SOME ASPECTS OF PHOTOPERIODISM IN RICE (*ORYZA SATIVA* L.)

R. BEST

STELLINGEN

I

Bij de verdeling van *Aleurites* met het doel het elaeostearinegehalte van de olie te verhogen, biedt de kruising van *A. montana* (LOUR.) WILS. met *A. Fordii* HEMSL. weinig kans op een gunstig resultaat.

WEBSTER, C. C. 1950. *Trop. Agr.*, 27: 179–220.

II

Bij grassen dient de ruimtelijke ordening der bladeren van individuele planten als een der belangrijkste criteria beschouwd te worden ter beoordeling van het potentiële productievermogen dezer planten in een gesloten grasmat.

COOPER, J. P. 1960. *8th Int. Grassl. Congress*, 1A/1: 2–5.
WARREN WILSON, J. 1960. *8th Int. Grassl. Congress*, 12A/2: 6–9.

III

De mening van LATIES en anderen dat de kinetische verschijnselen die door EPSTEIN werden waargenomen tijdens de "steady state uptake" van ionen, een dwingend bewijs zouden vormen voor het bestaan van de door EPSTEIN voorgestelde "carriers", is niet juist.

EPSTEIN, E. 1956. *Ann. Rev. Plant Physiol.*, 7: 1–24.
LATIES, G. G. 1959. *Ann. Rev. Plant Physiol.*, 10: 87–112.

IV

De exacte begrenzing van de "Donnan free space" ten opzichte van de "water free space", zoals deze door BRIGGS en medewerkers is voorgesteld, impliceert een statische conditie van de vaste phase van de cel, een statisch veld van Coulombse krachten aan het oppervlak van de vaste phase, en dientengevolge een adsorptie van ionen aan een diffuse dubbellaag (Gouy laag), hetgeen in strijd is met de aanname van de instelling van een Donnan evenwicht tijdens de "initial phase uptake".

BRIGGS, G. E., HOPE, A. B. AND PITMAN, M. G. 1958. *J. Exptl. Botany*, 9: 128–141.

V

De resultaten van het werk van SACHS sluiten de mogelijkheid niet uit dat bij *Cestrum nocturnum* L. onder continu behandeling met bepaalde daglengten bloemknopaanleg kan plaatsvinden.

SACHS, R. M. 1956. *Plant Physiol.*, 31: 185–192.

VI

Wanneer photoperiodiek gevoelige planten, die voldoende van suikers worden voorzien, in continu donker later bloemknopaanleg vertonen dan onder de optimale photoperiode, dan wordt dit voornamelijk veroorzaakt door het geringe transport van bloei-stimulus van de niet-assimilerende bladeren naar de groeipunten.

HAUPT, W. 1957. *Ber. deut. botan. Ges.*, 70: 191–198.
ZEEVAART, J. A. D. 1958. *Meded. Landbouwhogeschool Wageningen*, 58 (3): 1–88.

VII

In de equatoriale tropen kunnen bewolking en mist de natuurlijke daglengte in voldoende mate beïnvloeden om van landbouwkundige betekenis te zijn.

Dit proefschrift.

VIII

Wanneer getracht wordt de minimum hoeveelheid water benodigd voor het vermijden van oogstdepressies te schatten met behulp van meteorologische gegevens en de bedekkingsgraad van de bodem door het gewas, dan dient rekening te worden gehouden met de aard van het gewas en met mogelijke verschillen in de physiologische reactie van de planten tijdens opeenvolgende ontwikkelingsstadia.

PENMAN, H. L. 1956. *Neth. J. Agr. Sci.*, 4: 9–29.
WESSELING, J. AND WIJK, W. R. VAN. 1957. *Agronomy*, 7: 461–504.
WIT, C. T. DE. 1958. *Versl. Landbouwk. Onderz.*, 64 (6): 1–88.

IX

De curven, die het verband aangeven tussen de photoperiode en de bloemknopaanleg bij planten gekweekt onder wit licht en de optimale temperatuur, zijn eveneens geldig voor de inductie van de diapauze bij enkele schubvleugeligen (*Lepidoptera*), de Coloradokever (*Leptinotarsa decemlineata* SAY.), en een mijt (*Metatetranychus ulmi* KOCH).

LEES, A. D. 1959. In *Photoperiodism and Related Phenomena in Plants and Animals* (R. B. WITHROW, ed.): 585–600.
BEST, R. 1960. *Proc. Kon. Ned. Akad. Wetensch.*, 63: 676–691.

X

De qualiteit van geënsileerd gras kan aanzienlijk worden verbeterd door het gras vòòr de silage te kneuzen. Dit resultaat wordt bij gebruik van de maaikneuzer in een aantal gevallen echter onvoldoende bewerkstelligd. In dit verband dient als algemeen nadeel van de maaikneuzer gezien te worden dat droging van het gras niet aan de kneuzing kan voorafgaan, terwijl factoren zoals de verontreiniging van het gekneusde gras met zand, verliezen aan grassap en eventueel een onvoldoende intensieve kneuzing, eveneens een rol kunnen spelen.

WIERINGA, G. W. 1959. *Neth. J. Agr. Sci.*, 7: 134–137, 237–241.

XI

De argumenten waarmede DE VRIES stelling neemt tegen BOEKE'S concept ener dualistische economie, zijn onvoldoende gefundeerd.

BOEKE, J. H. 1930. *Dualistische Economie*, Leiden, p. 34.
VRIES, E. DE. 1947. *Inaug. Rede*, Wageningen, p. 15.

XII

In bevloeide rijstvelden kan de microbiologische stikstofbinding van essentiële betekenis zijn. De proeven van DE en MANDAL laten echter geen enkele conclusie toe omtrent de rol die blauw-groene algen (*Cyanophycea*) hierbij kunnen spelen.

BOND, G. 1955. *J. Exptl. Bot.*, 6: 303–311.
DE, P. K. AND MANDAL, L. N. 1956. *Soil Sci.*, 81: 453–458.
WATANABE, A. *et al.* 1959–'60. *J. Gen. Appl. Microb. Tokyo*, 5: 51–57, 85–91, 175–179.

SOME ASPECTS OF PHOTOPERIODISM IN RICE (*ORYZA SATIVA* L.)

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE LANDBOUWKUNDE OP GEZAG VAN DE RECTOR MAGNIFICUS IR. W. F. EIJSVOOGEL, HOOGLERAAR IN DE HYDRAULICA, DE BEVLOEIING, DE WEG- EN WATERBOUWKUNDE EN DE BOSBOUWARCHITECTUUR, TE VERDEDIGEN TEGEN DE BEDENKINGEN VAN EEN COMMISSIE UIT DE SENAAT DER LANDBOUWHOGESCHOOL TE WAGENINGEN OP VRIJDAG 27 JANUARI 1961 TE 16 UUR

DOOR

R. BEST

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Gaarne betuig ik op deze plaats mijn dank aan U, Hoogleraren, Lectoren en Docenten van de Landbouwhogeschool te Wageningen voor de wijze waarop U mijn studie hebt geleid.

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VOORWOORD EN SAMENVATTING

Dit proefschrift vormt een onderdeel van een algemene studie over de physiologie van de rijst, die in boekvorm zal worden gepubliceerd door Elseviers Wetenschappelijke Uitgeverij te Amsterdam onder de titel "Physiology of the Rice Crop". Voor het proefschrift zijn twee hoofdstukken uit dit boek gekozen waarin het belangrijkste deel van het eigen onderzoek over photoperiodiciteit wordt behandeld. Ter oriëntatie is aan het slot van dit voorwoord een korte inhoudsopgave van het boek gegeven waarin de titels der afzonderlijke hoofdstukken zijn vermeld. Wanneer in het hier gepresenteerde werk verwezen wordt naar één dezer hoofdstukken, of naar de appendix, dan betreft dit onderwerpen die niet tot deze dissertatie behoren.

De gebruikte proefopstellingen en materialen zijn niet in een afzonderlijk hoofdstuk besproken. Voor een gedetailleerde beschrijving hiervan zij verwezen naar de proefschriften van E. J. FORTANIER (*Meded. Landbouwhogeschool,* Wageningen, 57 (2): 1–116, 1957) en K. W. SMILDE (*Meded. Landbouwhogeschool,* Wageningen, 60 (5): 1–70, 1960).

De stof die in dit proefschrift is behandeld omvat onderzoek omtrent een vrij groot aantal aspecten van de photoperiodiciteit bij rijst. In het eerste hoofdstuk is het belangrijkste onderwerp de weergave van het photoperiodieke gedrag van een aantal rassen in de vorm van curven, die werden verkregen door de tijd van zaai tot bloemaanleg uit te zetten tegen de photoperiode.

In de literatuur wordt de photoperiodieke gevoeligheid van planten algemeen aangeduid met vrij vage termen zoals zwak-, matig-, of sterk-gevoelig, terwijl tevens van quantitatieve of qualitatieve korte- of lange-dagplanten wordt gesproken ter onderscheiding van een geringe en een hoge gevoeligheid. De specifieke photoperiodieke reactie van een bepaalde plant tracht men aan te duiden met de z.g. "critische daglengte" van deze plant. Een groot bezwaar van deze termen is dat hun waarde subjectief bepaald wordt en dat zij in feite zeer weinig over het photoperiodieke gedrag van de plant zeggen. Hiervan geven de curven, zoals deze in het eerste hoofdstuk van deze dissertatie behandeld zijn, echter een exacte weergave. De betekenis van deze curven voor de bestudering van de photoperiodiciteit bij planten in het algemeen werd eerder in een publicatie besproken (BEST, 1960).

In het tweede hoofdstuk is getracht het photoperiodieke effect van de natuurlijke dag te analyseren. Voor deze analyse werden twee richtingen van onderzoek gevolgd, namelijk de bepaling van een aantal photoperiodieke effecten onder gecontroleerde lichtcondities, en de metingen van het verloop van de lichtintensiteit in de ochtend- en avondschemering. onder verschillende weersomstandigheden Tevens werd gebruik gemaakt van een groot aantal gegevens van zaaidatumproeven in de tropen. De verkregen resultaten duiden erop dat bij photoperiodiek zeer gevoelige rijstrassen in de tropen de invloed van de bewolking op de dagelijkse photoperiode groot genoeg kan zijn om een belangrijke vervroeging of verlating van de bloei te veroorzaken.

Landbouwkundig is het belangrijkste aspect van de photoperiodiciteit de invloed van de natuurlijke daglengte op de vegetatieperiode van gevoelige rassen. Ten aanzien van de graanopbrengst kon vastgesteld worden dat de vegetatieperiode van deze rassen een vrij nauw begrensd optimum heeft. Een groeiduur korter of langer dan de optimale bleek de opbrengst vaak aanzienlijk te verlagen. Verschillen tussen rassen in de duur van de optimale vegetatieperiode kwamen voor, terwijl het optimum nauw gecorreleerd bleek te zijn met de stengelstrekking gedurende het vegetatieve stadium der planten. De vrij enge begrenzing van het optimum verklaart tevens de korte optimale zaaitijd van de gevoelige rassen.

Korte inhoudsopgave van het boek:

PHYSIOLOGY OF THE RICE CROP

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CHAPTER XXIV

PHOTOPERIODIC RESPONSE

1. INTRODUCTION

Broadly speaking rice may be regarded as a short-day plant. Probably there is no other single plant species of which the photoperiodic response has been investigated by so many research workers, and yet, when the data available in the literature are compared with the general review on photoperiodism presented in the preceding chapter, it is evident that in rice very little detailed analytical work has hitherto been devoted to the complex phenomenon of photoperiodism. Most experiments have been confined to observations on heading or flowering of rice plants exposed to a few different photoperiods and/or natural day length, whereas environmental conditions, other than the relative length of day and night, have neither been controlled nor analysed. It is not surprising, therefore, that various workers have obtained widely differing results in their experiments, and that many controversies are to be found in the literature.

In some respects rice is no doubt a very suitable plant for the study of photoperiodism: there is an extraordinarily wide range of differences in sensitivity to the photoperiod among commercial varieties, while inflorescence initiation can be accurately determined within a 24-hour period and the formation of the terminal inflorescence clearly separates vegetative and reproductive development. On the other hand there are many disadvantages: no grafting of leaves or stems is possible, there are no differences in flowering intensity indicating differences in the production of the floral stimulus, the study of the reaction of separate leaves has to be confined mainly to the leaf blades since the leaf sheaths largely envelop each other, the rice plant requires high light intensities for normal growth and development, the first leaves formed become senescent at an early age, etc. To overcome some of these disadvantages special techniques are required, one of the most important probably being the growing of rice plants in a medium which satisfactorily supplies the plant with an energy substrate for its growth and developmental processes. So far no research of this kind has been published on rice, and in our own work no satisfactory results have yet been obtained with this method. Therefore, in several cases, only approximate results can be given in the account on photoperiodic response presented in this chapter.

2. TYPES OF RESPONSE TO THE PHOTOPERIOD

2.1. *Effect of short day*

Probably the first research in which an artificially shortened day length was used in rice is the experiment of MIHARA (1923), who interrupted daylight between 10 a.m. and 2 p.m., thereby obtaining earlier flowering by about one month. In later work many authors reported that short days accelerated inflorescence initiation, heading or flowering (see *e.g.* YOSHII, 1927, 1929; SCVORZOFF, 1934; MIYASHIRO, 1935; LIN and CHEN, 1941, 1942; SARAN, 1945; YAMAMOTO, 1949; CHANDRARATNA, 1948, 1952, 1954; TAKASUGI and KOYAMA, 1951; MORINAGA *et al.*, 1954, 1955; and many others). Short-day treatments in these experiments were all photoperiods between 4 and 12 hours; shorter photoperiods proved to be lethal in all experiments. Where seasonal differences in day length have been compared, results amply confirmed that short days promoted reproductive development in rice (see *e.g.* VAN DER GOOT, 1923; MITRA *et al.*, 1924; LORD and DE SILVA, 1931; RAMIAH, 1933, 1936; HAIGH, 1936; JENKINS, 1936; JO, 1938; ADAIR, 1940; VAN DER MEULEN, 1941; JENKINS and JONES, 1944; KERLING, 1948, 1950; MURRAY, 1950; JODON, 1953; OKADA and KATO, 1935; WADA and NOJIMA, 1954; DORE, 1955 (a,b); ISHIKAWA, 1955; ASAKUMA, 1958).

Some authors reported that short photoperiods, of less than 9 or 11 hours, were less effective in shortening the vegetative period than slightly longer photoperiods (HARA, 1930; SUENAGA, 1936; OTANI and SHIRAKI, 1942–'48; CHANDRARATNA, 1948, 1951, 1954; MORINAGA and KURIYAMA, 1954; VELASCO and DE LA FUENTE, 1958). In general, these photoperiods have been accepted as being sub-optimal, although different interpretations for this have sometimes been given. In making comparisons between a sub-optimal and a near optimal photoperiod, KUILMAN (1937) and ABEYRATNE (1952) claimed to have established a long-day type of reaction in some *bulu* varieties from Java (KUILMAN) and in the Heenati group of *indica* varieties from Ceylon (ABEYRATNE). A long-day response was also supposed by GANGULEE (1954), who found in a sowing date experiment under greenhouse conditions in the U.S.A. that sowing in April resulted in earlier heading than sowing in December in the *bulu* variety Karang Serang. His experiments in India with the same variety were less conclusive, however. In his first experiment, non-photoperiodic effects such as low light intensity during the short days in winter, combined with relatively high greenhouse temperatures, might well have influenced the growth rate, and consequently the date of heading, more than the sub-optimum photoperiods in that season. Factors not related to photoperiodism have probably also contributed to aberrant results in some other experiments. RJABOV (1941) treated early and late maturing varieties with a 10 h photoperiod for 20 days. This treatment accelerated flowering in the late maturing varieties by 5 to 47 days, but delayed flowering in the early maturing varieties by 5 to 20 days. A similar type of response was reported by MISRA (1951, 1953, 1954) and SIRCAR and GHOSH (1954). MISRA worked with early and medium early maturing varieties in his experiments. A 10 h photoperiod delayed heading in all cases examined, the delay being at most 18 days. The delay was in general more marked when the treatment started earlier and when it was prolonged; SIRCAR and GHOSH (1954) exposed 7-day-old seedlings to an 8 h photoperiod for 28 days. Delay in heading in early varieties and a marked acceleration of heading in a late maturing variety were found. There are several factors unknown in these experiments, *viz.* the duration of the insensitive juvenile period of the varieties involved (*cf.* § 3), whether or not induction was completed before the short-day treatment was terminated (*cf.* § 4), and in which ways growth rate, inflorescence initiation and development were affected. It is, therefore, impossible to say which combination of factors brought about the results observed. The fact that only early maturing varieties showed delayed heading in these experiments is not surprising since late maturing varieties are mostly much more sensitive to the photoperiod, the effect of which usually masks all other effects in these varieties.

In several publications it is stated that short-day treatment for a limited period only, applied at early tillering, resulted in the plant coming into ear twice, or even three times (see *e.g.* KONDO *et al.*, 1932; BEACHELL, SIRCAR and PARIJA, 1945, 1949; WORMER, 1953). This may be explained by assuming that the main stem, and probably one or two of the oldest laterals, had passed the insensitive juvenile period before or during the treatment and subsequently reacted to the applied photoperiod, whereas other tillers were affected less and headed later, or were not affected at all and headed after induction in the natural day length; photoinduction in a particular stem being independent of induction in any other stem of the same plant (KONDO *et al.*, 1932, FUKE, 1942).

Transplanting at about the time of inflorescence initiation may cause rapid development of the inflorescence and early flowering (see Chapter XXVI, 4). The flowering of tillers in which initiation occurs after transplanting is much delayed and has been reported (TERAO and KATAYAMA, 1929; KATAYAMA, 1931) to be often very irregular.

In two experiments (*E. 323, E. 324*) with the varieties Nero di Vialone, Fortuna and Skrivimankoti, some additional data were obtained on the effect of short-day treatments for relatively brief periods. Single plants were grown in pots under natural day length conditions until the plants became sensitive to the photoperiod. The plants were thereafter exposed to short days (11 h) until 3 days after inflorescence initiation in the main stem, at which time initiation had just begun in some of the oldest laterals. At that stage the plants were transferred to natural day length conditions. The main data obtained in these experiments can be summarized as follows. Three heading periods were observed in the moderately sensitive variety Nero di Vialone but only one, relatively long, heading period was found in the very highly sensitive variety Skrivimankoti and in the almost day-neutral variety Fortuna.

A closer examination of heading in individual shoots revealed that in Nero di Vialone the main stem and one or two of the oldest tillers, which had initiated the inflorescence 3 days before the transfer to long days, headed first, followed about one week later by the tillers which had initiated their inflorescentes at or shortly after the transfer to long days, whereas younger tillers were induced under natural day length conditions and headed 6 weeks later. In Skrivimankoti the first two groups headed in one long heading period, but during the course of these experiments the younger tillers remained completely vegetative under the long days. Dissection of tillers showed that in some an inflorescence had been initiated, but had failed to grow out, a phenomenon also occasionally observed in Nero di Vialone. In the practically insensitive variety Fortuna all shoots of one plant headed in one period.

2.2. *Effect of long day*

The retarding effect of long photoperiods (13-24 h) on floral induction has been described by many workers (see *e.g.* SO *et al.*, 1927; FUKE, 1931, 1942; EGUCHI, 1937; MATSUO, 1942, 1952; OTANI *et al.*, 1949; MISRA, 1951, 1953, 1954; CHANDRARATNA, 1948, 1952, 1954; WORMER, 1953; YOSHIDA, 1954; MORINAGA *et al.*, 1955; YAMAGATA, 1957; VELASCO and DE LA FUENTE, 1958; BUI and NGIEM, 1959). The retardation was due to the fact that the photoperiods used were all super-optimal, as was well understood by several of the above mentioned authors. Reference should be made, however, to some reports which either show different results or give different interpretations of the long day effect. KONDO *et al.* (1932) found that a 24 h photoperiod applied for 30 or 45 days, slightly hastened the early maturing variety Kinai-wase to come into ear. Since this variety is almost indifferent to the photoperiod and differences of only a few days were found, this single result seems to be inconclusive. A favourable effect of long days on panicle emergence was also found by MORINAGA and KURIYAMA (1954) in their panicle emergence curves of the early maturing variety Norin-11. These curves show a small optimum at 21 h at one sowing date, but this optimum was not present at another sowing date. Therefore, it seems probable that the slight differences in heading time of varieties with a very low sensitivity to the photoperiod were rather the result of non-photoperiodic effects on developmental processes, such as temperature and the rate of photosynthesis.

2.3. *Indifferent reaction*

An indifferent (day-neutral) reaction to the photoperiod has been reported by some authors: MIYABAYASHI (1944) and MORINAGA and KURIYAMA (1954) for early Japanese varieties, KUILMAN (1937) for Menurun and WORMER (1953) for Karang Serang, two late maturing *bulu* varieties, and WORMER (1953) for Fortuna, a medium late maturing variety from the U.S.A. From the results of our experiments with the latter two varieties and with early maturing Japanese varieties (see § 8) it appeared, however, that a slight response to the photoperiod was always present. Some response to the photoperiod has previously been reported by CHANDRARATNA (1954) for varieties considered to be indifferent.

3. THE JUVENILE PHASE

In the preceding section the data in the literature have been discussed which give some general information on the photoperiodic response of rice plants. In this and the subsequent sections this information will be detailed, and each developmental stage of the plant from germination until grain maturation will be considered separately.

3.1. *Definition of the juvenile phase*

Following the outline given in the preceding chapter, the life cycle of the rice plant is divided, according to its response to the photoperiod, into a juvenile and an adult phase. The juvenile phase is considered to start at germination and to include the early growth stages in which the leaves formed are insensitive or have a sensitivity less than the maximum, whereas the adult phase is considered to start when the first leaf with a maximum sensitivity to the photoperiod attains its full sensitivity and to continue throughout the rest of the life of the plant. These definitions are in our opinion more accurate than those given previously for the juvenile phase in rice (BEST, 1959).

3.2. *The insensitive period*

During a certain period after germination short or long-day treatments have no effect on the time of floral initiation in rice. According to variety this period varies usually between about 2 and 5 weeks. Thus there seems to be a completely insensitive period for at least part of the juvenile phase.

In the literature FUKE (1931) was the first to report on the insensitive period in rice. He concluded from his experimental results that early maturing varieties had a short, and late maturing varieties a long insensitive period. KONDO and co-workers (1932) also recognized an insensitive period which would last for about 42 days after sowing. In a later experiment they (1933) established that continuous illumination during the first 70 days after sowing did not affect the time of heading in the varieties Shinriki and Kibiho, but when applied at later stages continuous illumination inhibited heading. CHO (1934) showed that night illumination during the nursery stage did not affect the time of panicle emergence in the varieties Rikuu 132 and Aikoku 20. OTANI and SHIRAKI (1942–1948) reported that long (24 h) and short (8 h) days during the first 35 days after sowing exercised no effect whatever in 7 out of 10 varieties, and produced only slight differences in time of heading in the other 3 varieties. In a later experiment they determined the insensitive period in one of the 3 varieties (Rikuu 20) to be about 30 days. In the work of CHANDRARATNA (1948) a 14-day treatment with short (6 h and 9 h) photoperiods had no effect on the time of heading when it was started at the age of 7 days, but exercised a marked effect when it was started at the age of 21 days. With the late maturing Indian varieties T 23 and T 36 MISRA (1950) established that no difference in time of heading occurred when a short-day treatment (10 h) commenced 30 or 40 days after sowing in T 23, but in T 36 earlier heading was obtained with the earlier treatment, which points to a shorter insensitive period in T 36 than in T 23.

WORMER (1953) used photoperiods of 12 and 18 h. Treatments started 10 days after sowing and lasted for 20 or 40 days, or during the whole life of the plant. In the medium-late maturing varieties Robarello and Nero di Vialone no response to the first treatment was found, whereas in the late maturing varieties Tjina, Baok and Nira even the second treatment did not affect the time of flowering. DORE (1955a) reported that the insensitive period lasted 4 weeks in the variety Siam 29. VELASCO and MANUEL (1955), who worked with the variety Elon-elon, found that when seedlings were transferred from long to short days at an age of 0, 15, 30, 45 or 60 days, the same heading date was obtained only in the first two treatments, from which they concluded that the insensitive period lasted 15 days in this variety. It may well be, however, that the insensitive period lasted 20 days or even longer. BUI and NGIEM (1959) stated that in the late maturing variety Tam Den the "photophase" begins on the 20th or 23rd day after sowing, whereas the medium-late maturing variety Chiem Chanh, sown in winter, started its "photophase" late, on the 90th to 100th day after sowing, as a result of low winter temperatures which inhibited its "progress to the photophase", even under short day lengths.

To indicate the insensitive period various terms have been used, such as "intrinsic vegetative period" (SUENAGA, 1936), "a certain balance" or "a certain leaf number" (YAMAMOTO AND MIYABAYASHI, 1944) and "basic vegetative growing habit" (ASAKUMA, 1958), but accurate analyses of the insensitive period were not made in these experiments.

Apart from these investigations, in which the duration of the insensitive period was tested, the existence of such a period seems to have been assumed by many workers, since most day-length treatments were started from 19 days (MIYABAYASHI, 1944) to 61 days (HARA, 1930) after sowing (see also SO *et al.*, 1927; NOGUCHI, 1930; BEACHELL, 1943; YAMAMOTO, 1949; NISHIMURA *et al.*, 1950; GHOSE and SHASTRY, 1954). Reference, however, should be made to some data in the literature which seem to contradict the existence of an insensitive period at the early stages of growth. SIRCAR (1944, 1946) reported that a short-day (8 h) treatment for 2 weeks after sowing caused earlier flowering in Bhasamanik, a winter paddy, but this result was not confirmed by SENGUPTA and SEN (1945), who treated the same variety with 8 h days during the first 20 days after sowing. In a second experiment with the 4 varieties, Bhasamanik, Indrasail, Kumargar and Tilakchary, the latter authors (see also SEN, 1948) induced heading 1 to 7 days earlier by exposure to long photoperiods (16 h) for 30 days after sowing. In experiments with early and medium-early varieties, MISRA (1951, 1953, 1954) found that ear emergence was delayed by short-day treatments which started 7 to 50 days after sowing. The effect increased the earlier the treatment was imposed and the longer it was maintained. Similar results have been reported by SENGUPTA and SEN (1945) and also by SIRCAR and GHOSH (1947, 1954). The conflicting results in these experiments are probably mainly due to factors not specifically related to photoperiodism. Short days, during the early stages of growth, alone or in combination with factors such as transplanting, high night temperatures, excess of nitrogen, low light intensities (cloudy weather), etc., may cause less vigorous growth and, as a consequence, later flowering or, conversely, long days may cause more vigorous growth and earlier flowering (see Chapter XXVI, § 2.4) while also a transfer from a short to a longer photoperiod shortly before initiation may have contributed to some of the results obtained (see § 3).

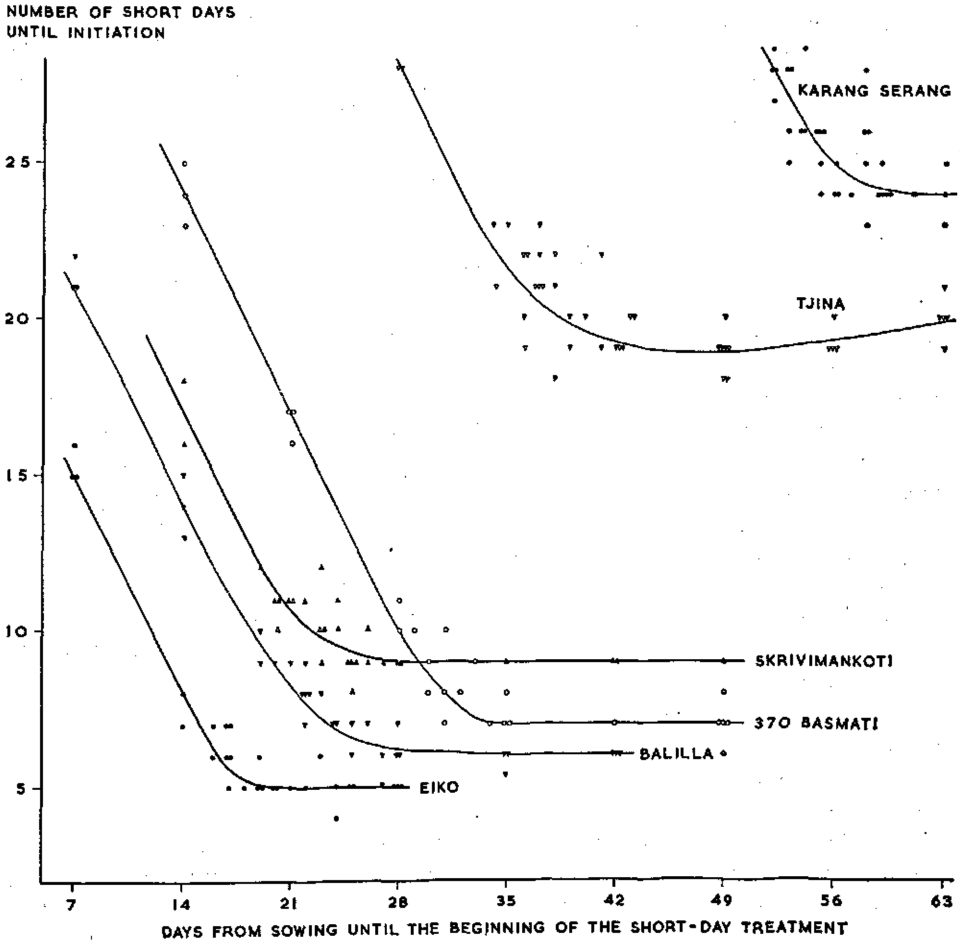
3.3. *The transitional period*

From the data in the literature reviewed above it is evident that the presence of an insensitive period after germination is quite common among rice varieties, while varietal differences in the duration of the insensitive period are often very marked. In addition, the insensitive period seems to be remarkably long in rice as compared with other annual plant species (*cf.* Chapter XXIII, § 3.5), and there is no clear evidence of a gradual transition of the insensitive to the fully sensitive period. As far as the author is aware a gradual transition has only been indicated in two cases. In the work of TAGUCHI *et al.* (1953) it has been suggested that young rice plants (variety Aichi-asahi) become gradually more sensitive to the photoperiod with an increase in age. The data presented did not indicate, however, whether some treatments included more of the insensitive period than did others, or that the differences found were due to real differences in sensitivity at different stages. VELASCO and MANUEL (1955), working with the variety Elon-elon, exposed different groups of plants grown in natural days to short days (10 h) at an age of either 0, 15, 30, 45 or 60 days. The first two treatments started during the insensitive period, whereas in the third, fourth and fifth treatments initiation occurred after 23, 13 an 6 short days respectively, which would indicate a transitional period as long as 20–40 days. In later experiments the same authors (1956) working with the same variety demonstrated repeatedly, however, that when 45-days-old plants were exposed to 10 h days, initiation occurred after 5 days (and under certain temperature conditions even after 4 days), which contradicts the earlier results and makes it probable that the transitional period is even shorter than 14 days in this variety.

To investigate the transition from the insensitive to the sensitive period a preliminary experiment (*E. 311*) was made with a number of *indica*, *japonica* and *semi-japonica* (*bulu*) varieties (Heenati 309, Kohumáwi B–11, Latisail, MYAC 104, Siam 29, Skrivimankoti, Tjina, Americano 1600, Balilla, Eiko, Kibiho, Rikuu 132, Rikuto

Norin 9, Karang Serang, Solo). The plants were grown under continuous illumination and at weekly intervals different groups of plants were transferred to the photoperiod which induced initiation most rapidly (*i.e.* 9 h in Tjina, 12½ h in Heenati 309, and 11 h in all other varieties). Data on the time of inflorescence initiation were recorded. In all varieties except Balilla and Tjina the completely insensitive period seemed to have changed to the fully sensitive period within a week. To determine the transition more accurately a second experiment (*E. 312*) was made in which plants were transferred to short days at daily intervals during a 10-day period from shortly before until shortly after the week in which the transition from the insensitive to the sensitive period occurred. Data on initiation obtained in this and in the previous experiment have been plotted in Graph 63.

It appears that although the transition is not abrupt, it actually occurs during a



Graph 63. Induction period curves demonstrating the transition of the photoperiodically insensitive to the sensitive period. Plants grown initially in continuous light were transferred at the age given on the abscissa to the photoperiod which induced initiation most rapidly (9 h in Tjina and 11 h in the other varieties), *(E. 311, E. 312)*.

few days in most varieties, which is, as far as the information at present available indicates, quite uncommon as compared with the response of other plant species, and indeed, even of other Gramineae. Throughout the adult phase the interval from the beginning of the short-day treatment until inflorescence initiation is fairly constant, with the exception of the variety Tjina, in which it increases again at later stages. In the section on photoperiodic induction this will be discussed in more detail.

3.4. *The sensitivity of individual leaves*

The long insensitive juvenile period may be explained by assuming some or all of the following:

(1) The first leaves formed are completely insensitive to the photoperiod.

(2) The sensitivity of the first leaves formed is so low that they do not reach an adequate level of induction to evoke floral initiation before the much more sensitive leaves formed at higher nodes have reached this stage; in other words, the induction of the initial leaves is so slow that it is completely masked by the rapid induction of the later formed leaves.

