

# DEVELOPMENTAL DIFFERENCES IN RICE PLANTS IN RELATION TO PHOTOPERIODISM <sup>1)</sup>

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## SUMMARY

Little is known about the development of rice when grown at photoperiods of a determined constant length. The second author made a careful examination of growth and development of 5 varieties cultivated at 12 h. daylight and photoperiods of 12 h. or 18 h. respectively. He made an investigation on the influence of a change in the length of the photoperiod.

In photoperiodically sensitive varieties earliness is induced by short photoperiods. Length of photoperiod influences leaf formation and leaf growth only in an indirect way. When the planting distance is small, tillering is not affected by the length of the photoperiod.

Some morphological characters of the axillary buds in various stages are described. Stem elongation in photoperiodically sensitive varieties proceeds more rapidly at a short photoperiod than at a long one. In photoperiodically sensitive varieties the size of the panicle is greatly affected by the length of the photoperiod.

A change in the length of the photoperiod from 12 h. to 18 h. retards growth and development and may cause serious malformations.

Based on these results, a picture of the development of rice in relation to photoperiodism is given.

## INTRODUCTION

The literature on photoperiodism of rice has been reviewed in detail by WAGENAAR (1951) and WORMER (1953). Though some of the data are contradictory, the following conclusions seem to be justified:

- 1 rice is flowering earlier when grown at a short photoperiod than when grown at a long photoperiod.
- 2 in Japan, China, India and Ceylon late varieties are said to be sensitive as to the length of the photoperiod, while varieties with a short growth period are said to be more or less indifferent. In Indonesia the awned varieties are regarded as being indifferent, the awnless varieties as being sensitive.
- 3 even sensitive varieties do not react to the length of the photoperiod in the first 4-6 weeks of their growth cycle.
- 4 a treatment of short duration with a short photoperiod can have a strong influence on the behaviour of the plant.
- 5 even in the tropics, where variation in daylength is small, the sowing date may have a strong effect on the length of the growing period.
- 6 a treatment with a short photoperiod, given on the nurserybed, where no tillers are formed, after the insensitive period mentioned in point 3, does result in an early earing of the main shoot, followed by the earing of the tillers at a normal or at a delayed time.

Though research on photoperiodism of rice was started as early as 1928, we still have a very limited knowledge of the influence of the photoperiod on the development of the riceplant. This is mainly due to:

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- 1 the failing of a careful dissection of the plants during growth and development.
- 2 the use of the "normal" or "natural" daylength as "control", which daylength in fact is no control at all.
- 3 the fact that no distinction is made between the photoperiodical and the photosynthetic action of light.

The first mentioned lack of exact knowledge — caused by the failing of a careful dissection of the plant — was already felt by KERLING in 1942. In order to get a clear picture of the growth and development of the rice plant she made an examination of as many plants as possible during the entire period of development. Her investigations yield an excellent report on the morphology of the plant and because she made sowings on various dates, they furnished at the same time some data on photoperiodism of rice.

#### THE SCOPE OF THE PRESENT INVESTIGATION

KERLING ends her publication with the remark: "The influence of a constant length of day on the developmental processes requires investigation, varietal differences need to be recorded". By this remark, the scope of the investigation dealt with in this article is delimited. For this purpose, an examination of the growth and development of five varieties, when grown at photoperiods of 12 h. and 18 h. respectively, has been made. These varieties are: *Nero di Vialone* (photoperiodically sensitive, arbitrarily awned, Italy), *Kameji* (sensitive, arbitrarily awned, U.S.A.), *Tjina* (sensitive, unawned, Indonesia), *Fortuna* (photoperiodically indifferent, unawned, U.S.A.) and *Karang Serang* (indifferent, awned, Indonesia). Besides this a second set of *Nero di Vialone* plants was grown. This set was submitted to a series of treatments, viz.

a photoperiod of 12 h. during the entire growing period,

a photoperiod of 18 h. during the entire growing period,

a photoperiod of 12 h. up till some days before the plant might enter the reproductive stage. From that moment a photoperiod of 18 h. was given,

a photoperiod of 12 h. up till the moment when the main axis entered the reproductive stage and the tillers were still in the vegetative stage. From this time a photoperiod of 18 h. was given,

a photoperiod of 12 h. up till the moment when both main axis and tillers entered the reproductive stage. From this moment a photoperiod of 18 h. was given,

a photoperiod of 18 h. up till the moment when the main axis of the plants grown at a photoperiod of 12 h. entered the reproductive stage. From this time a photoperiod of 12 h. was given.

a photoperiod of 18 h. up till the moment when both main axis and tillers entered the reproductive stage. From this time a photoperiod of 12 h. was given.

#### MATERIAL AND METHODS

A serious objection against the previous experiments mentioned in § 1, was the fact that no endeavour has been made to reach a distinction between the photoperiodical and the photosynthetic activity of light. In order to be able to

obtain such a distinction the authors manufactured the following two constructions :

1 An apparatus consisting of four carriages, each  $1.60 \times 1.20$  m, filled with soil and water, a shed and two pairs of rails. The shed was divided into two sections, one of which could be illuminated by three 40 W. fluorescent tubes. The plants in each carriage received an equal amount of daylight ; the carriages were shifted into the shed, where difference in length of the photoperiod was brought about by light of such a small intensity that practically it did not act in a photosynthetic way.

