

## BOTANY

# DEVELOPMENTAL PROCESSES OF THE RICE PLANT IN RELATION TO PHOTOPERIODISM

## II

BY

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5.5. *Stem elongation.* Before germination the insertion of the coleoptile, the leaf primordia and the growing point are at the same level. Two weeks after germination the horny, curved, pointed stem base has been formed, showing no signs of nodes or internodes. It lasts throughout the life-cycle. At the base of the 6th leaf the lowest internode is formed, which reaches its final length at the 16th day. After a leaf has reached maturity, the underlying internode extends. The successive internodes reach increasing lengths. The rate of the elongation depends on the variety and may also be influenced by external conditions. Fig. 10 and fig. 11 show the elongation of the main stem and the laterals respectively of the July-series of the Untung-variety and of the Baok-variety. In the latter the rate of elongation is much lower.

The laterals show no extended internode below the prophyll. As soon as a leaf of a lateral has reached maturity, the internode below it enters the grand period of growth. It is remarkable that such an internode, what even its place in the lateral, elongates to nearly the same extent as that internode of the main stem, that enters the grand period of growth at the same moment. It happened for instance that the 4th internode of the 9th lateral reached the same length as the 15th internode of the main stem at the 97th day.

Even young laterals with a small number of leaves react in the same way. Finally the peduncles elongate almost simultaneously: they are the top-most internodes between the bract at the base of the panicle and the insertion of the flag leaf. Earing of the main stem occurs first, immediately followed by earing of the laterals.

5.6 *Initiation and development of the inflorescence.* The first sign of the reproductive stage is an elongation of the growing-point from 0,080 mm to about 0,200 mm. It also increases in diameter. The highest primordium stops elongating and remains as a bract of about 0,250 mm under the inflorescence. The growing point is soon divided into lobes (fig. 12 and 13), which form the future flower-primordia. Each one splits off the 3 glumes, the palea, the lodicules and the 6 anthers (fig. 14 and 15). Finally the

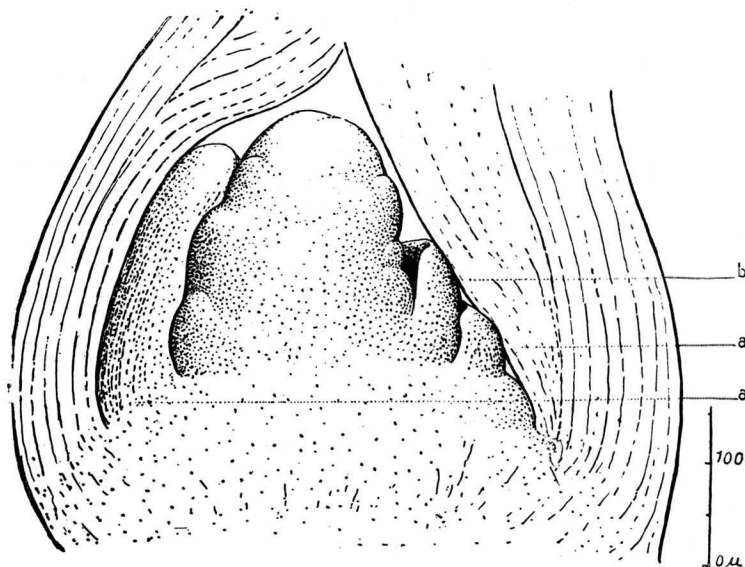


Fig. 12. Growing point of the main stem of a 51 days old plant of the Untung-variety (July-series), entered into the reproductive stage showing flower primordia.  
*a*: flag leaf; *b*: bract.