(3) The first leaves formed do not attain the induced state before the (early) senescence of these leaves.

(4) The total leaf area which must be present before the plant can react by floral initiation to the inductive day length is so large that it is only reached 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.

It was shown in Chapter XXIII, § 4, that the last possibility is unlikely, although it cannot be ruled out. In any case there does not seem to be a suitable technique to investigate this point in rice, since no grafting experiments can be made. In respect of the other four points it is only possible by experiments to clarify some aspects, but not sufficiently to discard any of these possibilities, as will be shown in the following survey of the work done on this subject. It remains possible, therefore, that a combination of all four points occurs in rice, and it may even be that this is the most likely explanation.

To study the various aspects involved in early insensitivity or low sensitivity it is necessary to investigate the individual leaves. The possibilities for this are limited in rice, however, since no grafting experiments can be made.

Morphologically the scutellum may be considered to be the first and the coleoptile the second leaf (*cf.* Chapter II, § 3), but it is unlikely that these organs either produce or store the floral stimulus since both function for a short time at only the very beginning of the life cycle of the plant. Besides, the plant responds to the photoperiod only after it has reached a fairly advanced stage of vegetative development. Furthermore, the marked response to the photoperiod of many varieties evidently opposes the possibility that the scutellum and/or the coleoptile store the floral stimulus.

In most varieties the first green leaf (which, for the sake of convenience, will further be referred to as the first leaf) has no leaf blade. The second leaf has a small blade, whereas the fourth and higher located leaves usually show a normal ratio between a long leaf blade and a short leaf sheath. The third leaf forms a transitional stage between the second and fourth.

Experiment 313. – To investigate the sensitivity of the first leaf it would be necessary to grow a plant with only this leaf functioning and with all other leaves removed or darkened as soon as they become visible. Working with the *indica* varieties Skrivimankoti and MYAC 104, and in later series also with the *japonica* varieties Nero di Vialone and Balilla, this appeared to be impossible, however, as a result of the very small area of the first leaf, which was entirely insufficient to supply the plant with the energy substrate required for its growth. Even a combination of the first, second and third leaves was insufficient to keep the plants alive for long periods. When more leaves were included the first leaf soon died and in most plants the second and sometimes the third leaf showed signs of yellowing before floral initiation occurred. Removal or darkening of leaves reduced growth so much, and consequently delayed floral initiation so markedly, that in this experiment the leaf number preceding the inflorescence was considered to be a more accurate criterion than the time from sowing to initiation by which to judge the response to the photoperiod.

In an 11 h photoperiod the highly sensitive varieties Skrivimankoti and MYAC 104 normally initiated their inflorescences on the main stems after the 12th and sometimes after the 11th leaf primordium had been differentiated, the last formed leaf primordium normally developing into the bract (see Chapter II, § 2, 6). When the first four, five or six leaves remained on the plant, initiation occurred after the primordium of the 16th or 17th leaf had been differentiated. In treatments with four leaves the results were, however, rather doubtful, since most plants died after a relatively short time. Of the plants which remained alive for longer periods, only two of Skrivimankoti and one of MYAC 104 initiated an inflorescence after the 17th leaf primordium had been formed, whereas all other plants remained vegetative.

When seven leaves remained on the plant, inflorescence initiation occurred after 13.5 leaves had been formed in Skrivimankoti and 13.7 in MYAC 104, and when eight leaves were left on the plant the results obtained, both in time and leaf number, were about the same as in the control. The 8th leaf was apparently the first fully sensitive leaf.

Most treatments used in this experiment were repeated in a second series with the addition of the much less sensitive varieties Balilla and Nero di Vialone. The results obtained showed the same tendencies as in the previous series, although differences between treatments were much less marked with the latter two varieties.

The results of this experiment indicate that under normal conditions the first three leaves formed probably always become senescent before the plant reacts to the photoperiod. To explain the results obtained with the 4th, 5th and 6th leaves three possibilities may be suggested, *viz.*

(1) The sensitivity of the leaves is very low and it takes a long time before the plant can react to the inductive day length by initiating flowers;

(2) the removal of leaves is, due to the morphology of the plant, confined to the leaf blade and in some cases the remaining parts of the sheaths may have produced the floral stimulus (either under the inductive day length or in darkness);

(3) the stimulus is produced in the stem.

At present it is not possible to discard any of these possibilities completely, although the second one is likely to be the most important in view of the almost similar results of the 5 and 6 leaf treatments. The 7th leaf evidently shows some sensitivity, although it is remarkable that after the 8th leaf had expanded, the plant fairly abruptly attained full sensitivity and became approximately comparable with the control both in leaf number and in the time from sowing until initiation. The effect of the removal of the 7th leaf or part of the 8th leaf shows that the total leaf area has something to do with this phenomenon. In later experiments (see Chapter XXV, § 2) it could be confirmed that for a rapid induction a large leaf area is required, suggesting that the rice leaves produce a relatively small amount of floral stimulus per unit area of leaf.

Summarizing the experimental results on leaf sensitivity in the juvenile phase it is probably justifiable to assume that the scutellum, coleoptile and the first three green leaves play no part owing to their relatively short life; that, with the four varieties used, the 4th, 5th and 6th leaves are either insensitive or of such low sensitivity that their effect is masked by that of later formed leaves; that the 7th leaf is partially sensitive and the 8th leaf probably fully sensitive, but that a fairly large total leaf area is required to evoke rapid floral induction. This may also explain the fairly abrupt change from the apparently insensitive to the sensitive period (see Graph 63). In different varieties a smaller or larger number of insensitive or practically insensitive leaves may occur, while, in varieties such as Tjina, with a relatively long transitional period, there may be more than one leaf with a sensitivity less than maximum (such as leaf no. 7 in *E. 313*). In fact, the conclusions of this experiment are still in terms of probabilities, mainly as a result of the impossibility of grafting leaves in rice, and it looks as if for the time being at least we must be content with a rough estimate of the sensitivity of different leaves during the juvenile phase in rice.

3.5. *Leaf number*

The results presented in this section give rise to some remarks about the minimum number of leaves formed before the inflorescence is initiated. This leaf number has been used as a more reliable criterion of photoperiodic response than the time from sowing to initiation, since, when leaves were removed, the treatments often retarded growth so much that plants which produced the same number of leaves differed a month or more in the time of initiation. This leaf number is by no means an absolutely constant value, however. Environmental conditions affecting growth rate may also affect leaf number. An influence of temperature, for instance, has been reported by OTANI and SHIRAKI (1942–1948). Using an 8 h photoperiod with the variety Rikuu 20 under outdoor temperature conditions they established that on the average 6.79 leaves were outwardly visible before the inflorescence was initiated, whereas this number was 6.38 under glasshouse temperatures.

Leaf number may also be influenced by other factors not related to photoperiodism, such as the mineral nutrition of the plant (see Chapter XXVI, § 4) and by the removal of tillers. YAMAGATA (1957) reported, for instance, that when all tillers were removed as they appeared in the period between transplanting and maturity, the leaf number preceding the inflorescence in the main stem increased. In the experiments *E 312* and *E 313*, discussed in the first part of this section, it was established that tiller removal had little effect on the leaf number of the main stem of the highly sensitive varieties Skrivimankoti and MYAC 104 when grown under short days, but the effect was more marked in the much less sensitive varieties Balilla and Nero di Vialone (on the average an increase in leaf number of 1.1 and 1.6 leaves respectively). Generally it was found that the more vigorous the growth of the stem, the more leaves were initiated prior to inflorescence initiation.

4. PHOTOPERIODIC INDUCTION

4.1. *General considerations*

Throughout the adult phase the interval from the beginning of a short-day treatment until inflorescence initiation is fairly constant in most varieties (*cf.* Graph 63). The duration of this induction period is usually shortest in an 11 h photoperiod and may vary, according to variety, from 5 days in, for instance, the varieties Siam 29, Radin Siak 34 and some early Japanese varieties such as Eiko, to 24 days in the variety Karang Serang; 6 to 12 days being the commonest. Under longer photoperiods the induction takes longer and, provided the variety used is not extremely sensitive to the photoperiod, inflorescence initiation can take place even under continuous illumination within a year from sowing. The question may arise whether this is achieved by building up the induced state in the leaves in the course of very many cycles or whether, when the vegetative period lasts very long, the rate of induction in less favourable photoperiods becomes more rapid. In view of the relatively short life of individual leaves, as compared with the very long induction periods under long days, it is likely that the latter possibility contributes, at least to some extent, to the effect. Experimental results on this subject have hitherto been inconclusive, however (see Chapter XXV, § 2.4).

4.2. *Effect of long days on subsequent induction in short days*

It was shown in Graph 63 that in the adult phase one variety, Tjina, showed a small increase in the induction period when the short-day treatment was applied later in the life of the plant. This phenomenon may either be brought about by a slower rate of induction in older plants or by an effect of the long-day condition preceding the short-day treatment. In a preliminary experiment (*E. 314*) to investigate this point, plants of the variety Tjina were grown in photoperiods of 13, 17 and 24 h. The photoperiods consisted of a 10 h daylight period and supplementary light of low intensity (3000 erg/sec/cm^2) and, with 24 h, also of high intensity (30,000 erg/sec/cm^2). At an age of 60 days (all treatments) and 85 days (17 and 24 h treatments) the plants were transferred to a 9 h day. The time of inflorescence initiation in the main stem was recorded.

The data obtained showed a general tendency for the induction in 9 h days to be prolonged when the preceding days were longer, when the intensity of the additional illumination in the long days was higher and when the duration of the preceding long-day treatment was longer. This indicates that the long-day conditions had an effect on the subsequent induction in short days. This effect was small, being at most 9 days, *i.e.* when high-intensity continuous illumination preceded the short-day treatment, and it was absent in those treatments in which the plants were exposed to a 17 h photoperiod for less than 85 days.

This type of response seems to be fairly specific for Tjina. In other experiments it was found with different varieties that high-intensity continuous illumination could lengthen the induction period in subsequent short days by 1–4 days, but this is likely to be mainly due to non-photoperiodic effects. It is thought that the unusual long induction period of Tjina under short-day conditions was at least partly responsible for this behaviour of the variety, but no experiments with other varieties with a very long induction period have been made to verify this view. The varieties with the longest induction period, *bulu* varieties from Java, are, due to their low response to the photoperiod, unfortunately unsuitable for this type of experiment.

4.3. *The building up of the induced state in short days*

There are very few data in the literature which give any information about the building up of the induced state in rice plants. OTANI and SHIRAKI (1942–'48) reported that in the variety Rikuu 20 no heading occurred when a transition from an 8 h photoperiod to natural day length was made approximately at the time of initiation. WORMER (1953), working with the variety Nero di Vialone, found that a transition from a 12 h to an 18 h photoperiod 8 days before initiation inhibited initiation completely. When the transition was made about 1–5 days before initiation, initiation was delayed for 30 days, and the panicle did not become any longer than 2 mm. Some plants partly returned to vegetative growth and produced malformed leaves. Dichotomy of the main stem was found twice. After initiation had occurred a transition to long days hampered panicle development, but did not inhibit it. Plants transferred from an 18 h to a 12 h photoperiod shortly before initiation, showed a more rapid development and an increased elongation of the panicle as compared with the plants that remained in the 18 h photoperiod.

As pointed out earlier (Chapter XXIII, § 3.4), induction involves two processes, *viz.* the building up of a state in which the floral stimulus is produced, and the formative effect of the stimulus on the apex. In addition, it is not known at which stage the induction has progressed sufficiently to bring about initiation in non-inductive day lengths, whether or not the completely induced state is obtained at the time of initiation, and if a continuous supply of floral stimulus is necessary to complete the early differentiation of the inflorescence. A distinction between the former two processes has not been attempted in our work, but the latter factors have been examined more closely in two experiments (*E. 315* and *E. 316*).

The results of these experiments showed that if an inductive day length was replaced by a non-inductive day length shortly before inflorescence initiation was due to occur, the induced state was already sufficiently advanced to evoke initiation. With a transition from an 11 h to an 18½ h photoperiod this stage was reached, dependent on variety, 2 to 4 days before initiation, although initiation was much delayed and further differentiation of the inflorescence was completely inhibited after the transfer. With different photoperiod combinations it was found that the effect of the transition decreased with a decrease in the difference between the two photoperiods used.

Transitions two days before initiation from an 11 h to longer photoperiods, showed that the shortest photoperiod which inhibited further differentiation of the inflorescence after the transfer was 13 h in a very highly, 14 h in a highly and 15½ h in a moderately sensitive variety. When the transition was made during or after inflorescence initiation, inflorescence development was often adversely affected and much delayed but not completely inhibited. With an increase in the duration of the short-day treatments these effects on inflorescence development decreased, and, with a transition from an 11 h to an 18½ h photoperiod 6 to 8 days after initiation, a development of the inflorescence comparable with that of the control (with regard to the number of rachillae and spikelets) was obtained. From this it was concluded that the completely induced state of the plant or of individual leaves was attained about 6 to 8 days after initiation, but this conclusion still lacks convincing experimental support.

A more detailed account of the experiments *315* and *316* is given below.

Experiment 315. – In this experiment the degree of induction shortly before, during and after inflorescence initiation was investigated. Six varieties were used: Balilla and Nero di Vialone having moderate, 370 Basmati high, and HMC 12, MYAC 104 and Skrivimankoti very high sensitivities to the photoperiod. Seedlings grown first in natural days in summer were exposed to 11 h days at the age of 32 days (42 days in 370 Basmati and HMC 12). The plants of each variety weve divided into 9 groups. One group remained in 11 h days (control), whereas the other groups were transferred to an 18½ h photoperiod at 8, 6, 4, 2 or 0 days before or after inflorescence initiation.

The time of initiation was normally very uniform among individual plants of one variety and deviations from the average were usually not more than one day, except in 370 Basmati and Nero di Vialone, where a deviation of two days was found in 10–14% of the plants.

The following data were obtained in this experiment:

(1) When the short-day treatment was terminated 8 days before initiation, all varieties remained completely vegetative.

(2) A transfer to long days 6 days before initiation caused variable results in individual plants of Nero di Vialone: some remained vegetative, others produced malformed leaves and stopped further terminal growth or showed the first stages of inflorescence initiation 31 to 39 days after the transition. Further development of the inflorescence was completely inhibited, however, and renewed tillering started about a week later. All other varieties remained vegetative.

(3) A transfer to long days 4 days before initiation delayed initiation 18 to 27 days in Nero di Vialone. The highly and very highly sensitive varieties showed a disturbed vegetative growth and produced malformed leaves.

Balilla remained vegetative and continued normal growth.

(4) The transition 2 days prior to initiation delayed initiation 5–12 days in 370 Basmati and Nero di Vialone.

In all other varieties initiation occurred within three weeks after the transition, although the inflorescences did not become any longer than 2–5 mm and stopped growth thereafter.

(5) During inflorescence initiation a transfer to long days retarded further development of the panicle, reduced its size and caused incomplete extrusion of the panicle out of the sheath of the flag leaf, but a complete inhibition of panicle growth at young stages was only found in some plants of MYAC 104 and HMC 12.

(6) With a further increase in the duration of the short-day treatment there was a decrease in the effect on panicle development caused by of the transition to long days. A development comparable with that of the control (with regard to the number of rachillae and spikelets) was found when the short-day treatment continued until 6 days after initiation (varieties Skrivimankoti, MYAC 104, 370 Basmati and Balilla) or until 8 days after initiation (varieties HMC 12, Nero di Vialone).

An interesting phenomenon, also observed in *E. 315*, was that a transition from short to long days at an early stage of induction, *i.e.* 8 days (Nero di Vialone) or 4 days (Balilla) prior to initiation, caused an unusual prolongation of the vegetative growth under the long-day conditions. Plants of these varieties grown continuously in an 18½ h photoperiod initiated the inflorescence after 14–15 leaves had been formed, but in the transferred plants initiation occurred after 18 to 20 leaves had been formed. It would be of interest to know in which way a termination or destruction of the induced state at this stage may bring about an extension of the vegetative growth of the stem, and if this phenomenon occurs also in other varieties, but this awaits further experimental work.

Experiment 316. – The transition from an 11 h to an 18½ h photoperiod used in the previous experiment was modified by transferring groups of plants, two days before initiation, from: (1) an 11 h photoperiod to photoperiods of 12, 13, 14, 15½, 17, 18½, 20, 22 or 24 h, and (2) from an 18½ h photoperiod to photoperiods of 8, 11 and 24 h.

In the first series the varieties Nero di Vialone, 370 Basmati and Skrivimankoti were used. The varieties responded to the treatments according to their sensitivities. With the transition from the 11 h to longer photoperiods, the shortest day which caused a complete inhibition of further development of the inflorescence primordium was 13 h in Skrivimankoti, 14 h in 370 Basmati and 15½ h in Nero di Vialone. A transfer to longer photoperiods accentuated the long-day effect on inflorescence differentiation, and in continuous light of high intensities only a partial differentiation of the apex was found which developed into all sorts of malformed and fused leaves, whereas in most plants the apex was unable to resume normal vegetative growth. Instead branch shoots and tillers were produced in abundance.

In the second series the varieties Nero di Vialone, Americano 1600 and 370 Basmati were used. The transition from the 18½ h to short days two days before initiation caused slightly earlier initiation and a more rapid development of the inflorescence, whereas the transition to continuous illuminations had little or no effect in Nero di Vialone and Americano 1600, but retarded inflorescence initiation and development markedly in 370 Basmati.

From the data presented above it appears that if the inductive day length is replaced by a non-inductive day length shortly before inflorescence initiation, the induced state may already be sufficiently advanced to evoke the differentiation of the apex. Just how many days before initiation this stage of induction is reached appeared to depend on varietal characteristics such as the reaction to the photoperiod and the duration of the induction period, and also on the non-inductive day length used. The varieties of very high sensitivity apparently did not reach this stage any earlier than 2 days before initiation, whereas Nero di Vialone, of moderate sensitivity, reached it 6 days before initiation, and Balilla, also moderately sensitive, 2 days before initiation (the induction period in 11 h days being 6 days in Balilla and 10 days in Nero di Vialone). The figure of 6 days before initiation, given for Nero di Vialone, applies only to 10–16% of the plants, which corresponds approximately with the percentage of plants which was found (p. 13) to initiate the inflorescence 2 days earlier than the average in this variety. It seems justified, therefore, to assume that the induction was not sufficiently advanced to evoke floral initiation any earlier than 4 days before initiation was due to occur in the inductive day length.

Considering the inductive short days, it appears then that in Nero di Vialone the induced state which could just bring about initiation was reached after about 6 cycles out of the 10 necessary for normal initiation, in Balilla the cycles were 4 out of 6, in 370 Basmati 5 out of 7, and in the very highly sensitive varieties 7–9 out of 9–11. In percentages this is 60–66% in the moderately sensitive varieties, about 71% in the highly sensitive variety, and about 78–82% in the very highly sensitive varieties. These results were obtained with the transition from an 11 h to an 18½ h photoperiod. With different photoperiod combinations it was found that the effect of the transition decreased with a decrease in the difference between the two photoperiods used.

4.4. *Induction in short days as affected by intervening long days*

In the preceding pages it was shown that when a short-day treatment was changed to a long-day treatment shortly before initiation was due to occur, the varieties with a very high sensitivity to the photoperiod attained a state of induction which could bring about initiation in the long-day conditions much later than the moderately sensitive varieties. This may also be explained differently, however, by saying that in the very highly sensitive varieties the long days produce a greater destructive effect on the induced state built up in short days than they do in varieties of only moderate sensitivity. The possible destructive effect of a long day on the early stages of induction in short days have been studied in the following experiment.

Experiment 317. – Plants of the varieties Skrivimankoti, 370 Basmati and Nero di Vialone, grown in natural days in summer, were transferred to an 11 h photoperiod 32 days after sowing. The plants of each variety were then divided into several groups, each of which was exposed to a different combination of day length treatments (Table 25), whereas the control remained continuously in the 11 h photoperiod.

TABLE 25

EFFECT OF A LONG-DAY CYCLE ON THE INDUCTION BUILT UP IN ONE OR MORE SHORT-DAY CYCLES IN VARIETIES OF A VERY HIGH (SKRIVIMANKOTI), HIGH (370 BASMATI) AND MODERATE (NERO DI VIALONE) SENSITIVITY TO THE PHOTOPERIOD

Treatments consisting of one or more short (11 h) days followed by one long day (20 h); each treatment was repeated 5 times and was then followed by continuous short days	*Number of short days to initiation (the figures in brackets are the number of short days from the last long day until initiation)*		
	Nero di Vialone	*370 Basmati*	*Skrivimankoti*
control – no intervening long days	(9.9)	(7.1)	(9.2)
1 short–1 long (5 ×).... short . .	15.1 (10.1)	11.8 (6.8)	14.9 (9.9)
2 short–1 long (5 ×).... short . .	16.4 (6.4)	14.7 (4.7)	20.4 (10.4)
3 short–1 long (5 ×).... short . .	17.0 (2.0)	14.0 (–.–)	23.8 (8.8)
4 short–1 long (5 ×).... short . .	15.8 (–.–)	10.5 (–.–)	25.3 (5.3)

From the results presented in Table 25 it can be calculated that the intervening long day destroys, as an average of the 5 cycles used, the equivalent of about 1.2 inductive short days in Nero di Vialone, about 1.5 in 370 Basmati and 3.1 in Skrivimankoti. The differences between these varieties show a striking correlation with their photoperiodic sensitivities, but much work is still needed with many varieties to show whether this is the rule or an exception in rice. In view of the induction built up in the short-day periods, more detailed work is also necessary to show whether the effect of the long day gradually diminishes from the first to the fifth long day given. In addition, experiments still have to be made on the exact relationship between the destructive effect of the long-day interval on the induction in short days when different short and long days are used, and when the duration of the long-day interval and short-day sequences are altered.

5. REPRODUCTIVE DEVELOPMENT

The reproductive development of the rice plant may be divided into four stages, *viz.* inflorescence initiation, inflorescence development, anthesis, and grain development. Data on each of these stages will be discussed separately.

5.1. *Inflorescence initiation*

Microscopic analysis of the growing point may reveal a change from the vegetative to the reproductive stage within 24 hours, a fact first reported by NOGUCHI (1929). A detailed morphological study of the initiation and development of the inflorescence in rice was published by KERLING (1948, 1950), who confirmed NOGUCHI's finding. (For particulars see Chapter II, § 6.) Inflorescence initiation has been used as a criterion for the response of rice plants to the photoperiod by several workers (see *e.g.* EGUCHI, 1937; OTANI and SHIRAKI, 1942–'48; YAMAMOTO and MIYABAYASHI, 1944; WORMER, 1953; SIRCAR and SEN, 1953; CHANDRARATNA, 1954; MORINAGA and

KURIYAMA, 1954; VELASCO and MANUEL, 1955). The length of the treatment required to induce inflorescence initiation depends on variety, photoperiod and other environmental factors. Details have been presented in the preceding sections and more will be given in § 8.

5.2. *Inflorescence development*

Inflorescence development can be defined as the period between inflorescence initiation and the stage when the panicle and the terminal internode of the culm are fully grown.

Particulars of photoperiodic effects on inflorescence development were first published by NOGUCHI (1929, 1929–'30) and HARA (1930). NOGUCHI established that an 8 h photoperiod was scarcely effective after the inflorescence primordia had developed to a certain extent in the early, medium and late maturing varieties Kameno–o, Shinriki and Aikoku. Similar observations have been reported by many other workers (see *e.g.* HARA, 1930; TABATA *et al.*, 1934; ENOMOTO, 1935; EGUCHI, 1937; YAMAMOTO and MIYABAYASHI, 1944; WORMER, 1953). In all these cases short days had either no effect or slightly hastened inflorescence development as compared with long days. LIEN and KUANG (1944) concluded from their experiments, however, that long days slightly hastened inflorescence development and that short days were ineffective in this respect. The former may have been due to a non-photoperiodic effect, probably an increased growth rate under long-day conditions. OTANI and SHIRAKI (1942–1948) claimed that an 8 h photoperiod, when it was continued for a few weeks after initiation, inhibited heading in the variety Rikuu–20. In glasshouses, with relatively high temperatures, an even shorter treatment was sufficient to inhibit heading. These results may have been brought about by factors not related to photoperiodism and are contradicted by the observations of other authors. In the work of MATSUO (1942), for instance, no failure of heading occurred when the variety Rikuu–20 was exposed to an 8 h photoperiod, whereas no similar result was reported by other workers who used 8 h photoperiods, such as ENOMOTO (1935) or WADA (1942), who tested 93 and 134 Japanese rice varieties respectively.

A very marked effect on panicle development of extremely small differences in day length has been reported by KERLING (1948, 1950) in the variety Untung. In her experiments under natural day length conditions at Buitenzorg (Java), two sowing dates were used, *viz.* January 16 and July 21. Flowering occurred 100 days after sowing in both plots, but panicle initiation was found in the first plot 70 days, and in the second plot 50 days after sowing, which shows that even the small variations of the local day length at a latitude of 6°34′ may cause a marked difference in the time of initiation. Day length conditions after initiation influenced panicle development so much in the opposite way, however, that the influence of day length on panicle initiation was just compensated, resulting in flowering at exactly the same age in both plots. In this experiment the effect of the photoperiod on the two stages, panicle initiation and development, can be better understood if we take the fluctuating local day length into consideration. The plot sown on January 16 started growth under "long" day conditions, decreasing slowly, but long enough to retard panicle initiation until the 70th day after sowing. After that period the further decrease in day length forced the second stage, panicle development, and reduced its duration to only 30 days. Day length influence on the plot sown on July 21 was just the reverse. The largest differences in day length between sunrise and sunset amounted to about 44 minutes. This case illustrates clearly that the time of heading or flowering is inadequate as the sole criterion by which to estimate the varietal photoperiodic response in rice.

CHANDRARATNA (1954) exposed the very sensitive variety Kohumawi B–11 to a 10 h photoperiod until inflorescence initiation had occurred, and thereafter to photoperiods varying from 6 h to 13 h. Compared with initiation he found a much less pronounced, but still marked, effect of the photoperiod on inflorescence development.

The results of our investigations on the effect of the photoperiod on inflorescence development generally confirm the data known from literature. A report of this work is presented in § 8. Broadly speaking three types of response could be distinguished among varieties, *viz.* a day-neutral, a moderate and a marked short-day reaction. A neutral or moderate short-day reaction being the most common, whereas in some varieties with a relatively high sensitivity to the photoperiod during the inflorescence development stage, continuous illumination with high-intensity light could inhibit panicle emergence almost completely, a finding reported earlier in the work of CHO (1930).

5.3. *Anthesis*

The third stage in reproductive development, anthesis, has not, as far as the writer is aware, been studied specifically in rice. In the present work on this subject two experiments (*E. 318* and *E. 319*) have been made. The results, although still largely of a preliminary nature, indicate that either the last stages of flower bud maturation or anthesis itself are not completely indifferent to the photoperiod although, under normal conditions, this will be completely masked by temperature effects. A more detailed account of these experiments is presented below.

In a preliminary experiment (*E. 318*) to investigate possible effects of day length on anthesis, five varieties with different sensitivities to the photoperiod, China 1039, Nero di Vialone, 370 Basmati, Tjina and Skrivimankoti, were used. The plants were grown in an 11 h photoperiod until one day before anthesis was due to occur in the first spikelets of the panicle of the main stem (*i.e.* when the yellow anthers began to show feebly through the pales of these spikelets). The plants were then transferred to photoperiods of 0, 4, 8, 12, 15½ and 24 h for 7 days, after which the 11 h photoperiod treatment was resumed. In all treatments anthesis began at about 10–11 a.m. (in the continuous dark treatment this was established by bringing 2 plants into the light at one-hour intervals during the daytime. In each panicle the duration of anthesis lasted from 3 to 5 days from the first to the last flower; this was similar to the control, which had remained under the 11 h photoperiod. A closer study revealed that anthesis was mainly governed by temperature under these conditions: anthesis began in the daytime as soon as the temperature in the greenhouse had reached 25° to 28° C. To avoid this effect, controlled temperature conditions during anthesis were used in a second experiment (*E. 319*). Plants of the variety 370 Basmati were grown in a 14 h photoperiod, and tillers were removed as they appeared. Panicles were initiated late in this treatment (108–110 days after sowing) and were large. One day before anthesis was due to occur in the first spikelet, plants were transferred to 12 h, 16 h and 24 h photoperiods under rigidly controlled temperature conditions (28° ± 0.5° C). In the 12 h photoperiod treatment, anthesis started the first day 3 to 4 hours after the light was switched on, still showing the same behaviour as in the greenhouse; in the following days anthesis started earlier, however, and on the last day anthesis was observed, individual flowers opened at irregular times during the photoperiod, a phenomenon which was more marked and occurred earlier when the photoperiod was longer (16 h and 24 h treatments). After the treatments the plants were again transferred to the greenhouse. The percentage of sterile spikelets appeared to be high (32.8%) in the 24 h treatment as compared with the 16 h (12.3%) and the 12 h (15.7%) treatment and the control (14 h) in the greenhouse (8.7 %). In repeating the 24 h and 12 h treatments with a second series of plants (*E 320*), differences in sterility were again found to be marked: 41.3 % in the 24 h and 19.5 % in the 12 h treatment. In the 24 h treatment it was observed in this experiment that the plumose stigmas of several flowers which opened on the 7th and 8th day after the beginning of the treatment had a dry and shrivelled appearance, as if anthesis had occurred at least half a day earlier, which would indicate a protogynous effect. No definite proof was obtained of this, however. As compared with the 11 h photoperiod in the first series, the duration of anthesis in a given panicle from the first to the last flower was longer, *viz.* 5 to 8 days as compared with 3 to 5 days. Different experiments in the greenhouse showed later, however, that this is apparently mainly brought about by the preceding treatment. A long duration of anthesis in a given panicle was common in plants that had grown continuously in photoperiods which prolonged the vegetative period considerably.

5.4. *Grain development*

The fourth and last developmental stage, covering the period between fertilisation and grain maturity, has not been reported in the literature in connection with photoperiodism. From experiments (*E. 321–322*) which were carried out on this part of the developmental cycle, and in which plants were exposed to a range of photoperiods either during their whole life period or from anthesis, it appeared that although various differences were found in grain weight, the development of the endosperm, the shape of grain, etc., between plants which were exposed to different photoperiods, no photoperiodic action could be credited for these differences. In most cases the main influence on grain development appeared to be the rate of photosynthesis, although in some cases also other environmental conditions came into play. Formative influences on the awn attached to the lemma, caused by the photoperiod, will be discussed in Chapter XXVI, § 6.

6. VARIETAL CLASSIFICATION

As early as 1927 and 1929 YOSHII showed varietal differences in response to fixed day lengths. Flowering in the late maturing variety Shinriki was accelerated by an 8 h photoperiod, but not in the early variety Kameno–o (the terms early and late maturing apply to the vegetative period of these varieties under local natural day length conditions). A similar type of response, *i.e.* late maturing varieties being on the whole more sensitive to the photoperiod than early maturing varieties, was reported later by many other workers (see *e.g.* KONDO *et al.*, 1932; TABATA *et al.*, 1932; ENOMOTO, 1935; EGUCHI, 1937; MORINAGA *et al.*, 1938; LIN, 1941; MATSUO, 1942; KAR and ADHIKARI, 1945; YAMAMOTO, 1949; GHOSE and SHASTRY, 1954; CHANDRARATNA, 1954; ISHIKAWA, 1955; BUI and NGIEM, 1959). According to OKADA and KATO (1953), working with the varieties of the Tôhoku region, such a distinction can only be made in respect of the sensitivity to short days, however.

In the U.S.A. sensitivity to the photoperiod has not been related to earliness or lateness (see *e.g.* JENKINS, 1936; ADAIR, 1940; BEACHELL, 1943; JENKINS and JONES, 1944; JONES *et al.*, 1953).

In Java VAN DER GOOT (1923) made a distinction between the late maturing *bulu* varieties, which would all be insensitive, and the *tjereh* varieties, which were subdivided into insensitive early maturing varieties and late maturing varieties which could be either insensitive, moderately sensitive or very sensitive. WAGENAAR (1951) doubted the reliability of VAN DER GOOT's classification, however. He reported that experimental results with 58 *tjereh* varieties from Java showed that of the early maturing ones 50% were sensitive; for medium late and late maturing varieties the percentages were 30 and 70 respectively, giving a slight indication on greater sensitivity in late maturing varieties. If, however, *bulu* varieties had also been included in this experiment, the indication might even have been the reverse.

Chandraratna (1952) mentioned one late variety in Ceylon, Devaredderi, which did not react much to variations in local natural day length, but which appeared to be of a fairly high sensitivity when exposed to a range of fixed photoperiods.

In a preliminary experiment (*E. 325*), in which 417 rice varieties imported from practically all the rice growing countries in the world were used, plants were grown in photoperiods of 11 h, 15 h and 21 h to get a rough idea of varietal differences in response to the photoperiod. It appeared that a correlation between the earliness or lateness of these varieties in their native countries and their photoperiodic sensitivity was found more often in the temperate and subtropical zones than in the tropics, but in none of these zones was the correlation absolute.