2 An apparatus consisting of two cisterns, each with an area of  $3.15 \times 0.50$  m and a depth of 0.60 m filled with soil and water. Over each cistern a wooden frame was constructed. Against this frame sheets of hardboard could be placed, which caused an absolute darkness inside the frames. One of these cisterns could be illuminated by one 40 W. fluorescent tube.

The four carriages were used in 1951 for the growing of *Nero di Vialone*. Of this variety, 338 plants were examined in the first set, and 58 in the second. In 1952, both the carriages and the cisterns were employed for cultivating about 120 plants of each of the other varieties. Only the second set of *Nero di Vialone* was grown in pots in order to avoid root damage during transport from one photoperiod to the other : therefore, no examination of the roots could be made, but all the other parts of the plants were carefully analysed and measured. Axillary buds and tips of culms were cleared in chloralhydrate before counting and measuring the leaf primordia.

#### THE GROWTH OF THE LEAVES

a *The growth of the leaves in general.* A description of the embryo, germination and growth of the young seedling has been given by KERLING. In the embryo the coleoptile and three leaf primordia can be distinguished. After germination, the first and the second leaf primordia grow out rapidly. The third primordium elongates to a small extent. When the first leaf nearly reaches its full length, the primordium of the fourth leaf is split off.

The growth rhythm of a shoot in the vegetative stage is described by KERLING as follows :

"Every growing point in the vegetative period is always surrounded by the following sequence of leaves :

one or more mature leaves ; one which has nearly reached maturity : one in the grand period of growth : one primordium from 0.080 to 0.200 mm in length : one primordium of 0.080 mm or less, just developed.

*The blade and the sheath of a preceding leaf have to reach maturity before the next leaf primordium can enter the grand growing period"* (Italics by us). "At that moment the growing point is surrounded by two younger primordia not yet elongating. The blades of the highest leaves, however, start elongating at the time the sheath of the precedent leaf still shows immature cells at the base".

Our findings, however, do not agree completely with the description of KERLING which we put in italics. When a leaf indicated by  $n$  enters the grand period of growth the first part that grows out is the blade. The sheath, being at

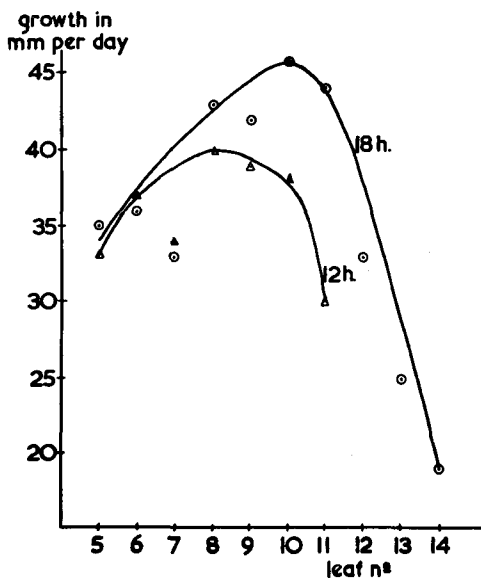


FIG. 1. MEAN GROWTH OF THE LEAVES ON THE MAIN STEM OF NERO DI VIALONE IN MM PER DAY BEFORE AND AFTER INITIATION OF THE PANICLE.

first not longer than 5 mm, starts growing out when the blade has nearly reached maturity. Simultaneously with the elongation of the sheath of this leaf the blade of the next leaf,  $n + 1$ , is elongating.

The primordium of the leaf  $n + 2$  elongates to a smaller extent; it reaches a length of  $\pm 5$  mm. Meanwhile, the primordium  $n + 3$  grows out from  $\pm 0.1$  mm to  $\pm 0.5$  mm, and the primordium  $n + 4$  is split off. Consequently, according to us, a shoot in the vegetative stage consists of:

- 1 one or more mature leaves,
- 2 one leaf with a nearly mature blade and a sheath in the grand period of growth,
- 3 one leaf with the blade in the grand period of growth,
- 4 one leaf with a length of  $\pm 0.5$  to  $\pm 5$  mm,
- 5 one primordium from  $\pm 0.1$  to  $\pm 0.5$  mm,
- 6 one primordium recently split off, with a length of 0.1 mm or less,
- 7 the growing point.

