971
IR747-82-6	Philippines	68	64	77	73	13	29	Mar 1970
IR773A1-36-2	Philippines	96	86	103	116	30	51	Oct 1969
IR790-28-2	Philippines	86	–	113	118	32	51	May 1971
IR883-6-2	Philippines	62	80	80	86	24	27	Mar 1972
IR883-34-1	Philippines	60	89	93	95	35	25	Mar 1972
IR841-5-1	Philippines	68	94	92	91	23	33	Aug 1972
IR87882-62-2	Philippines	103	102	115	114	13	67	Mar 1970
IR930-2-6 (Navlamp)	Philippines (Peru)	95	82	109	122	40	47	Mar 1972

Variety	Country	Photoperiod[a]				PSP[b]	BVP[c]	Date of test[d]
		10	12	14	16			
IR930-31 (Cica 4)	Philippines (Colombia)	90	94	92	90	4	55	Mar 1972
IR1052 (Variety R)	Guyana	86	82	–	96	14	47	Feb 1974
IR1055 (Variety S)	Guyana	78	86	–	118	40	43	Feb 1974
IR1480-116-3	Philippines	74	102	100	106	32	39	Aug 1972
IR1480-125-2	Philippines	74	108	108	107	34	39	Aug 1972
IR1514A-E666-9	Philippines	81	76	94	120	44	41	Mar 1973
IR1529-72-5	Philippines	88	106	107	106	19	53	Aug 1972
IR1529-382-4	Philippines	76	103	106	104	30	41	Aug 1972
IR1529-430-3	Philippines	78	104	105	103	27	43	Aug 1972
IR1529-548-1	Philippines	78	103	104	101	26	43	Aug 1972
IR1529-677-2	Philippines	87	106	107	105	20	52	Aug 1972
IR1529-680-3	Philippines	81	105	106	104	25	46	Aug 1972
IR1541-76-3	Philippines	84	96	101	100	17	49	Aug 1972
IR1541-102-6	Philippines	71	101	103	101	32	36	Aug 1972
IR1561-149-5	Philippines	68	87	91	92	24	33	Aug 1972
IR1561-228-3	Philippines	67	82	85	90	23	32	Aug 1972
IR1561-228-3-3	Philippines	67	69	78	–	11	32	May 1976
IR1632-93-2-2	Philippines	75	72	92	–	20	37	May 1976
IR2035-117-3	Philippines	88	93	119	–	31	53	May 1976
IR2058-78-1 -3-2-3	Philippines	73	79	102	–	29	38	May 1976
IR2061-214- 3-2-41	Philippines	78	78	–	97	19	43	Feb 1974
IR2061-214- 3-2-71	Philippines	80	80	–	96	16	45	Feb 1974
IR2061-214-3-3-1	Philippines	79	74	–	92	18	39	Feb 1974
IR2061-214-3-3-7	Philippines	86	82	–	96	14	47	Feb 1974
IR2061-214- 3-3-11	Philippines	76	76	–	88	12	41	Feb 1974
IR2061-214- 3-3-17	Philippines	77	75	–	90	15	40	Feb 1974
IR2061-214- 3-3-19	Philippines	82	74	–	99	25	39	Feb 1974
IR2061-214- 3-3-22	Philippines	80	77	–	88	11	42	Feb 1974
IR2061-214- 3-3-28	Philippines	78	75	–	83	8	40	Feb 1974
IR2061-214- 3-3-32	Philippines	77	73	–	81	8	38	Feb 1974
IR2061-214- 36-20	Philippines	75	75	–	82	7	40	Feb 1974
IR2061-214- 3-6-21	Philippines	74	72	–	82	10	37	Feb 1974
IR2061-214- 3-6-34	Philippines	84	80	–	94	14	45	Feb 1974
IR2061-214- 3-6-39	Philippines	74	75	–	83	9	39	Feb 1974
IR2061-214- 3-6-41	Philippines	82	78	–	92	14	43	Feb 1974
IR2061-214- 3-6-51	Philippines	73	73	–	81	8	38	Feb 1974
IR2061-214- 3-6-62	Philippines	81	77	–	91	14	42	Feb 1974

Variety	Country	Photoperiod[a]				PSP[b]	BVP[c]	Date of test[d]
		10	12	14	16			
IR2061-214-3-6-68	Philippines	82	80	–	93	13	45	Feb 1974
IR2061-214-3-8-1	Philippines	74	73	–	85	12	38	Feb 1974
IR2061-214-3-8-2	Philippines	75	72	–	82	10	37	Feb 1974