In addition to earliness and lateness some Japanese workers have used several classifications to arrange varieties according to their photoperiodic sensitivity. To distinguish between varietal behaviour in short and in long days Hara (1930) used his *coefficient of sensitivity*, defined as

$$\frac{T - Y}{Y} \times 100 \text{ for short days} \qquad \frac{L - Y}{Y} \times 100 \text{ for long days}$$

where Y is the period from sowing to heading in days in local natural day length, T in 8 h days and L in 24 h days.

Suenaga (1936) constructed response curves by plotting the day length on the abscissa against the time from sowing to heading on the ordinate, and used the angle between the super optimal part of this curve and the abscissa as a criterion for varietal sensitivity. He also modified this method and constructed curves by plotting the day length, P, on the abscissa against

$$\frac{V_p - V_o}{V_o}$$

on the ordinate, where V_p is the vegetative growth period in a given photoperiod and V_o the vegetative growth period in the optimum photoperiod. The angle between this curve and the abscissa was also used as a criterion for varietal sensitivity.

Wada (1942) originally classified Japanese varieties into 3 groups: *viz.* (1) those with a high sensitivity to temperature and a low sensitivity to the photoperiod, (2) those with a low sensitivity to temperature and a high sensitivity to the photoperiod, and (3) those with a high sensitivity both to temperature and photoperiod. Varieties from Formosa, South China, Indo-China, the Philippines and Java, which Wada (*l.c.*) also used in his experiments, were regarded as belonging to the second group. In a second and third publication Wada (1952, 1954) extended his classification to 7 classes according to photoperiodic sensitivity and 8 classes according to the length of the "basic vegetative growth" (*i.e.* the period from sowing to heading under short days, in fact, indicating differences in the length of the juvenile phase).

Fuke (1942) classified varieties into 4 groups: *viz.* varieties of (1) a high or (2) a low sensitivity to both long and short days or (3) a high sensitivity to long and a low sensitivity to short days or (4) the reverse, a high sensitivity to short and a low sensitivity to long days.

Matsuo (1952) expressed varietal sensitivity to temperature as the difference in the number of days of local day length between the heading periods under outdoor and glasshouse temperatures, and varietal sensitivity to the photoperiod as the difference in the number of days between the heading periods under (1) a 10 h photoperiod, and (2) natural days, both under outdoor temperature conditions. In Chapter I it was outlined that Matsuo (*l.c.*) used the following taxonomic classification of rice varieties:

japonica	plant *type A*	Japan (temperate islands)
	plant *type B*	Java (tropical islands)
indica	plant *type C*	S. China to India (Asian continent)

The relations between these groups and varietal photoperiodic sensitivity was, according to MATSUO: *type A* > *type C* > *type B*. In trying to find some expression for varietal differences in the duration of the juvenile phase, he exposed plants to a 10 h photoperiod under high (glasshouse) temperatures, named the short growth period under these conditions the "basic vegetative growth" (*cf.* WADA, 1952), and arranged the taxonomic groups according to the length of this period in the order: *type B* > *type C* > *type A*.

However, none of the above classifications provides a suitable criterion by which to make accurate distinctions in varietal sensitivity to the photoperiod. This can only be accomplished by using response curves based on inflorescence initiation in a wide range of photoperiods, as will be discussed in more detail in the subsequent sections. SUENAGA's (1936) first classification came nearest to this.

7. EARLY WORK ON RESPONSE CURVES

Few investigators have used a range of photoperiods to study varietal photoperiodic behaviour, and only in three cases have the dates of heading obtained in their experiments been used to construct response curves by plotting the time from sowing to heading on the ordinate against the photoperiod used on the abscissa. The data obtained in the other experiments permit the construction of such curves, however, and have therefore been included in the review presented in this section.

HARA (1930), who was the first to test varieties in a range of photoperiods, used eight fixed day lengths between 4 and 24 h. In his first experiment earliest heading was obtained in photoperiods of 8 and 12 h, but the treatment had started very late, on the 61st day after sowing. In a second experiment, with earlier day length treatments, photoperiods of 8 and 10 h appeared to be the most effective in all four varieties used. KONDO *et al.* (1932) exposed six varieties to photoperiods of 4, 8, 12 and 14 h and to natural day length during the whole life period of the plants. All plants perished in 4 h days but heading was earliest in 8 and 12 h photoperiods.

SUENAGA (1936) worked with eight varieties and used in addition to natural days two ranges of photoperiods, *viz.* 7, 8, 9, 10 and 24 h and 9, 10, 11, 12, 13, 14 and 24 h. Differences in temperature were obtained by sowing on the 15th of alternate months. Day length treatments started after the third leaf had expanded. SUENAGA used the dates of heading obtained in these experiments to construct response curves and showed that the optimal photoperiod, depending on temperature, was denoted by the minimum of the curve. He either used the angle between the super optimal part of the curve and the abscissa as a criterion for varietal photoperiodic behaviour, or worked out more complicated methods by using ratios between the dates of heading in optimal and superoptimal photoperiods (see § 6). Furthermore, he reported that varieties differed in the range of photoperiods in which heading could be obtained. These ranges would be limited (would show "critical day lengths") on one or both sides.

MATSUO (1942) tested 15 Japanese varieties in six day lengths, 4, 8, 12, 24 h and natural day length with or without supplementary artificial illumination until 9 p.m. In all varieties heading was earliest in the 12 h day. MIYABAYASHI (1944), who worked with six varieties, used 7, 9, 11, 12, 13, 14 and 17 h photoperiods and natural day length. In establishing optimal photoperiods at 11–12 h, he reported that with a progressive extension of super-optimal photoperiods, the number of days from sowing to heading first increased gradually, then rapidly, and again gradually. Had these dates of heading been used to construct response curves, sigmoid curves would have been produced. MIYABAYASHI (*l.c.*) was the first to report this characteristic type of response in a range of super-optimal photoperiods.

Independently of this earlier Japanese work, CHANDRARATNA (1952) investigated the response of some varieties from Ceylon and one from Burma to a range of photoperiods between 6 and 12 h (in one experiment up to 16 h) in stages of 30 minutes. The heading curves obtained in these experiments clearly showed the extremely strong response of some tropical varieties to photoperiods exceeding 12 h. In his second publication on this subject CHANDRARATNA (1954) worked with 8 varieties from Burma, Ceylon, India and Indonesia. The conditions under which the experiments were made caused high mortality in the very short and also in the long photoperiods used, which had not been reported by workers in subtropical and temperate regions. This high mortality rate may have influenced CHANDRARATNA to confine himself to the range between 8 h and 14 h, thus limiting the scope of his work.

In interpreting the data on heading in the 8–14 h range, second order polynomials of the form $y = a + bx + cx^2$ were fitted to the response curve, where y is the germination to heading interval in days, x the photoperiod in hours and a, b and c are constants. The minimum value of the germination–heading interval, $d^2y/dx^2 = 0$ was called the *minimum heading duration*, and the photoperiod corresponding to it the *optimum photoperiod*. CHANDRARATNA further stated that, with the equation $y = a + bx + cx^2$ as a basic, the best estimates of sensitivity, the minimum heading duration and the optimum photoperiod, were provided by the parameters $2c$, $a - b^2/4c$, and $- b/2c$ respectively. It is doubtful, however, if $2c$ does provide an estimate of sensitivity. Sensitivity is the rate of change of y with change of x, *i.e.* dy/dx. This has a value of $b + 2cx$, and, being dependent on the photoperiod, cannot be a constant. The second differential, $d^2y/dx^2 = 2c$, but this is the rate of change of sensitivity with change of x. Apart from this, objections can be raised against the substitution of initiation or heading curves by second order polynomials. Response curves are obviously the sum of many factors. The polyfactorial nature of the response curves finds its expression in their irregular shape and, in a number of varieties, also in the clearly asymmetric limbs of the curve near the minimum (see *e.g.* Graph 70, p. 30). Fitting a mathematical equation to part of the curve, therefore, is liable to give a wrong picture of the response to different photoperiods. However, CHANDRARATNA'S theoretical approach to his experimental results does not detract from the value of his publications, in which it was stressed for the first time that response curves covering the range of photoperiods around the optimum, *i.e.* between 8 and 14 h, could be used as a standard for varietal photoperiodic behaviour.

MORINAGA and KURIYAMA (1954) have published the most recent Japanese work on response curves. They used varieties from Japan, Burma, India and Java. In the first experiment 12 different photoperiods were used, *viz.* 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 24 h and natural day length. Photoperiodic treatments were started either immediately (A), 20 days (B) or 40 days (C) after germination. Heading curves for plots A and B only showed significant differences for very short photoperiods (C being on the whole much later), while, in general, the minima of the two curves were not clearly distinguishable. In the second experiment two limbs of the response curves were partially constructed by using two ranges of photoperiods: 3, 4, 5, 6 and 7 h and 16, 17, 18, 19, 20, 21 and 24 h. Two sowing dates, *A* on May 2 and *B* on June 10, were used to compare temperature influences. In general, plot *B* (higher temperatures) showed considerably earlier heading than plot *A*, but under very short photoperiods the order was often reversed.

It is remarkable that although several important features of the response curves were recognized in the early work, complete response curves between limits of, for instance, 6 and 24 hours with small intervals between the photoperiods used, have never been constructed. Probably as a result of this the significance of response curves for the interpretation of varietal photoperiodic behaviour was very incompletely understood. It may be that an insufficiently accurate analysis of the reaction of the plant to the photoperiod is partly responsible for this. In most work there was evidently no clear understanding of the insensitive juvenile stage, of separate photoperiodic effects on inflorescence initiation and development, of the actual temperature effect (apart from rough approximations in comparing outdoor and glasshouse conditions), of photosynthesis and of other non-photoperiodic effects on reproductive development. In addition there has been a notable tendency not to study the response curves themselves but to use these as data in the calculation of other criteria to judge photoperiodic behaviour.

8. CONSTRUCTION OF RESPONSE CURVES

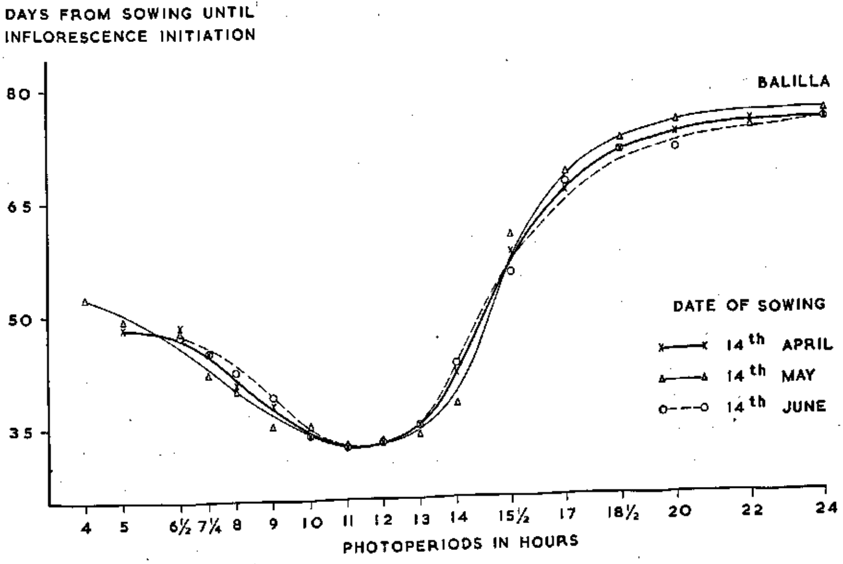
In § 6 there was a brief discussion of some results of a preliminary experiment (*E. 325*) in which 417 varieties from different parts of the world were exposed to photoperiods of 11, 15 and 21 h. The dates of heading recorded in this experiment made possible the selection of 28 varieties on the basis of their differences in photoperiodic behaviour. The varieties may, broadly speaking, be classed into six groups, *viz.* (1) varieties with a very low sensitivity to the photoperiod and a short juvenile phase, (2) varieties with a very low sensitivity to the photoperiod and a long juvenile phase, and varieties with various durations of the juvenile phase and either a low (3), moderate (4), high (5) or very high (6) sensitivity to the photoperiod. In most experiments the plants were exposed to 16 different photoperiods, ranging from 5 to 24 h, whereas in some cases a 4 h photoperiod was used in addition. Inflorescence initiation was determined by examining with a microscope, a preparation of the growing point heated in chloralhydrate (see *Appendix 1.7*).

8.1. *Initial experiments*

The work on the construction of response curves was initiated with some varieties of moderate sensitivity to the photoperiod, which were grown at three successive periods in summer to investigate the influence of the prevailing glasshouse conditions in different parts of the summer season on the time of initiation when the plants were exposed to a range of photoperiods.

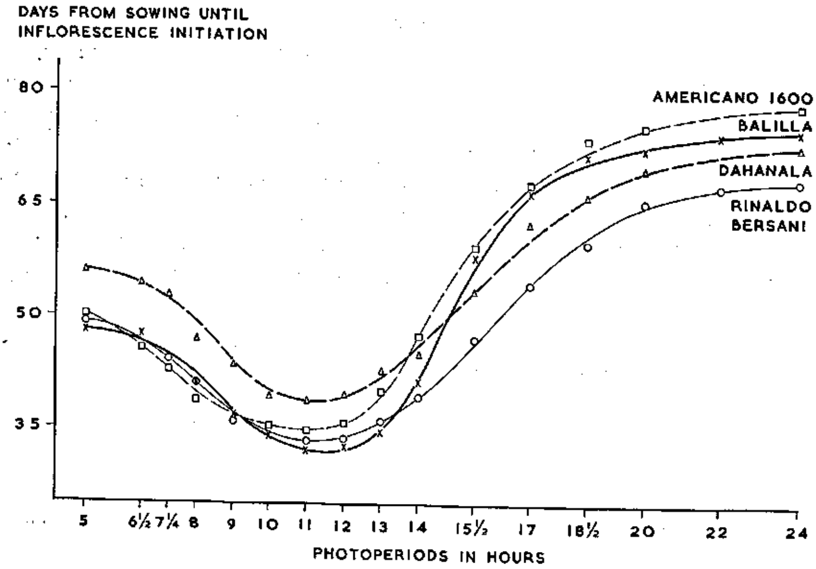
Experiment 326. – In this experiment, with the variety Balilla, three sowing dates were used, *viz.* April 14, May 14 and June 14. The seedlings, grown in natural days, were exposed to different photoperiods from an age of 16 days. In the range of photoperiods between 8 and 13 h the examination of growing point started after the 7th leaf had fully expanded, and this range was gradually extended after initiation had been established in plants grown in the optimal and near-optimal photoperiods. The general method adopted in these early experiments was to examine 3 plants daily and if initiation was found in any of these, to examine an additional 7 plants. When 7 or more out of 10 plants had initiated an inflorescence on a particular day, that day was used as the date for inflorescence initiation in the construction of the response curves. As a rule this date was found within two days of establishing initiation for the first time, and in most cases it was found on the first day.

The data obtained in the three series (sowing dates) showed a remarkably small variation (Graph 64) in the first year when the average greenhouse temperatures during the vegetative period did not differ greatly between the series. In the second year it was found, however, that a cold spell, in particular in the latter part of the vegetative period, could delay initiation markedly (*cf.* Chapter XXVI, § 3). The results obtained in the first year showed that although a separate curve could in fact be constructed for each series used (Graph 64), all of these showed the same specific varietal characteristics.



Graph 64. Photoperiodic response curves of the variety Balilla. Each curve represents the response of a group of plants sown on various dates (*E. 326*).

Experiment 327.– The foregoing experiment was repeated with the varieties Americano 1600, Dahanala and Rinaldo Bersani. The results obtained with Balilla were confirmed and it was found that when the data of the three series were averaged (Graph 65) it did not make an appreciable difference if the number of growing points analysed per treatment was cut down to one per day or per two days, and if, for a confirmation of the first time inflorescence initiation was found, 5 instead of 10 plants were analysed. This simplified method, which requires much fewer plants per treatment, has been used in most other experiments.



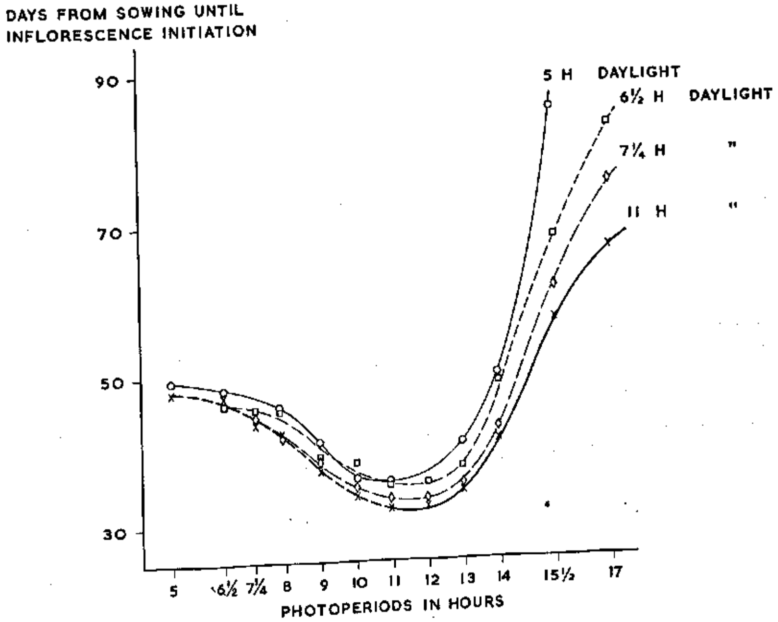
Graph 65. Photoperiodic response curves of four varieties based on average dates of inflorescence initiation obtained in three experimental series (*E. 327*).

8.2. *Non-photoperiodic effects of very short daylight periods*

The photoperiods used in the experiments *E. 326* and *E. 327* consisted of a daylight period of 11 h with or without supplementary artificial illumination (daylight fluorescent tubes (see *Appendix, 2.4*) with an intensity – at the level of the top leaves – of about 3000 erg/sec/cm^2). Shorter photoperiods were obtained by using shorter daylight periods. It was realized, however, that in the sub-optimal part of the curve, in photoperiods shorter than 11 h, or possibly even in daylight periods shorter than 12 or 13 h, non-photoperiodic effects may have influenced the time of inflorescence initiation to an appreciable extent. In particular photosynthesis, which has to supply the plant with sufficient energy substrates for a normal rate of growth and development, is likely to be much reduced in short days. In addition, other non-photoperiodic factors, probably mainly temperature and mineral nutrition, may have affected the results in both experiments. The following experiments were designed to investigate these points.

Experiment 328. – Seedlings of the varieties Americano 1600 and Balilla, grown under natural day length conditions in May, were exposed to various combinations of daylight period and total photoperiod at an age of 16 days. Seven daylight treatments were used, *viz.* 5, 6½, 7¼, 8, 10, 12 and 14 h. Each daylight period was supplemented with low intensity (about 3000 erg/sec/cm^2) to obtain a series of photoperiods with a maximum of 17 h. Data on the time of inflorescence initiation and the leaf number of the main stem were recorded. The data on initiation have been used to construct response curves of which those for Balilla are presented in Graph 66.

The curves in Graph 66 show that non-photoperiodic factors markedly affected initiation in the very short days. To determine the magnitude of this effect for each photoperiod a comparison has to be made with a super-optimal photoperiod which has about the same effect on the time of initiation as the sub-optimal photoperiod. As an example the 5 h daylight period curve in Graph 66 may be considered. Both the 5 h and 14 h photoperiods cause approximately the same delay in initiation, but with the 14 h photoperiod a comparison can be made between the 5 h and 11 h daylight period treatments, initiation being 9 days earlier in the latter. This difference of 9 days in delay of inflorescence initiation under the same photoperiodic conditions is an estimate of the non-photoperiodic effect on initiation of the lack of light in the 5 h daylight period. This number of days should therefore be subtracted from the days to initiation in the 5 h photoperiod to obtain an approximation of the actual photoperiodic effect exerted by that photoperiod. In the same way a correction can be made of the days to initiation in the 6½ and 7¼ h photoperiods.



Graph 66. Photoperiodic response curves of the variety Balilla. The curves present the effect of photoperiod treatments consisting of either a 5 h, 6½ h, 7¼ h or 11 h daylight period supplemented with low-intensity light (*E. 328*). The curve for the 11 h daylight period–photoperiod treatments is identical with the one in Graph 65.

The 8, 10, 12 and 14 h daylight period curves resembled the 11 h daylight period curve obtained in the previous experiments so closely in the photoperiod range of 8–15½ h that these curves have not been constructed separately in Graph 66. Only in a 17 h photoperiod was a greater delay in initiation found with an 8 h as compared with 10, 11 or 14 h daylight periods.

In a second experiment (*E. 329*) with the varieties Americano 1600 and Balilla, a 24 h photoperiod was used consisting of daylight periods of 8, 9, 10, 11, 12 and 14 h and supplementary low-intensity light. As compared with the 11 h daylight period inflorescence initiation was delayed 9–14 days, when an 8 h daylight period was used, and 2–7 days when the 9 h daylight period was used. No consistent differences were found between the 10, 11, 12 and 14 h daylight periods. In using (*E. 330*) varieties more sensitive to the photoperiod, Rizotto, 370 Basmati and Tjina, and also the very highly sensitive variety Skrivimankoti, a comparison of daylight periods of 8 h and 12 h in various photoperiod treatments showed that there is no specific delay in initiation when the daylight period is restricted to 8 h, as long as the total duration of the treatment does not last any longer than about 36 days. With longer treatments results differed according to variety. In general it may be concluded, therefore, that in the sub-optimal part of the response curves, the duration of daylight periods affected the time of initiation only in photoperiods shorter than 8 h, provided, particularly in varieties with a long juvenile phase, that the plants were exposed to long daylight periods during the insensitive period or at least during part of it, so as to limit the treatment with an 8 h daylight period to less than 36 days.

In experiments *E. 328* and *E. 329*, some observations were made on the number of leaves formed prior to the initiation of the inflorescence. As an example, the data for the 5 h daylight period treatments and the corresponding controls are presented in Table 26 for the variety Balilla.

TABLE 26

EFFECT OF DIFFERENT PHOTOPERIOD: DAYLIGHT PERIOD TREATMENTS ON THE LEAF NUMBER PRECEDING THE INFLORESCENCE IN THE MAIN STEM; DIFFERENCES BETWEEN THE TREATMENTS (4) AND (5) ATTAINED STATISTICAL SIGNIFICANCE (0.05 LEVEL), BUT THOSE BETWEEN (2) AND (3) WERE INSIGNIFICANT (*E. 328*)

No.	*Light treatments in hours*			*Average number of leaves preceding the inflorescence of the main stem* *
	Daylight	*Supplementary light*	*Total photoperiod*	
1	5	–	5	11.9
2	5	6	11	11.1
3	11	–	11	11.4
4	5	9	14	12.8
5	11	3	14	13.6

* Bracts not included.

These results were rather contrary to expectations, but all other observations indicated that vigorously growing plants initiated more leaves before inflorescence initiation than more slowly growing plants (see also Chapter XXVI, § 4).

Experiment 329. – This experiment was designed to investigate the effect of different photoperiods when preceded by a favourable daylight treatment during the insensitive stage of the juvenile phase. The varieties Balilla and 370 Basmati were used in this experiment. Seedlings were exposed to daylight periods of 5, 6½, 7½, 8 and 11 h beginning 0, 16, 20 (Balilla) or 27 (370 Basmati) days after sowing (the last two being the respective durations of the insensitive periods of the two varieties). Prior to the photoperiodic treatments, the seedlings were grown under natural daylight conditions in June. The results showed that the longer the natural daylight treatment lasted, the less the non-photoperiodic effect of the subsequent very short days on initiation (Table 27).

TABLE 27

NUMBER OF DAYS FROM SOWING UNTIL INITIATION WHEN SEEDLINGS WERE EXPOSED TO NATURAL DAYS PRIOR TO A SHORT-DAY TREATMENT (*E. 329*)

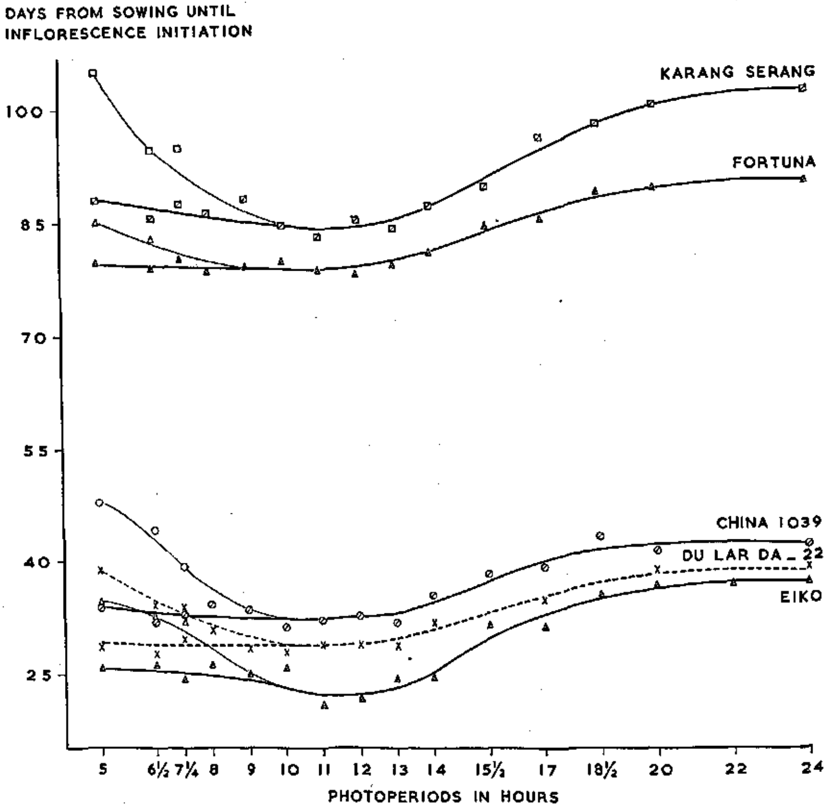
Variety	*Age of seedlings in days at the beginning of the photoperiodic treatments*	*Photoperiods (daylight) in hours*				
		5	*6½*	*7½*	*8*	*11*
Balilla	0	59.7	51.6	47.5	43.5	33.7
	16	48.2	47.1	44.4	41.8	32.8
	20	45.3	45.5	43.7	42.2	33.9
370 Basmati	0	77.4	70.6	61.3	56.7	43.0
	16	69.8	67.5	56.9	51.0	42.1
	27	63.7	61.2	57.8	52.1	42.3

Experiment 330. – The non-photoperiodic effects of very short daylight periods were studied in this experiment by interrupting the night period with a short break of high-intensity light. Seedlings of the varieties Balilla and 370 Basmati, grown under natural day length conditions, were transferred at an age of 16 days to daylight periods of 5, 6½ and 11 h. The night period was interrupted by high-intensity light (27,000 erg/sec/cm^2 from 500 W incandescent lamps) for 30 minutes. Photoperiodic treatments with low-intensity supplementary light (3000 erg/sec/cm^2, fluorescent tubes) were used as controls (Table 28).

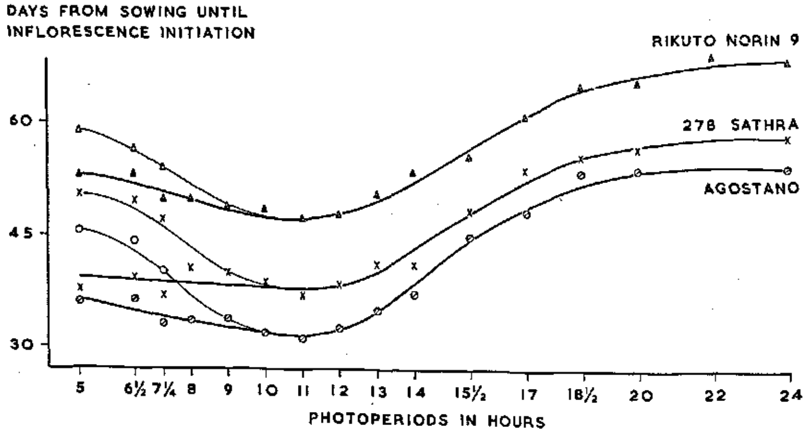
TABLE 28

EFFECT ON THE TIME OF INITIATION OF SUPPLEMENTARY LOW-INTENSITY LIGHT AND LIGHT BREAKS OF HIGH-INTENSITY LIGHT WHEN THE DURATION OF THE LONGEST UNINTERRUPTED DARK PERIOD WAS SIMILAR IN BOTH TREATMENTS (*E. 330*)

Photo- and nyctoperiods in hours					*Days from sowing until initiation*	
Daylight period	*Supplementary light period*	*Dark period*	*Light break*	*Dark period*	*Balilla*	*370 Basmati*
5	—	5½	½	13	35.8	50.3
5	6	—	—	13	36.1	52.7
5	—	8½	½	10	54.2	121.7
5	9	—	—	10	50.7	128.5
6½	—	4	½	13	36.9	47.1
6½	4½	—	—	13	35.8	46.0
6½	—	7	½	10	49.0	113.2
6½	7½	—	—	10	48.5	110.8
11	—	—	—	13	33.9	42.4
11	—	2½	½	10	40.1	105.3
11	3	—	—	10	40.6	101.8



Graph 67. Photoperiodic response curves of some varieties with very low sensitivities to the photoperiod. Sub-optimal parts of the curves corrected for non-photoperiodic effects. The uncorrected curve is given in thin lines (*E. 331*).

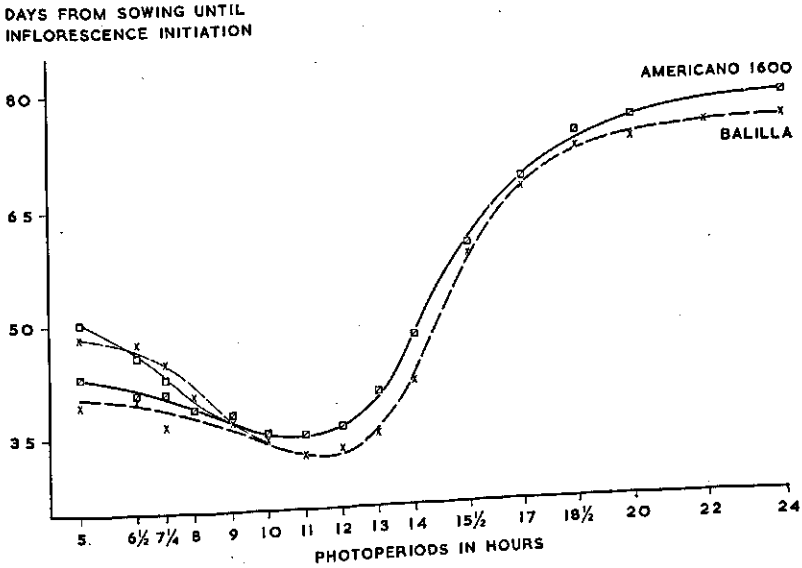


Graph 68. Photoperiodic response curves of some varieties with a low sensitivity to the photoperiod (*E. 331*). Explanation of curves as in Graph 67.

The differences between the two types of treatment, although sometimes significant (0.05 level) were inconsistent and did not indicate a specific favourable effect of supplementary light on growth rate and the time of initiation. This result was anticipated since no formative effects on leaf area as a result of low-intensity supplementary illumination had been observed in the experiments previously discussed.

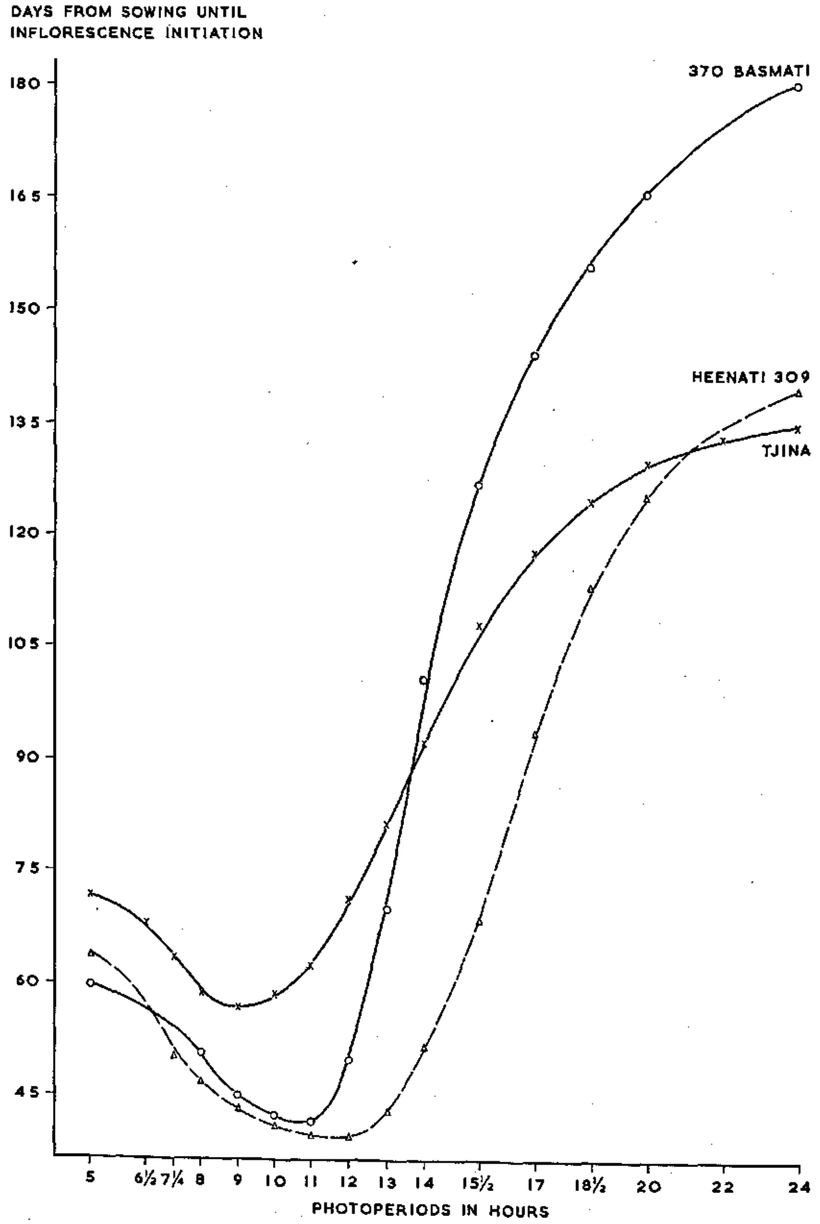
In subsequent research on the construction of response curves seedlings were grown in natural days in summer during the insensitive period and were transferred thereafter to different daylight period: photoperiod treatments. Non-photoperiodic effects on the duration of the vegetative period, which still occurred in plants grown in 5, 6½ and 7½ h days, were corrected according to the method described earlier (p. 25) and the sub-optimal parts of the curves were adjusted accordingly.