Normally, the blade of the leaf  $n + 1$  mentioned above is somewhat longer than the sheath of  $n$ , so that the tip of this blade is just visible. This condition which we found to be present in all the varieties investigated by us was overlooked by KERLING. Although it may remain possible that the varieties which she used — *Baok* and *Untung* — possess a rhythm which is different from those we investigated her statement is probably incorrect. Each of the successive leaves reaches a greater length than the preceding one, up till the moment at which the initiation of the inflorescence becomes distinguishable. When this happens the leaves grow out to a smaller extent than before. Fig. 1 shows the mean growth of the leaves of *Nero di Vialone* in mm per day before and after the initiation of the panicle. When observing the data given in this figure, one should keep in mind that the plant of the 12 h. series entered the reproductive stage when the 8th and 9th leaf were in the grand period of growth: in the

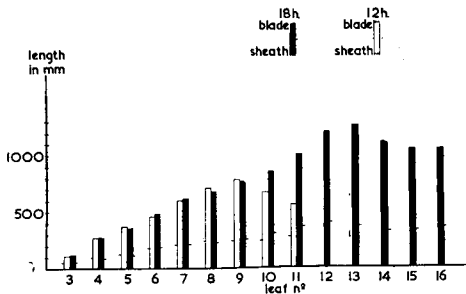


FIG. 2. MEAN LENGTH OF THE LEAVES ON THE MAIN STEM IN MM IN VARIETY KAMEJI.

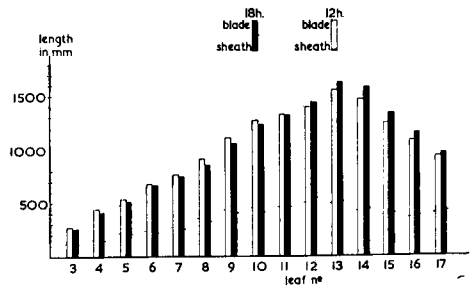


FIG. 3. MEAN LENGTH OF THE LEAVES ON THE MAIN STEM IN MM IN VARIETY KARANG SERANG.

18 h. series, however, this happened when the 11th and 12th leaf were elongating rapidly.

It can easily be seen that the rapidness of growth gradually increases during the vegetative stage and gradually diminishes after the reproductive stage has been reached.

Figs. 2 and 3 show the length of the leaves in two varieties. They show that each successive leaf is longer than the preceding but that the rate of growth in each of them diminishes after the initiation of the inflorescence.

b *The influence of the length of photoperiod on the growth of the leaves.* The data given in figs. 1, 2 and 3 prove that the length of the photoperiod has no influence on the formation and the elongation of the leaves until the plant enters the reproductive stage. In photoperiodically sensitive varieties this phenomenon occurs earlier at a 12 h. photoperiod than at a 18 h. photoperiod. Consequently, plants grown at 12 h. photoperiod have a smaller number of leaves in comparison with those grown at 18 h. photoperiod. Because initiation of the inflorescence coincides with inhibition of leaf growth, the uppermost leaves of plants grown at 12 h. photoperiod do not reach the same length as the leaves which grow during the same term on plants cultivated at 18 h. photoperiod. The latter remark holds only for photoperiodically sensitive varieties: with photoperiodically indifferent varieties differentiation of the growing point occurs independently of the length of the photoperiod, and no influence of photoperiod on leaf growth could be detected. The very small differences shown in fig. 3 are obviously not reliable.

Therefore we may conclude that photoperiod exerts an influence on leaf-growth only in an indirect way.

## TILLERING

a *Tillering in general.* The axillary bud can be distinguished under the microscope as soon as the leaf to which it belongs has reached a length of  $\pm 1$  mm. Somewhat later the primordium of the prophyll is split off, followed by three leaf primordia. When the supporting leaf has reached its full size, the bud is just closed by the prophyll and has a half-circular shape. When the next leaf has reached maturity the bud contains three leaf primordia and is triangular. When tillering occurs the first leaf breaks through the prophyll of the elongating bud.

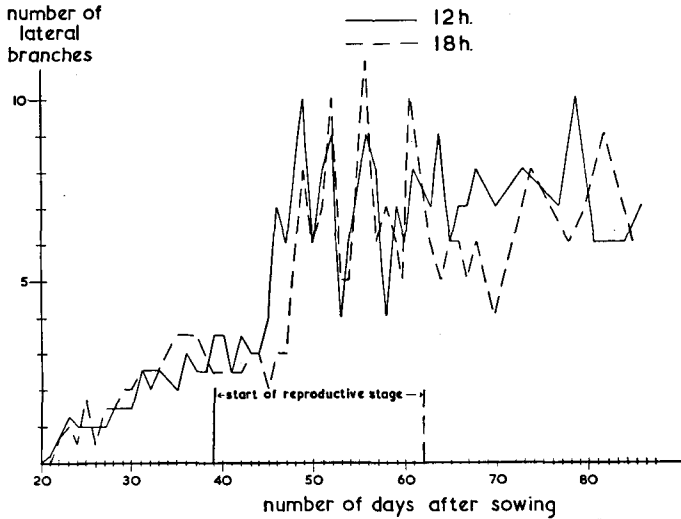


FIG. 4. COURSE OF TILLERING IN NERO DI VIALONE.

From this moment the bud may be considered as a shoot. With the lower buds this happens at a length of  $\pm 60$  mm and with the buds in the middle and topmost parts of the culm at a length up to 220 mm.

b *The influence of photoperiod on tillering.* No detailed information could be obtained as to the influence of the length of the photoperiod on the number of laterals formed, because tillering was limited by narrow spacing. *Fortuna* formed  $\pm 2$ , *Karang Serang* and *Tjina*  $\pm 4$  tillers per plant. No difference could be observed which might be ascribed to length of photoperiod. Especially the data of *Nero di Vialone*, however, show some interesting features.

