BOTANY

DEVELOPMENTAL PROCESSES OF THE RICE-PLANT IN RELATION TO PHOTOPERIODISM. I [1])

BY

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1. Introduction. There is an extensive literature dealing with the influence of environmental conditions on the development of the rice plant. The influence of nutrients, temperature and light on the germination, the tillering, the time of earing and on the processes of ripening has been studied. Nevertheless the developmental processes succeeding each other or occurring simultaneously in a normal freely developing rice plant, are not yet fully understood. In most cases the plants have only been observed externally, without the systematic dissection necessary to determine their condition. With a better knowledge of the developmental processes occurring in control series, the results of many experiments on rice could have been interpreted more succesfully. The physiology of wheat and rye is far better known.

This knowledge may be the key to the solution of practical problems: the time of application of fertilizers depends on the requirements during the different phases of growth; abnormal development in case of diseases or physiological disturbances can only be recognized if the normal course of development is known. The mèntèk-disease in Java has been considered for a long time as a "yellowing", until KUILMAN [19] observed a shortening of the leaf-sheaths, a phenomenon which he could reproduce by cultivating plants on modified solutions. Moreover, knowledge of varietal differences in development will make it possible to choose varieties with factors adapted to prevailing conditions as daylength, altitude, water supply, etc. By breeding new varieties with a combination of favourable factors, earliness and a high yield may be promoted.

The scope of this paper is confined to the study of the development of two rice varieties under known conditions and to the effect of different daylengths on the developmental processes.

2. Literature. After the morphology of the rice plant had been studied (VAN BREDA DE HAAN [8]; BALSAC [3]; BHALERAO [5]; JULIANO and ALDAMA [16], compiled by COPELAND [11]), more attention was

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1) The experiments have been carried out at the "Algemeen Proefstation voor de Landbouw", Buitenzorg, Java. They were ended by war circumstances.

directed to the physiological processes. Germination has been studied frequently (VALETON [41]; JONES [15]; CHIEN LIAN PAN [10]), as well as the process of tillering. Exact data on this part of the developmental cycle have been given by RAMIAH and NARASIMHAM [36], KUILMAN [21, 22] and others, cited by the latter. Both authors pay more attention to the individual plant than had been done before. KUILMAN studied the behaviour of plants on nutrient solutions under controlled conditions. In the Untung-variety the process of tillering started about 18 or 19 days after germination, with an interval after the appearance of the first lateral shoots and a second pause from about the 45th to the 65th day. In the Baok-variety an interval in the process of tillering occurred between the 75th and the 85th day. Similar intervals have been observed by SUMMERS [40], ADAIR [2] and RAMIAH and NARASIMHAM [36]. Afterwards tillering increases again, though many buds die off or remain dormant. Attention has also been paid to stem elongation as well as to the development of the inflorescence (NOGUCHI [29]). RAMIAH [34] gave a growth-phase concept, similar to the schemes of PURVIS and GREGORY [32] for rye and of KCKINNEY [25] for wheat. In rice the photophase is far more important than the thermophase, which may even be lacking.

The effect of daylength on the time of flowering has been studied in many rice growing countries (NOGUCHI [30]; FUKE [13]; KONDO [18]; EGUCHI [12]; KUILMAN [20]; BEACHELL [4]; and others). The awned varieties are either indifferent to daylength or ear initiation is delayed to a small extent by short days. In the unawned varieties, endemic in northern regions, short days hasten earing. Japanese varieties introduced into Java flowered at such an early stage, that the yield was reduced. The reverse was observed by BEACHELL [4], who states, that tropical varieties introduced into the Southern States of the U.S.A. "fail to head, or head too late". The long days of summer prevent heading and the low temperature in autumn retards maturity.

Even in the same country the growing period may vary, depending on the date of sowing. The effect of this date on the length of the growing period has been described by MITRA [28]; by JENKINS [14]; by ADAIR [1] and by BEACHELL [4]. Two groups of varieties may be distinguished: 1. those whose growing period is shortened if the date of seeding is delayed. These "timely fixed" (MITRA) or "sensitive" (JENKINS) varieties flower at a particular time, irrespective of the date of sowing. They head when the days are shortening. 2. The second group of varieties flowers at a definite length of time more or less irrespective of their date of sowing. They are "periodically fixed" or "indifferent". Some sensitive varieties, if sown late, give a reduction in growth period as well as in yield.

SCRIPCHINSKY [38] interpreted the experiments of RAMIAH [35], LORD and DE SILVA [24] and HAIGH [17]. He comes to the conclusion that the seasonal variation of daylength, though small in the tropics, may be the cause of the seasonal growth habit.

At Buitenzorg (Java), VAN DER MEULEN [27] controlled the growth period of some awned or bulu-varieties and some unawned or tjereh-varieties by monthly sowings throughout the year. The awned varieties endemic in the tropics, showed only slight differences throughout the seasons. Of the unawned varieties the growth period of Bayang and Skrivimankoti was shortest if grown between May and October, longest if grown between November and April. A difference of 60 days or more occurred (fig. 1). Daylength at Buitenzorg (7° Lat. S.) differs between