Investigations have also been made on the effects of temperature and mineral nutrition on the time of initiation in plants grown in very short days. The experiments will be detailed in Chapter XXVI, § 3.4. The main results can be summarized as follows: a high nitrogen level prolonged the vegetative period, a high phosphate level tended to shorten it, whereas high temperatures tended to shorten the vegetative period when the plants were grown under favourable photosynthetic conditions, but tended to prolong it when photosynthesis was limited. The nitrogen level with which earliest initiation was obtained depended on the rate of photosynthesis. The optimum level in 12 h days, for instance, was excessive in 5 h days and consequently caused a marked delay in initiation in that treatment. Therefore, a very low nitrogen level was used in the very short days and a higher level in the longer days in all further experiments. Low night temperatures favoured early initiation in the very short days, but under

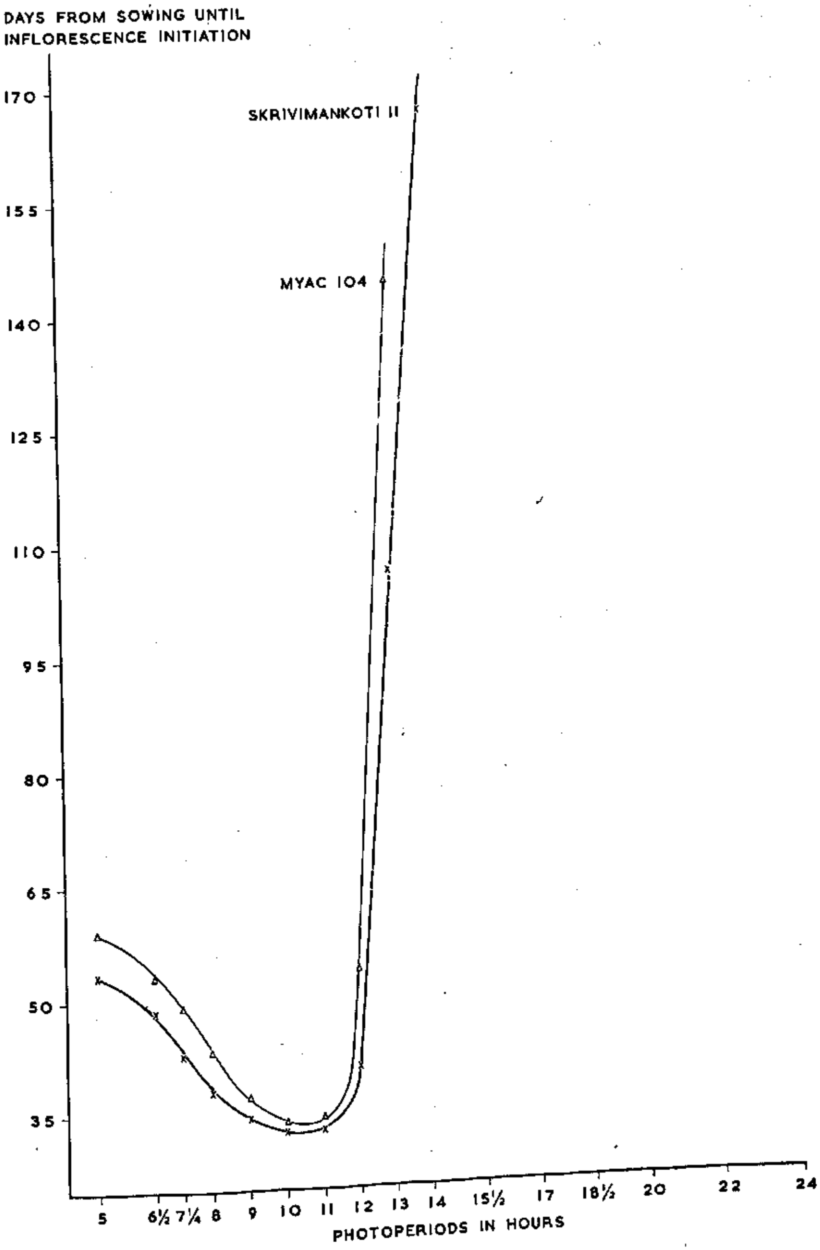


Graph 69. Photoperiodic response curves of two varieties with moderate sensitivities to the photoperiod (*E. 331*). Explanation of curves as in Graph 67.

the experimental conditions used the temperature during the dark period could not be lowered below the glasshouse temperature. With the method employed to determine non-photoperiodic effects on initiation in short days, the temperature effect could, however, be measured.



Graph 70. Photoperiodic response curves of three varieties with high sensitivities to the photoperiod. The sub-optimal parts of the curves have been corrected for non-photoperiodic effects (*E. 332*).

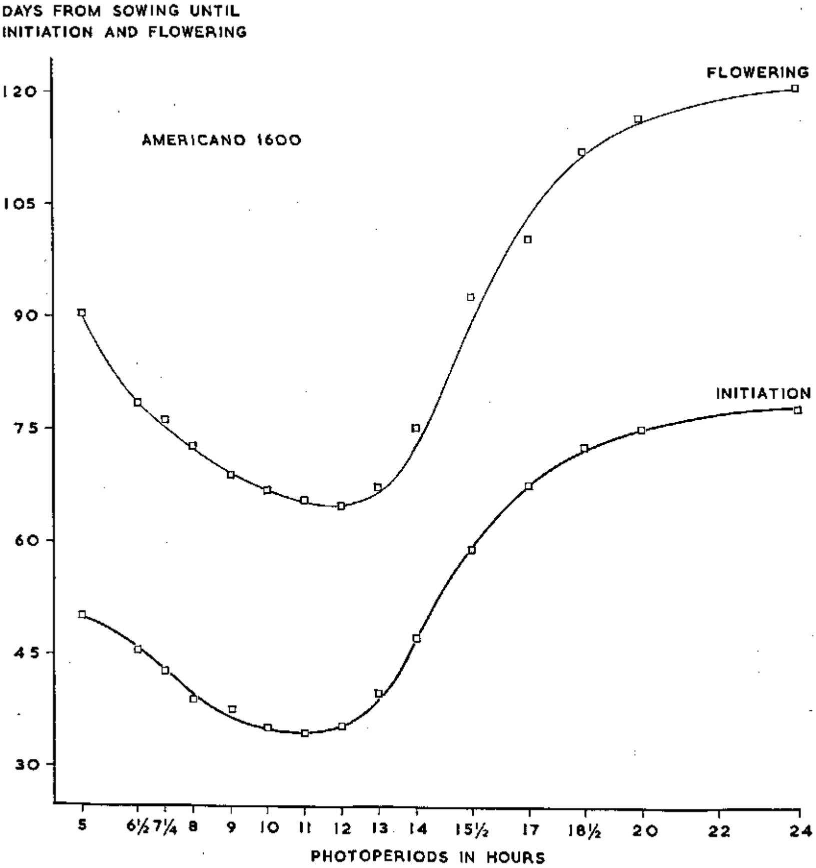


Graph 71. Photoperiodic response curves of two varieties with very high sensitivities to the photoperiod. Sub-optimal parts of the curves have been corrected for non-photoperiodic effects (*E. 333*).

8.3. *Differences in varietal photoperiodic behaviour*

Working with the methods outlined above three experiments have been made using altogether 24 varieties. In the first experiments (*E. 331*) varieties of very low, low and moderate sensitivities to the photoperiod were used. Some of the results obtained have been plotted in Graph 67 and 68. In Graph 67 an example is given of varieties which, although varying little in their photoperiodic behaviour, show large differences in their time of inflorescence initiation as a result of the differences in the durations of their juvenile phases.

Comparison of the uncorrected and corrected sub-optimal parts of the curves show that in some varieties the non-photoperiodic effects of very short days are marked while in others they are only slight. This is in spite of the almost identical photoperiodic behaviour of these varieties.



Graph 72. Photoperiodic response curves based on inflorescence initiation and flowering (*E. 334*).

In Graph 69 the corrected curves of the varieties Balilla and Americano 1600 are presented as an example of varieties with a moderate sensitivity to the photoperiod.

In the second experiment (*E. 332*), varieties with a high sensitivity to the photoperiod have been used. The largest difference in the positions of the minima of the curves (the optimal photoperiod) were found in this group, *viz.* a photoperiod of 9 hours in the variety Tjina and one of 12½ hours in the variety Heenati 309 (Graph 70.)

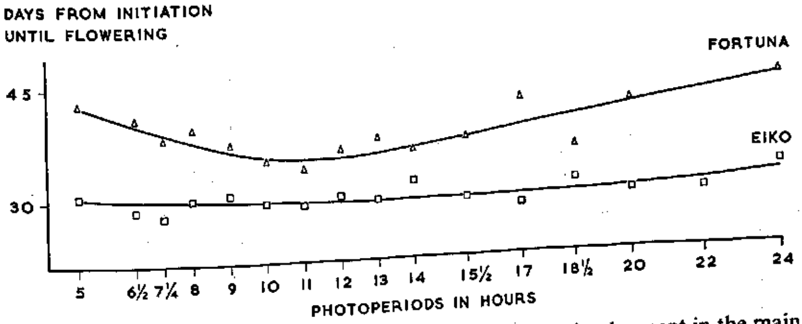
Finally, in the third experiment (*E. 333*), varieties of a very high sensitivity to the photoperiod were used. Two curves, characteristic for the response of these varieties, are presented in Graph 71.

The latter curves clearly show that these varieties are extremely sensitive to photoperiods exceeding 12 h, but not to shorter ones. The construction of the response curves of such varieties is naturally to the point where a particular long photoperiod lengthens the vegetative period so much that growth abnormalities or physiological disorders finally occur. Furthermore, data on inflorescence initiation after very long vegetative periods become increasingly disturbed by non-photoperiodic effects. This will be discussed in more detail in Chapter XXVI.

8.4. *Response curves based on flowering and inflorescence development*

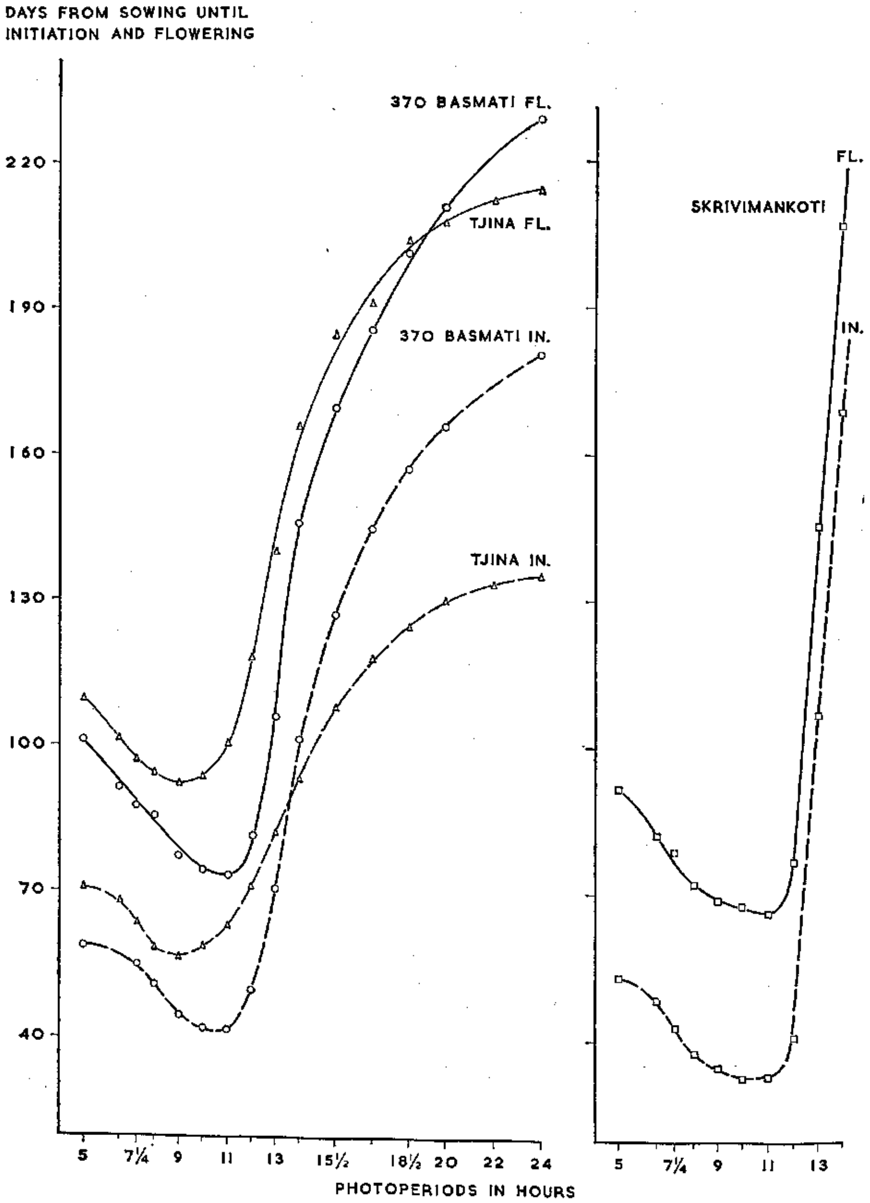
Following the methods outlined in the preceding part of this section, response curves have been constructed by plotting the times from sowing until initiation and flowering on the ordinate against the photoperiod used on the abscissa (*E. 334*). Anthesis in the first spikelets of the panicle of the main stem was taken as the date of flowering. An example of the results for a moderately sensitive variety is presented in Graph 72.

The distance between the two curves indicates the duration of inflorescence development between initiation and early flowering. The curve shows that this stage is little affected by the photoperiod in the variety Americano 1600. Similar observations were made on all varieties used in this experiment. The low sensitivity to the photoperiod is demonstrated better when the period from inflorescence initiation until flowering is plotted on the abscissa against the photoperiod used on the ordinate (Graph 73).



Graph 73. Response curves showing the duration of inflorescence development in the main stem in two varieties with very low sensitivities to the photoperiod (*E. 334*).

To investigate the response of inflorescence development to photoperiods of 5, 6½ and 7½ h the same method was used as for inflorescence initiation, since the same considerations apply. It was generally found, however, that the non-photoperiodic effect of very short days on inflorescence development (in terms of the period between initiation and earliest anthesis) was very small, at most a few days. This is not surprising since the total response to the photoperiod was itself very small, although panicle size and spikelet number were markedly reduced. In most cases the measurements of non-photoperiodic effects showed large variations, however, and have to be



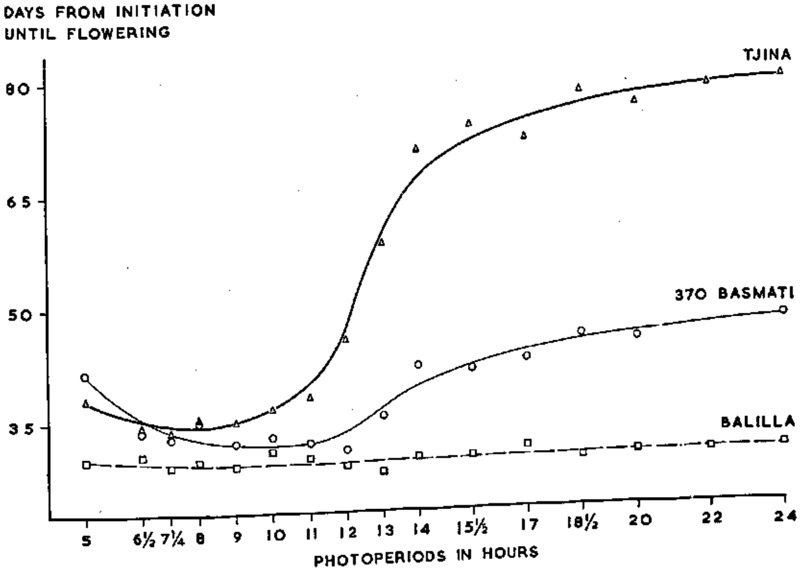
Graph 74. Response curves showing the duration of inflorescence development between the initiation of the inflorescence and early flowering in the main stem. Sub-optimal parts of the curves corrected for non-photoperiodic effects (*E. 335*).

considered as much less accurate than the ones made with inflorescence initiation. The finding that inflorescence development was in many cases more susceptible to temperature than to photoperiodic effects, may largely explain this.

Experiment 335. – Working along the same lines as in the preceding experiment the sensitivity to day length of inflorescence was investigated in varieties of high and of very high sensitivity to the photoperiod. In some of these varieties a marked effect of day length on the duration of panicle development was found, although this stage was practically day-neutral in others. In Graph 74 three characteristic examples are presented.

Of the varieties with very high sensitivities to the photoperiod, MYAC 104 showed a response similar to Skrivimankoti, but panicle development was somewhat sensitive in GEB–24. In the highly sensitive varieties a low to moderate response was found in Heenati 309 and Bengawan, but in the variety Tilakchary the response was relatively very high, even exceeding that of Tjina.

Examples of a completely day-neutral, a moderate and a high response of panicle development to the photoperiod are shown in Graph 75.



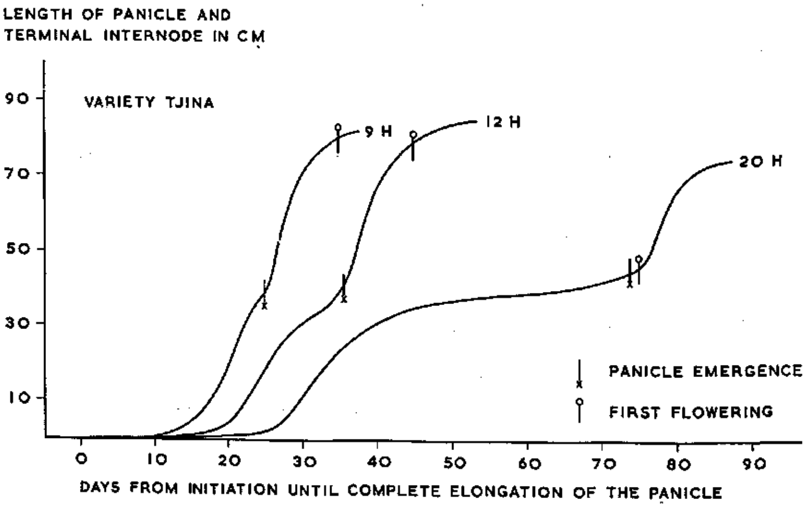
Graph 75. Response curves showing the duration of inflorescence development between inflorescence initiation and early flowering. The sub-optimal parts of the curves have been corrected for non-photoperiodic effects (*E. 335*).

It was realized that the photoperiodic treatment during the first stage of reproductive development could have an after-effect on panicle development, in which case the data obtained in the previous experiments would give an incorrect picture of the specific day length effects during the panicle development stage. This was investigated in a separate experiment (*E. 338*) in which plants of the varieties Balilla, 370 Basmati, Skrivimankoti and Tjina were grown in an 11 h photoperiod until 6 days after inflorescence initiation and were then transferred to a whole range of different photoperiods varying from 4 to 24 h. Data on panicle development and flowering were recorded. With the method used in this experiment the panicle development of plants in long days was usually a few days shorter than for those kept continuously under long-day conditions, but this difference may be attributed to the period the plants were kept under short days after the initiation of the panicle. It may be concluded, therefore, that, after the primary differentiation of the inflorescence, photoperiodic conditions during floral induction had little if any effect on the photoperiodic response during the inflorescence development stage.

8.5. *Particulars of inflorescence development in the variety Tjina*

The marked response of inflorescence development to the photoperiod in the variety Tjina has been studied in more detail. In § 4 the term "inflorescence development" was used to designate the development and elongation of the inflorescence and of the terminal internode of the stem (the internode between the nodes of flag leaf and bract). In this study an attempt was made to distinguish between photoperiodic effects on these two elongation processes.

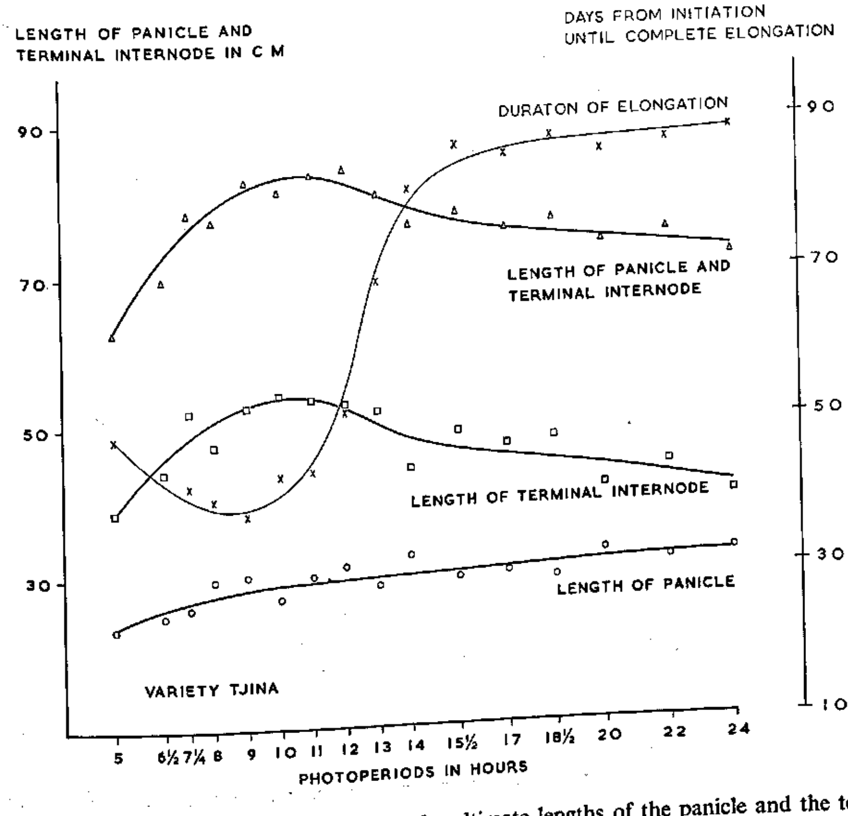
Experiment 337. – Plants of the variety Tjina were grown for their first 30 days in natural days in April and were then transferred to photoperiods of 9, 12 and 20 h. After inflorescence initiation had occurred 5 plants per treatment were analysed daily to measure the lengths of the inflorescence and the terminal internode of the main stem. In addition, data on panicle emergence and flowering were recorded. The results have been presented in Graph 76.



Graph 76. Curves showing the elongation of the panicle and the terminal internode of the main stem in plants of the variety Tjina, exposed to day lengths of 9, 12 and 20 h (*E. 337*).

The curves in Graph 76 show that at about the middle of elongation the process was seriously hampered, either for a short time (in short days) or for a long time (in long days). The dissection of plants at daily intervals during elongation showed that after its initiation the panicle was at first slow to elongate while further differentiation of rachillae and spikelets reacted similarly. Thereafter development became rapid but was again slow when the panicle was nearly full grown. At that stage the elongation of the terminal internode started; this also was very slow at first, and it was at this early stage that the photoperiod had its marked effect: long days inhibited the elongation for a much longer period than did short days, and it was this inhibition which brought about the almost horizontal part in the middle of the curves presented in Graph 76. Furthermore, it was established that the maturation of flower buds was affected less by the photoperiod than was the elongation of the terminal internode, so that under long days anthesis immediately followed or even preceded the emergence of a spikelet. In the 9 h photoperiod, on the other hand, anthesis did not start until elongation was almost complete. It is evident, therefore, that the beginning of flowering, as used in the preceding experiments, is an inaccurate criterion with which to mark the end of inflorescence development, at least in those varieties in which inflorescence development is clearly affected by the photoperiod. The end of flowering in a panicle would be a better indication of the termination of the panicle development stage in most cases.

It was, furthermore, established that in the main stem, anthesis from the first to the last flower lasted 3–4 days in the 9 h, 4–5 days in the 12 h and 6–8 days in the 20 h photoperiod treatment (*cf.* § 4). Long days not only hampered the rate of elongation of the terminal internode, but also reduced its final length (Graph 77). In other

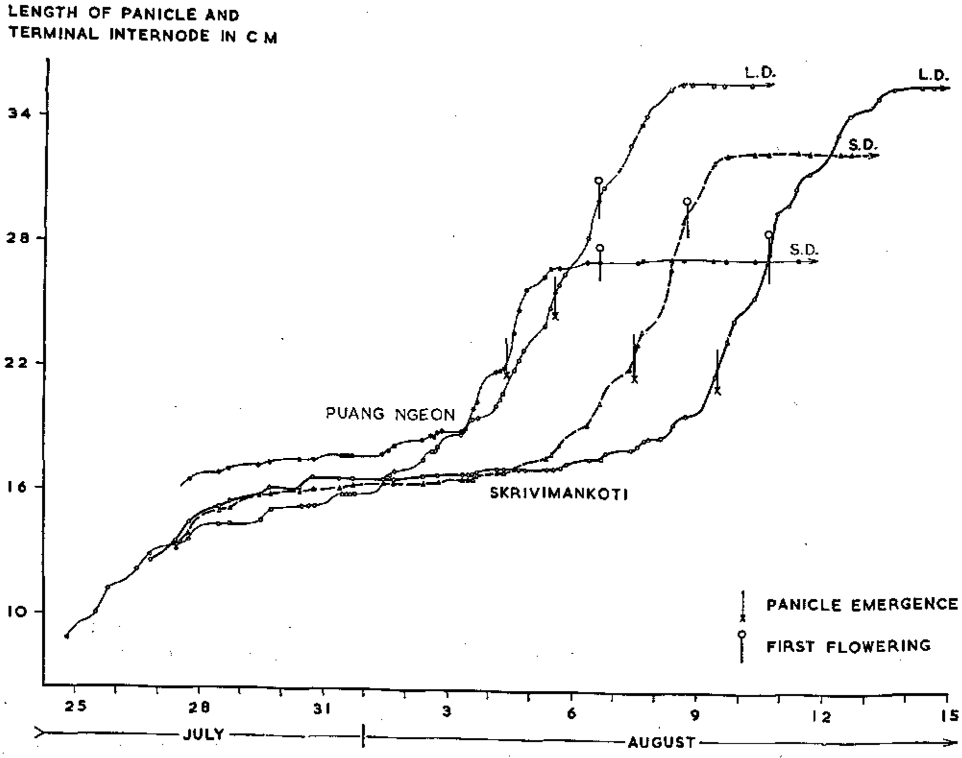


Graph 77. The effect of the photoperiod on the ultimate lengths of the panicle and the terminal internode of the stem. Comparison with the curve for the duration of panicle and internode elongation shows that there is no correlation between the time required for elongation and the ultimate length attained (*E. 337*).

words, the extension of the panicle from the sheath of the flag was less in long than in short days, a phenomenon which Tjina has in common with many other varieties although in others long days seem to promote panicle elongation (*cf.* Graph 78).

8.6. *The daily course of inflorescence elongation*

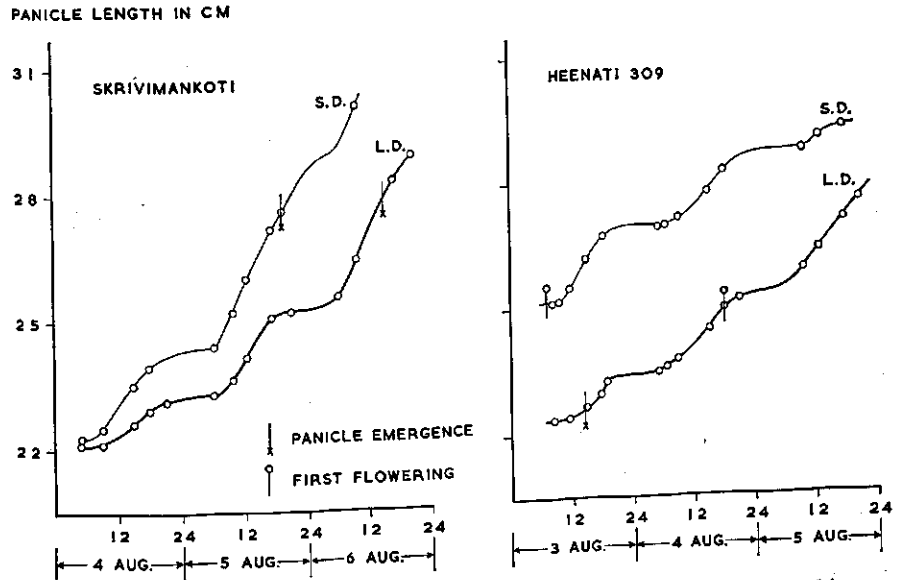
Experiment 338. – From the method used in the preceding experiment a general picture of inflorescence elongation was obtained by constructing curves based on the measurement of many inflorescences. The actual course of the elongation of an individual inflorescence, and its elongation over 24 h periods, could not be studied, however. To obtain this more detailed information, particularly in the period when the photoperiod hampered elongation most, a different method was used in this experiment. Plants were grown in an 11 h photoperiod until 6 days after inflorescence initiation and were then either transferred to natural days in July or remained under short-day conditions. Measurements of young panicles, still enveloped by the sheath of the flag leaf, were made by placing a strong light source behind the sheath of the flag leaf. The contours of the young panicle then shone feebly through the leaf sheath and the distance between the node of the flag leaf and the top of the young panicle could be measured at different times of the day. In most cases measurements could not be made with sufficient accuracy before the panicle had reached a length of about



Graph 78. Effect of day length on the elongation of the inflorescence and the terminal internode of the main stem. Measurements in each treatment were made on one particular inflorescence (*E.338*).

12 to 14 cm, *i.e.* shortly before or at the time of the main inhibition period in the elongation process. An example of the type of curves obtained is presented in Graph 78. A more detailed picture of the elongation process per 24 h is presented in Graph 79.

The results obtained with the *indica* varieties used (Heenati 309, Puang Ngeon, Skrivimankoti and Tjina) showed the same pattern as those obtained with three *japonica* varieties (Americano 1600, Eiko and Rikuto Norin 9).



Graph 79. Effect of day length on the elongation of the inflorescence and the terminal internode of the main stem during 24 h periods. Measurements in each treatment were made on one particular inflorescence. In the variety Skrivimankoti the short-day treatment was interrupted for 5 minutes at 6 a.m. on August 5 to make an additional measurement (*E. 338*).

9. DISCUSSION

Briefly reviewing the work discussed in this chapter, the following points may be noted: in § 2 two phases have been distinguished in the development of the rice plant, *viz.* a juvenile phase and an adult phase. Relatively few investigations have yet been made on the juvenile phase in plant species, but a comparison between the data discussed in the preceding chapter and the results obtained with rice show that the juvenile phase in rice has some special features for an annual plant. There is, relatively spoken, a very long, completely insensitive period and a brief transition period between the insensitive and the most sensitive (adult) stages. Whether the insensitive period was due to the first formed leaves being completely insensitive or only of very low sensitivity to the photoperiod could not be established convincingly. The experimental results obtained indicated that one of the reasons for the brief transition was probably the fairly large leaf area of fully sensitive leaves necessary to obtain rapid induction under favourable photoperiodic conditions.

The experiments on the induction period (§ 3) showed that the induced state was built up gradually. The smallest number of short-day cycles, from the beginning of the treatment until inflorescence initiation, was found when the plant was exposed to the optimal photoperiod during the adult stage. More cycles were required in photoperiods that deviated from the optimum, and in a few varieties more cycles were also required when the optimal photoperiod (or other short-day lengths) were preceded by long days; in other words, there was an after-effect of the long-day treatment.

The periods of induction in the optimum photoperiod differed markedly among varieties, the shortest was found to be 5 days and the longest 24 days. No correlation was found between the length of the induction period and varietal photoperiodic behaviour. The experimental results showed, furthermore, that in short days, a few days before inflorescence initiation was due to occur, the plant had already reached a state in which inflorescence initiation could be induced in long days, but a normal number of rachillae and spikelets were differentiated only when the short-day treatment was continued until 6 or 8 days after initiation. From this it was concluded that the induced state was not completely attained until a few days after initiation, although no experiments could be made to verify this view.