Fig. 4 gives a picture of the tillering in this variety. Two conclusions may be drawn from this figure, viz. A) there was an ample variation in the number of tillers in the various plants, B) there was no difference in the number of tillers in plants grown at photoperiods of 12 h. and 18 h. respectively. Moreover, the mean number of tillers in thirty plants grown at 12 h. photoperiod was as high as 7.1 and that of thirty plants grown at 18 h. photoperiod amounted to 7.4, with a statistically insignificant difference of 0.3. From figure 4 can be seen, that the 12 h. series entered the reproductive stage while tiller formation was proceeding, whereas the progress of tillering had ended at the day when the 18 h. series moved into the reproductive stage. The consequences of these facts are shown in figs. 5 and 6. Fig. 5 gives the total number of shoots (main axis and tillers) as well as the number of shoots showing the inflorescence for the 12 h. series. It can easily be seen that the main axis and the early developed tillers entered the reproductive stage soon after each other; consequently, the number of shoots in the reproductive stage became as high as the total number of shoots. The tillers which developed later had to reach a certain vegetative development before they could enter the reproductive stage. For that reason the total number of shoots surpassed the number of reproductive shoots considerably for another 8 days, after which time the newly formed shoots had arrived also

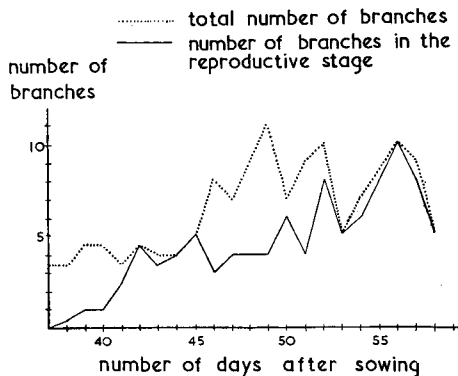


FIG. 5. TOTAL NUMBER OF SHOOTS AND NUMBER OF SHOOTS IN THE REPRODUCTIVE STAGE IN VARIETY NERO DI VIALONE, 12 H. SERIES.

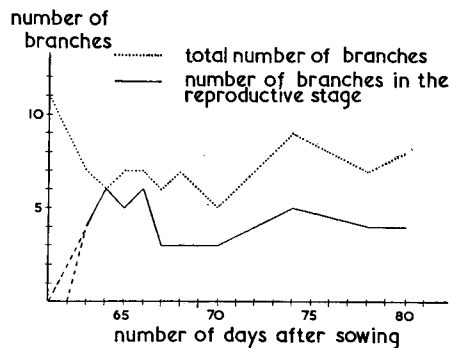


FIG. 6. TOTAL NUMBER OF SHOOTS AND NUMBER OF SHOOTS IN THE REPRODUCTIVE STAGE IN VARIETY NERO DI VIALONE, 18 H. SERIES.

at the reproductive stage. The picture given by the 18 h. series is quite another one. Fig. 6 shows that in the latter case there was no gradually increasing number of reproductive shoots, but that the final quantity of such shoots originated almost simultaneously. This behaviour is demonstrated again in the process of earing. The number of panicles completely visible at the exterior on the plants grown at 12 h. photoperiod increased slowly whereas at 18 h. photoperiod all panicles became visible on one and the same day.

From the figures 5 and 6 one more conclusion can be drawn. Fig. 5 proves that nearly all the shoots of the 12 h. series entered the reproductive stage. On the contrary, only part of the shoots entered the reproductive stage at 18 h. photoperiod (fig. 6).

This is caused by an inhibition in the process of tillering, a phenomenon already observed by KERLING (1950) and KUILMAN (1940, 1940 and 1941). Though in our experiments tillering was limited by narrow spacing, here the presence of this inhibition process can also be demonstrated. With respect to this the following three phenomena are worth mentioning, viz.:

- 1 at regular times plants were taken for dissection. In this way the plants became gradually more widely spaced; nevertheless after approximately the 55th day after sowing no more tillers were formed.
- 2 at approximately the 55th day sowing the already elongating buds suddenly stopped their growth. After this moment many long buds could be found which did not develop into a shoot.
3. at the same time the growth of many young tillers came to an end. They dried up, and died at last.

From fig. 4 it can be seen that this inhibition occurred after the 12 h. series entered the reproductive phase and before the 18 h. series did so. Thus, all the shoots of the 12 h. series entered the reproductive stage, after which part of them ceased their development. On the other hand, part of the shoots of the 18 h. series ceased their development even before they had formed an inflorescence. The shoots which escaped this inhibition grew out, entered the reproductive stage, and practically always bore a well developed panicle,

whereas the other ones remained in the vegetative stage. The result was an equal number of earbearing culms in both series.

#### THE BEHAVIOUR OF THE AXILLARY BUDS

a *The axillary buds in general.* It is easy to understand that only a small number of buds become a shoot. In this paragraph we shall give a description of the behaviour of those buds which do not enter this stage.