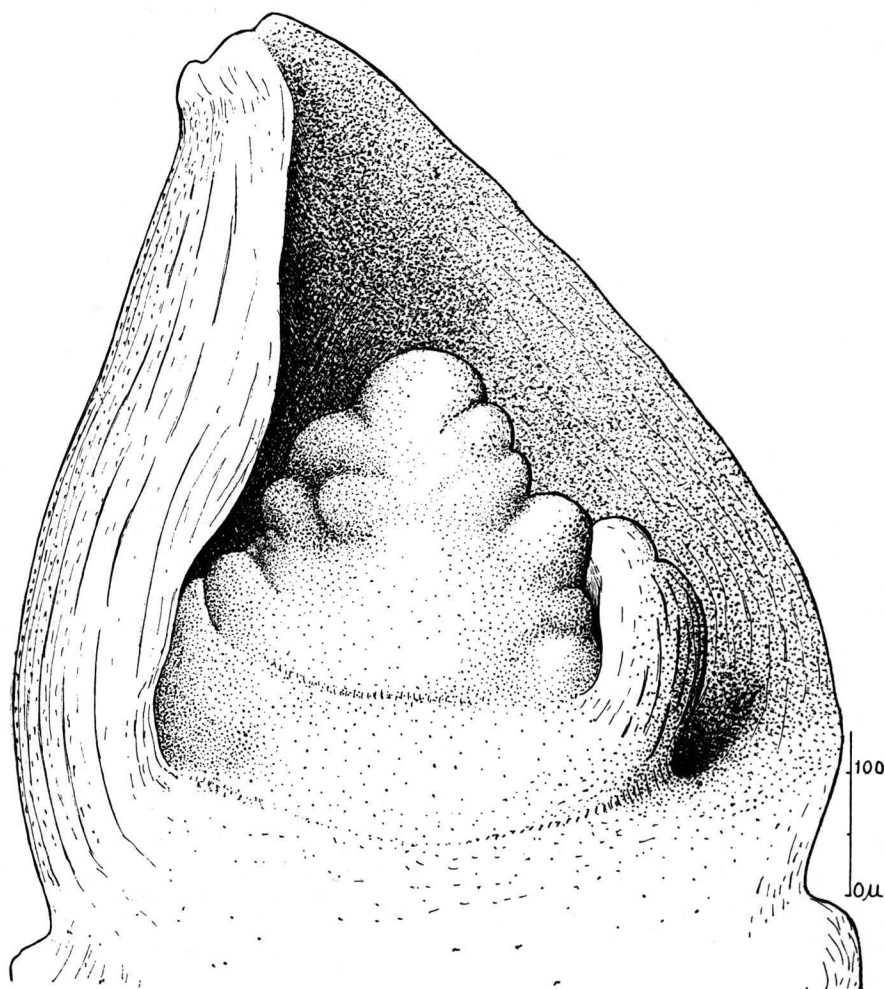


Fig. 13. Growing point of the main axis of a 52 days old plant of the Untung-variety (July-series), in the reproductive stage, surrounded by the 15th and the 16th leaf.

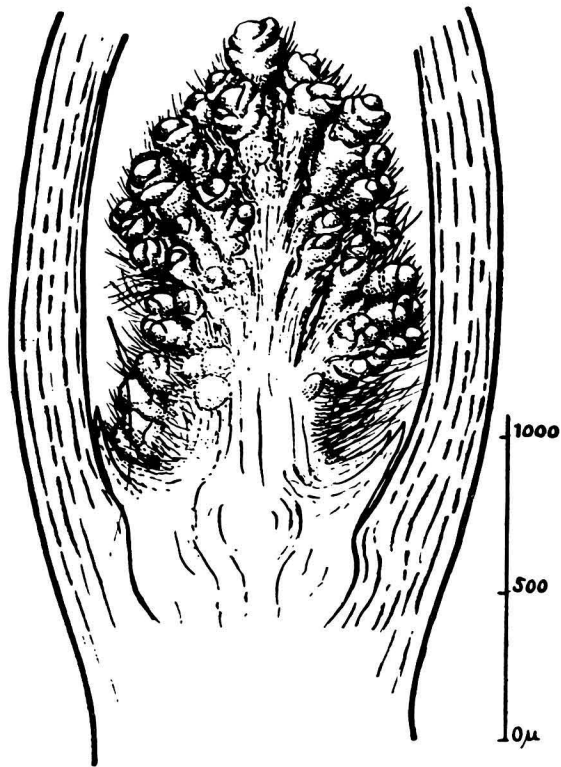


Fig. 14. Plumule of the main axis of a 66 days old plant of the Untung-variety. The topmost flowers with paleas and glumes developed.

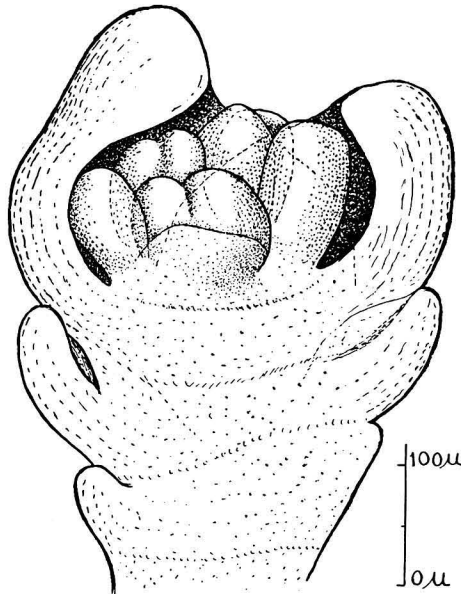


Fig. 15. Flower primordium of a 69 days old plant of the Untung-variety with paleas and glumes. The primordium of the 5th anther is just visible.

pistils are formed and the rest of the growing point changes into the ovary (fig. 16). At this stage the flower has a length of 1,5 mm to 2 mm. Maturity is reached after 24 to 30 days. The main stem reaches the reproductive