The exact moment at which the plant reached a state in a short-day treatment in which initiation could be induced in long days, appeared to depend on the length of the induction period, the photoperiodic behaviour of the variety, and the particular short and long-day lengths used. A more marked effect of long days on the induction built up in short days was found when the plants were exposed to an intervening long day in the early stages of induction. The long-day effect showed a striking correlation with varietal photoperiodic behaviour, and in a very highly sensitive variety a 20 h day was even found to destroy the induction built up in 3 preceding short days. Such an effect is unusually great compared with other plant species (see *e.g.* CARR, 1955). The correlation between varietal photoperiodic behaviour and the long-day effect was found in the three varieties used in these experiments, and it remains to be seen, therefore, if this applies to rice varieties in general.

The reproductive stage (§ 4) was divided into inflorescence initiation, inflorescence development, anthesis and grain development. Day length effects on each of these stages have been studied. In a few varieties day length appeared to effect markedly the development as well as the initiation of the inflorescence, which is uncommon for a short-day plant (*cf.* GREGORY, 1948; HAMNER, 1948; LANG, 1952). Preliminary results showed that the possibility of a photoperiodic effect on the last stages of flower bud maturation and/or on anthesis may not be ruled out. Grain development was completely insensitive, however.

The principal item dealt with in this chapter was the construction of response curves. With inflorescence initiation as the criterion for photoperiodic response, experiments were conducted in which rice plants were exposed to a range of photoperiods between 5 and 24 h. Photoperiodic response was expressed in the shape of a curve which was obtained by plotting the time from sowing to initiation against the photoperiod used. All curves showed an optimal photoperiod between 9 h and 12½ h which induced initiation most rapidly. All varieties showed a similar type of response, although there was a wide range of quantitative differences between them, varying from varieties practically insensitive to the photoperiod to varieties with a very marked short-day response. The curves which showed not only the varietal differences in photoperiodic sensitivity but also the specific response of each variety to the wide range of photoperiods used, were therefore considered to be the best criterion by which to judge varietal photoperiodic behaviour. The significance of the curves for general considerations on photoperiodism in plants has been dealt with earlier (Chapter XXIII, § 7.2).

In the construction of the response curves the number of days from sowing until inflorescence initiation was used to express the effects of the photoperiods used. This may be criticized on the ground that such a time interval is susceptible to non-photoperiodic effects. Experimental results (p. 10) showed, however, that the leaf number preceding the inflorescence, the other criterion which can be used, also has a relative value only since growth rate, mineral nutrition and temperature may affect this leaf number considerably (sometimes by as much as 2 leaves). Vigorous growth, a high nitrogen level and relatively low temperatures tended to increase the number of leaves. Therefore, completely reproducible results in terms of a time unit or of a leaf number may be expected only if the photoperiodic treatments are carried out under rigidly controlled conditions of environment and if the plants which are compared show exactly the same growth rate.

Non-photoperiodic effects have received special attention in respect of the sub-optimal part of the curve. The period of photosynthesis is considerably curtailed in very short days, and possible effects of this and of temperature on initiation have been investigated by comparing sub- and super-optimal photoperiods which cause the same delay in initiation, and by varying the daylight period in the super-optimal photoperiod (§ 8.2). In this way an estimate of the non-photoperiodic effects was obtained which seemed to be fairly accurate. It has to be kept in mind, however, that it is based on the comparison of sub- and super-optimal photoperiods, in which the photoperiodic effect may be of a different nature. A fully satisfactory determination of the non-photoperiodic effects would only be possible if, in addition to a completely controlled environment, a nutrient medium had been used which could supply the plants with adequate sugars, and which, therefore, would make the plant independent of photosynthesis in any treatment.

CHAPTER XXV

SPECIFIC LIGHT EFFECTS

1. INTRODUCTION

In the preceding chapter a general picture of the responses of different varieties to a range of photoperiods was presented, but there remain several aspects of the photoperiodic action of the light which require a more detailed study. Firstly, there is the perception of the photoperiodic treatment by the leaves and possibly also by other parts of the plant. Some work on this subject has been presented in the discussion of the juvenile phase and the transition of the juvenile to the adult phase, but most points have not yet been touched upon. Secondly, the intensity of the light which is still photoperiodically active remains to be discussed. Thirdly, little attention has yet been paid to the effect of an interruption of the photoperiod with a dark period or of the nyctoperiod with a light period, and, fourthly, particular photoperiodic conditions, such as a continuous alteration of photoperiods or of a gradual increase or decrease of the photoperiod during the induction period remain to be considered.

The study of these specific light effects is a necessary preliminary for the analysis of the photoperiodic effect of natural days, the principal subject dealt with in this chapter. The natural day is, in fact, the most complicated and difficult of all photoperiods to study, and there are so many effects of light and of other external conditions which may effect the transition from vegetative to reproductive development, that at best only an approximate understanding of its photoperiodic action can be obtained.

2. PERCEPTION OF THE PHOTOPERIODIC TREATMENT

2.1. *Variation in sensitivity of leaves of different ages*

In rice plants which are still in their vegetative stage, only leaf blades and part of the leaf sheaths are directly exposed to light. Hence, under normal conditions, the photoperiod can be perceived in the leaves only.

In the published work very few papers cover experiments on the perception of the photoperiodic treatment. FUKE (1942) exposed either the top parts (young leaves) or the basal parts (older leaves) of rice plants to short days. In the latter case induction was much delayed and not complete, whereas in the former case early and perfect induction followed the short-day treatment. VELASCO and MANUEL (1956), working with the highly sensitive variety Elon-elon, used two methods to investigate the sensitivity of leaves, *viz.* selective defoliation prior to a short-day treatment, or a short-day treatment applied to certain leaves only. Plants were grown in summer under relatively long day conditions and were transferred to short (10 h) days 49 days after sowing. The treatments used were the removal of the youngest fully expanded leaf or of one of the three preceding leaves, the control plants remaining unaltered.

Removal of the youngest leaf delayed flowering about two weeks compared with the other treatments, which indicates the importance of the youngest fully expanded leaf in the perception of the photoperiodic treatment. Non-photoperiodic effects, caused by the removal of a large area of the photosynthetic apparatus of the plant, undoubtedly affected the results in this experiment. In a second experiment either the two basal leaves or the two top leaves were exposed to a 10 h photoperiod whereas the other leaves remained in natural days. Flowering was earlier when the top leaves were

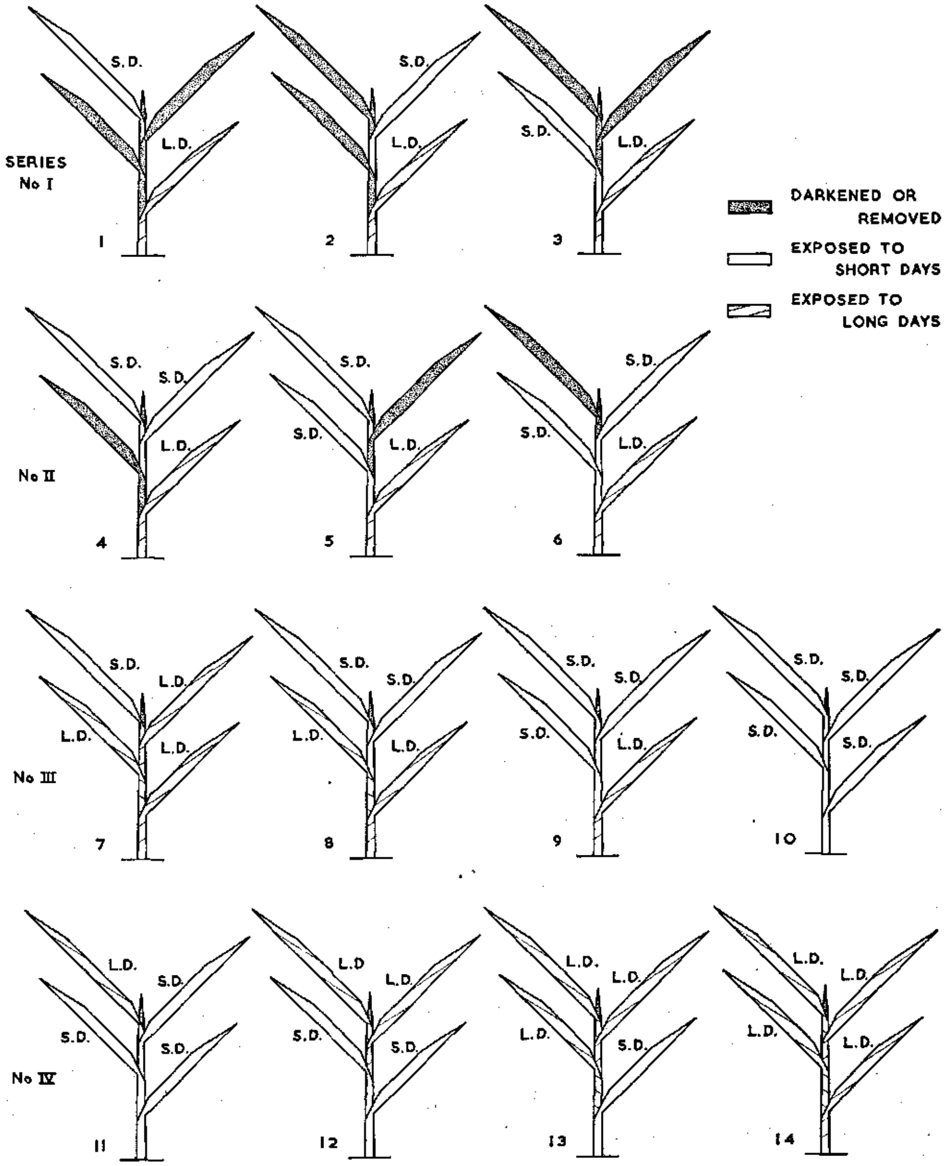


Fig. 17. Schematic presentation of the treatments used in *E. 342*.

exposed to short days than when the basal leaves were thus exposed. This result is inconclusive, however, since, as in FUKE's (*l.c.*) experiment, the flower-inhibiting effect of non-induced leaves located more acropetally than the induced leaves was overlooked.

In the present work on the variation in sensitivity of leaves of different ages (*E. 342*), plants of the varieties Nero di Vialone and 370 Basmati were grown in natural days in summer and, at the age of 40 days (Nero di Vialone) and 50 days (370 Basmati), the tillers were removed and the number of green leaves on the main stem was reduced to four. Thereafter individual leaves were either removed, kept in continuous darkness, exposed to short days (11 h) or to long natural days. The still unfolded leaves were darkened in all treatments to avoid possible effects of these leaves when they began to unfold during the induction period. A diagram showing the 14 different treatments used is presented in Fig. 17. The fourth series of these treatments was designed to investigate the flower-inhibiting effect of non-induced leaves located more acropetally than the induced leaves. Untreated plants exposed either to short (11 h) days or to natural day length were used as controls.

It was realized that by removing a considerable part of the photosynthetic apparatus of the plant or by excluding it from the light, non-photoperiodic effects would certainly influence the time of flower formation. To keep this effect as small as possible, no more than two leaves were removed or darkened in any treatment, while the plants were already fairly large and had accumulated a certain amount of starch in their leaf sheaths and stems before treatments were started. In addition, the normal duration of the induction period in 11 h photoperiods was fairly short, 10 days in Nero di Vialone and 7 days in 370 Basmati, and it was therefore expected that the duration of the treatments would be sufficiently short to avoid a serious reduction in growth rate.

The experimental results (Table 26) indicate that the youngest fully expanded leaf is the most sensitive one, and that the sensitivity decreases progressively with an increase in the age of the leaves (most differences between leaves of different ages were significant at 0.5 level). The sensitivity of the fourth leaf from the top has not been examined specifically in any of these treatments, but from a comparison of the results of treatments 9 and 10 it is evident that this leaf had hardly any effect on flower formation when the more acropetally located leaves perceived the photoperiodic stimulus. The darkening of leaves seemed in most treatments to delay initiation more than their removal, but the differences were insignificant. A comparison between the series I, II and III remains inconclusive in respect of possible specific effects of the removal of one or two leaves on the time of initiation.

2.2. *Considerations on leaf sensitivity*

Factors other than the age of the leaves may have contributed to the effects observed in Table 26. The following points have been examined more closely:

(1) The apparent differences in leaf sensitivity may be a result of the differences in the size of the leaves and not of differences in the rate of production of the floral stimulus per unit of leaf area.

(2) If the transport of the floral stimulus is assumed to depend on the transport of carbohydrates to the growing point (Chapter XXIII, § 4), then the total amount

TABLE 26

EFFECT OF SHORT-DAY TREATMENTS OF INDIVIDUAL LEAVES ON THE TIME OF INFLORESCENCE INITIATION (*E. 342*)

Series	No.	a = *top leaf*, b = *second*, c = *third and* d = *fourth leaf from top*			*Days from the beginning of the treatments until initiation*	
		Leaves exposed to:				
		Darkness or removed	*Short (11 h) days*	*Long (natural) days*	*Nero di Vialone*	*370 Basmati*
I	1	– b c	a – – –	a – – –	12.8	10.7
	1*	– b c	a – – –	a – – –	13.2	10.8
	2	a – c	– b – –	– – – d	13.9	12.0
	3	a b –	– – c –	– – – d	15.1	15.4
	3*	a b –	– – c –	– – – d	15.4	15.6
II	4	– – c	a b – –	– – – d	11.2	8.8
	5	– b –	a – c –	– – – d	11.5	10.3
	6	a – –	– b c –	– – – d	13.3	14.1
	6*	a – –	– b c –	– – – d	13.2	14.6
III	7	– – –	a – – –	– b c d	14.7	12.3
	8	– – –	a b – –	– – c d	12.4	9.5
	9	– – –	a b c –	– – – d	9.8	7.2
	10	– – –	a b c d	– – – –	10.1	6.9
IV	11	– – –	– b c d	a – – –	15.6	15.4
	12	– – –	– – c d	a b – –	19.5	—
	13	– – –	– – – d	a b c –	20.3	—
	14	– – –	– – – –	a b c d	20.7	—
	**	– – –	a b c d	– – – –	9.9	7.1
	**	– – –	– – – –	a b c d	22.1	93.0

* Leaves not removed but darkened.

** Controls with young folded leaves not darkened at the beginning of the photoperiodic treatment.

of both carbohydrates and stimulus transported from a particular leaf to the growing point may be a more important factor in the effect of that leaf on flower formation than the total amount of stimulus which it produces. This would add to the difficulty of estimating the actual sensitivity of each leaf.

(3) If young leaves are more sensitive than older leaves, this may be caused by the age of the leaf (senility) or by the number of non-inductive cycles to which the leaves have been exposed prior to the short-day treatment. In other words: long days may be able to inactivate at least part of the mechanism which perceives the photoperiodic stimulus.

Some preliminary experiments have been made on the factors mentioned under (1) and (3).

Experiment 343. – To investigate the effect of leaf size on the perception of the photoperiodic stimulus, different groups of plants of the variety Skrivimankoti were exposed to treatment no. 1 (Fig. 17) at different ages (Table 27).

TABLE 27

EFFECT OF THE AREA OF THE YOUNGEST FULLY EXPANDED LEAF BLADE EXPOSED TO SHORT DAYS ON THE TIME OF INFLORESCENCE INITIATION, VARIETY SKRIVIMANKOTI (*E. 343*)

No.	*Age of plants in days at the beginning of the treatments*	a = *top leaf,* b = *second,* c = *third and* d = *fourth leaf from top*			*Average leaf area in cm²*		*Days from the beginning of the treatments until initiation*
			Leaves exposed to:				
		Leaves removed	*Short (11 h) days*	*Long (natural) days*	*Top leaf blade*	*Two leaf blades below top leaf*	
1	40	b c	a – – –	– – – d	62	—	14.7
2		b c	a* – – –	– – – d	50	—	16.5
3		– –	a b c d	– – – –	63	109	9.2
4		– –	a b c d*	– – – –	50	109	11.3
5	55	b c	a – – –	– – – d	87	—	12.8
6		– –	a b c d	– – – –	85	134	8.9
7	70	b c	a – – –	– – – d	103	—	10.1
8		b c	a* – – –	– – – d	75	—	11.4
9		b c	a* – – –	– – – d	50	—	15.8
10		– –	a b c d	– – – –	105	177	9.0
11		– –	a b c d*	– – – –	75	177	9.1
12		– –	a b c d*	– – – –	50	177	9.7

* Part of leaf (a) removed.

The results indicate that a large leaf area is required to obtain the shortest induction period under inductive day length conditions, *viz.* a leaf area in the order of 100 cm² at probably the most sensitive stage in the variety Skrivimankoti (*cf.* treatments 7–12). A more precise determination of the required area does not seem justified since it is likely that non-photoperiodic effects have affected the results of the treatments in which only the top leaf was exposed to short days.

The results of treatments 4 and 9 are not fully comparable since in treatment 4 part of the leaf area of the two leaves below the top leaf belonged to the less-than-fully sensitive leaves formed at the end of the juvenile phase. A comparison between treatments 5 and 6, and also between 7–9 and 10–12, indicates that in this variety a unit area of the top leaf affects flower formation about twice as much as the same area of the next two leaves below. This seems a greater variation than was found with the two varieties tested previously (see Table 26), and it indicates that the youngest fully expanded leaf is probably markedly more sensitive than the more basipetally located leaves, although only grafting experiments could give convincing evidence in this respect (see under (2) p. 44). It is not likely that in this experiment the size of the leaves below the top leaf (*cf.* treatments 6 and 11) affected the results obtained, although such an effect cannot be ruled out completely.

Working along the same lines as in the preceding experiments, a preliminary study (*E. 344*) was made of the effect of a pre-treatment with long days on the perception of the photoperiodic stimulus in short days. Plants of the variety Skrivimankoti were exposed to photoperiods of either 14, 19 or 24 h (10 h day light period supplemented with artificial illumination of low or high intensities). At an age of 90 days, the youngest expanded leaf of the main stem was removed and the top part of the plant was darkened with a black paper bag, while the other leaves, which had received a number of long-day cycles, were exposed to an 11 h photoperiod.

TABLE 28

EFFECT OF A PRE-TREATMENT WITH LONG DAYS ON THE PERCEPTION OF THE PHOTOPERIODIC STIMULUS IN SHORT DAYS, VARIETY SKRIVIMANKOTI (*E. 344*).

No.	*Photoperiod in hours prior to short-day treatment*	*Intensity of supplementary light (in erg/sec/cm²) during the long-day treatment*	a = *top leaf*, *b* = *second*, c = *third and* d = *fourth leaf from top* *Leaves exposed to short days*	*Days from the beginning of the short-day treatment until inflorescence initiation*
1	14	3,000	a b c d*	9.2
2	14	3,000	– b c d**	13.3
3	19	3,000	a b c d*	9.0
4	19	3,000	– b c d**	14.7
5	24	3,000	a b c d*	9.3
6	24	3,000	– b c d**	14.5
7	24	30,000	a b c d*	10.2
8	24	30,000	– b c d**	17.4

* Folded top leaf darkened.
** Ditto, in addition, leaf (a) removed.

The results (Table 28) indicate that leaves which had been exposed to a 14 h photoperiod remained more sensitive to the photoperiod than those exposed to 19 or 24 h photoperiods. With intact plants (treatments 1, 3 and 5) these differences were apparently compensated by the sensitivity of the top leaves, which had been exposed to none or a few long days after the unfolding of the leaf blade, when continuous light of high intensities was used (treatment no. 7). In the latter case, either the sensitivity of the top leaf was diminished by a few long-day cycles or the sensitivity of the other leaves was affected more than in the other treatments, or both. A comparison of treatments 6 and 8 actually shows that the after-effect of the long days increased with an increase in light intensity.

There is no indication to show whether the decreased sensitivity of the other leaves was due only to the photoperiod to which they had been exposed or also to the increased senility of the leaves. The latter may be the most likely explanation.

It is difficult to decide if the effect of long days on the sensitivity of leaves in subsequent short days would be general in rice. Experiments such as *E. 344* can only be made with highly to very highly sensitive varieties, since in varieties of lower sensitivity the vegetative period cannot be sufficiently prolonged in moderately long day lengths such as the 14 h photoperiod. Judged by the magnitude of the differences in Skrivimankoti (Table 28) it is likely that an after-effect of long days would either be small or absent in varieties of moderate or low sensitivity to the photoperiod. Earlier (p. 11), however, it was reported that Tjina, a variety much less sensitive than Skrivimankoti, showed a relatively marked after-effect of long days, but this may be a result of the extraordinarily long induction period of this variety. It is evident that there is still much prospect for further experimental work on this subject in rice.

2.3. *The perception of the photoperiod in long days followed by short days*

In rice plants of moderate sensitivity to the photoperiod, the induced state is gradually built up and eventually results in flower formation under long-day conditions. The question may arise whether leaves which have reached an advanced state of induction under long days still react to short days. The following experiment was carried out to elucidate this point.

Experiment 345. – Plants of the varieties Americano 1600, Balilla and Nero di Vialone, all of moderate sensitivity, were exposed to a 20 h photoperiod until 24, 12, 4 or 2 days before inflorescence initiation was due to occur in the main stem. Different groups of plants were then transferred to an 11 h photoperiod. Plants which were continuously exposed to an 11 h or to a 20 h photoperiod, served as controls.

The transfer 12 and 24 days before inflorescence initiation brought about earlier initiation and more rapid panicle development in all varieties as compared with the continual 20 h treatment, but no other particular phenomena occurred, and the duration of the induction period in short days was the same in both treatments. In the other treatments, however, not only were initiation and panicle development accelerated, but in most plants the axillary bud of the flag leaf also developed into a complete panicle in most plants and the axillary buds of the three preceding leaves showed, on microscopic examination, a much more advanced differentiation of the panicle primordium than in plants which initiated the terminal inflorescence under 20 h photoperiods, or under continual 11 h photoperiods. The lower the buds were located on the stem, the less the differentiation of their panicle primordia. The most probable explanation of this pattern of panicle development in axillary buds is that the flow of carbohydrates (and floral stimulus) directed to these buds when they were formed, have determined their development. The later a bud was formed, the more carbohydrates and stimulus it must have received from the "double induced" leaves and the more advanced the differentiation of its panicle primordium became.

The results obtained in this experiment indicate that under the applied conditions an advanced state of induction under long days and a subsequent induction under short days have a cumulative effect which surpasses the effect of either a continuous short or long-day treatment. This "cumulative effect" can probably be explained best by assuming that, after the transfer to short days, the leaves attained the fully induced state in a relatively short time and consequently produced more floral stimulus in the period of axillary bud development than leaves which remained continuously under either long or short-day conditions.

Earlier, WORMER (1953) had reported a similar phenomenon: transference of plants of the variety Nero di Vialone from an 18 h to a 12 h photoperiod shortly before inflorescence initiation was due to occur, accelerated reproductive development. In several plants the axillary bud of the flag leaf developed into a panicle, in which normal flowering and seed development occurred.

It is remarkable that only in *japonica* varieties are panicle primordia found in axillary buds of plants that have entered the reproductive stage. In *indica* varieties a panicle primordium may be found in the axillary bud of the flag leaf, but this primordium usually dies after a short time and only some shrivelled remnants are present when the terminal panicle has reached the flowering stage. All other axillary buds remain vegetative. At present there does not seem to be a readily acceptable explanation for this disparity between the two groups of varieties.

2.4. *Effect of the age of the plant on the perception of the photoperiodic treatment*

It was mentioned earlier (Chapter XXIV, § 3) that the induced state is gradually built up in long days. It has even been shown (§ 2.3) that under certain conditions the induction, which had advanced considerably under long days, could be rapidly completed under short days. On the other hand, evidence has also been obtained (§ 2.2) that, at least in some highly and very highly sensitive varieties, the leaves become less responsive to short days after they have been exposed to long days, an effect which increases with the length and the light intensity of the long days. These two phenomena seem to be contradictory.

Furthermore, it has been observed with, for instance, 370 Basmati exposed to a 20 h photoperiod, that usually 4 and sometimes 5 green leaves were present on the main stem about 50 days after sowing when the plants had already entered the adult phase. At an age of 110 days, elongation of the stem had already proceeded for more than a month and again 4 green leaves were found on the main stem, but none of these was the same as on the 50-day-old stem. Similarly, when the inflorescence was finally initiated in plants 167 days old, none of the green leaves present was the same as on the 110-day-old stem. The question may then arise how the induced state can be built up in the leaves when they die before they can evoke floral initiation.

The following explanations may be suggested:

(1) The induced state is gradually built up in the stem and not in the leaves.

(2) The induced state is gradually built up and maintained in the youngest leaves and in the growing point.

(3) Each leaf produces a small amount of floral stimulus which accumulates in the stem until a certain threshold value is reached which can bring about floral initiation.

(4) With an increase in the age of the plant the last formed leaves become gradually less sensitive to long days, and leaves are eventually formed which attain the induced state under the long-day conditions.

(5) With an increase in the age of the plant, growth processes become slower and the growing point reacts more readily to small amounts of floral stimulus.

At present there are still far too few data available to justify a positive conclusion about the explanations suggested before, but a few points may be mentioned. (1) An induced state of the stem may be present, but it would be difficult for the stimulus to reach the apex in sufficient quantities when the main supply of carbohydrates would have to come from non-induced leaves. (2) None of the experimental data at present available indicates that the induced state is either built up or maintained in very young (still folded) leaves or in the growing point. (3) If a low level of induction was present in leaves exposed to long days, this would always shorten the induction period when the leaves were subsequently exposed to short days. The experimental results presented in this section do not indicate such an effect. (4) If, with an increase in age of the plant, the newly formed leaves became less sensitive to long days, this would mean that the leaves formed on older plants would react differently to short and long-day treatments than those on younger plants, but this remains to be investigated. (5) In all varieties which could be kept vegetative for long periods under long-day conditions, it was found that the growth rate gradually decreased when the plants became older, in particular when the vegetative period lasted longer than 6 to 7 months, and that the apex became more conical in shape as compared with young plants (*cf.* Chapter II, § 6), but so far no evidence has been obtained which indicated an increase in sensitivity of the apex to the floral stimulus with an increase in age of the plants.

It must be concluded that the extent to which plant age influences photoperiodic perception in long days is still not clear but it is difficult to account for flower formation in long days without assuming that in some way the age of the plant affects its reaction to the photoperiodic treatment.

2.5. *Perception of the photoperiodic treatment by the leaf sheaths*

In the preceding investigations attention was paid only to the leaf blade as the site of perception of the photoperiodic stimulus. In the following experiment information was sought on the role of the leaf sheath in this respect.

Experiment 346. – A selective short-day treatment of leaf sheaths is technically more difficult than that of leaf blades. Two methods were chiefly employed, *viz.* (1) plants exposed to long photoperiods were left intact, but the still folded top leaves were covered with a black paper bag and the leaf sheaths were wrapped in dark paper; the wrappings of the sheaths were removed for 11 hours during the daytime, the leaf blades in this way receiving a long-day treatment and the leaf sheaths a short-day treatment; (2) plants of highly sensitive varieties were kept vegetative for a long period under long day length conditions and after they had formed at least eight markedly elongated internodes, the still folded top leaf was darkened, while all leaf blades and yellowing and dead leaf sheaths were removed, leaving the green leaf sheaths as the only parts of the plant directly exposed to the light. Different groups of plants thus treated were exposed to either short or long photoperiods.

Working with the very highly sensitive varieties Skrivimankoti and Siam 29, inconclusive results were obtained with the first method, but the results obtained with the second method clearly showed that the leaf sheath can perceive the photoperiod: plants in the long-day treatment remained vegetative, whereas inflorescence initiation occurred in the 11 h photoperiod. However, in both varieties the induction period was more than three times longer when the stimulus was perceived by the leaf sheaths than by the leaf blades.

With the variety Siam 29 it was furthermore found that when the sheath of the youngest fully expanded leaf was permanently covered, initiation was 12 days later than when it was exposed to an 11 h photoperiod (all other leaf sheaths were exposed to 11 h days in both treatments). This indicates a relatively high sensitivity of the youngest leaf sheath, similar to that of the corresponding blade, while it also shows that the photoperiodic stimulus can be perceived by the older leaf sheaths.

The results of *E. 347* give the impression that leaf blades are much more sensitive to the photoperiod than leaf sheaths. This, however, may not be correct, for leaf sheaths normally largely cover each other, and preliminary comparisons of the total surface of leaf sheaths and of leaf blades exposed to the light showed that per unit area leaf sheaths do not differ much in sensitivity from leaf blades, but this matter awaits further confirmation after more detailed experiments.

2.6. *Perception of the photoperiodic treatment by the stem*

The sensitivity of the stem to the photoperiod can only be studied under specific conditions, *i.e.* when a long elongated stem is present in vegetative plants. In the first experiment on this subject (*E. 347*), the variety 370 Basmati was used. In plants 150 days old, grown in continuous light, all leaf blades, leaf sheaths and tillers were carefully removed from the main stem, except for the youngest, still expanding leaves at the top, which were darkened with a black paper bag. The weak, whitish bare stems became firm and turned dark green a few days after being exposed to sunlight. The stems either remained under continuous illumination, or were exposed to an 11 h photoperiod. For their further growth plants depended entirely on the starch that had previously accumulated in the stem and on the photosynthetic activity of the chlorenchyma of the stem. Under these conditions non-photoperiodic effects must have influenced the behaviour of the plants considerably. Untreated plants which either remained under continuous illumination or were transferred to an 11 h photoperiod, served as controls.

Treated plants exposed to an 11 h photoperiod either continued to remain vegetative until physiological disorders became apparent and the experiment had to be terminated, or they initiated an inflorescence after the same number of leaves had been formed as in the 24 h photoperiod control. It was concluded from this that the stem was unable to perceive the photoperiodic treatment and that the floral initiation which had been observed in some plants was probably brought about by some floral stimulus which had been formed in the leaves prior to the defoliation and which had been retained in the stem.

On closer examination these conclusions seemed unsatisfactory, however. The data were obtained with a few plants only and it was unknown to what extent non-photoperiodic effects had influenced the results obtained. To verify the earlier findings a second experiment was made a few years later with a larger number of plants and a different variety.

Experiment 348. – Plants of the variety HMC 12, with a very high sensitivity to the photoperiod, were grown under natural day length conditions for 120 days, and were thereafter exposed to a fixed photoperiod of 16 h. Tillers were regularly removed, and, as a result, the main stem made very luxurious growth. After the plants had started to form elongated internodes, the leaf sheaths of yellowing or dead leaves were regularly removed. For some time these plants had a bare dark green lower part of the stem and 4 or 5 green leaves on the higher part. At an age of 150 days all leaves and leaf sheaths were removed as in the preceding experiment and the top parts of the plants were also darkened. Thereafter a division was made into two groups of 25 plants, one group being transferred to an 11 h photoperiod, the other remaining under the 16 h photoperiod. Data on inflorescence initiation and leaf number were recorded. The plants with stems exposed to a 16 h photoperiod all remained vegetative, but in the 11 h photoperiod treatment inflorescence initiation did occur, although the duration of the induction period varied markedly among individual plants, *viz.* from 37 to 51 days.

This result clearly indicates that, at least in this variety, the bare stem is capable of producing the floral stimulus.

2.7. *The retention of the induced state*

The marked effect of non-inductive day length on the duration of inflorescence development in some varieties indicates that in these cases a transfer from inductive to non-inductive day lengths after initiation still reduces the amount of floral stimulus transported to the inflorescence primordium. The reason for this effect may either be that the fully induced state is gradually destroyed under the influence of non-inductive day lengths, or that the young leaves which are not yet fully induced and the leaves which begin to expand after the transfer to non-inductive day lengths provide the young panicle with much of its carbohydrates and thus dilute the supply from the lower leaves which were fully induced and capable of producing floral stimulus. The latter factor is likely to have some effect, but little is known about the former factor – a possible destruction of the fully induced state in non-inductive day lengths.

In an experiment (*E. 349*) to investigate this point, it was found that the induced state could be retained in the leaves when they were moved to long-day conditions, but that very long days had a destructive effect on the induced state. In continuous light, consisting of a daylight period and low-intensity supplementary light, the induced state could be partly destroyed in some varieties; in others, however, this required high-intensity supplementary light. In a very highly sensitive variety the latter condition was apparently sufficient to destroy so much of the induced state that no flower formation occurred. In a second experiment (*E. 350*) the possibility that the stem could retain the floral stimulus was investigated. The results, as with leaves, indicated that the stems could retain the floral stimulus even under long-day conditions, but that their effect on flower formation was less than that of induced leaves. Consequently, when both are present, the effect of the stems is probably masked by that of the leaves. Furthermore, it was found that very long days may partly destroy either the retained stimulus or the induced state, or both, in the stems. Details of the two experiments are presented below.

Experiment 349. – In earlier work (BEST, 1951) it was shown that pieces of stem with one or more leaves, or even without leaves, can be successfully used as cuttings. Rooting occurred first on the node which was in contact with the wet soil, thereafter the axillary bud corresponding with this node grew out into a shoot which rooted, formed tillers, etc., and eventually could not be distinguished from a plant grown from seed. This method of striking cuttings has been used to investigate whether or not the induced state is retained in the leaves under different day length conditions.