The first possibility is that of a bud not entering the grand period of growth. Such buds have a length of not more than  $\pm 10$  mm and are to be found in great numbers. When a bud does come in the grand period of growth, it normally becomes a shoot, but as we saw in the foregoing paragraph, it may happen that elongation is inhibited. An elongated bud the growth of which is inhibited, can have a length of 100 mm or even more. It is flat, pressed between the stem and the leaf-sheath, gradually gets brown and decayed, and finally dies off. These long flat buds can be found above the tillers lastly developed.

The small dormant buds and the elongated buds do not always stay in this dormant stage. Sometimes it happens that the plant enters a second period of tillering, in which many dormant buds suddenly elongate and become a shoot. This happened for instance with the 12 h. series of *Kameji* at the time when the main shoot and the first laterals were earing. Another possibility is that the dormant buds show their renewed activity by splitting off one or more leaf primordia. Meanwhile the prophyll and sometimes also the first leaf of such a bud are thickened to a considerable amount, while in many cases the axillary buds of the prophyll and of one or more leaves grow out to a length of  $\pm 3$  mm. If this happens it occurs at the end of the growing period of the plant. This form of activity starts with the buds at the base of the culm and advances in apical direction.

When this process reaches the flattened, elongated buds — which, as already said, are situated above the tillers lastly developed and therefore in the middle part of the culms — it can be observed that the base of such an elongated bud can be thickened as well. Dissection, however, shows that in many cases not the growing point of this bud, but that of the axillary bud of the prophyll is developing. Shortly before, during or after ripening of the seeds these thickened buds as well as the axillary buds within the thickened buds grow out and sometimes give rise to a very large number of shoots.

Up till now little is said about the internal situation of the buds. A bud developing into a shoot in the first period of tillering is always in the possession of a prophyll and four leaf primordia. The same holds for a bud which does not develop but stays dormant. The buds which develop after the culm entered the reproductive stage — these are the axillary buds of the top-most leaves — can be in the vegetative as well as in the reproductive stage. This depends on variety and on circumstances. Such a bud can have three or four leaf primordia, whereas the differentiation of the panicle mostly advances as far as the initiation of the lateral branches. Equally it can happen that buds formed when the supported culm was still in the vegetative stage, reach the reproductive stage. These buds, situated at the middle or the lower parts of the stem, of course have four leaf primordia.

The description given just now does not agree with the data given by KERLING. She mentions elongated buds as well as thickened buds, but according to her



observations thickening occurred immediately after the process of bud inhibition had started and the thickened buds gradually died. These differences are probably due to varietal influences.

Our descriptions hold for all buds with the exception of the one belonging to the uppermost leaf of the stem, the so-called flagleaf. This bud can be lacking or present. In the latter case it appears to contain an ear with a length of  $\pm 3$  mm which dries and dies off, or it grows out to a well developed panicle bearing flowers and eventually even ripe seeds.

b *The influence of photoperiod on the behaviour of axillary buds.* No influence of the length of photoperiod on bud behaviour could be observed in the photoperiodically indifferent varieties *Fortuna* and *Karang Serang*. Merely small dormant buds in the vegetative stage with four primordia were present. The axillary bud of the flagleaf could not be detected. At the end of the growing period a very few buds at the base of the culms thickened and formed a shoot. The 18 h. series of *Tjina* did not reach flowering before the short, dark days of October. Therefore, the last part of the growing period must be regarded as passing in an abnormal way. All the buds of the plants of the 12 h. series were in the vegetative stage whereas the axillary bud of the flagleaf was absent. Some three weeks after ripening of the seeds the buds became slightly thickened, had five leaf primordia but did not form new shoots.

The axillary buds of the four topmost leaves of *Nero di Vialone* deserve our special interest. In the axil of the flagleaf a small panicle of  $\pm 3$  mm in length at least could be observed, but in the 12 h. series of this variety some 13 % of these buds grew out into a panicle bearing 10–25 flowers or seeds, hidden in the sheath of the flagleaf. Moreover, in the 12 h. series the axillary buds of the 2nd and 3rd leaf from the top were nearly always in the reproductive stage, and  $\pm 10$  % of the buds of the 4th leaf reached that stage. On the contrary, the percentage of reproductive buds in the plants of the 18 h. series amounted to  $\pm 40$  %,  $\pm 30$  % and  $\pm 5$  % for the 2nd, the 3rd and the 4th leaf from the top, respectively. Another difference between the two series of this variety could be observed in the process of the thickening of the buds. At the 18 h. series this process started when flowering nearly finished. Elongation occurred when the seeds were ripe. In the plants of the 12 h. series bud thickening started six days later than in the 18 h. series. At this moment the seeds were completely ripe, and elongation of the buds occurred soon after.

Still more striking differences could be detected in *Kameji*. In the 18 h. series of this variety, all the buds were in the vegetative stage, and the bud of the flagleaf — containing a very small panicle and in this way the only exception — seldom could be found. In the 12 h. series, however, all the buds reached the reproductive stage, even those buds which developed before the supporting shoot entered this stage. These buds formed an inflorescence within two weeks after the shoot to which they belonged did so. No opinion can be given on the lowermost buds because they were destroyed by penetrating roots soon after their appearance.