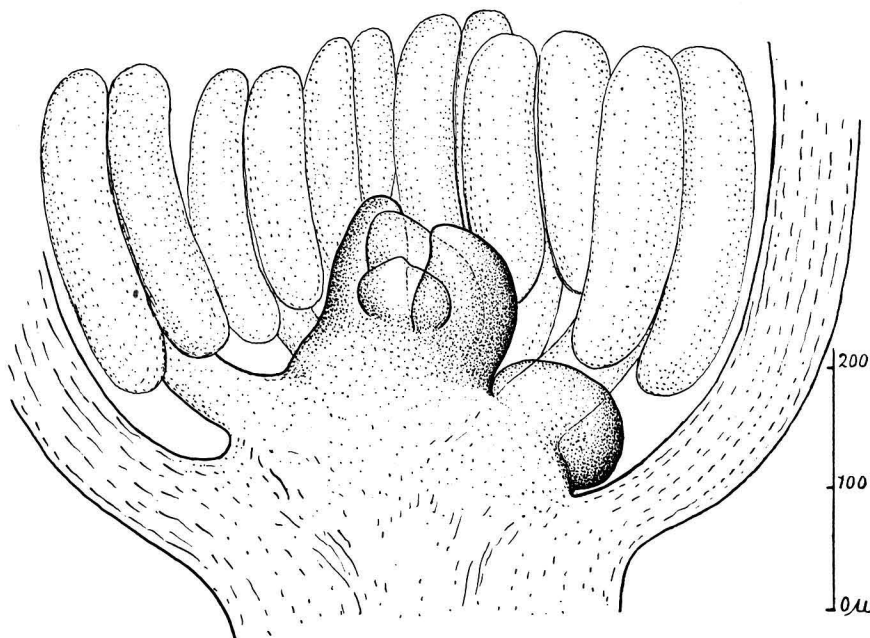


Fig. 16. Flower with anthers, carpels and lodicules of a 83 days old plant of the Untung-variety. The growing point has changed into ovary.

stage first, followed in turn by the biggest laterals of the first order and within a week by the smaller ones of the second and the third order. The same order of succession occurs in the elongating of the peduncles and in flowering.

5.7. *The period of inhibition.* After the described period of vigorous growth, a period of inhibition sets in. Especially bud development is retarded. No correlation could be found between the beginning of the period of inhibition and the time of stem elongation and earing. In the Untung-variety (July-series) the beginning of the inhibition period could be detected after stem elongation had started and after the flower-primordia were initiated. In the Baok-variety, however, the first signs of inhibition were visible long before (fig. 17). Only in one case a correlation was found between the time of earing and another phenomenon of inhibition. It concerns the elongation of the sheaths of the successive leaves of the main stem which are of increasing lengths until the growing point changes into an ear primordium. The sheaths which are immature at that time, elongate to a lesser extent than could be expected (fig. 18).

Concerning bud initiation, it was observed that the rate of initiation decreased in the Untung-variety (July-series) from the 55th day on.

Between the 75th and the 95th day, however, a period of a somewhat increased bud initiation and bud development could be observed in the midst of the inhibition period which lasted until the ears had ripened. Thus the observation of KUILMAN [21 and 22] was confirmed.

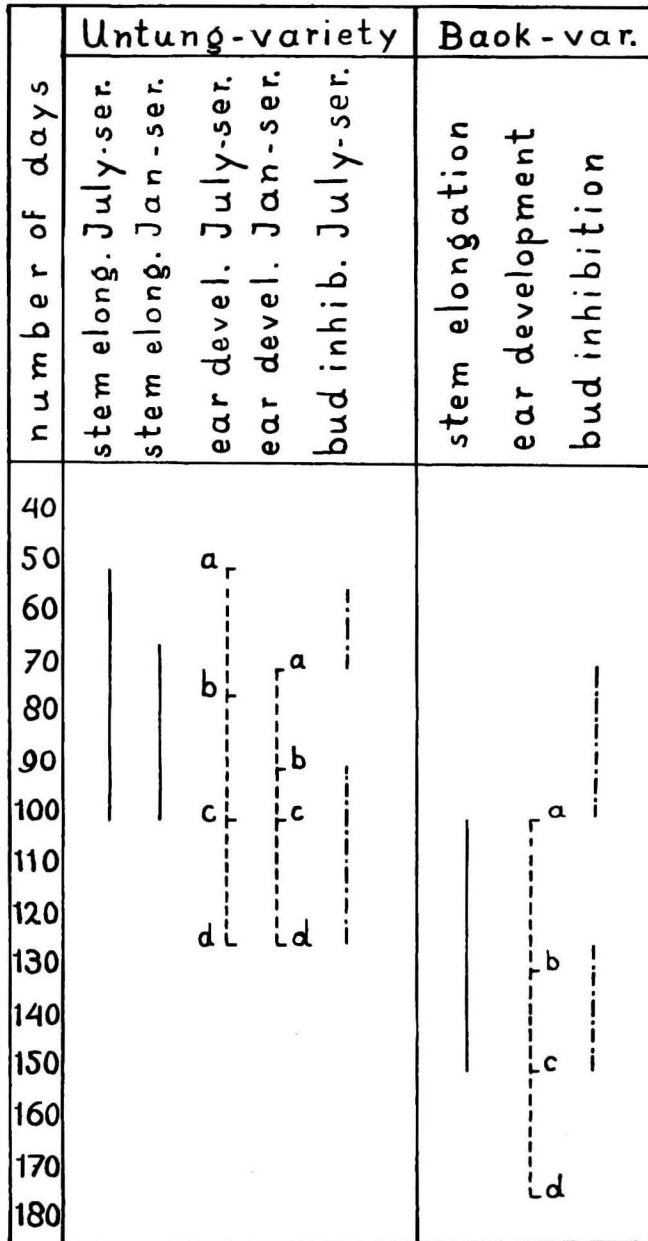


Fig. 17. Periods of stem elongation, ear development and bud inhibition in the 3 series. *a*: ear initiation; *b*: the peduncles start elongating; *c*: earing; *d*: panicles are mature.