IR2061-214-3-8-5	Philippines	77	75	–	86	11	40	Feb 1974
IR2061-214-3-8-7	Philippines	75	74	–	89	15	39	Nov 1972
IR2061-464-2-4-4-6	Philippines	83	81	94	–	13	46	May 1976
IR2061-465-1-5-5	Philippines	68	68	84	–	16	33	May 1976
IR2061-522-6-9	Philippines	80	72	90	–	18	37	May 1976
IR2061-628-1-6-4-3	Philippines	76	71	91	–	20	36	May 1976
IR2070-414-3-9	Philippines	71	73	100	–	29	36	May 1976
IR2070-423-2-5-6	Philippines	75	78	99	–	24	40	May 1976
IR2071-105-9-1	Philippines	85	87	109	–	24	50	May 1976
IR2071-137-5-5-1	Philippines	69	72	89	–	20	34	May 1976
IR2071-486-9-2-6	Philippines	69	72	79	–	10	34	May 1976
IR2071-586-5-6-3	Phllippines	82	86	120	–	38	47	May 1976
IR2071-588-1-1-1	Philippines	80	86	120	–	40	45	May 1976
IR2071-588-5-4-5	Philippines	81	87	124	–	43	46	May 1976
IR2153-26-3-5-6	Philippines	80	82	104	–	24	45	May 1976
IR2153-338-3	Philippines	74	76	86	–	12	39	May 1976
IR2307-64-2-2	Philippines	64	65	76	–	12	29	May 1976
IR2307-86-1-2	Philippines	72	78	96	–	24	37	May 1976
IR2328-51-1-2-1	Philippines	79	76	98	–	22	41	May 1976
IR2681-163-5-2-2	Philippines	84	90	118	–	34	49	May 1976
IR2688-39-4-2-3	Philippines	90	93	117	–	27	65	May 1976
IR32748-99-3-2	Philippines	83	88	118	–	35	48	May 1976
IR2798-115-2-3	Philippines	84	90	119	–	35	49	May 1976
IR2823-399-5-6	Phllippines	73	77	108	–	35	38	May 1976
IR2832-141-2-1	Phllippines	93	96	122	–	29	58	May 1976
IR2863–6-3	Philippines	87	86	108	–	22	51	May 1976
IR2863-35-3-3	Philippines	74	85	112	–	38	39	May 1976
IR2863-38-1-2	Phllipplnes	76	87	118	–	42	41	May 1976
IR2863-39-2-1	Philippines	81	91	113	–	32	46	May 1976
IR4422-51-1	Philippines	83	84	105	–	22	48	May 1976
IR4432-103-6	Philippines	76	87	102	–	26	41	May 1976
IR4816-70	Philippines	75	80	110	–	35	40	May 1976
IR8234-OT-9-2	Thailand	93	112	143	147	54	58	Dec 1982
Italpatna	Italy	76	74	79	90	16	39	Nov 1972
Jayanti (IET1039)	India	79	82	–	120	41	44	Feb 1974
Jeratus Molam	Indonesia	93	–	99	–	6	58	Mar 1974
Jinhung	Korea	56	56	81	136	80	21	Jan 1967

Variety	Country	Photoperiod[a]				PSP[b]	BVP[c]	Date of test[d]
		10	12	14	16			
Kala or Black Aman	India	77	146	*	*	200+	42	Jul 1982
Kalar Harsall	India	75	142	*	–	200+	40	Jul 1975
Kamuning	Indonesia	56	124	–	*	200+	21	Dec 1981
Kaohsiung 68	China	104	107	113	118	14	69	Aug 1963
Kapuas	Indonesia	61	137	–	*	200+	26	Dec 1981
Karang-Duku 1	Indonesia	63	118	–	*	200+	28	Dec 1981
Karang Serang	Indonesia	115	111	114	121	10	76	Dec 1966
Karang Serang Sel.	USA	139	123	132	153	30	88	Dec 1966
Karpaddy	India	86	115	*	*	200+	51	Jul 1982
Kataktara	Bangladesh	72	72	81	84	12	37	Aug 1970
Kattuvanam	India	83	134	*	*	200+	48	Jul 1982
Katumbar Kuning 1	Indonesia	66	117	–	*	200+	31	Dec 1981
Katurnbar Putih 1	Indonesia	68	126	–	*	200+	33	Dec 1981
Kekowa Bao	India	59	123	*	–	200+	24	Jul 1975
KH17854	India	-	60	97	**	50	25	Feb 1979
Khao Bai Sri	India	64	125	–	*	200+	29	Feb 1978