#### STEM ELONGATION

a *Stem elongation in general.* Stem formation occurs in three periods. In the first period the horny, curved, pointed base of the stem is formed by the

internodes of the first four or five leaves. Nodes or internodes, however, are not visible in this part. In the second period trapezium-shaped internodes are formed, having a length of 0.5–2 mm and each being somewhat longer than the preceding one. These internodes are demonstrated by making a longitudinal section, but they are not visible externally, because this part of the stem is covered by the insertions of the leaves. The number of these internodes depends on variety and circumstances. The third period of stem formation covers the grand period of growth. The internodes formed in this period can be distinguished externally. They have a length of 10 mm to 300 mm or even more.

Stem elongation in the tillers is different from the process in the main shoot. The tillers are composed of a smaller number of internodes, which implies that some internodes or all of them formed in the first and second period may be missing and that the number of elongated internodes may be smaller in the tillers than in the case of the main shoot.

*b Stem elongation in relation to length of photoperiod.* Again, all the plants of the photoperiodically indifferent varieties *Karang Serang* and *Fortuna* showed the same picture. In both varieties stem elongation started before the reproductive stage, whereas no differences due to the length of the photoperiod could be observed. Stem elongation in *Kameji* is shown in fig. 7. It can be seen that stem elongation started at 12 h. photoperiod after and at 18 h. photoperiod before the initiation of the inflorescence. Moreover, the growth was more rapid at 12 h. than at 18 h. photoperiod. The differences between *Kameji* and *Nero di Vialone* are of a quantitative nature. Similarly as in *Kameji*, in *Nero di Vialone* stems elongated at 12 h. photoperiod after and at 18 h. photoperiod before differentiation of the panicle. *Nero di Vialone* is, however, somewhat less sensitive than *Kameji*, so the difference in time between both series for the starting of the stem elongation was  $\pm 40$  days for *Kameji* and 14 days for *Nero di Vialone*.

As can be seen from fig. 8, stem elongation in *Tjina* went off differently as compared with the varieties mentioned above. In both series the internodes extended before the plants came in the reproductive stage, but at 12 h. photoperiod this happened some days earlier than at 18 h. photoperiod. In the 12 h. series the first extended internode was nearly always the one at the base of the

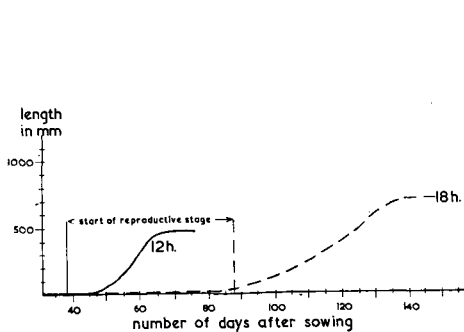


FIG. 7. LENGTH OF MAIN STEM IN MM IN VARIETY *KAMEJI* AT PHOTOPERIODS OF 12 H. AND 18 H.

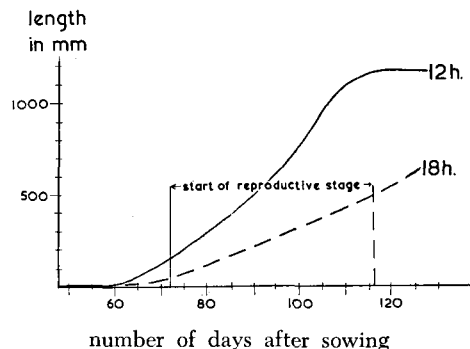


FIG. 8. LENGTH OF MAIN STEM IN MM IN VARIETY *TJINA* AT PHOTOPERIODS OF 12 H. AND 18 H.

12th leaf, in the 18 h. series the one at the base of the 13th leaf. As in *Kameji* and *Nero di Vialone*, growth was more rapid at 12 h. than at 18 h. photoperiod.

THE FORMATION OF THE PANICLE

a *The influence of photoperiod on the formation of the panicle.* In the photoperiodically indifferent varieties *Karang Serang* and *Fortuna* no differences could be detected in the rapidness of growth of the plants grown at photoperiods of 12 h. or 18 h. In *Kameji* and *Nero di Vialone* the panicle extended faster at 12 h. than at 18 h. whereas in reference to *Tjina* no comparison could be made because earing at 18 h. photoperiod took place late in autumn and was quite abnormal.

b *The size of the panicle in relation to the length of the photoperiod.* Table 1 gives some data on the panicle of the main axis of *Nero di Vialone*, *Kameji*, *Fortuna* and *Karang Serang*. As said before, flowering in the 18 h. series of *Tjina* was abnormal.

Table 1. The size of the panicle of the main stems of four varieties grown at photoperiods of 12 h. and 18 h. resp.