During the period of inhibition the buds of about 4 mm do not enter the grand period of growth as readily as before, though the growing point does not stop initiating new leaf primordia. Thus thickened buds of a spherical shape can be found with a great number of short leaves, sur-

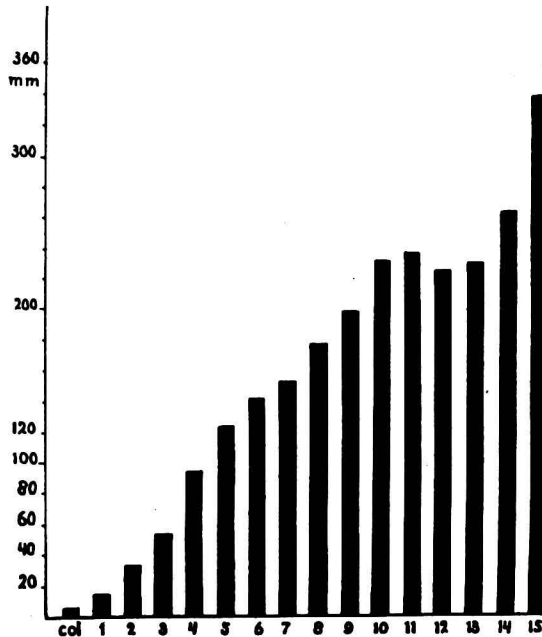


Fig. 18. Average lengths of the sheaths of 195 plants of the Untung-variety sown in July. Abcissa: the numbers indicate the place of the sheaths and the coleoptile at the main stem; ordinate: length in mm

rounding each other (fig. 19 and 20; table 1, 76 and 84 days). Here again the rate of leaf production seems to be rather independent of the factors causing inhibition of the further development.

The rate of elongation of those buds already in the grand period of growth decreases at the time inhibition sets in. As they do not reach the stage of a "shoot" as readily as before, the result is an increasing number of buds between 4 mm and 60 mm. They are flat, pressed between stem and leaf sheath (fig. 19).

These buds die off after the 70th day (Untung-variety, July-series), becoming brown, decayed or shrivelled. The thickened buds die off as well, though less readily than the flat ones. The outer leaves are first in decaying. The growing point may finally die as well, or it may still be living at the time the plant resumes vegetative growth after the ripening of the ears. In that case it may play a rôle in the secondary vegetative development (p. 1625). The flat and the thickened types of bud are found at the base of culms with a developing ear, just above the insertion of the highest lateral in the generative stage. The processes of decaying and

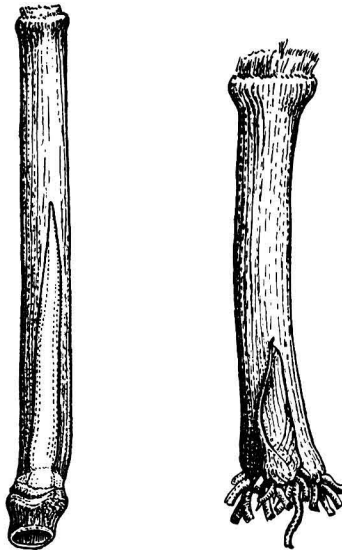


Fig. 19. An elongated and a thickened axillary bud of the axis  $1/5/2$  of a 80 days old plant of the Untung-variety.  $2\times$ .

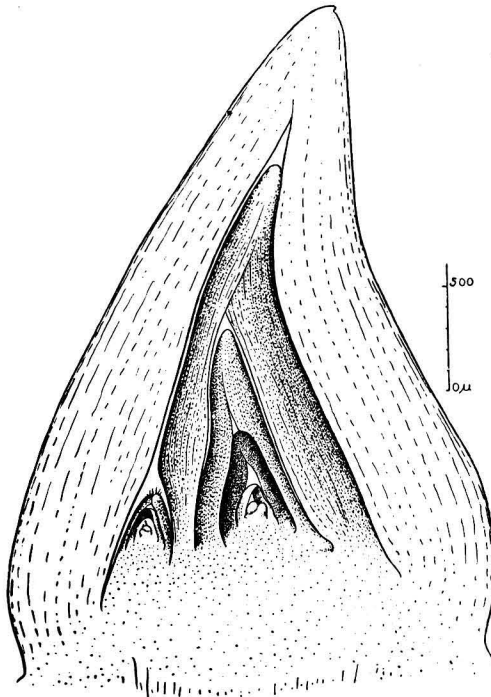


Fig. 20. The thickened bud  $1/6/3$  of a 84 days old Untung-plant with 5 primordia under the prophyll.