Khao Lo	Laos	54	–	130	–	76	19	Mar 1974
Khao Med Lek	Thailand	58	131	*	–	200+	23	Jul 1975
Khao Phe	Laos	59	–	*	–	200+	24	Mar 1974
Kinalabao	Philippines	82	85	–	100	18	47	Feb 1978
Kinanda	Philippines	99	100	–	121	22	64	Feb 1978
Kinandang Pula	Philippines	81	89	–	104	23	46	Feb 1978
Kinandang Puti	Philippines	92	90	–	109	19	55	Feb 1978
Kriau 1	Indonesia	60	126	–	*	200+	25	Dec 1981
Ku-70-1	Thailand	58	–	106	–	48	23	Mar 1974
Ku-104	Thailand	55	–	205	–	150	20	Mar 1974
Ku-113-1	Thailand	64	–	*	–	200+	29	Mar 1974
Kwansansaek	Korea	-	49	94	100	51	14	Feb 1979
Lac 5	Liberia	96	–	111	–	15	61	Mar 1974
Lac 23	Liberia	98	–	119	–	21	63	Mar 1974
Lakatan Gadur 1	Indonesia	59	123	–	*	200+	24	Dec 1981
Lakatan Hirang 1	Indonesia	56	129	–	*	200+	21	Dec 1981
Lakatan Kuning 1	Indonesia	64	122	–	*	200+	29	Dec 1981
Lakatan Lakatut 1	Indonesia	72	116	–	*	200+	37	Dec 1981
Lakatan Lakatut 2	Indonesia	70	–	–	8	200+	35	Dec 1981
Lakatan Pahu 1	Indonesia	58	132	–	*	200+	23	Dec 1981
Lakhi	India	66	119	*	*	200+	31	Jul 1982
Laki 192	India	40	94	*	–	200+	5	Jul 1975
Lalkanai	India	66	91	*	*	200+	31	Jul 1982
Latisail	Bangladesh	55	84	*	*	200+	20	Mar 1974
Layang Kuning 1	Indonesia	64	125	–	*	200+	29	Dec 1981
Layang Putih 1	Indonesia	67	128	–	*	200+	32	Dec 1981
Layang Putih 2	Indonesia	61	121	–	*	200+	26	Dec 1981
Leb Mue Nahng 111	Thailand	60	126	*	–	200+	25	Jul 1975
Lemo 1	Indonesia	64	137	–	*	200+	29	Dec 1981
M148	Philippines	77	109	115	147	70	42	Aug 1972
M1FB-253-3	Philippines	83	90	–	106	23	48	Feb 1966
Macan Piña	Philippines	88	91	–	105	17	53	Feb 1978

Variety	Country	Photoperiod[a]				PSP[b]	BVP[c]	Date of test[d]
		10	12	14	16			
Macan Pulot	Philippines	50	66	–	*	200+	15	Feb 1978
Magkompol	Philippines	56	91	–	*	200+	21	Feb 1978
Magsanaya	Philippines	68	75	–	99	31	33	Feb 1978
Mahsuri	India	96	120	131	137	41	61	Oct 1982
Mahsuri	Malaysia	90	110	*	*	200+	55	Jul 1982
Malagkit Sungsong	Philippines	76	104	–	*	200+	41	Feb 1966
Mangarez	Philippines	92	91	–	113	22	56	Feb 1978
Maratelli	Italy	68	62	68	85	23	27	Nov 1972
Mas	Indonesia	82	93	130	144	62	47	Jul 1967
Meung Naung 62 M	Thailand	63	103	*	*	200+	28	May 1963
Mil for (6) 2	Philippines	108	108	111	–	3	73	Jan 1963
Mil tex	Philippines	95	–	104	–	9	60	Mar 1974
Moddai Karuppan	Sri Lanka	84	–	–	–	200+	49	Mar 1974
Moroberekan	Guinea	94	–	104	–	10	59	Mar 1974
Nahng Mon S-4	Thailand	55	79	*	*	200+	20	May 1963
Nang Tay C	Vietnam	58	128	*	–	200+	23	Jul 1975
Nato	USA	81	78	89	–	11	43	Jul 1962
Nizersail	Bangladesh	64	96	*	*	200+	29	Aug 1970
Nongkwang	Korea	54	55	86	137	83	19	Jan 1967
Norin 17	Korea	69	70	79	89	20	34	Jan 1967
Norin 18	Japan	61	73	120	138	77	26	Aug 1963
Norin 20	Japan	49	48	48	59	11	13	May 1963
Norin 25	Japan	59	60	81	151	92	24	May 1963
Norin 29	Korea	56	56	88	118	62	21	Jan 1967
Oryza nivara		53	52	108	107	56	17	Mar 1973
OS4	W. Africa	90	82	92	105	23	47	Mar 1973
OS6	W. Africa	85	82	92	105	23	47	Mar 1973