Plants of the varieties 370 Basmati and Skrivimankoti were grown in continuous light (11 h daylight supplemented with low-intensity artificial light) until 150 days after sowing when they were transferred to an 11 h photoperiod. Two and four weeks after inflorescence initiation had occurred, different groups of plants were harvested and stem cuttings with one node and an accessory leaf were taken, which leaf had been exposed to 18–21 short days. The cuttings were planted in soil flooded with 0.5 cm of water. The node was just covered with soil and the leaf was enveloped by a polythene bag until one week after the planting, when the cuttings had rooted. The axillary buds grew out into shoots which, as soon as they protruded from the sheath of the corresponding leaf, were covered with black paper bags. In this way they depended entirely on the induced leaf for their carbohydrate supply, and possibly also to some extent on the piece of stem of the cutting. Different groups of cuttings were exposed to photoperiods of 11, 14, 18 and 24 h consisting of 11 h daylight supplemented with low-intensity light (3000 erg/sec/cm^2), and to a 24 h photoperiod using high-intensity light (30,000 erg/sec/cm^2).

The results showed that the axillary buds, which generally had 3 leaf primordia when the cuttings were taken, differentiated one or two more when they began to grow out, and then formed an inflorescence primordium. This occurred slightly earlier in the 11 h photoperiod treatment than in the other treatments, but differences were insignificant (0.05 level). The only marked effect of the long days was that in the 24 h treatment Skrivimankoti initiated 3 or 4 leaf primordia before an inflorescence was formed. In the 24 h treatment with high light intensities the same phenomenon occurred in cuttings of 370 Basmati, whereas several shoots reverted to vegetative growth after a few days or did not initiate an inflorescence before the experiment was cut short. With Skrivimankoti all cuttings remained vegetative in the 24 h high light intensity treatment.

Experiment 347. – Working with the same methods and varieties as in the preceding experiment the possibility was investigated whether the stem could retain the floral stimulus when transferred from inductive to non-inductive day lengths. Cuttings were used consisting of smaller or larger pieces of stem, either with one, two or three nodes. Only one leaf with the corresponding bud was left intact. Other leaves and buds were removed carefully. The results indicated that the size of the piece of stem had no effect on flower formation in the shoot.

In a second series of treatments the varieties Nero di Vialone, 370 Basmati and Skrivimankoti were used. The plants were exposed to a 12 h photoperiod until flowering. Thereafter the panicle was cut off and all leaves and buds on the stem were removed, except for the one most basipetally located on the elongated stem, for this was the only bud still vegetative on the elongated stem in Nero di Vialone. A small piece of leaf sheath, just covering the bud, was left intact to prevent it from drying. The treated plants thus consisted of an intact root system and a number of long bare stems with one intact bud at the base of each stem. After the bud had started growth and become visible, it was covered with a black paper bag. Different groups of plants thus treated were exposed to day lengths of 12, 18 and 24 h. The shoots which grew out at the base of the stem all initiated inflorescence primordia after 2 (Nero di Vialone) or 4–6 (370 Basmati and Skrivimankoti) leaves had been formed. Only Skrivimankoti showed, in some plants, a delay in initiation in continuous light. No high-intensity supplementary light was used in this series of treatments.

These results indicate that the stems can retain the floral stimulus, even under long day length conditions. Observations which point to the same phenomenon have been reported by VELASCO and MANUEL (1956) in the Philippines, who found that when the stubble of Elon-elon rice was allowed to produce new tillers, these young shoots flowered in August, although the day length was then unfavourable for this very highly sensitive variety. This indicates that the floral stimulus was retained in the stubble and probably moved with the translocation of carbohydrates from the stubble to the young shoots.

3. ALTERNATING PHOTOPERIODS

To investigate the effect of alternating photoperiods on flower formation a preliminary experiment (*E. 350*) was made with the moderately sensitive varieties Balilla and Nero di Vialone. Plants of these varieties were grown in natural days until 35 days after sowing and each was thereafter exposed to sequences of short, medium and long photoperiods. Plants exposed to constant photoperiods were used as controls.

TABLE 29

NUMBER OF DAYS FROM THE BEGINNING OF THE TREATMENTS UNTIL INITIATION WHEN 35-DAY-OLD PLANTS WERE EXPOSED TO SEQUENCES OF VARYING AND CONSTANT PHOTOPERIODS (*E. 350*)

Daily photoperiods in hours to which the plants were exposed; average photoperiod in brackets	*Average number of days; leaf number in brackets*			
	Balilla		*Nero di Vialone*	
11–14–20–11–14–11–17–repeated–....(14).......	23.4	(14.8)	24.9	(14.1)
14–20–17–20–21–14–20–repeated–....(18).......	39.5	(16.0)	44.3	(15.9)
Controls:				
11	5.8	(10.9)	10.0	(11.0)
14	15.0	(12.7)	16.4	(12.3)
17	30.3	(15.1)	21.9	(13.7)
18	35.0	(15.4)	26.3	(14.2)
20	36.2	(15.5)	32.5	(14.2)
21	37.1	(15.4)	33.1	(14.5)

The experimental results presented in Table 29 show that the sequences of daily changing photoperiods delayed inflorescence initiation much more than the average photoperiods of these sequences (the 14 h and 18 h controls). In both sequences the plants seem to have responded most to the long days. In the second treatment, with predominantly long days, the duration of induction was even longer than in the 21 h control, which was the longest photoperiod used in this treatment. This effect was more marked in Nero di Vialone, with a 10-day induction period in short (11 h) days, than in the somewhat more sensitive Balilla, with a 6-day induction period under the same conditions. These results may be partly explained by the destructive effect of long days on the induced state built up in preceding short days (p. 14), but this destructive effect was previously found (p. 15) to be smaller than the effects observed in this experiment. It is likely, therefore, that, in addition to the destructive effect of long days, a second factor has also contributed to the results obtained. Possibly the observation reported in the preceding chapter (p. 13) that the destruction of the induced state at a certain stage could bring about an unusual prolongation of the induction period, has something to do with it, but this awaits further research.

4. INCREASING AND DECREASING PHOTOPERIODS

The effect of gradually increasing or decreasing photoperiods on the duration of the induction period was investigated in an experiment (*E. 351*) with the varieties Balilla and Nero di Vialone. The plants were grown under natural day length conditions until 35 days after sowing and were thereafter exposed to a range of photoperiods from 11 to 20 h in ½-hour steps. Treatments and results are presented in Table 30.

Two main points are suggested by the figures presented in Table 30, *viz.*

(1) The total duration of the induction period was apparently mainly determined by the sum of the inductive effects of the different photoperiods to which the plants were exposed.

(2) The relatively small differences in varietal photoperiodic behaviour of the two varieties caused marked differences in their response to the ranges of photoperiods used.

TABLE 30

NUMBER OF DAYS FROM THE BEGINNING OF THE TREATMENTS UNTIL INITIATION WHEN 35-DAY-OLD PLANTS WERE EXPOSED TO SEQUENCES OF INCREASING, DECREASING AND CONSTANT PHOTOPERIODS (*E. 351*)

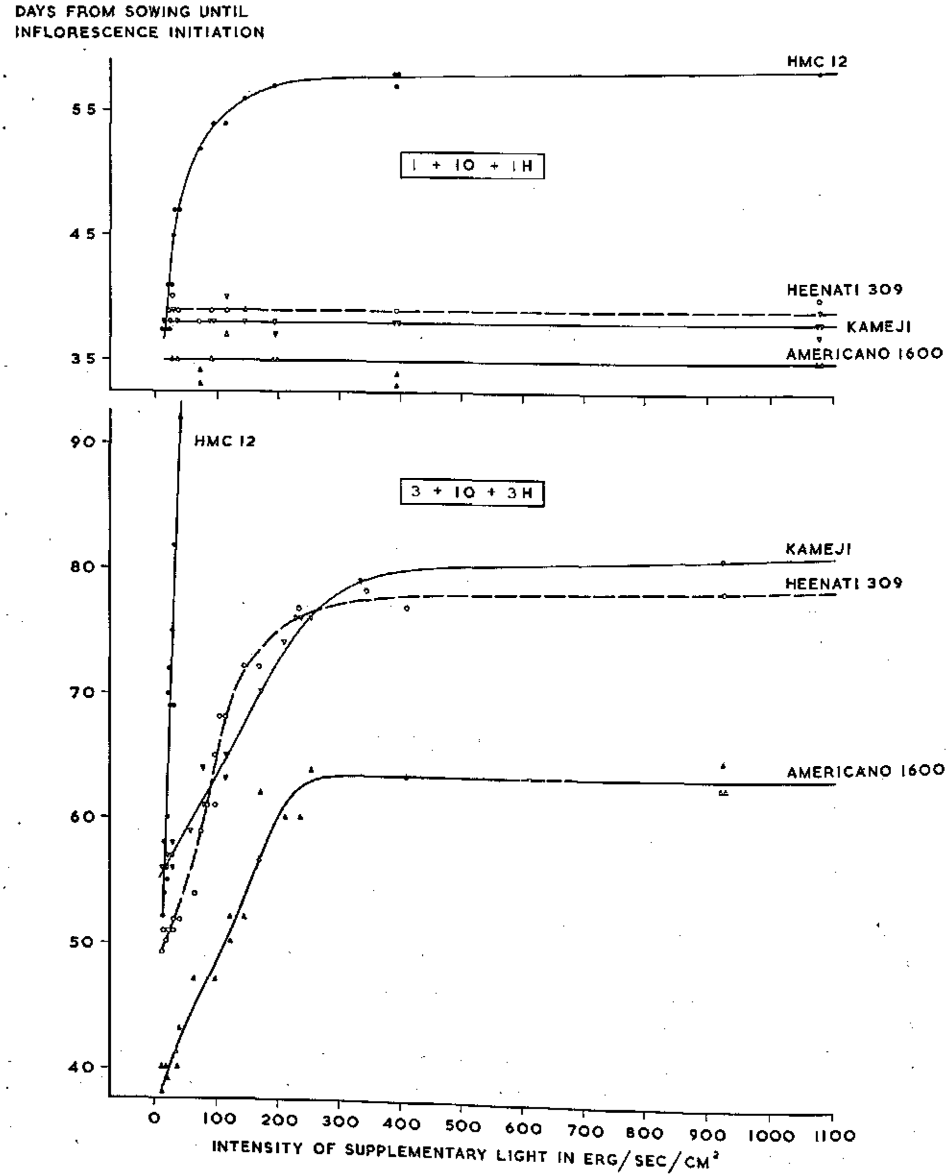
Daily photoperiods in hours to which the plants were exposed; average photoperiod in brackets	*Average number of days; leaf number in brackets*			
	Balilla		*Nero di Vialone*	
11–11½–12–etc. increasing to 20....(16)	7.8	(11.0)	15.7	(12.1)
20–19½–19–etc. decreasing to 12....(16)	16.3	(12.4)	14.9	(12.2)
Controls:				
11	5.8	(10.9)	10.0	(11.0)
16	23.7	(14.0)	19.9	(12.8)
20	36.2	(15.5)	32.5	(14.2)

At present it is not justifiable to extend these findings to rice in general, or even to generalise about the varieties used. Quite different results might have been obtained, for instance, had the range of increasing day lengths started with a 12 h or 13 h photoperiod. Furthermore, the marked effect of small differences in varietal behaviour found in this experiment is a warning that quite different results may be obtained with other varieties. The only general conclusion which seems to be justified from this (*E. 351*) and from the foregoing experiment (*E. 350*) is that the duration of the induction period is apparently delayed much more by irregular variations in successive daily photoperiods than by a gradual increase or decrease of the photoperiod.

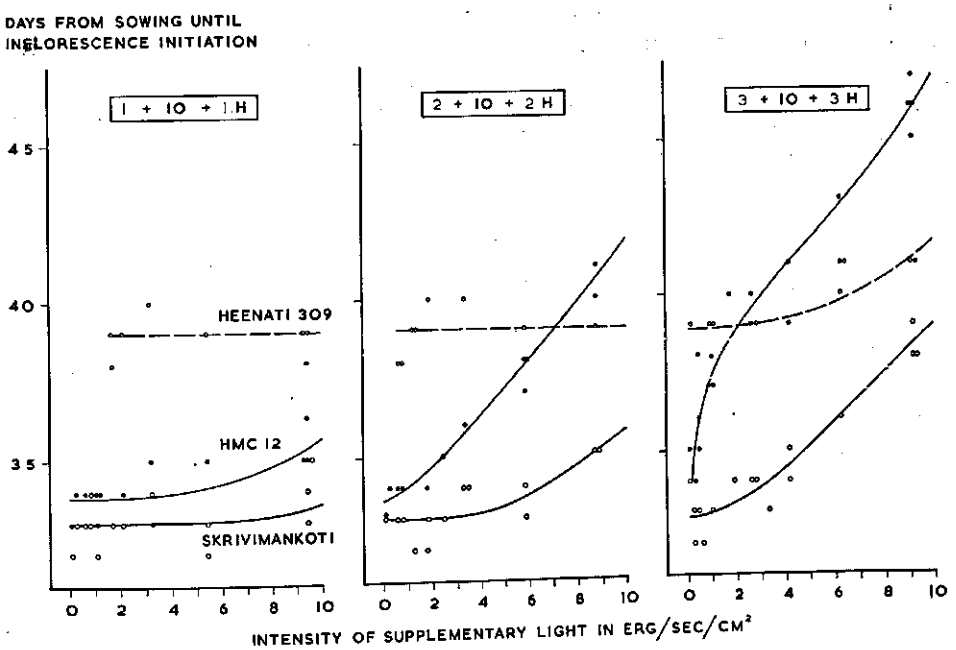
5. LIGHT INTENSITY

5.1. *Review of literature*

With few exceptions, the intensity of any supplementary artificial illumination is seldom given in published work. CHO (1930) first showed that illumination throughout the night with supplementary light as weak as 0.1 f.c. could retard the time of ear emergence by nearly 20 days in the *japonica* variety Kameji. The brighter the illumination, the stronger the retarding effect. Light intensities of over 0.65 f.c. inhibited the complete emergence of the panicle from the sheath of the flag leaf. FUKE (1931) and KUILMAN (1937) reported that daylight screened to such an extent that the plants could hardly be seen was effective as a dark period in their experiments. MIYABAYASHI (1943) exposed rice plants about 70 days after sowing to a 24 h photoperiod consisting of 9 h daylight and supplementary illumination at intensities varying from 0 to 10 f.c. He reported that the time of ear emergence was retarded for 7 days by 0.1 f.c., for 26.5 days by 1 f.c. and for 59.5 days by 10 f.c. WORMER (1954) used a daylight period of 12 h and, in addition, 6 h of supplementary light with an intensity ranging from 1 to 80 f.c. With the variety Nero di Vialone the differences in light intensity hardly affected the time of heading, a somewhat earlier heading occurred only in plants exposed to 1–2.5 f.c. as compared with higher light intensities, but the other variety tested, Kameji, showed a marked response to the differences in light intensity. The brighter the illumination, the greater the retardation of heading, particularly between 1 and 4 f.c.



Graph 80. The effect of the intensity of supplementary light on the time of initiation when a 10 h daylight period is supplemented with 2 h or 6 h of low-intensity artificial illumination (*E. 353*).



Graph 81. The effect of very low intensity supplementary light on the time of initiation when a 10 h daylight period is supplemented with 2, 6 or 14 h of artificial illumination (*E. 353*).

5.2. *Light intensity in relation to the photoperiod*

The work presented in this section is confined to the effect of the intensity of supplementary light. Data on the intensity of light breaks during the nyctoperiod will be presented in § 7. The effect of different light intensities given during the whole of the photoperiod has not been investigated.

Experiment 352. – Three factors have been considered in relation to one another in this experiment, *viz.* (1) varietal differences in sensitivity to the photoperiod, (2) the duration of the photoperiod, and (3) the intensity of the supplementary light.

Plants of the varieties HMC 12, Heenati 309, Kameji and Americano 1600 were exposed to a 10 h daylight period and low-intensity supplementary light from fluorescent tubes (daylight type) (see *Appendix,* 1.4). A whole range of different light intensities was obtained by placing the plants in rows at different distances from the fluorescent tube. The spacing between the rows was 10 cm. In addition, different plots were exposed to high-intensity supplementary light, either by using 12 fluorescent tubes (about 30,000 erg/sec/cm^2) or 3 high-pressure mercury vapour lamps (about 45,000 erg/sec/cm^2) at plant top level.

In a second series, with the varieties HMC 12, Skrivimankoti and Heenati 309, only very low light intensities were used. Data on inflorescence initiation and leaf number were recorded. By plotting the time from sowing to initiation on the ordinate against the light intensity used on the abscissa, the curves presented in Graph 80 and 81 have been obtained.

The curves in Graphs 80 and 81 clearly show that the lowest light intensity which is still photoperiodically active and the shape of the initiation curve depend on the variety and on the photoperiod. Low light intensities are more effective with long photoperiods and in varieties of high sensitivity.

The highest light intensity given (Graph 80) is about 1000 erg/sec/cm^2. A further increase in light intensity had little influence (Table 31).

TABLE 31

NUMBER OF DAYS FROM SOWING UNTIL INITIATION WHEN 10 H DAYLIGHT WAS SUPPLEMENTED WITH 6 H LAMP LIGHT OF MODERATE TO VERY HIGH INTENSITIES (*E. 352*)

Varieties	*Intensity of supplementary light in erg/sec/cm²*		
	*1,800**	*30,000**	*45,000***
Americano 1600	63.2	65.8	66.0
Kameji	81.0	85.9	86.7
Heenati 309	78.3	83.1	87.2

* Fluorescent tubes (daylight type).
** High-pressure mercury vapour lamps.

Whether the small effect of very high light intensities on the time of initiation was due to photoperiodic or non-photoperiodic effects has not been investigated.

5.3. *Light intensity at the beginning and at the end of the photoperiod*

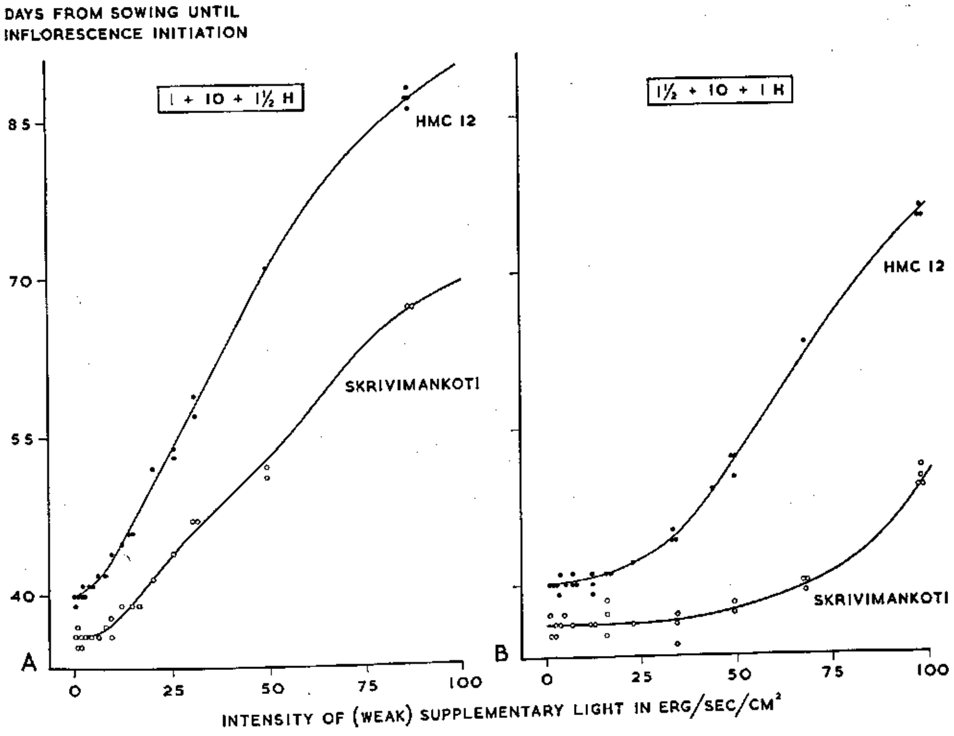
In the preceding experiment the supplementary illumination was given partly before and partly after the daylight period. The effect of low light intensities may be different when the photoperiod begins, *i.e.* after the dark period, and when the photoperiod ends, *i.e.* after the plant had been exposed to high light intensities (daylight). To investigate this point the following experiment was designed.

Experiment 353. – The varieties HMC 12 and Skrivimankoti were exposed to a 10 h daylight period, either preceded by 1½ h of high-intensity supplementary light (30,000 erg/sec/cm^2) and succeeded by 1 h of low-intensity light of different intensities, or the reverse, preceded by 1 h of low-intensity light and succeeded by 1½ h of high-intensity light. Data on inflorescence initiation were recorded. The results are presented in Graph 82.

The curves in Graph 82 clearly show that low light intensities affect inflorescence initiation markedly more when the plant is exposed to these intensities after a dark period than after a period of high-intensity light. This implies that in the preceding experiment (*E. 352*) a very low light intensity may have influenced initiation in the morning, whereas in the evening the plant reacted to the same intensity as if it was exposed to darkness. We will return to this in § 8.

5.4. *Effect of light intensity on inflorescence development*

In addition to the data recorded in *E. 352* on the time of inflorescence initiation, observations have been made on the time of heading and of flowering. With these



Graph 82. Effect of the intensity of supplementary light on the time of initiation when the low intensity light is given at the beginning (A) or at the end (B) of the photoperiod (*E. 353*).

data the influence of light intensity on the duration of inflorescence development could be measured. Little effect was found with Americano 1600 and HMC 12, but with Heerati 309, and even more so with Kameji, light intensity did affect inflorescence development to some extent in long days but not in short days, differences being at most 7 days. Observations on other varieties exposed to some fixed photoperiods (Chapter XXIV, § 8) and to natural day length, indicated that differences in light intensity during the period of supplementary light affected inflorescence development in a few varieties only. The most marked effect was found in varieties such as Tjina and Tilakchary, which are sensitive to the photoperiod during the inflorescence development stage. In some experiments, when plants were exposed to continuous illumination of high intensities, it was observed that in a few varieties, Kameji and Kibiho for instance, the extrusion of the panicle from the sheath of the flag leaf was completely inhibited by the high-intensity light. Such an effect did not occur in Tjina, however.

Summarizing the available data it may be concluded that inflorescence development is markedly affected by the intensity of supplementary light in a few varieties only, independently of their photoperiodic sensitivity in respect of floral initiation, and that the effect tends to be more marked in longer photoperiods.

6. WAVE LENGTH DEPENDENCIES

The influence of spectral composition of supplementary light on the photoperiodic response in rice has only been studied, as far as the writer is aware, by KONDO *et al.* (1942). They reported that green supplementary light had practically no effect on the time of flowering in rice.

To compare the influence on the photoperiodic response in rice of supplementary light from fluorescent tubes (daylight type) with sources emitting light with either a higher proportion of red or blue light, a preliminary experiment (*E. 354*) was made with varieties of different photoperiodic behaviour. In addition to a 10 h daylight period the plants were exposed to supplementary light, beginning 18 days after sowing, from either fluorescent tubes (Philips TL/55, daylight type), 40 Watt Philips incandescent lamps ("red" light) or 60 Watt Philips incandescent lamps with bulbs of blue glass ("blue" light).

The results (Table 32) show that red light was most active, while blue was least active and, at a relatively low intensity, it exerted an effect only in the most sensitive variety. It has to be kept in mind, however, that the "colours" used in this experiment were very impure, and that the results therefore have to be considered with caution.

TABLE 32

EFFECT OF DIFFERENCES IN SPECTRAL COMPOSITION OF SUPPLEMENTARY LIGHT ON THE PHOTOPERIODIC RESPONSE OF THREE VARIETIES; 10 H DAYLIGHT SUPPLEMENTED WITH 6 H LAMP LIGHT, EXCEPT FOR THE CONTROL WHICH RECEIVED DAYLIGHT ONLY (*E. 354*)

Supplementary light		*Days from sowing until initiation*		
Type	*Intensity in erg/sec/cm²*	*Americano 1600 (moderate sensitivity)*	*Heenati 309 (high sensitivity)*	*HMC 12 (very high sensitivity)*
"red"	1000	62.4	78.3	—
"white"	1000	63.2	76.8	—
"blue"	1000	51.9	66.6	—
"red"	50	45.0	62.8	132.9
"white"	50	41.5	53.1	93.6
"blue"	50	35.3	40.0	72.4
none (control)		35.4	39.3	34.7

7. INTERRUPTED LIGHT AND DARK PERIODS

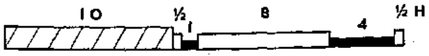
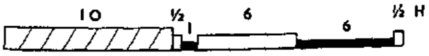
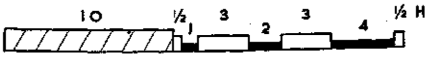
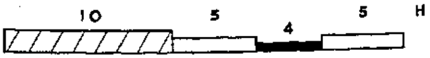
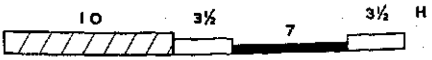
7.1. *Interrupted light periods*

Daily interruptions of the photoperiod were studied first by MIHARA (1923) who exposed rice plants grown in natural days to 4 h of darkness between 10 a.m. and 2 p.m. Flowering occurred about a month earlier than in untreated plants. FUKE (1931) showed that a continuous 8 h photoperiod was more effective in accelerating flowering than a discontinuous photoperiod, *viz.* 4 h in the morning and 4 h in the afternoon. KONDO *et al.* (1932, 1933) have worked extensively on interrupted photoperiods. With most of their treatments, which were within the range of 8 to 12 h, the differences in the time of heading were too small to be conclusive. In a second series, plants of the varieties Shinriki and Kibiho were exposed to light from 6 to 10 a.m. and from 2 to 10 p.m. (continuous nyctoperiod of 8 h). No heading was found in this treatment before the experiment was terminated, and only those plants which received a continuous photoperiod of 16 h (nyctoperiod 8 h), produced panicles shortly before the end of the experiment. Non-photoperiodic effects were probably responsible for these results: the plants in the former treatment received much less daylight than in the latter treatment. BEACHELL (1943) interrupted natural days for 5 hours, in one plot from 8 a.m. until 1 p.m. and in another from 1 p.m. until 6 p.m. In general, heading was later than in the controls (natural days) and in sensitive varieties was delayed more by a dark period in the afternoons than in the mornings, but this was reversed in less sensitive varieties. The differences were small, however, and may well have been attributable to a retardation of plant growth through lack of light.

In summary it can be said that several treatments were insufficiently accurate to permit any conclusion, but that some results of the work of FUKE (*l.c.*) and KONDO (*l.c.*) indicated that the response of the plants was more closely related to the length of the continuous nyctoperiod than to the total daily photoperiod.

TABLE 33

EFFECT OF DAILY INTERRUPTIONS OF THE PHOTOPERIOD ON THE TIME OF INFLORESCENCE INITIATION (*E. 355*)

No.	▨ DAYLIGHT □ LAMP LIGHT 3000 ERG/SEC/CM² ■ DARKNESS	*Days from sowing until initiation; leaf number between brackets*	
		Americano 1600	*Heenati 309*
	periods of light and darkness per 24 h cycle*		
1		76.2 (15.0)	126.2 (19.2)
2		70.3 (15.1)	114.1 (18.0)
3		74.1 (14.9)	123.9 (19.5)
4	 20 HOUR PHOTOPERIOD CONTROL	75.6 (15.0)	125.8 (19.4)
5	 18 HOUR PHOTOPERIOD CONTROL	71.4 (14.7)	112.7 (18.1)
6	 17 HOUR PHOTOPERIOD CONTROL	66.9 (14.5)	93.1 (16.3)

* Treatments started 18 days after sowing.

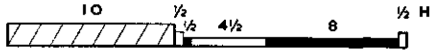
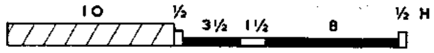
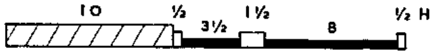
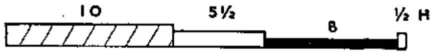
To investigate the effect of daily interruptions of the photoperiod on the time of inflorescence initiation under accurately controlled photoperiodic conditions, an experiment (*E. 355*) was made with the varieties Americano 1600 and Heenati 309. The results (Table 33) show clearly that the response of the plants is determined by the longest dark period.

7.2. *Interrupted dark periods*

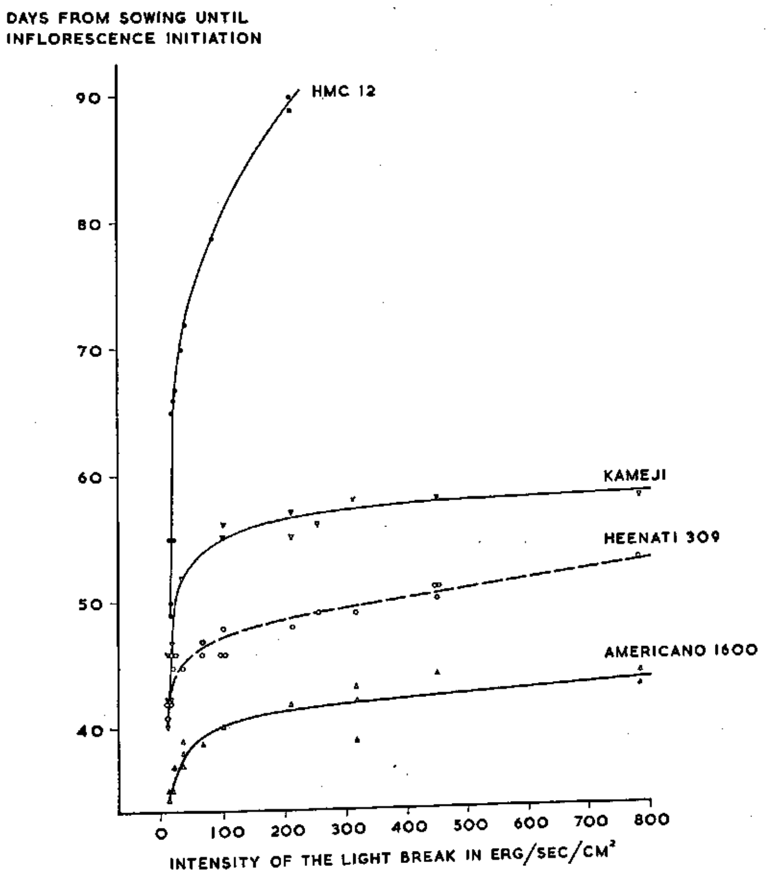
Luong and Okuda (1950) interrupted the nyctoperiod of an 8 h 45 min photoperiod for 15 minutes in the middle of the dark period. A 9 h photoperiod, natural day length and a 24 h photoperiod were used as controls. The short day and broken night treatments were applied 10 days after transplanting and lasted only 9 days. Plants were then transferred to natural days and data on the time of heading were recorded. Differences between treatments were small. In the 3 varieties used heading

TABLE 34

EFFECT OF DURATION AND INTENSITY OF LIGHT BREAKS DURING THE DARK PERIOD ON THE TIME OF INFLORESCENCE INITIATION (*E. 356*).

No.	▨ DAYLIGHT ☐ LAMP LIGHT 3000 ERG/SEC/CM² ▭ LAMP LIGHT 100 ERG/SEC/CM² ▬ DARKNESS	*Days from sowing until initiation; leaf number between brackets*	
		Americano 1600	*Heenati 309*
	periods of light and darkness per 24 h cycle*		
1		46.0 (12.7)	63.6 (14.1)
2		42.3 (12.0)	52.1 (13.3)
3		40.2 (12.0)	47.8 (13.0)
4		46.4 (12.8)	65.0 (14.3)
5		55.7 (13.3)	73.5 (15.0)
6	 16 HOUR PHOTOPERIOD CONTROL	63.5 (14.1)	78.0 (15.2)
7	 11 HOUR PHOTOPERIOD CONTROL	35.4 (11.0)	41.3 (12.1)

Treatments started 18 days after sowing.



Graph 83. Effect of differences in light intensity during the ½ h light break in the cycle 11 h light – 4½ h dark – ½ h light – 8 h dark on inflorescence initiation (*E. 357*).

was earliest in the short-day treatment, followed by natural day length, the broken night treatment and the 24 h photoperiod. This indicates that the photoperiodic response of the plants tended to be affected most by the longest uninterrupted nyctoperiod. The treatments were very short and included several photoperiodic and non-photoperiodic effects on initiation and inflorescence development. Definite conclusions about the influence of the interrupted dark period on the photoperiodic response of the plant are, therefore, not justified.

To investigate the effect of the duration and intensity of a light break during the dark period, an experiment was made with the varieties Americano 1600 and Heenati 309 (Table 34).

The results show that with the light intensity of 100 erg/sec/cm² the effect of a light break during the nyctoperiod was determined by the product of its duration and intensity. With the 3000 erg/sec/cm² light intensity the results indicated a similar tendency, but this was much less clear, whereas the effects of the two light intensity treatments, 100 and 3000 erg/sec/cm², were not comparable on the basis of the products of their duration and intensity. This indicates that the effect of the light intensity on the time of initiation did not increase markedly between 100 and 3000 erg/sec/cm^2. To investigate this point a second experiment (*E. 357*) was made with four varieties. The treatments used were in principle similar to treatment no. 4 in Table 34, but the light intensities to which different rows of plants were exposed varied between 12 and 780 erg/sec/cm^2. The results are presented in Graph 83.