thickening advance in an apical direction. Fig. 21 shows the schemes of 3 of the dissected plants. In the 51 days old plant the buds are still "normal", in the 84 days old plant dead buds are found for instance at the culm 1/5/1, above the insertion of the earing shoot 1/5/1/3. If the lateral 1/11

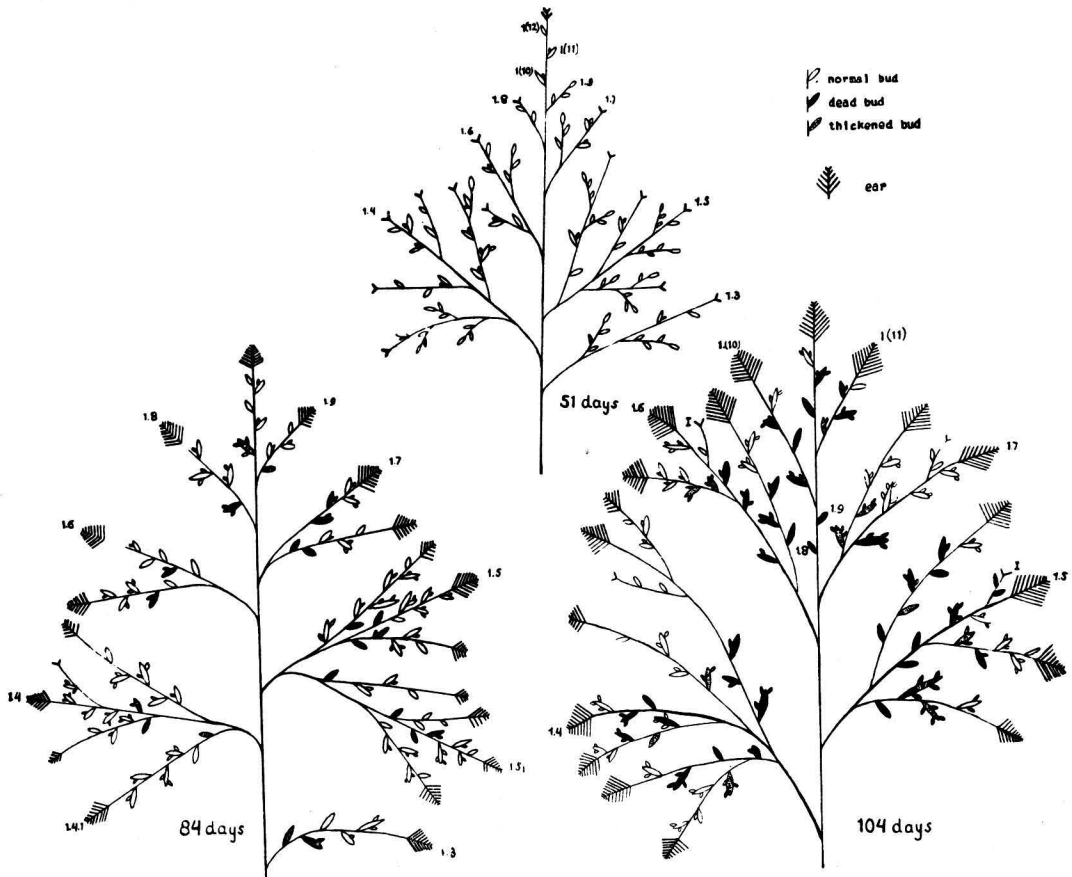


Fig. 21. Schemes of 3 dissected plants (Untung, July-series). The leaves are omitted and the internodes are lengthened at random, to show the place and the types of the buds.

is the highest earing culm, the buds 1/12 and 1/13 may die off which often happens as in the case of the 104 days old plant. At the time the ears reach maturity only a few normal buds are left at the top of the culms. Though the number of "normal" buds decreases, the total number of buds increases during the period of inhibition, as well as the number of decayed flat and thickened buds.

5. 8. *Which shoots are "ripe to flower"?* Ripeness to flower is reached if the minimal leaf number necessary for ear initiation has been laid down. Probably this number depends on the variety and may differ for the main stem and for the laterals which may need fewer leaves. Also day-



length may be of influence. In the Untung-variety a shoot with a mature prophyll, one mature leaf at the top of an elongated internode, one leaf in the grand period of growth and 2 leaf primordia were ripe to flower in August. The internode may have a length of 20 mm or as little as 5 mm provided it has a cylindrical shape. Shoots never initiate a flower-primordium while they still have immature flat internodes. In most cases 6 leaves is the minimum number for an earing lateral, though culms with 4, even with 3 leaves were recorded at the end of the generative period. On the other hand, after the ripening of the ears of the main stem and the biggest laterals, shoots with 8 or more leaves might still be vegetative, a difference which could not be explained. May be the plant is not able to initiate an ear primordium just after having entered a second vegetative period under all circumstances, may be the shoots developed during September and October were influenced by the increasing daylength, which inhibits ear initiation.