Padi Gadabal	Indonesia	66	121	–	*	200+	31	Dec 1981
Palawan	Philippines	87	83	–	121	38	48	Feb 1978
Palingkau 1	Indonesia	57	121	–	*	200+	22	Dec 1981
Palkwoeng	Korea	60	60	89	125	65	25	Jan 1967
Paltal	Korea	60	59	80	121	62	24	Jan 1967
Pate Blanc MN3	Ivory Coast	113	–	113	–	0	78	Mar 1974
Perola	Brazil	82	–	89	–	7	47	Mar 1974
Perunel	India	83	84	*	*	200+	38	Jul 1982
Peta	Philippines	70	85	125	145	75	35	May 1963
Piniling Daniel	Philippines	63	91	–	131	68	28	Feb 1978
Pinulot	Philippines	92	100	–	113	21	57	Feb 1978
Pinursigue	Philippines	49	60	–	132	83	14	Feb 1978
Podiwi A-8	Sri Lanka	76	136	*	–	200+	41	Jul 1962
Pokkali	Sri Lanka	85	110	*	*	200+	50	Oct 1982
Po Ngern	Thailand	61	148	*	–	200+	26	Jul 1975
Ponkambi Samba	India	85	108	*	*	200+	50	Jul 1982
Ponni	India	95	116	*	*	200+	60	Jul 1982
Ponta Rubra	Portugal	67	67	72	74	7	32	Nov 1972
Poongar	India	73	71	*	*	200+	36	Jul 1982
Precoce 6	Portugal	74	75	77	83	9	39	Nov 1972
PTB28	India	66	57	113	110	56	22	Mar 1973
Puang Nahk 16	Thailand	68	90	*	*	200+	33	May 1963
Pungok	Korea	64	64	87	128	64	29	Jan 1967
Raden Sawo 1	Indonesia	67	119	–	*	200+	32	Dec 1981
Radin China 4	Malaysia	65	116	*	*	200+	30	May 1964
Radin Kling	Malaysia	66	89	123	144	78	31	May 1964

Variety	Country	Photoperiod[a]				PSP[b]	BVP[c]	Date of test[d]
		10	12	14	16			
Radin Siak	Malaysia	88	116	153	171	83	53	May 1964
Ramilon	Philippines	74	135	–	*	200+	39	Feb 1978
Raminad Str. 3	Philippines	69	121	*	*	200+	34	May 1964
Rayada 16-02	Bangladesh	108	126	–	–	140+	73	Nov 1982
Rayada 16-03	Bangladesh	108	124	–	–	140+	73	Nov 1982
Rayada 16-05	Bangladesh	109	126	–	–	140+	74	Nov 1982
Rayada 16-06	Bangladesh	108	124	–	–	140+	73	Nov 1982
Rayada 16-08	Bangladesh	105	125	–	–	140+	70	Nov 1982
Razza	Italy	76	72	76	83	11	37	Nov 1972
RD3	Thailand	83	87	101	100	18	48	Mar 1970
Rendah Padang 1	Indonesia	62	121	–	*	200+	27	Dec 1981
Rendah Padang 2	Indonesia	61	121	–	*	200+	26	Dec 1981
Rexoro	USA	99	111	–	*	200+	64	Feb 1978
Ribe	Italy	69	66	75	83	17	31	Nov 1972
Roma	Italy	71	64	74	82	18	29	Nov 1972
Romeo	Italy	65	61	73	84	23	26	Nov 1972
Roncarolo	Italy	63	59	65	78	19	24	Nov 1972
Rosa Marchetti	Italy	67	70	72	75	8	32	Nob 1972
Sai Bur	Thailand	59	128	*	–	200+	24	Jul 1975
Sarang Burung	Indonesia	61	118	–	*	200+	26	Dec 1981
Saran Kraham	Cambodia	52	123	*	–	200+	17	Jul 1975
Sarapalli Samba	India	87	91	94	94	7	52	Jul 1982
Sequial	Spain	64	60	87	92	32	25	Nov 1972
Serandah Kuning 60	Malaysia	51	109	*	*	200+	16	May 1964
Seraup Besar	Philippines	69	102	129	129	60	34	Mar 1972
Seraup Besar15	India	50	136	*	*	200+	15	Aug 1972
Shirogame	Korea	59	60	80	124	65	24	Jan 1967
Slam 29	Philippines	61	112	*	*	200+	26	Jan 1964
Slam 48	Malaysia	51	80	*	*	200+	16	May 1964
Sibung Rendah 1	Indonesia	71	128	–	*	200+	36	Dec 1981
Sibung Tinggi	Indonesia	68	131	–	*	200+	33	Dec 1981
Sinampablo	Philippines	89	99	–	108	19	54	Feb 1978