The curves in Graph 83 show that there is a linear relationship between light intensity and the delay in floral initiation at very low light intensities, but not, for instance, between 100 and 800 erg/sec/cm^2, where most curves begin to approach an asymptote, which explains the results obtained in the preceding experiment (*E. 356*).

8. NATURAL DAY LENGTH

8.1. *General outline*

In the tropics the influence of natural day length on the time of heading in rice has been appreciated for a long time. The old classification of date-fixed and period-fixed varieties, winter and summer varieties, and *maha* and *yala* varieties *, is based on this effect, although the cause of the differences in the vegetative periods was not fully understood until the late 1930s. KUILMAN (1937) was probably one of the first to suggest that the slight variations in day length occurring in the tropics could induce differences in the time of flowering in the so-called date-fixed varieties. A few years later SCRIPČINSKIĬ (1940) and VAN DER MEULEN (1941) came to the same conclusion. CHANDRARATNA (1948), KERLING (1948) and JAGOE (1952) showed in their experiments that this supposition was right.

The type of experiment which is generally used to investigate the influence of natural day length is the date-of-sowing experiment. These experiments are undoubtedly of great importance for the practical grower, but they are not very suitable for research on photoperiodism, since so many specific and non-specific effects may influence the photoperiodic response of the rice plants under these conditions.

Temperature, the total light energy to which plants are exposed during different growth stages, the quality of the irrigation water, the E_h of the soil, the humidity of the air, etc., are among the non-photoperiodic factors which may influence the time of initiation to a lesser or greater extent under field conditions. A study of these factors is presented in the subsequent chapter. This section will be confined to the photoperiodic effect of the natural day.

Several light conditions may influence day length. Of these, the most important are: cloudiness, haze and fog (which affect light intensity), the duration of the twilight periods in morning and evening (which affects day length and which varies with season), and seasonal variations in the period between sunrise and sunset (which affect day length). We can thus distinguish both seasonal and daily changes in day length which may occur during the period of floral induction when plants are exposed to natural days. Each of these factors will be discussed in more detail in the subsequent parts of this section.

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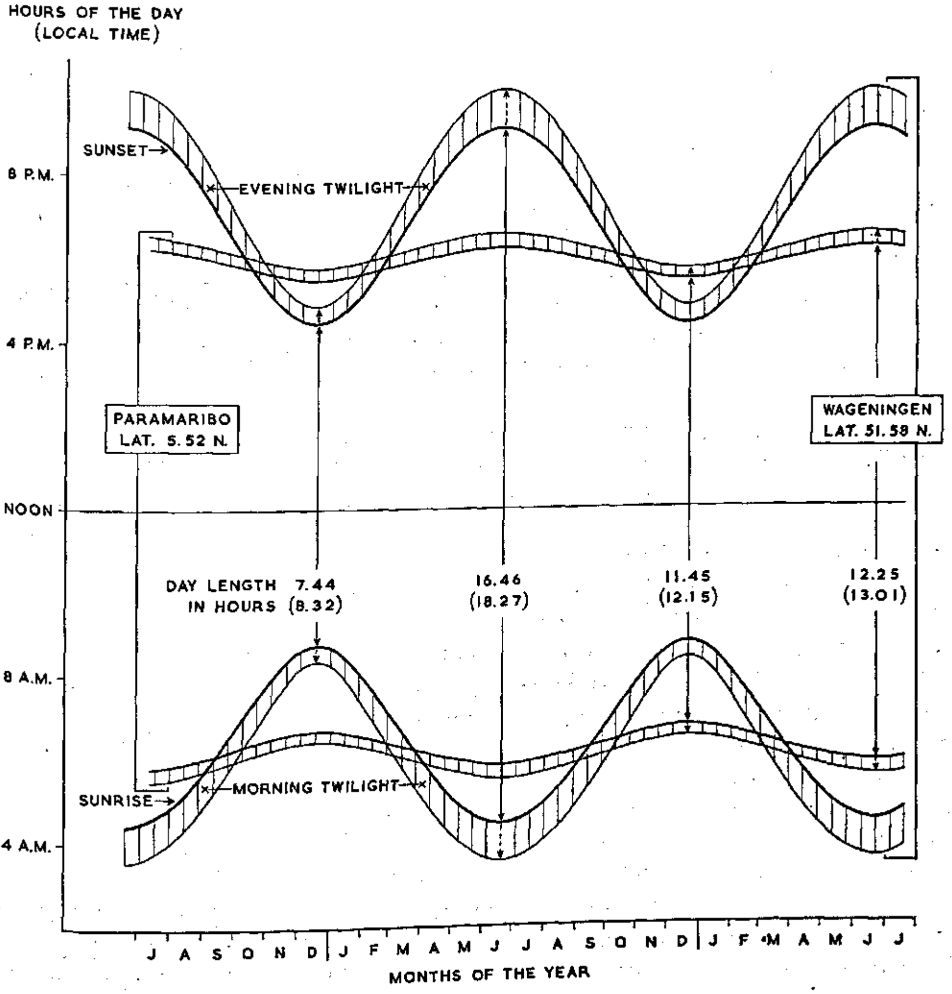
* *Yala*, SW monsoon season; *maha*, NE monsoon season.

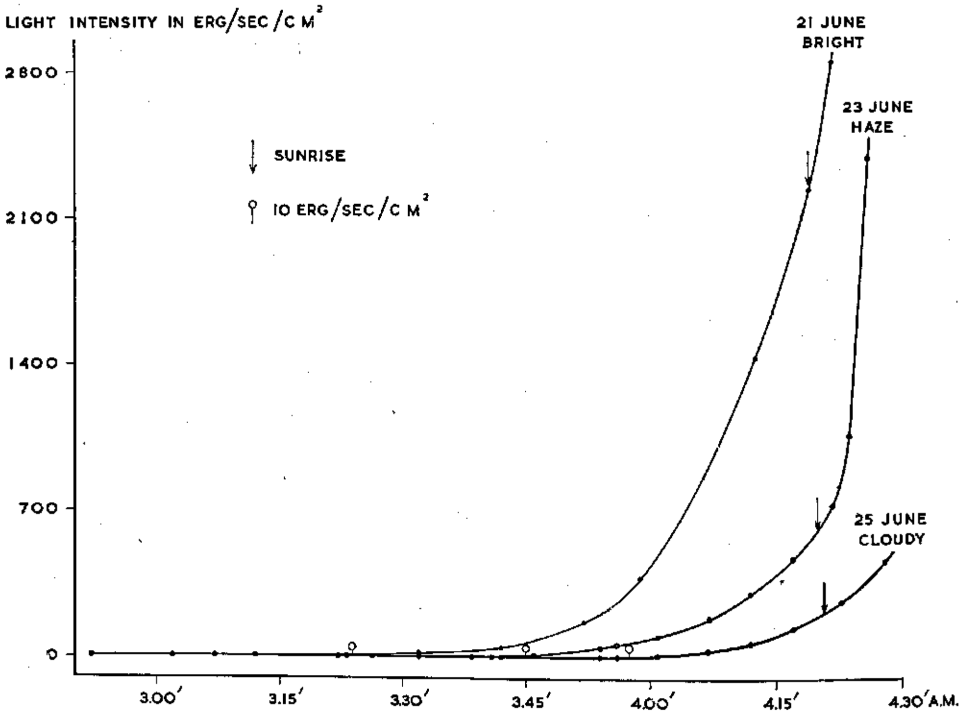
8.2. *Seasonal changes in day length*

The light intensity of the greater part of the twilight period in morning and evening is sufficiently high to affect flower formation. The duration of the twilight period differs according to season and latitude (Graph 84) and actually accentuates the seasonal differences in day length.

When the seasonal variations in day length are taken into consideration, it is evident that rice plants sown at different dates may be exposed to either increasing or decreasing day lengths or combinations of these during their induction period. Different varieties may react differently to these conditions according to their photoperiodic behaviour (*cf.* § 4). It must be kept in mind, however, that the day length curves in Graph 84 are constructed for the theoretical case of perfectly clear days all



Graph 84. Seasonal differences in the period between sunrise and sunset and of twilight (with a minimum intensity of 10 erg/sec/cm^2) for perfectly clear days at Paramaribo (Surinam) and Wageningen (The Netherlands).



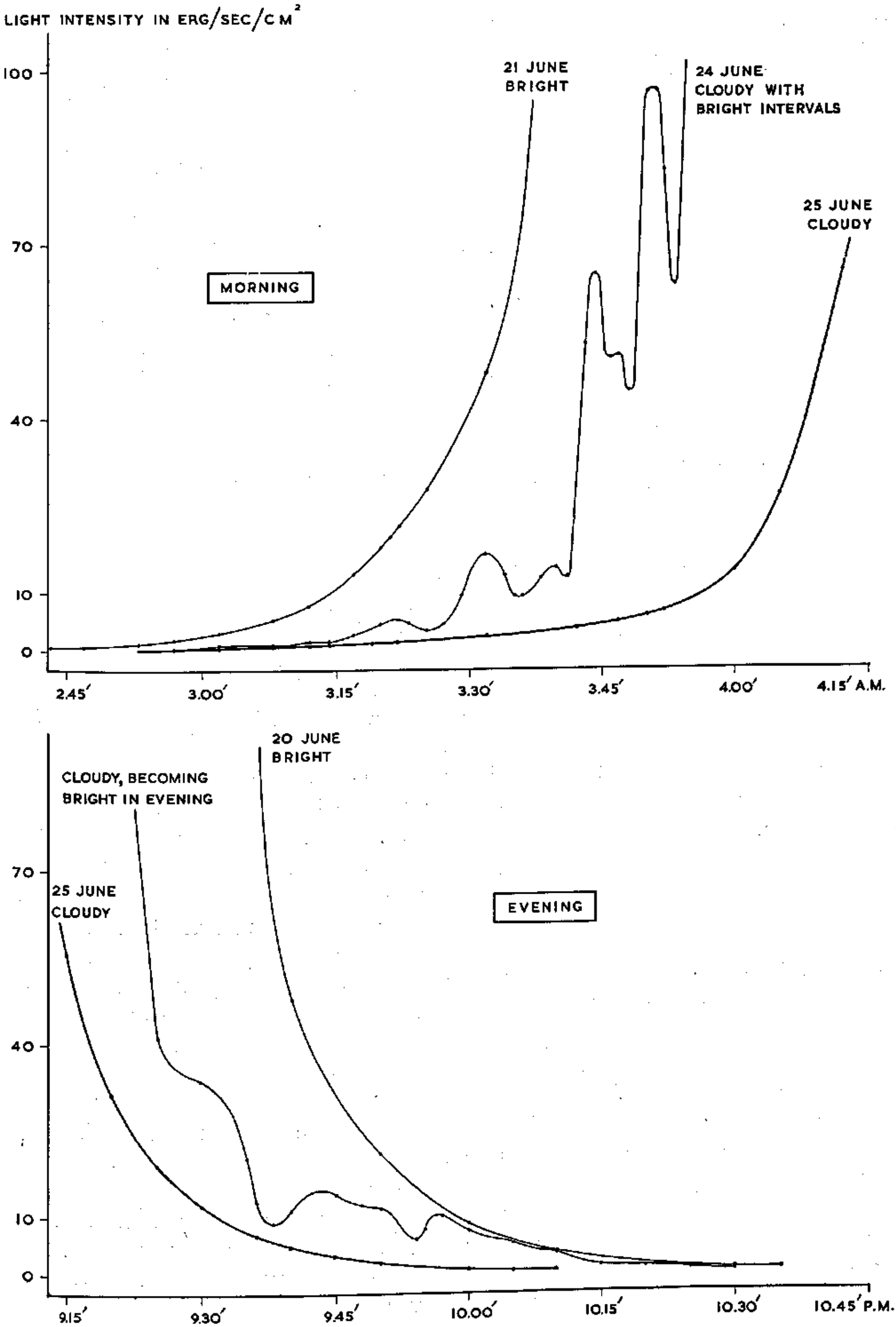
Graph 85. Effect of weather conditions on the course of light intensity during the morning twilight period in summer at Wageningen (The Netherlands).

the year round, and that the photoperiodic effect of natural days is, in fact, much more complicated than a seasonal variation in day length, as will be discussed in more detail in the subsequent parts of this section.

8.3. *Daily changes in day length*

The duration of the twilight period in morning and evening may be markedly affected by weather conditions. Haze, fog and cloudiness can reduce light intensity considerably and thus curtail the duration of the photoperiodically active period of twilight. This reduction in light intensity may be a regular one, for instance, in the case of a completely clouded sky, or an irregular one, *i.e.* when clouds and bright periods alternate. At Wageningen (Lat. 51°58′ N) many measurements have been made of light intensities during the twilight periods. The data obtained have been used to construct curves by plotting light intensity in erg/sec/cm² against the time of the day in hours and minutes. Some examples of these curves are presented in Graphs 85 and 86.

In general it may be assumed that the photoperiodic effectiveness of daylight increases in the morning with an increase in intensity until a certain saturation value is reached (*cf.* § 5.2), and then shows little change until the light intensity decreases in the evening. The changes in light intensity and in effectiveness of the light during the twilight period are mainly responsible for daily changes in the photoperiodically active day length and these will be examined more closely in this section.



Graph 86. Effect of weather conditions on the course of light intensity in early morning and late evening in summer at Wageningen (The Netherlands).

In Graph 85 the point has been indicated where the morning twilight reaches an intensity of 10 erg/sec/cm^2. When this light intensity was used as the limit of day length in morning and evening, differences in day length between bright sunny days and cloudy rainy days, which occurred within a week's time, were found to be at most 2.04 h. The choice of the value of 10 erg/sec/cm^2 is entirely an arbitrary one, however, and does not indicate the lowest light intensity which is still photoperiodically active. No constant value can be given for such an intensity, since it depends on varietal photoperiodic behaviour. Earlier (§ 5.2) it was found that low light intensities are more effective with long photoperiods and in varieties of high sensitivity as compared with short photoperiods and varieties of moderate sensitivity. Experimental results (§ 5.3) furthermore showed that rice plants are more sensitive to low light intensities after a dark period than after a period of high-intensity light. It is probable, therefore, that the plants respond to a lower light intensity in the morning than in the evening and that the total duration of the photoperiodically active light period in natural days is longer for highly as compared with moderately sensitive varieties.

It is probable that twilight is relatively more active than daylight, since it contains a higher proportion of the red part of the spectrum (*cf.* § 6), and it is likely that very sensitive varieties can react to very low light intensities in the morning. Under the prevailing changeable weather conditions at Wageningen it was unfortunately not possible to investigate the actual magnitude of the lowest light intensity in natural days which was still photoperiodically active, but judging by the experimental results obtained under controlled conditions (§ 5.6), it may be considered possible that, with very highly sensitive varieties, intensities in the order of 0.08–6.0 erg/sec/cm^2 in the morning and 8–35 erg/sec/cm^2 in the evening (dependent on day length, *cf.* § 5.2), are still effective.

In the range of very low light intensities in early morning and late evening, an alternation of clouds and bright periods may cause light intensities to fluctuate markedly (Graph 86) and to surpass or drop below the lowest still photoperiodically active intensity at irregular intervals, thus causing irregular changes in the effectiveness of the light and irregular interruptions of the photoperiod. Experimental results (§ 7) showed that with interrupted photo- or nyctoperiods the plants reacted to the longest uninterrupted nyctoperiod, while the effect of light breaks depended on their intensity. In the case of twilight these intensities are so low that the plants are likely to respond as if exposed to a nyctoperiod longer than the longest uninterrupted one, while the irregular differences in the effectiveness of twilight are also likely to shorten the duration of the effective photoperiod.

When dark cloudy weather, prevailing over long periods, is interrupted by one or a few bright sunny days, the photoperiodic effect will be one of relatively "short" days with one or a few intervening "long" days. Experimental results obtained so far (*cf.* Chapter XXIV, § 4) showed that intervening long days had a destructive effect on the induction built up in preceding short days, which effect depended on the state of induction and on varietal photoperiodic behaviour. Long days were in this respect more effective at an early than at an advanced state of induction, and in highly as compared with moderately sensitive varieties.

The reverse, *i.e.* bright weather interrupted by one or a few dark cloudy days ("long" days with a few intervening "short" days) will probably have approximately the same effect as continuous "long" days, although under certain conditions the destruction by long days of an early stage of induction built up under short days has been found (Chapter XXIV, § 4.3) to cause an unusual prolongation of the vegetative period of the plant. Changeable weather conditions prevailing over long periods may cause irregular differences in daily photoperiods. Under controlled conditions (§ 3) these have been found to be able to cause a delay in inflorescence initiation which may markedly exceed the effect of the longest photoperiod to which the plant was exposed.

Seasonal changes in day length bring about a gradual increase or decrease of the daily photoperiod (*cf.* 8.2) and will normally occur in combination with one or more of the above-mentioned specific light effects.

From this survey it appears that the photoperiodic effects of some of the above-mentioned weather conditions are so complicated that in many cases no accurate estimation of the photoperiodic effect of the natural day is possible. Furthermore, only the main photoperiodic factors have been mentioned in this brief survey. There may be other effects which influence the perception of the photoperiodic action under conditions of low-intensity light, such as the water film which covers leaves exposed to rain, possible specific effects of dense fog, etc., but these are not likely to be of much importance.

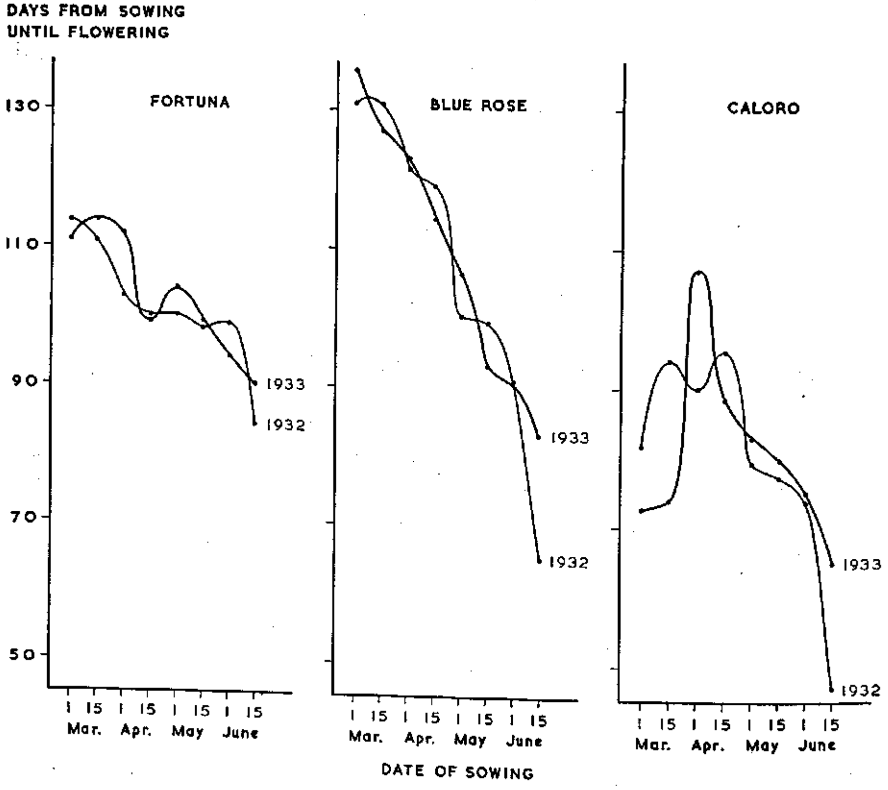
8.4. *Seasonal changes in cloudiness*

If in a particular area weather conditions show a regular annual pattern, for instance, in the case of a summer or winter rainy period, cloudiness will naturally also follow this pattern and one could then speak of seasonal changes in cloudiness. When the rainy period covers a long period of dark cloudy weather, not interrupted by bright days, and when the dry period covers a long period of bright sunny days, not interrupted by rainy days – *i.e.* conditions which occur in some of the monsoon areas – then weather conditions may cause a seasonal fluctuation of the photoperiodically active day length which may either accentuate or diminish the differences in day length between the summer and winter seasons.

At relatively high latitudes the effect of weather conditions on the photoperiodically active day length will be comparatively of much less importance for the response of the locally grown varieties (which are at most of a fairly high sensitivity to the photoperiod) than the seasonal variations in day length, but in the tropics, where such variations are small, daily and seasonal changes in cloudiness are comparatively much more important for the response of extremely sensitive tropical varieties, and at the equator they may be the only changes in day length which occur. In the next part, § 8.5, the practical consequences of these conditions on the time of flowering in paddy rice exposed to natural days will be discussed.

8.5. *Effect of sowing date*

In the temperate zone rice can be grown in the warm summer season only and, as a consequence, sowing dates are limited to a few months of the year. At these latitudes the very marked seasonal differences in day length and the effect of temperature are likely to mask most other effects on the duration of the vegetative period of the rice plant. As an example the date-of-heading curves are presented in Graph 87 of a sowing date experiment made in the U.S.A.



Graph 87. Effect of sowing date on the date of heading in three rice varieties at Crowley (Lat. 30° 11′ N), Louisiana, U.S.A. Data after JENKINS (1936).

The curves show that the dates of heading were correlated to some extent with the increasing and thereafter decreasing day length in one variety, Caloro, only. In the other two varieties a marked delay in heading occurred when the plants were sown very early in the year. This cannot be explained by day length effects only and was due probably to low temperatures early in spring which seem to have affected these varieties markedly more than Caloro. Thereafter day length effects would probably have become more important and would have affected mainly the duration of the vegetative period later in the year. This with the notable exception of the summer conditions in 1932, which caused very early heading in all varieties used, probably as a result of high temperatures during induction and floral initiation.

The data published by JENKINS (1936) are, in fact, much more extensive than those presented in Graph 87 and cover 5 years (1929–1933) and 12 varieties. In general, varietal behaviour showed more or less the same pattern as with Fortuna and Blue Rose and the effect of natural days in 1929–1931 was roughly comparable with the results obtained in 1933; the most marked variations in the dates of heading occurred at the very early sowing dates.

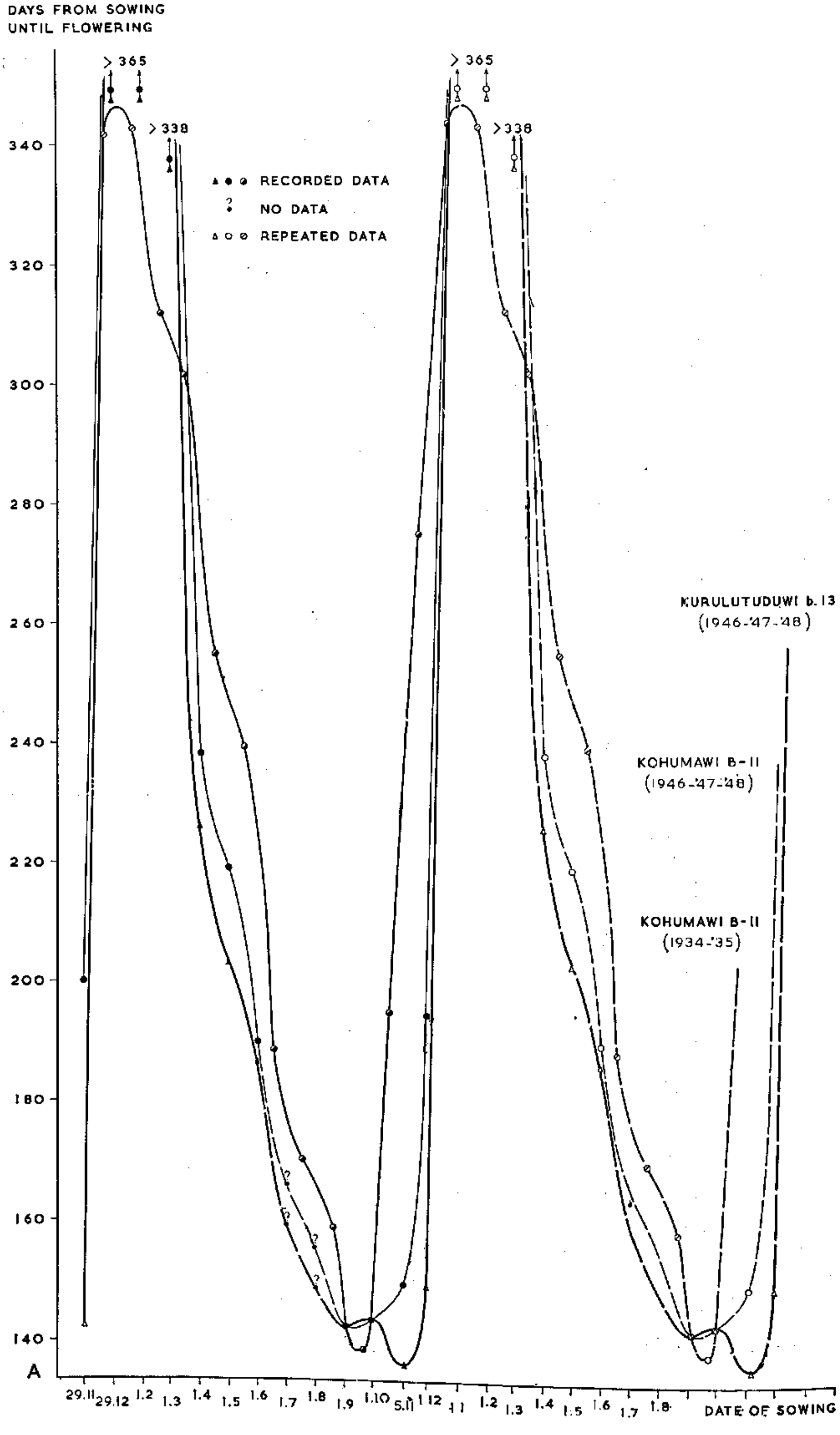
In the tropics, where rice can be grown throughout the year, some interesting results have been obtained in sowing-date experiments. Compared with experiments in the temperate zone, the interpretation of the data obtained in these experiments is complicated less by factors not related to photoperiodism. In particular this is because the variation in temperature between day and night, between successive days, and even between seasons, is rarely of a sufficient magnitude to affect the photoperiodic reaction of the plant (*cf.* Chapter XXVI, § 3).

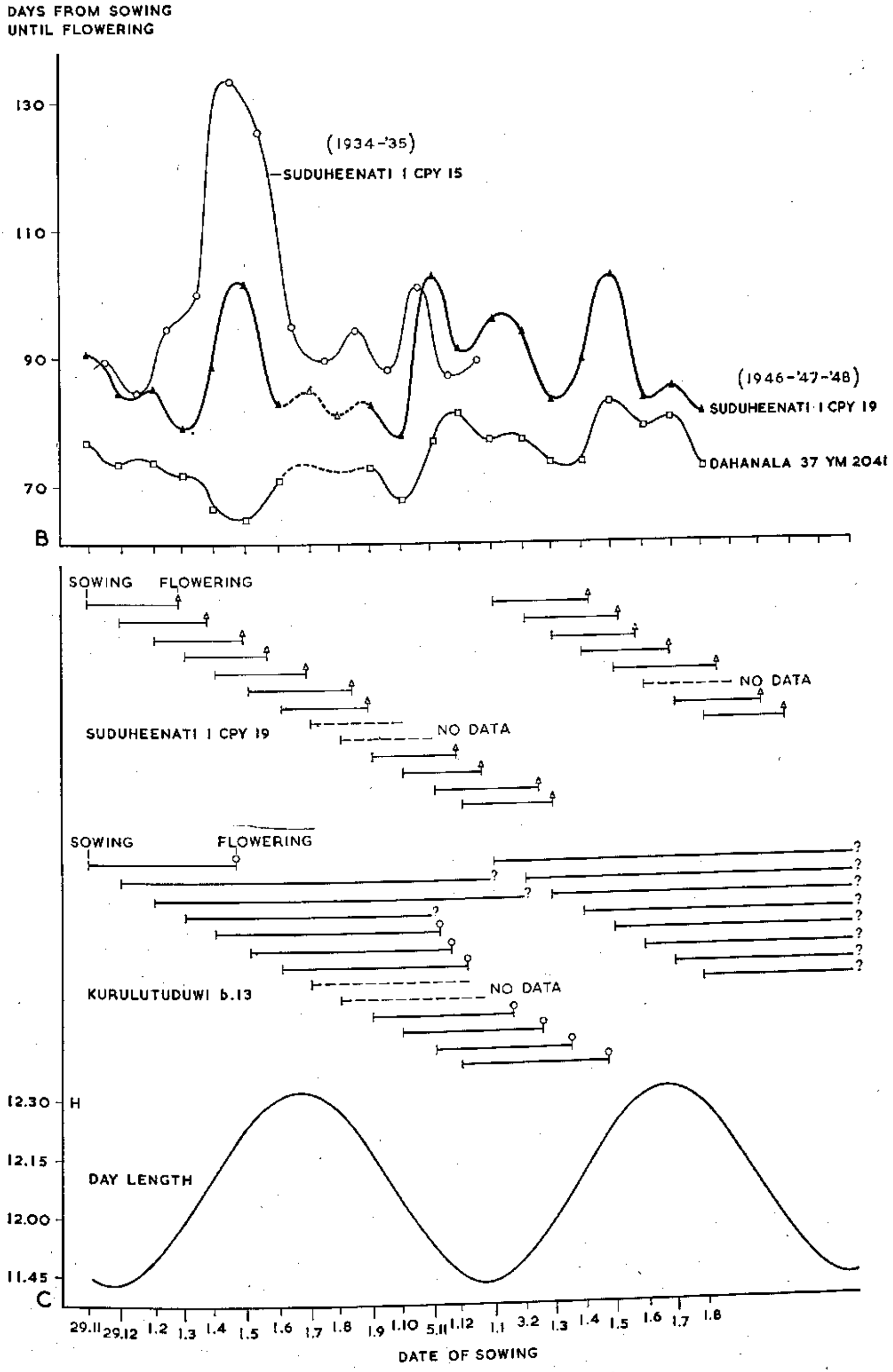
As examples of the results obtained with sowing-date experiments in the tropics, the date-of-heading and flowering curves are presented in Graphs 88 and 89 for varieties differing widely in sensitivity, and in the duration of the insensitive period of the juvenile phase. The curves in Graph 88 show that in the very highly sensitive varieties seasonal differences in day length have a very great effect on the growing period. These differences do not explain, however, the unusual prolongation of the growing period to more than a year of plants exposed to the longest days during part of their induction periods, since, at an advanced age, these plants have been exposed to the shortest days of the year. An accurate interpretation of this phenomenon is not possible, since no detailed data of growth conditions, meteorological conditions or inflorescence initiation are available, but it may be suggested that the very long growing period is due to either: (1) a specific photoperiodic effect, (2) senility of the plant and/or physiological disorders, (3) non-photoperiodic effects caused by environmental conditions or (4) a combination of these factors.

In respect of specific photoperiodic effects it is possible, for instance, that a phenomenon similar to that found earlier under controlled conditions had occurred (p. 13), *viz.* that a destruction by long days of an early state of induction built up under short days caused the plants to remain vegetative for a very long period or that irregular changes in day length, caused by an irregular alternation of cloudy and bright days during part of the induction period, brought about a delay in initiation exceeding the effect of the longest photoperiod to which the plant was exposed (*cf.* § 3). It is remarkable, in this respect, that the curve of the variety Kohumawi B-11 for the exceptionally dry and sunny season 1934–1935 follows the seasonal variation in day length much more regularly than the 1946–'47–'48 curve, while only in the latter case sowing at the end of December or the beginning of February caused a delay in flowering of more than a year (the plots were discarded after one year). The second point, senility of the plant and/or physiological disorders, will be discussed in the next section, while non-photoperiodic effects may be assumed to have been relatively small under the conditions at the experimental stations (*cf.* Chapter XXVI, § 4).