At the time the ears are initiated, about 88 % of the shoots is not yet ripe to flower. It might be expected that they would gradually reach this stage by a continuous process of leaf initiation and elongation. By the inhibition process, however, they stop developing and only a few buds at the top of the main stem and earing laterals, having escaped inhibition, reach a stage of ripeness to flower and join the first group in flower initiating later on. In each dissected plant a few ear primordia were found much younger than the others. They flower and mature 2 to 3 weeks after the first group (fig. 10 and 11, the laterals 1/15, 1/16 and the younger ones). These culms are cut 2 to 3 weeks after the harvest.

5. 9. *The second vegetative stage.* After the ripening of the ears, the inhibition stops rather suddenly and a vigorous vegetative development of all living buds and meristematic tissues occurs. In a short time the apparently dead culms are covered with green needle shaped shoots, the internodes of which at once show an increased elongation. A culm partly developed during the generative and partly during the second vegetative period, may show short internodes, originating from a thickened bud with many leaves at the base, sharply separated from the longer topmost internodes, which bear longer leaves. Flower initiation of these shoots is delayed. The moment of ear initiation could not be determined, as the old decaying culms could not bear the heavy load of new shoots and succumbed. The behaviour of the buds and shoots was further studied by examining cuttings.

5. 10. *The behaviour of rice cuttings.* Pieces of old stems each with a thickened bud or a young shoot rooted easily helped by the high number of adventitious roots. Cuttings of the Untung-variety were taken from the field directly after harvesting in February. Cuttings were taken weekly up to 7 weeks after harvesting. The first set tillered abundantly and flowered after 84 days. Every plant developed about 8 ears, each with

about 170 spikelets. The other groups showed less tillering: the longer the buds remain on the mother plant, the less they tiller after transplanting, which might be due to the lack of nutrients in the early stages. All cuttings flowered, however, at the same time, the ears having been initiated simultaneously, independent of the time of transplanting and probably influenced by daylength. The shoots cut 7 weeks after harvesting only showed 1 to 3 ears per plant, each with about 20 to 60 spikelets. From all sets the number of leaves of a culm varied between 3 and 9; most culms showed 5 leaves, independent of the date of transplanting. Such a small number of leaves necessary for earing is characteristic for laterals of a high order. All shoots developed by the cuttings seem to retain their original character as laterals of high order, forming only a small number of leaves before ear initiation. None of the shoots behaved as a main stem, forming 15 or more leaves before entering the generative period. Yield was reduced by this readiness to flower.

From the varieties: Skrivimankoti, Bayang, Brondol poetih, Tjina and Baok cuttings were taken directly after harvesting. From Skrivimankoti and Bayang respectively 66 % and 43 % failed, a fact probably due to the coarse unbranched root system. Cuttings of these varieties, as well as those of Brondol poetih eared before tillering. After 75 days Skrivimankoti flowered irregularly and did not produce tillers afterwards. Bayang produced only a few tillers after earing, but Brondol poetih produced such a great amount of tillers after earing at the 40th day, that the plants showed an even more vigorous growth than seedlings of the same age. Of the Tjina- and Baok-variety 100 % of the cuttings succeeded: the plants tillered abundantly before earing and the growth was as vigorous as of seedlings. Probably the long growing period and a high number of leaves required before earing, are favourable factors.

The circumstances of the war stopped the experiments. For a rapid propagation of new valuable varieties further study of the behaviour of cutting may be of interest.

5. 11. *Developmental differences between the January- and the July-series of the Untung-variety.* Fig. 1 shows, that the duration of the growth-periods of Bayang and of Skrivimankoti are nearly equal, when sown in January and when sown in July. Earing occurs after the same number of days. However, it is not surprising that processes preceding a phenomenon of such a complex character as earing: e.g. leaf and ear initiation, leaf and stem elongation, may proceed in different ways. The plants of the January-series were exposed to decreasing daylengths, those of the July-series to increasing daylengths. Both flowered after 100 days though the plants of the July-series were more irregular. Concerning development the following facts were established:

a. The number of leaves on the main stem. In the July-series ear initiation took place at the 50th day, after 15 leaves and leaf primordia

had in most cases been formed. The 16th primordium is the bract under the panicle. The number of leaves in the January-series increased until the 62nd day, when the 19th leaf primordium was developed. At the 70th day the ear primordium was differentiated.

*b.* The process of inhibition. As mentioned before the sheaths of the leaves, which are still immature at the time of ear initiation remain shorter than might be expected. In the July-series those of the 12th and of the 13th leaf (fig. 16), in the January-series those of the 16th and of the 17th leaf were thus shortened. The delay in the process of bud inhibition enabled the plants of the January-series to tiller longer and more abundantly than those of the July-series.

*c.* The rate of leaf initiation and leaf development. As mentioned before the rate of leaf initiation is independent of daylength. In both series, 15 leaves were initiated before the 45th day. Between the 45th and the 70th day the January-series initiated 5 leaves more before ear initiation. Did elongation of a leaf continue to take 3 to 5 days, the January-series might be expected to flower 15 to 25 days later than the July-series. Flowering occurred, however, in both cases after about 100 days. This is due to the fact that after the 45th day leaf elongation proceeds with increasing speed in the January-series and is retarded in the July-series.