Sinariaya	Philippines	51	80	–	127	76	16	Feb 1978
Sirumani Aman	India	72	87	*	*	200s	37	Jul 1982
Siyam	Indonesia	61	129	–	*	200+	26	Dec 1981
SK 36 Str. 482	Philippines	73	125	*	*	200+	38	May 1964
Subang	Malaysia	56	112	*	*	200+	21	May 1964
Subang Intan 117	Malaysia	59	89	*	*	200+	24	May 1963
Sukanandi	Indonesia	117	113	120	163	50	78	May 1963
Sunson	Korea	55	54	81	127	73	19	Jan 1967
Suwon 82	Korea	62	63	81	131	69	27	Jan 1967
Suwon 118	Korea	71	71	80	91	20	36	Jan 1967
T-3	India	77	86	–	120	43	42	Feb 1966
T-3 W356	India	82	90	127	137	55	47	Dec 1966
T-21	India	77	82	103	98	26	42	Dec 1966
T-136	India	66	69	88	92	26	31	Dec 1966
T442-36	Thailand	65	94	131	130	66	30	Mar 1972
T442-57	Thailand	73	117	140	142	69	38	Aug 1972
Tah Pow Gaew	Thailand	61	82	*	*	200+	26	May 1963
Taichung 172	China	87	83	90	99	16	48	Jan 1964
Taichung (N)1	China	83	84	105	–	22	48	Jan 1963
Tainan 3	China	89	89	97	114	25	54	Jan 1964
Tampokong Kuning	Indonesia	55	127	–	*	200+	20	Dec 1981
Tangkai Rotan	Malaysla	83	105	160	179	96	48	Jul 1967

Variety	Country	Photoperiod [a]				PSP [b]	BVP [c]	Date of test [d]
		10	12	14	16			
Tau Binh C	Vietnam	63	129	*	–	200+	28	Jul 1975
TD-47	Thailand	75	–	*	–	200+	40	Mar 1974
TD-48	Thailand	71	–	*	–	200+	36	Mar 1974
TD-51	Thailand	70	–	*	–	200+	35	Mar 1974
Tempokong Putih 1	Indonesia	56	131	–	*	200+	21	Dec 1981
Thailand	Philippines	65	79	–	101	36	30	Feb 1978
Thiorno	Senegal	77	–		–	200+	42	Mar 1974
Tjere Mas	Philippines	73	105	134	133	61	38	Aug 1963
TKM-6	India	69	68	–	118	50	33	Dec 1968
TNR1	India	90	116	*	*	200+	55	Jul 1982
TY12	Japan	–	45	100	**	65+	10	Feb 1979
Urnbang Gadabung 1	Indonesia	58	119	–	*	200+	23	Dec 1981
Urnbang Gadabung 2	Indonesia	60	121	–	*	200+	25	Dec 1981
Urnbang Kabatik 1	Indonesia	64	–	–	*	200+	29	Dec 1981
Urnbang Kabatik 2	Indonesia	64	122	–	*	200+	29	Dec 1981
Umbangju	Korea	57	57	89	122	65	22	Jan 1967
Usubang Inai	Indonesia	66	132	–	*	200+	31	Dec 1981
Usubang Kencana 1	Indonesia	59	98	–	*	200+	24	Dec 1981
Usubang Putih 1	Indonesia	70	113	–	*	200+	35	Dec 1981
Usubang Sampahiring	Indonesia	56	124	–	*	200+	21	Dec 1981
Usubang Sarnpahiring 1	Indonesia	58	122	–	*	200+	23	Dec 1981
Vanam Villai	Sri Lanka	84	–	*	–	200+	49	Mar 1974
White Ottadan	India	84	112	*	*	200+	49	Jul 1982
Yamabiko	Japan	–	48	97	**	62	13	Feb 1979

[a] The plants received 10 h of natural light, from 0700 to 1700. The light intensity in the dark-rooms was 400 Ix and the temperature 20ºC. *No panicle initiation after 200 d of growth. [b] Photoperiod-sensitive phase. Growth duration at longest photoperiod minus shortest growth duration obtained in the test. [c] Basic vegetative phase. Minimum growth duration minus 35 d. [d] Variations in growth duration can occur because of differences in greenhouse temperature during growth.

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