	12 h.	18 h.	P <sup>2)</sup>
<i>Nero di Vialone</i>			
Number of flowers	149	208	0.00
Number of side-axes of first order	7.36	10.53	0.00
Number of side-axes of 2nd order	28.5	42.8	0.00
Length of panicle in mm	203	220	0.00
Total length of side-axes of first order in mm	817	968	0.00
Number of flowers per 100 mm of side-axes of first order	18.3	21.5	0.00
Number of side-axes of 2nd order per 100 mm side-axes of first order	3.52	4.42	0.00
<i>Kameji</i>			
Number of flowers	110	227	0.00
Number of side-axes of first order	6.1	13.7	0.00
Length of panicle in mm	184	246	0.00
Total length of side-axes of first order in mm	583	1154	0.00
<i>Fortuna</i>			
Number of flowers	312	286	0.61
Number of side-axes of first order	18.2	18.0	0.83
Length of panicle in mm	288	282	0.32
Total length of side-axes of first order in mm	1922	1891	0.84
<i>Karang Serang</i>			
Number of flowers	98	99	0.92
Number of side-axes of first order	10.6	10.8	0.61
Length of panicle in mm	339	364	0.02
Total length of side-axes of first order in mm	1167	1241	0.19

The figures given in table 1 are self-evident as regards the influence of length of photoperiod on the size of panicles of photoperiodically sensitive varieties. Some remarks, however, must be made. The figures for *Nero di Vialone* prove

<sup>2)</sup> If we assume equality of the distributions of both compared quantities, P is the probability of those values of WILCOXON'S statistic which deviate from expectation as much as the experimental value, or more.

clearly, that the panicle is built more compactly at a 18 h. photoperiod than at 12 h. photoperiod. Nevertheless, the number of side-axes of first order must be considered as the most important factor for obtaining a high number of flowers. One may put the question if this number of side-axes is determined either by the length of the photoperiod at the moment of initiation of the inflorescence or by the vegetative mass of the plant at this moment. An experiment to solve this dilemma failed for the greater part owing to extremely high temperatures in the hothouse, but probably the latter explanation is the right one.

As mentioned in § 2, *Nero di Vialone* and *Kameji* are arbitrarily awned. In both varieties the seeds of the plants grown at 12 h. photoperiod were practically awnless. In the 18 h. serie of *Nero di Vialone* the seeds bore long awns. In the 18 h. serie of *Kameji* some plants had seeds with long awns, others were intermediately awned.

#### THE INFLUENCE OF A CHANGE IN THE LENGTH OF THE PHOTOPERIOD

As described on p. 203, in the second set of *Nero di Vialone* certain changes in the length of the photoperiod were made. The results of these experiments throw some light on the problem mentioned in § 1, point 6, viz. the possibility that a treatment with a short photoperiod before tillering occurs, results in early earing of the main shoot and delayed earing of the tillers.

When studying the results of a change in the photoperiod from 12 h. to 18 h., one should keep in mind that the tillers of plants grown at 12 h. photoperiod entered the reproductive stage some days later than the main shoot: therefore, the development of the tillers must be regarded as being somewhat behind the development of the main axes.

In applying the changes in photoperiod, the data of the first set of *Nero di Vialone* could be used. The first change was made 5 days before the main shoot of the plants constantly grown at 12 h. photoperiod showed the inflorescence and some 8 days before the tillers did so. The main shoot came in the reproductive stage 35 days after the change was made, the stem reached a length of not more than 150 mm and the panicle a length of no more than 2 mm and often appeared to be seriously malformed. The retardation of the tillers was still more striking; with one exception, all tillers remained in the vegetative period, even after the plants constantly grown at 18 h. photoperiod became reproductive. Elongated internodia could be found, but the stem of a tiller never did get higher than 50 mm.

The next change from 12 h. to 18 h. was made when the growing point of the main shoot had differentiated and those of the tillers had not. Also this treatment caused a serious drawback, but to a lesser degree. The growth of the stem and the panicle of the main shoot was delayed, and the length of a plant grown constantly at 12 h. photoperiod could not be reached, but flowering occurred normally. The behaviour of the tillers in this group was the same as that of the main axis of the group dealt with in the preceding alinea.

The third change from 12 h. to 18 h. was made at the moment when all the tillers had become reproductive and the panicle of the main shoot was  $\pm 2$  mm in length. In the main shoot earing was delayed and length of the stem diminished, but only slightly. As could be expected, the tillers of this group behaved as did the main shoots of the second group.

Changes from 18 h. to 12 h. photoperiod were made for the first time when the plants were in the vegetative stage, and for the second time when they were in the reproductive stage. The first time the change was made at the moment when comparable plants grown at 12 h. photoperiod were entering the reproductive stage. Consequently, these plants could be considered as being ripe to flower. By dissecting one plant each day it could be ascertained that a period of 10 days was necessary before the initiation of the inflorescence became visible under the microscope. Stem elongation was very rapid.

Changing the photoperiod from 18 h. to 12 h. i.e. when such a plant — main shoot and laterals at the same day — reached the reproductive stage, demonstrated again that a short photoperiod hastens elongation of both stem and panicle. The plants of this group flowered when the experiments had to be ended owing to the late season whereas at that moment the plants grown constantly at an 18 h. photoperiod were not yet flowering.