*d.* Elongation of the internodes and the peduncle. Till the 50th day in the July-series the stem consisted of about 10 small internodes, the 5 lower ones each with a length of 0,5—1 mm, the higher ones not surpassing 4 or 5 mm. When earing occurred, total stemlength was 20 to 25 mm. After the 50th day it was the internode under the 11th leaf that suddenly showed an increased elongation. It reached a length of 40 mm, in some plants even of 50 mm. Each of the following internodes elongated to a higher extent; the stem had entered the grand period of growth simultaneously with ear initiation. Finally, at the 100th day, when earing occurred, total stemlength was about 600—700 mm (fig. 17). In the January-series, the 10 lowest internodes formed a stem of only about 10 or 11 mm, the biggest internodes not surpassing 5 mm. Here it was the 14th internode that suddenly elongated to an extent of 30 mm at the 64th day. In this series the stem had entered the grand period of growth before ear initiation, which occurred at the 70th day, when stemlength was already 175 mm. After 100 days, at the time of earing the total stemlength was about 1200 mm. The youngest internodes of the January-series, below the leaves 15 to 18, together with the peduncle, needed less time for elongation than those of the July-series under the leaves 11 to 14. From the moment the flag leaf became visible till ear emergence the former needed only 8 to 10 days, the latter about 15 to 16 days.

*e.* The number of grains in the ear. The ears of the main stem of 13 plants of the July-series had an average of 135 grains, of the January-series over 200 grains. Ears of the laterals had averages respectively of 100 and of 150 grains.

## 6. Discussion

6. 1. *The interrelation between the developmental processes.* Fig. 17 shows, that in the July-series of the Untung-variety the process of stem elongation was immediately followed by ear initiation and inhibition. In the Baok-series inhibition occurred first, followed by the entering of the stem in the grand period of growth and finally by ear initiation. A correlation was found between ear initiation and inhibition of the rate of elongation of those leaf sheaths, which were still immature at that time. Between inhibition of bud development and earing, however, no correlation could be found. On the contrary, after the first period of bud inhibition in the Baok-series bud development increased again when stem elongation and ear differentiation were observed. The only coincidence between these processes can be observed at the beginning of the second vegetative period when maturity has been reached and bud inhibition stops suddenly.

Concerning bud inhibition, RAMIAH and NARASIMHAM [36] consider a lack of food as the causal factor of the abortion of tillers, the mother shoots taking so much of the available nutrients that no adventitious roots can be formed. "All the late and undesirable tillers are thus eliminated by the time the plant passes into the reproductive phase". KUILMAN [21, 22] considered his second interval in the process of tillering to be correlated with formation and development of the ear; later he saw in the elongation of the internodes the causal factor. None of these opinions has been proved exactly.

Concerning the coincidence of the developmental processes, the 3 series behaved in different ways, no causal connection could be established. They may be caused independent of each other by different factors. The influence of growth substances as auxin or of the still hypothetic caulocaline formed in the roots, causing stem elongation under certain conditions, (WENT [42]), will not be discussed here. Before a theory of flowering and flowering hormones can be formulated for rice, as has been done by PURVIS and GREGORY [32] for rye and by VAN DE SANDE BAKHUYZEN [37] for wheat, a considerable body of experimental work still has to be completed.

6. 2. *The influence of daylength; earliness and lateness.* Though in the vegetative period of the January-series the average number of hours of insolation was far less than in the July-series, the plants tillered to a greater extent. The long days of January and February may delay bud inhibition and therefore promote tillering. They delay ear initiation, inhibit leaf- and stem elongation and promote lateness. The shorter days of March and April, however, induce flowering and provoke a rapid leaf- and stem elongation and a rapid earing; just as in winter rye elongation and ear-initiation are influenced by the same factors (PURVIS [31]). The reverse can be said of the conditions and their effect on the development

of the plant of the July-series. From the graphs given by VAN DER MEULEN ([27], fig. 1), it is clear that the life cycle is shortest under daylength conditions as short as possible at Buitenzorg. Earliness is promoted, but yield is lowest. It must be stated that the Untung-variety is better adapted to the light conditions prevailing during the first half than during the second half of the year. Possibly the decreasing or the increasing daylengths are decisive, more likely the absolute daylength determines development. In that case the number of hours of daylength necessary to obtain flower initiation as early as possible is still an unknown factor. On the other hand it is known that continuous light suppresses heading (KONDO [18]) or heading may occur at some delayed moment (FUKE [13]).

The influence of daylength on the different developmental processes has to be studied separately as far as possible. Long days may have an after-effect on stem elongation during a following period of decreasing daylength (PURVIS [31]).

Whether there is an obligate minimum number of leaves which has to be initiated before the ear can be differentiated, is another question to be elucidated. In winter rye this number is 7; for different rice varieties this number is still unknown. That a certain stage has to be reached before flowering can be induced has been reported by ALAM: "all varieties require a minimum period of 30 days for vegetative growth" (WHYTE [43], p. 329), and by FUKE [13], who discriminates two tillering stages. The effect of short day-conditions on plants in the first and on plants in the later part of the tillering stage was similar. Probably the minimum number of leaves required for flower initiation had not yet been reached in the earlier stages. Thus short day conditions had no effect on the growing point, as the stems were not yet "ripe to flower".