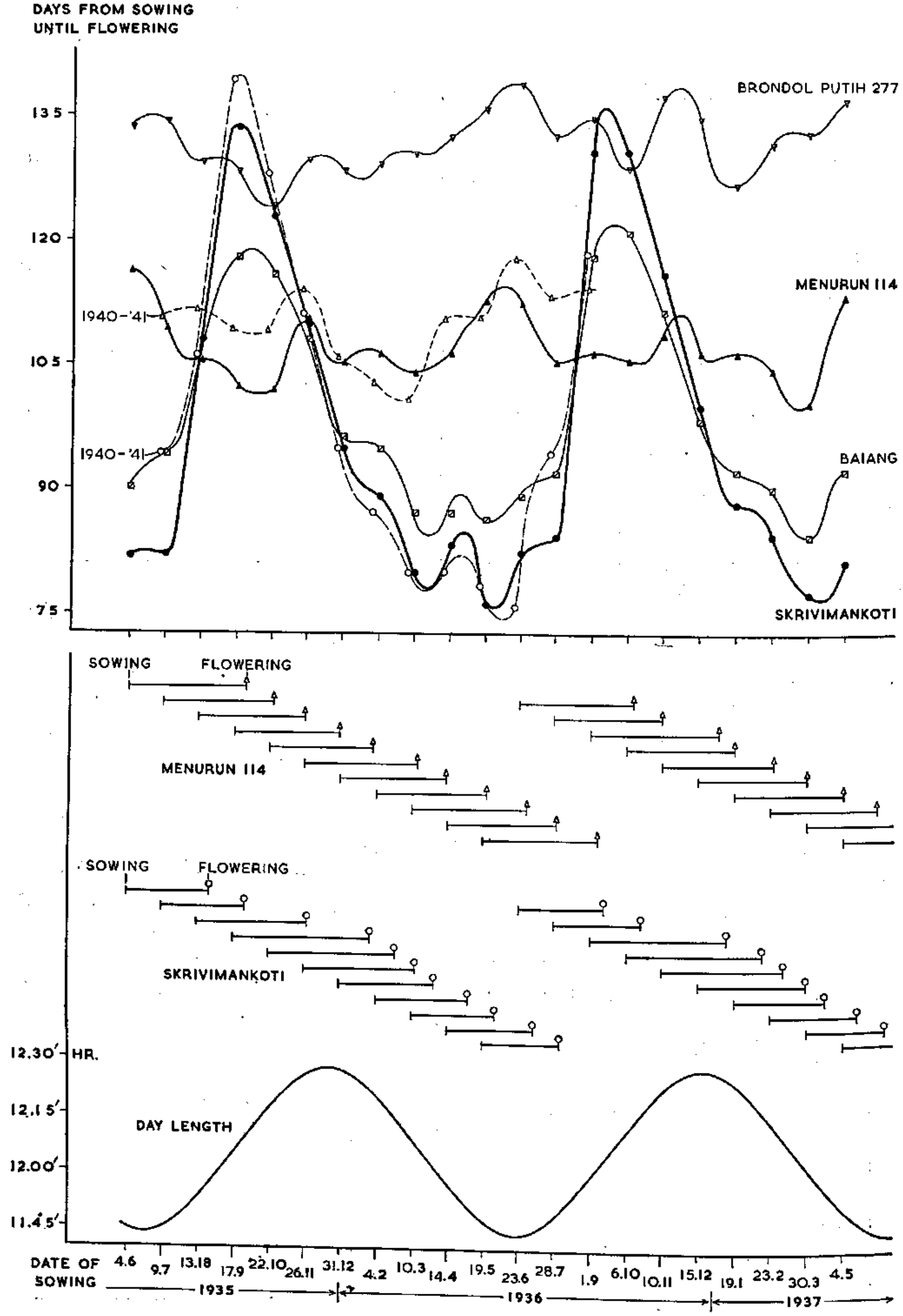
The curves in Graph 89 again show a clear response of the highly sensitive varieties to seasonal differences in day length, and a response of the moderately sensitive varieties which is much less regular and which seems partly the opposite: some peaks of the curves correspond with the shortest day length conditions of the year.

The meteorological conditions at Buitenzorg are characterized by a wet monsoon in the "summer" period and a dry monsoon in the "winter" period. As a consequence, long periods of cloudy weather occur in the period with the longest days, and most bright weather in the period with short days. In the transitional periods cloudy and bright days normally alternate irregularly, whereas rainy days often occur also during the dry monsoon. The intensity of cloudiness and the number of cloudy days may vary markedly in different years, but a very high number of rainy days is normal (see Table 35, p. 77).


DAYS FROM SOWING UNTIL FLOWERING
> 365
> 338
> 365
> 338
340
320
300
280
260
240
220
200
180
160
140
A
▲ ● ⊘ RECORDED DATA
? NO DATA
△ ○ ⊘ REPEATED DATA
KURULUTUDUWI b.13 (1946-'47-'48)
KOHUMAWI B-11 (1946-'47-'48)
KOHUMAWI B-11 (1934-'35)
?
?
?
29.11
29.12
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
1.10
5.11
1.12
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
DATE OF SOWING



Graph 88. Effect of sowing date on the date of flowering in three *maha* varieties (A) and three *yala* varieties (B) at Peradeniya (Lat. 7° 19′ N, elev. 470 m), Ceylon. Data after CHANDRARATNA (1948) for the varieties Kohumawi B-11, Kurulutuduwi b. 13, Suduheenati 1 CPY 19 and Dahanala 37 YM 2041; HAIGH (1936), for the varieties Kohumawi B-11 (1934–'35) and Suduheenati 1 CPY 15.



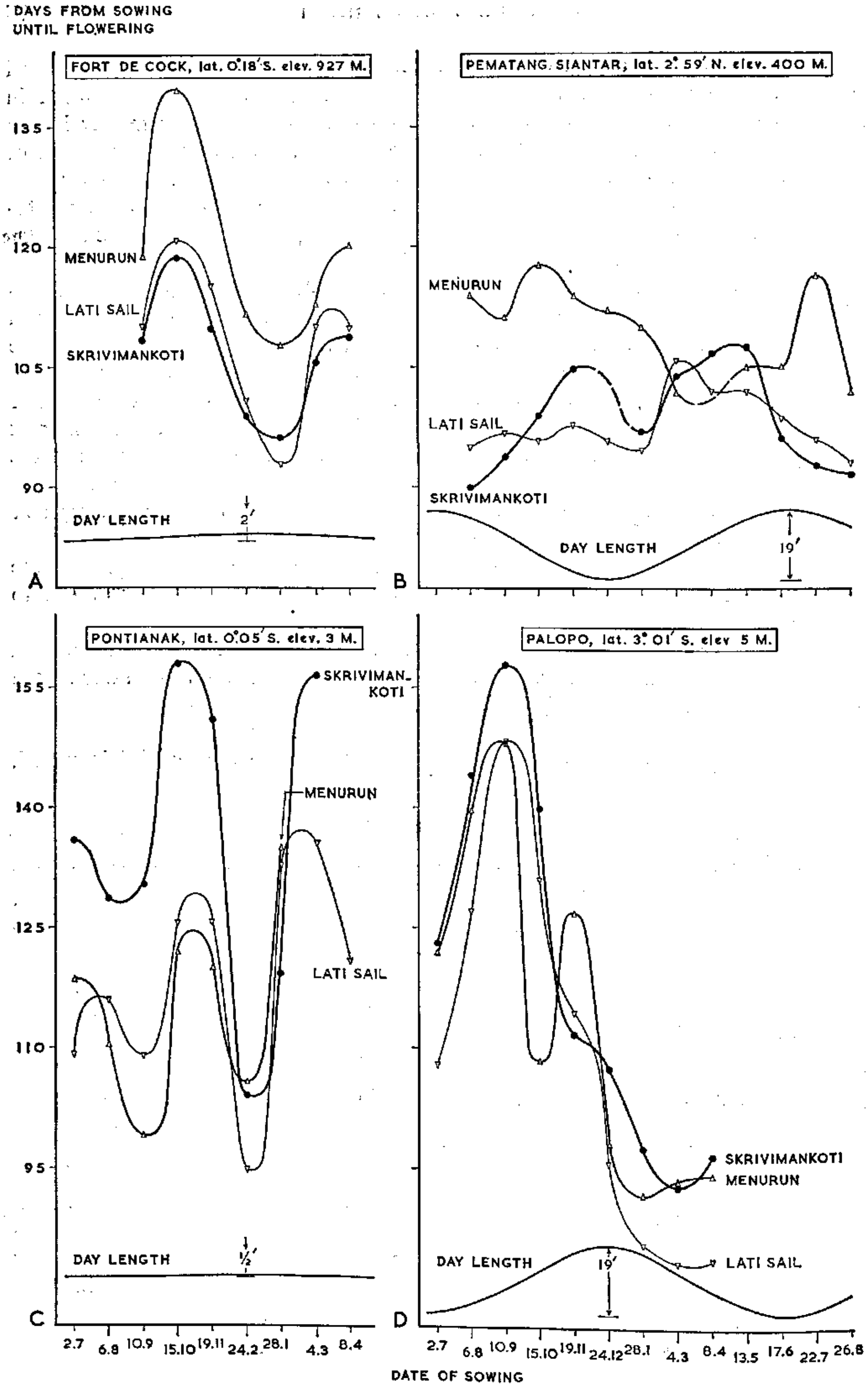
Graph 89. Effect of sowing date on the date of heading in two *indica* (Baiang and Skrivimankoti) and two *semi-japonica* (*bulu*) varieties (Brondol Putih 277 and Menurun 114) at Buitenzorg (Lat. 6° 32′ S, elev. 266 m), Java. Data after VAN DER MEULEN (1941).

With this general pattern of seasonal weather conditions in mind, the general course of the curves of the highly sensitive varieties Baiang and Skrivimankoti in Graph 89 may be explained by assuming that seasonal differences in day length caused the main maxima and minima in these curves, while day length effects of cloudiness were responsible for the secondary maxima and minima. The latter were probably mainly caused by irregular differences in the length of the daily photoperiod which occurred particularly in the transitional periods between wet and dry monsoon and in rainy spells in the dry monsoon.

The moderately sensitive *bulu* varieties Brondol Putih 277 and Menurun 114 reacted differently and were apparently more affected by irregular daily changes in cloudiness than by seasonal changes in day length, which may also explain why the curves of these varieties are more irregular in shape than those of the highly sensitive varieties (*cf.* Graph 88B). Furthermore, a comparison of the 1935–1936 and 1940–1941 curves of the varieties Menurun 114 and Skrivimankoti, clearly shows that in different years markedly different curves may be obtained for Menurun 114, but that the curves of Skrivimankoti differed significantly only in the period of short days, when seasonal differences in day length apparently became relatively less important (*cf.* Graph 71 for the effect of photoperiods of 12 and 13 h).

It may be asked whether it is justifiable to ascribe the maxima and minima in the curves which are not correlated with seasonal differences in day length mainly to specific day length effects caused by cloudiness. In our opinion there is sufficient evidence in favour of this view to accept it. Most of the data involved have been discussed earlier in this chapter, while the specific effect of cloudiness on day length could be confirmed in the following experiment:

Experiment 358. – In two successive years plants of the variety Skrivimankoti, sown on April 1, were exposed to morning twilight, 11½ h daylight (starting at sunrise), and thereafter to ½ h of high-intensity supplementary light. In view of the change in the times of sunrise during the course of the experiment, an adjustment of the 12 h high-intensity light period was made every 5 days. Plants sown at the same date, but exposed to fixed photoperiods of either 12, 13 or 14 h served as controls. In the first year, with exceptionally few bright days in spring and summer, inflorescence initiation occurred 62 days after sowing. Interpolation in the data obtained with the controls showed that this time of initiation corresponded with a photoperiod of 12 h 17 min. In the second year, with a fairly sunny spring and a very sunny summer, inflorescence initiation occurred 127 days after sowing, which corresponded with a photoperiod of 13 h 21 min. Yet the difference in light period between the treatments in the two successive years was only a difference in the intensity of the morning twilight. The dates of initiation in the controls differed in the two years by 1.4 days for the 12 h treatments (insignificant at 0.05 level) and 5.5 days for the 13 h treatments (significant at 0.05 level). Temperature conditions in the greenhouse differed much more (see *Appendix*, part 2, for the years 1954 and 1955) than the most marked differences ever measured in those regions in the tropics where the sowing-date experiments previously discussed were made. This indicates that it is unlikely that temperature effects were of much importance for the results obtained in those experiments.



Graph 90. Effect of sowing date on the time of heading in four varieties at (A) Fort de Cock (Sumatra), (B) Pematang Siantar (Sumatra), (C) Pontianak (Borneo) and (D) Palopo (Celebes). Data after VAN DER MEULEN (1943).

The view that weather conditions may have a marked effect on the length of the photoperiodically active natural day in the tropics finds further strong support in the results of unpublished sowing-date experiments by VAN DER MEULEN, carried out in 1940 and 1941 in different parts of the Malayan Archipelago. These experiments, the results of which have been kindly placed at our disposal for publication by Mr VAN DER MEULEN, were made at different latitudes and at different altitudes. The experiments were unfortunately terminated by the Japanese occupation during the Second World War, and less data have been received from some stations than from others, but the available data are of considerable interest and some of these have been used to construct date-of-heading curves. In Graph 90 examples are given of the curves obtained at the equator at sea level (Pontianak) or at high altitudes (Fort de Cock), and at a latitude of 3° north (Pematang Siantar) and 3° south (Palopo).

Graphs 90 (A) and (C) are particularly interesting since seasonal differences in day length are practically absent at Fort de Cock and Pontianak, and the photoperiod is governed by cloudiness only. The maxima of the curves are correlated with the sowing dates of plants which were exposed to the maxima of the rainy periods (frequent and irregular daily changes in cloudiness) during the latter part of their induction periods, and the minima of the curves are correlated with the sowing dates of plants which were exposed to the maxima of the dry periods (many bright days, regular photoperiodic conditions). In contrast to the curves presented in Graph 89, all curves follow the same trend.

The dates of flowering of the plants at the high altitude (927 m) of Fort de Cock (Graph 90 A) show that low temperatures, especially at night, did not seem to have a marked specific effect on the dates of heading, although the much less marked peaks of the curves compared with those obtained at Pontianak may have something to do with the phenomenon that low night temperatures may hasten floral initiation, in

TABLE 35

AVERAGE NUMBER OF RAINY DAYS AT THE PLACES WHERE SOWING-DATE EXPERIMENTS WERE MADE

Place	*Lat.*	*Elev. in m.*	*Months of the year*											
			J.	*F.*	*M.*	*A.*	*M.*	*J.*	*J.*	*A.*	*S.*	*O.*	*N.*	*D.*
Kandy (nr. Peradeniya)	7°.17′N.	470	10.4*	*6.4*	11.3	13.9	11.8	21.5	**21.7**	19.9	*17.5*	**20.0**	18.7	17.9
Buitenzorg	6°.32′S.	266	**26.0**	24.8	25.9	23.4	18.9	15.8	*14.1*	15.5	17.1	22.4	23.7	24.1
Pontianak	0°.05′S.	3	16.3	*12.5*	14.4	**15.7**	15.5	12.9	*10.3*	12.7	13.0	19.3	**20.3**	18.7
Fort de Cock	0°.18′S.	927	18.4	*14.1*	17.6	**18.3**	15.0	11.7	*10.9*	14.8	16.1	19.3	18.9	**20.0**
Palopo	3°.01′S.	5	17.7	17.4	18.5	**21.7**	20.6	19.1	16.1	12.2	*10.9*	11.7	14.9	14.8
Pematang Siantar	2°.59′N.	400	10.2	*7.5*	9.5	10.5	**11.5**	*7.7*	8.5	10.3	12.9	**15.3**	10.9	10.8

* Average of the years 1946–1956 (*The Trop. Agr. Ceylon*). All other data: averages of 16 to 44 years (*Verh. no. 18, Kon. Mag. Meteor. Observ.*, Batavia).

particular in sensitive varieties and under long-day conditions (*cf.* Chapter XXVI, § 3). Other factors may have contributed to this effect, however. Light conditions during the twilight periods may, for instance, have been affected by the mountain range surrounding Fort de Cock.

The Graphs 90 (B) and (D) show that when weather conditions differ markedly at two places having the same latitude, day length effects may also differ markedly. Alternating bright and cloudy days during the "summer" period caused a marked "long-day" effect at Palopo, Lat. 3°01'S (which exceeded the effect of "long" days reduced by almost continuous cloudiness at Buitenzorg, Lat. 6°32'S, Graph 89), whereas at Pematang Siantar, with typical double equatorial rainy periods but few rainy days, seasonal differences in day length seem to have little effect on the growing periods of the plants sown at different dates.

In Table 35 the average monthly numbers of rainy days are presented of those places where the sowing-date experiments were made.

It has to be kept in mind, however, that the figures in Table 35 give only a very rough idea of cloudiness in the respective months of the year. Unfortunately, sunshine data have been published in very few cases, and of the places where the sowing-date experiments previously discussed were made, data of a number of years were only available of Pematang Siantar. It appeared that in this region the number of sunshine hours per month was higher than would have been expected from the number of rainy days, while the sunshine hours in the morning were higher than in the afternoon in all months of the year. This indicates that cloudiness occurred mostly in the afternoon, with as a consequence that on many rainy days twilight was not affected by clouds in the morning.

In summary, it can be concluded that the view held previously that small seasonal differences in day length occurring in the tropics may affect the growing period of extremely sensitive rice varieties very markedly, probably needs some modification. The data presented in this section indicate that the slight differences in day length caused by cloudiness may affect the growing period of these varieties to such an extent that these effects are significant from an agricultural point of view. Since no measurements of light intensities during twilight periods have been made in the tropics, and no detailed data are available of daily weather conditions during the sowing-date experiments, it is not possible to give an accurate interpretation of the photoperiodic effect of weather conditions, but the available data seem to suggest the following:

(1) The effect of the daily photoperiod is shortened when more than 22 rainy days occur per month (Buitenzorg).

(2) Irregular changes in the daily photoperiod may cause a delay in flowering which exceeds the effect of the longest day to which the plants were exposed. Such conditions apparently occurred sometimes in months with, on the average, 14 to 22 rainy days.

(3) Bright weather conditions (regular photoperiods) tended to give early flowering, *i.e.* in months with on the average less than 14 rainy days.

It is evident that there is still ample scope for detailed work on the photoperiodic effect of weather conditions in the tropics, but at present it may suffice to draw attention to the possible magnitude of such effects and the agricultural significance of the shortened or prolonged vegetative period of the plant (see also § 8.7).

8.6. *Varietal sensitivity*

The behaviour of a number of varieties under natural day length points to some adaptation of photoperiodic sensitivity to ecological conditions. The most sensitive varieties from the tropical regions can be grown as a crop only under the day length conditions of those regions. If transferred to the higher latitudes of non-tropical regions, suitable photoperiodic conditions for floral induction occur too late in the year and the growing season is curtailed by the onset of low winter temperatures. The higher the latitude the shorter the growing season and the longer the photoperiod during the growing season; this implies that only varieties which are capable of sufficiently early floral initiation under those longer photoperiods are suitable for such conditions.

Varieties with a response ranging from almost insensitive to sensitive can be found in all regions. For instance, certain early varieties in Japan and some late awned varieties in Java are practically insensitive, but the most sensitive varieties in Java (tropics) are much more sensitive than the most sensitive varieties in Japan (temperate zone).

A few varieties of low photoperiodic sensitivity show a great ecological adaptability, for instance, the early maturing variety Taichu 65 from Taiwan and the fairly late maturing varieties Fortuna and Blue Bonnet from the U.S.A., which can be grown successfully in both subtropics and tropics.

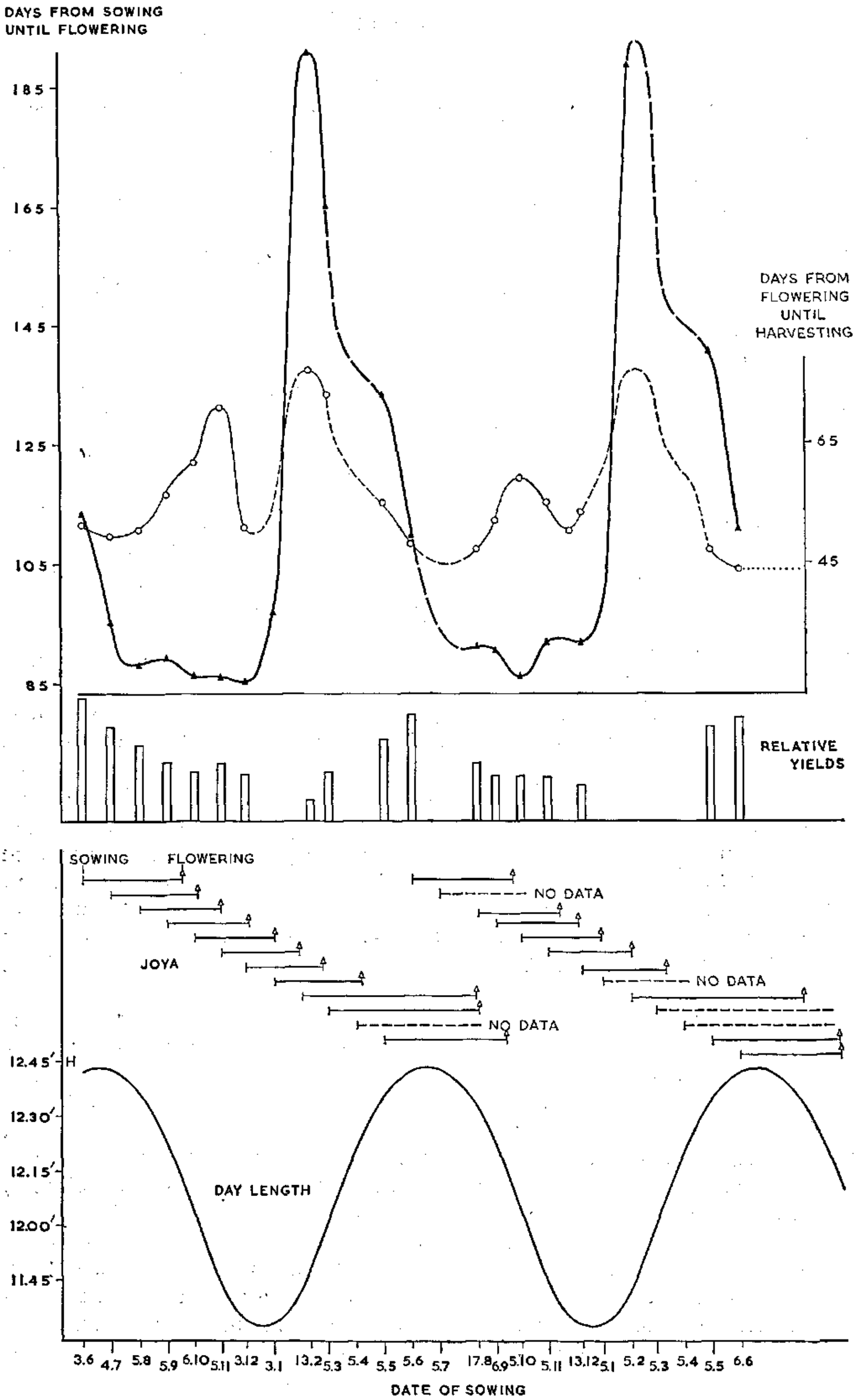
8.7 *Day length effect on yield*

Several workers have investigated the effects of day length on yield in sowing date experiments. As an example the results obtained by MURRAY (1950) are presented in Graph 91.

MURRAY's results show that the best yields were obtained with a medium short growing period. In other experiments, made elsewhere and with different varieties, variable results were obtained, however. In some cases the longest growing period gave the best yield, but in others the shortest or a medium long growing period gave the best results, and there does not seem to be a consistent trend in these data.

Some interesting differences exist, for example, in the effect of different sowing dates on yield in regions having approximately the same latitude. For instance, we find that varieties extremely sensitive to the photoperiod are planted in Java in December ("long" days), reach maturity and yield well. When planted out of season, "short" days cause premature heading and poor yields (see *e.g.* VAN DER GOOT, 1923; KUILMAN, 1937, 1940). In Ceylon and India the situation is just the reverse. Very sensitive varieties are planted in the season with short days and mature early (for Ceylon see *e.g.* LORD and DE SILVA, 1931; HAIGH, 1936; for India: RAMIAH, 1954). When planted out of season, *i.e.* under long-day conditions, the vegetative period may be extended to more than a year (*cf.* Graph 88), while yield is reduced by sterility and reduced panicle size.

The respective behaviour of sensitive varieties in Java, compared with Ceylon and India, seems to be contradictory. Differences in sensitivity between varieties exist, however, although several factors are involved and an explanation of the differences in varietal behaviour requires a closer examination of the day length effect on yield.



Graph 91. Effect of sowing date on the growing period and yield of the variety Joya at St. Augustine (Lat. 10° 40′ N, elev. 16 m), Trinidad. Data after MURRAY (1950).

The most fundamental process which affects yield when rice is grown in different day lengths is photosynthesis. An increase in photosynthesis, produced by a longer vegetative period (to a certain extent), by lengthening the assimilation period per day, or by increasing the assimilation rate (brighter weather), potentially increases the yielding capacity of the plant. To mention a few examples: the highest yield obtained at experimental stations is about twice as high in the temperate zone as in the tropics. The best late varieties outyield the best early varieties. The same varieties of rice grown in the dry monsoon (bright weather) may yield up to about 25% better than in the wet monsoon (cloudy weather). A detailed discussion of these factors, in particular of the differences in radiation at different latitudes during the growing period of the crop, will be given in Chapter XXX. In respect of the photoperiodic effect of natural daylength the principal factor related to yield is the influence of daylength on the duration of the vegetative period of the plant and, in some varieties, on the duration of panicle development.

In an experiment (*E. 359*) to investigate the relation between the vegetative period and yield of highly sensitive varieties it was found that when the photoperiod forced initiation to occur very early, for instance, 40 days after sowing, panicles were small and yield was low in all varieties used (HMC 12, Kohumawi B-11, MYAC 104, Skrivimankoti). With a series of photoperiods increasing in steps of 10 minutes between 12.00 and 13.10 h yield increased with longer vegetative periods until an optimum was reached. With still longer vegetative periods panicle size gradually decreased, and sterility increased rapidly to 70–100%.

The optimum vegetative period for yield differed slightly among the varieties used, and occurred 96 (Skrivimankoti) to 108 days (Kohumawi B-11) after sowing (period from sowing to flowering 129–147 days). An explanation of this phenomenon might be that the optimum vegetative period was determined by the optimum vegetative development of the plant under the given photosynthetic conditions and that at later stages senility and, as a result, physiological disorders, would begin to affect the capacity of the plant to produce high yields. With regard to photosynthesis this view appeared to be incorrect, however. When the light intensity during the daytime was lowered by screening the light with a vitrage cloth, dry plant weight and yield decreased markedly under all photoperiodic conditions, but the optimum vegetative period was not affected.

A closer examination of the development of the plant revealed that the optimum vegetative period was correlated with the elongation of the stem. When the vegetative period of the rice plant is sufficiently prolonged, the elongation of the stem begins about two months after sowing in most varieties as was shown in Chapter XXIII, § 3.8. The first elongated internodes normally remain small, and plant growth is not affected at that stage. But when more markedly elongated internodes are formed and a fairly long stem begins to develop in vegetative plants, plant growth gradually declines. It appeared that the optimum vegetative growth for yield occurred before this stage.

These results may account for several of the data obtained in sowing date experiments with very highly sensitive varieties. In these experiments high yields occurred with vegetative periods which were, compared with the vegetative periods obtained at other sowing dates, either long, medium long or short, but the actual duration of the optimum period between sowing and flowering was in the order of 130–140 days in all cases, which is in accordance with the results of *E. 358*. It has to be kept in mind, however, that these results apply to a small number of varieties only. With less sensitive varieties (*E. 359*) it was found, for instance, that the optimum vegetative period was, in general, shorter and differed more markedly among varieties as compared with the very highly sensitive varieties. In addition, non-photoperiodic effects may greatly complicate the yield figures obtained in sowing-date experiments.

A second photoperiodic effect which, in some varieties, may affect yield significantly, is that of day length on panicle development. In an experiment (*E. 360*) to investigate this effect, it was found that for a given vegetative period, the best panicle development and the highest yield were obtained when panicle development was hastened by short days. A delay of panicle development under relatively long days resulted in a smaller number of rachillae, less spikelets per panicle and an increased sterility. This phenomenon was marked in the varieties Kohumawi B-11, Tjina and Tilakchari, but practically absent in MYAC 104 and Skrivimankoti.

Earlier KERLING (1950) reported that plants of the variety Untung, exposed to relatively "long" natural days which gradually decreased, initiated an inflorescence 70 days after sowing and flowered 30 days later (rapid panicle development under "short" days). These plants produced large panicles and gave a good yield. Under the reverse conditions, *i.e.* plants exposed to relatively "short" days which gradually increased, the inflorescence was initiated 50 days after sowing and flowering occurred 50 days later. Panicles were smaller and yields were much lower in this plot. These results point to the same phenomenon as observed in *E. 360*, although in KERLING's work the vegetative periods of the plants differed and non-photoperiodic effects may have contributed to the results.

It may be concluded that the main photoperiodic effect of natural day length in sensitive varieties is the regulation of the vegetative period, which has a rather critical length for maximum yield. Day length may consequently increase yield when it forces initiation to occur when the optimum vegetative period is reached, or decrease yield when it forces initiation to occur earlier or later. Furthermore, if the panicle development of a variety is markedly affected by the photoperiod, yields may be higher when panicles develop in short as opposed to long days.

9. DISCUSSION

In view of the many data dealt with in this rather extensive chapter it seems useful to summarize some of the main findings of the specific light effect studied under controlled light conditions before discussing the analysis of natural days.

The results of experiments on the perception of the photoperiodic treatment (§ 2) indicated that the youngest fully expanded leaf is the most sensitive one, and that sensitivity decreases progressively with an increase in the age of the leaves. It was realized that factors other than the age of the leaves could have contributed to these results. In experiments to investigate this point it was found, for instance, that the apparent differences in leaf sensitivity could have been due partly to differences in leaf size. A large leaf area appeared to be required to obtain the shortest induction under inductive day length conditions. Furthermore, it was found that a pretreatment with long days may diminish the sensitivity of the leaves to subsequently applied short days, although a very advanced state of induction under long days and a subsequent induction under short days appeared to have a cumulative effect which even surpassed the effect of either a continuous short or long-day treatment. The latter was explained by assuming that after the transfer to short days the leaves probably attained the fully induced state in a relatively short time. Of some other factors no conclusive data were obtained and it remains uncertain, for example, to which extent the age of the plant may influence leaf sensitivity and/or the reaction of the growing point to the floral stimulus, while it is also not known if, in respect of leaf "sensitivity", the total transport of carbohydrates and floral stimulus from a particular leaf to the growing point is a more important factor in the effect of that leaf on flower formation than the total amount of floral stimulus which it produces.

In addition to leaf blades, leaf sheaths and even bare stems appeared to be capable of perceiving the photoperiodic treatment. Furthermore, it was established that leaves and stems could retain the floral stimulus under non-inductive day length conditions, although very long days and high-intensity light could, at least partly, destroy the induced state and/or the floral stimulus.

In § 3 the effect of irregular changes in the daily photoperiod on the time of initiation was investigated. It appeared that these conditions may cause a delay in floral initiation which exceeds the effect of the longest photoperiod to which the plant was exposed. Gradually increasing or decreasing photoperiods (§ 4) were found to have a much less marked effect.

In respect of light intensity (§ 5) it was established that low light intensities were more effective with long photoperiods and in varieties of high sensitivity as compared with short photoperiods and moderately sensitive varieties, while low light intensities were, moreover, much more effective when these were given at the beginning of the photoperiod (in the "morning") than at the end of the photoperiod (in the "evening"). As with many other plant species (see *e.g.* MEIJER, 1959), red light was photoperiodically more active than blue light in rice.

The investigations presented in § 7 showed that the photoperiodic response of the rice plant depends more on the length of the longest uninterrupted dark period than on the sum of either light or dark periods given during the course of 24 h, which is also a type of response common among plants (*cf. e.g.* LANG, 1952).

An attempt has been made in this chapter to analyse the photoperiodic effect of natural day length and to interpret the agricultural significance of this effect in terms of yield.

To investigate natural day length two lines of research have been followed: firstly, various specific light effects which may occur in natural days were studied under controlled conditions and, secondly, detailed measurements of light intensity during the twilight periods of natural days were made. By deducing light effects in natural days from the data obtained under controlled conditions, by testing the effect of twilight directly in an experiment, and by using numerous data from the literature on sowing date experiments a general picture of the photoperiodic effect of natural day length was obtained. At the same time it was made clear, however, that this effect is usually too complicated to permit a detailed and accurate analysis of the daily photoperiod.

The main conclusions drawn from this study were that twilight contributes significantly to the natural daily photoperiod, that the effective duration of this photoperiod differs for varieties with different sensitivities and that the natural daily photoperiod is not only determined by seasonal differences in day length but also by weather conditions such as cloud and fog, which may shorten the effective daily light period markedly. At low latitudes in the tropics, where very small differences in day length may cause marked differences in the vegetative period of extremely sensitive varieties, the effect of weather conditions on the daily photoperiod may have a significant effect on the time of flowering in these varieties.

From the finding that the duration of the vegetative period is a factor determining yield, and that in many varieties yield decreased rapidly with vegetative periods differing only slightly from the optimum, it was concluded that the natural daily photoperiod, which can effect the duration of the vegetative period markedly, may, as a result, largely determine yield in highly sensitive varieties. Furthermore, the limited range of vegetative periods giving maximum yields may explain the restricted planting season of the highly sensitive varieties in the tropics.

This very brief survey of the analysis of natural day length and the conclusions drawn from the results obtained, give, in fact, too simple a picture of the very complex phenomenon of the natural day length. It has to be borne in mind that this study is a first attempt to analyse the photoperiodic effect of natural days, that many of the specific light effects involved have been investigated with a few varieties only and that no accurate measurements of twilight under different weather conditions in the tropics have been made, while several factors are still insufficiently known or completely unknown with regard to light conditions and the reaction of the plant to certain combinations of photoperiods.

It is realized, therefore, that several of the conclusions in this chapter still require further confirmation in experiments with different varieties and under different environmental conditions, and that for a more detailed interpretation of the photoperiodic effects of natural day length much detailed research work still remains to be done.

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