The change from a long to a short photoperiod has another striking effect: it stimulates reproductive development of the axillary buds. In § 6, we reported already that at 12 h. photoperiod sometimes the bud of the flagleaf develops into a large panicle. This did not happen in the second set of *Nero di Vialone*. However, when a change in length of photoperiod was made from 18 h. to 12 h. during the vegetative stage, 55 % of the axillary buds of the flagleaves grew out and became well developed panicles. Moreover, the development of the other buds was stimulated when the change was applied in the vegetative stage or in the reproductive stage. A greater number of buds showed an inflorescence and in this inflorescence flower primordia could be detected. Normally, panicle development in a reproductive bud proceeds as far as the differentiation of the side-axes.

## DISCUSSION

The data, obtained by our experiments, enable us to give the following picture of the behaviour of photoperiodically sensitive varieties of rice:

In the first weeks of the growing cycle rice is indifferent to the length of the photoperiod. Some authors contend that this period of insensitivity ends earlier for a short photoperiod than for a long one, but this, of course, cannot be true: in the sensitive period a plant is susceptible to any length of photoperiod. The explanation of this controversy lies in the use of the "normal daylength" as "control". Let us assume that we have an experiment at a latitude where daylength in the experimental period fluctuates from 14 h. to 16 h.: we use a sensitive variety, and give it a photoperiod of 10 h. or 16 h. during 30, 40, 50, 60, 70 or 80 days, starting at the sowing date. Now it happens that the plants of the 10 h. series enter the reproductive stage after 40 days, those of the 16 h. series after 70 days and the plants of the control after 60 days. This means, that all the plants receiving a 10 h. photoperiod during 40 days or longer, will ear earlier than the control. The conclusion will be made that for a 10 h. photoperiod the indifferent stage ends after 40 days. The plants of the 16 h. series which grew at this photoperiod during 30 to 50 days, after this treatment arrived at a convenient photoperiod for becoming reproductive at the 60th day after sowing, viz. the local daylength. This means, that they will ear at the same day as the control, and it seems as if the indifferent stage for a long photoperiod ends after 60 days. It is

easily to understand that only a wrong idea on the significance of the "normal daylength" as "control" leads to this incorrect conclusion.

After the initiation of the inflorescence the plant remains photoperiodically sensitive. This is proved by the fact that stem elongation proceeds more rapidly at 12 h. than at 18 h. photoperiod. Of course, the influence of the length of the photoperiod in this stage cannot be as strong as in the stage when no inflorescence was visible. When the shoot has reached the sensitive stage but the inflorescence is not yet visible, it depends on the photoperiod at which moment the growing point will develop into a panicle. When the inflorescence has appeared, the length of the photoperiod is decisive on the rate of growth, but this is quite another phenomenon.

Within a plant important processes may go on without being traceable at the outside. This is proved by the second set of *Nero di Vialone*. A plant which within 10 days will show the inflorescence cannot be distinguished from one which is not yet so far advanced. The results of the set of plants mentioned show, that these days are the most critical in the life cycle of the plant as regards photoperiodism. However, our experiment renders no complete picture, which is the more evident when we examine fig. 8. This figure demonstrates that stem elongation in the 12 h. series of *Tjina* started  $\pm 12$  days before the differentiation of the growing point. If we take it for granted that *Tjina* in the same way enters a critical phase 10 days before this differentiation it remains to be asked what might happen when a change in the length of the photoperiod was applied  $\pm 18$  days before the formation of the panicle, i.e.  $\pm 6$  days before stem elongation started.

There exists no more doubt as to the early flowering of the main shoot and the delayed flowering of the tillers mentioned in § 1, point 6. Axillary buds may enter the reproductive stage under the influence of the stage which the shoot has reached at which they are situated. However, the initiation of the panicle in the axillary bud takes place a few weeks later than on the shoot itself. Moreover it has not been ascertained that the buds lower situated, i.e. those which contribute to the tillering, are induced also. In *Nero di Vialone* this certainly was not the case, whereas in *Kameji* it is still uncertain. This means that if we administer a sufficient number of short photoperiods to a non-tillering plant, the growing point of the stem will give rise to a panicle, but the axillary buds will stay in the vegetative stage for a considerable time. When the treatment with short photoperiods ends, and the buds can grow out and become a shoot, they will not undergo the influence of the reproductive main stem but they are at the moment which is imposed by the photoperiod at which the tillers developed. Consequently, if we want to reach earliness in earing of both main stem and tillers, we should proceed with the treatment until all the shoots are entering the reproductive stage.

Only a few data could be obtained on the influence of photoperiod on tillering. Because, normally, tillering occurs in the indifferent period, it is not likely that the length of the photoperiod could be responsible for a loss in yield owing to the formation of a smaller number of tillers. In freely developing plants of a highly sensitive variety, the number of tillers probably will be smaller at a short photoperiod than at a long photoperiod, because in the latter case the number of axillary buds is much greater than in the former.

One might ask whether the presence of awns depends on the size of the plants.

VERVELDE (1953) made clear that in intermediately awned cereals the more robust ones bore awns, whereas the small ones were awnless. This could be an explanation for the fact that the plants of the 18 h. series of *Nero di Vialone* and *Kameji* were awned, whereas the plants of the 12 h. series, that were much smaller, did not possess any awns. Observations in our greenhouses, however, do not support this supposition.

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