6. 3. *Breeding of rice varieties based on developmental characters.* In the Untung-variety factors may be distinguished independent of the date of sowing, such as the rate of leaf-initiation before the 45th day, the relation of the lengths of the mature sheaths and the increasing lengths of the successive internodes. Others are dependent on the date of sowing, such as the number of leaves and internodes initiated in the first vegetative period, the rate of leaf- and stem-elongation, the moment of inhibition of bud development and the number of spikelets per ear.

In a variety sensitive to daylength these factors could be recognized under different lengths of day; in varieties indifferent to daylength, factors for earliness and for a high yield can be determined as well: the tendency to develop a small number of leaves or the tendency to rapid leaf- and stem-elongation. In breeding for earliness in combination with a high yield, knowledge of the physiology of the parent plants is of highest importance. The program proposed for the wheat plant by MCKINNEY and SANDO [26] can be applied to rice hybrids as well: "populations which are segregating for earliness and lateness should be tested and

classified as far as practicable under several suitable conditions of temperature and daylength. This should facilitate the selection of genotypes homozygous for the several characters influencing earliness and lateness". Lines still heterozygous to a small degree may segregate for some developmental factors. By selection of types with the most favourable factors more homogeneous material may be obtained. The factors discussed here have not to be considered as units of heredity. They have to be studied first before the physiological factors depending on a single gene can be analyzed, in the way it is proposed by BOONSTRA [6].

### *Summary*

The development of 3 series of rice plants was studied by the dissection method:

1. Two series of the variety "Untung", one sown in January, the other in July. Untung is an unawned pure line, grown at Buitenzorg, Java. The growing period depends on the date of sowing.

2. One series of the variety "Baok", sown in January, an awned pure line with a growing period of 130 days, independent of the date of sowing.

Both varieties were grown on nutrient solution.

The following facts were established:

The growing point of the embryo is surrounded by a coleoptile, two young leaves, closely packed together and a third primordium. After germination a fourth primordium is formed exactly when the coleoptile starts elongation. The same principle is maintained during the vegetative stage, as every growing point during that period is always surrounded by: a young primordium of about 0,200 mm; a primordium of about 0,200 mm to 1 or 2 mm; a leaf in the "grand period of growth"; one or more mature leaves. A primordium only elongates when the preceding leaf has reached maturity and a new primordium has been formed.

When a leaf has reached maturity the internode below starts elongating, the peduncle being last of all. The immature internodes of the main stem and of all flowering laterals elongate to nearly the same extent at the same moment. The growing point of the sufficiently developed laterals change almost simultaneously into ear-primordia which develop in about 25 to 30 days. The simultaneous elongation of the peduncles synchronises flowering. In the Untung-variety ripeness to flower may be reached if a lateral has a minimum number of 5 leaves. At a certain stage, depending on the variety, an inhibition of the process of tillering prevents the younger shoots from reaching this stage. Buds, apparently in the grand period of growth, are found to be dead, pressed between stem and leaf sheath. In younger buds leaf primordia are still initiated but as no elongation occurs, the buds become spherical in shape. These two types of inhibition continue from the base of a flowering shoot in an

apical direction. At the time of maturity only the uppermost buds are still in a normal condition.

At that time the plant enters a second vegetative stage: the buds at the top and the thickened ones develop quickly into shoots, which may flower some 3 weeks after the first set.

The behaviour of the shoots was studied further with cuttings.

The period in which stem elongation and in which bud inhibition takes place, as well as the date of ear initiation depend on the variety and on the environmental conditions. An interrelation between these processes has not yet been determined.

Daylength at Buitenzorg (7° Lat. S.) is 12 h. + 31' in December and 12 h. — 17' in June. This difference of 48' throughout the year may induce a difference of 50 or 60 days in growth period in some varieties, depending on the date of sowing. When sown in January and July an equal number of days is required for earing.

Both the series of Untung examined reached maturity after 120 days, though the developmental processes were different:

The vegetative period of the July-series lasted 50 days, that of the January-series 70 days, with 15 and with 20 leaves initiated respectively. In the July-series the elongation of the uppermost leaves and the peduncle took 50 days, in the January-series these processes took only 30 days. Flowering occurred in both cases at the 100th day, though in the July-series the ears were smaller and flowering occurred more irregularly. Probably in the July-series short days promote flower initiation, resulting in earliness, but the longer days of September delay leaf and stem elongation. In the January-series the long days delay flower initiation but promote vegetative development. In March and April the shorter day-length promotes elongation and earing, resulting in earliness.

The influence of a constant length of day on the developmental processes requires investigation, varietal differences need to be recorded. Attention should be paid to those simple developmental factors which control earliness. New varieties may be obtained by crossings of varieties combining factors favourable for earliness and for a high yield under certain conditions.

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