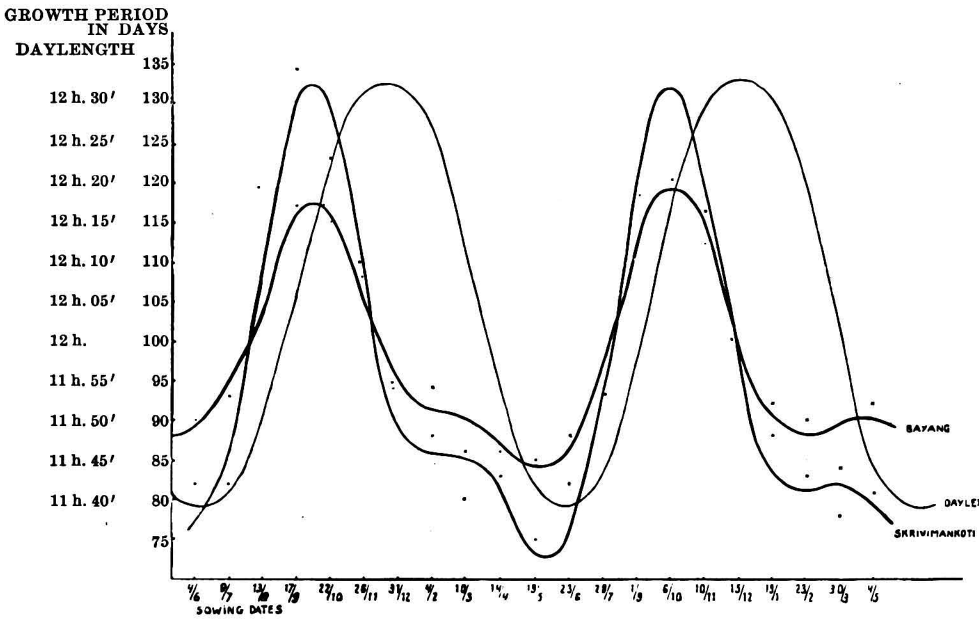

Fig. 1. Daylength at Buitenzorg and lengths of the periods from sowing to ripeness of the varieties "Bayang" and "Skrivimankoti" throughout the year (after VAN DER MEULEN, 27).

12 h + 30′ and 12 h — 18′. That a difference by only 48′ can induce such a difference in growth period is made clear by the same experiment North of the equator: the varieties reacted in the same way, but here the longest growth period occurred between May and October, the shortest between November and April (VAN DER MEULEN, unpublished).

Inducing earliness by short-day treatment has been tried frequently with more or less effect. A review has been given by KUILMAN [23]. One of the most striking reports is that of SIRCAR and PARIJA [38], who obtained an earlier flowering by short-day treatment of a Bengal variety. They could reduce the period before flowering from 133 to 47 days.

The way in which the developmental processes are influenced, in all experiments mentioned, has not yet been elucidated, a fact affirmed by WHITE ([43], p. 328).

3. Material and methods. In examining the developmental processes by the dissecting method used by BLAAUW and his coworkers

(Wageningen), care must be taken that all individuals are of the same genetic composition, of the same sowing date and that environmental conditions are similar. Three series of plants were grown on the nutrient solution used by KUILMAN and modifed by VAN RAALTE [33] [1]):

1. Two series of the variety "Untung", one sown January 16th, the other July 21st. Untung is an unawned or tjereh-variety, a pure line, selected by VAN DER MEULEN from an Indian variety named "Tilakkacheri". The growth period is dependent on the date of sowing;
2. One series of the variety "Baok", sown in January, an awned or buluvariety, a pure line with a growth period of 130 days, independent of the date of sowing;
3. Plants of the same varieties and of the same date of sowing from the rice fields were examined as well.

The plants were grown in the garden of the laboratory at Buitenzorg, Java. The temperature of the salt solution and of the air varied between 21° and 32° C; the number of hours of sunshine was determined; the daily light period was obtained from the Meteorological Institute. The grains were soaked in water for 24 hours; for another 24 hours they were kept in closed jars on moist paper in darkness, as germination is more regular under these conditions. Germination was continued on gauze covering the top of cylinders filled with the nutrient solution. In the early stages each seedling was kept on a 1 litre container, in the later stages a 4 litre container was used for every plant. In the seedling stage 10 plants were dissected every day; after the 16th day only 2 or 3 plants could be examined daily. In the later stages dissection of a plant with its tillers took so much time, that only 2 or 3 plants a week could be examined. The total number of dissected plants was about 300. In order to determine the stage of the growing-point and of the primordia a binocular microscope was used. Axillary buds and tips of culms were cleared by chloralhydrate in order to facilitate examination.

4. Nomenclature. As the conceptions concerning the morphologic status of the parts of the Gramineae-embryo differ greatly, the nomenclature of the laterals gave some difficulties. The opinion of BOYD and AVERY [87], who regard the meristematic epiblast as the ligule of the scutellum seems most satisfactory. The scutellum is thus the first leaf, the coleoptile the second, the first green leaf that becomes visible after germination must then be considered as the third leaf. This system is difficult to use in practice, just as all other systems, in which the first green

[1])

distilled water. . .	1 litre	$Fe_2(SO_4)_3$	25 mg
NH_4NO_3	340 mg	ferric citrate . . .	10 mg
KNO_3	170 mg	$MnSO_4 . 4H_2O$ . . .	20 mg
$MgSO_4 . 7H_2O$ . . .	250 mg	H_3BO_3	0,5 mg
$CaSO_4 . 2H_2O$ . . .	100 mg	$Fe_3(PO_4)_2$	400 mg
KCl	300 mg	$Ca_3(PO_4)_2$	400 mg

leaf of the main stem is not indicated by number one. For convenience therefore I labelled the first green leaf number one, its axillary bud was called 1/1, the lateral in the second leaf 1/2 etc. Every lateral has a closed prophyll at the base, which can be compared with the coleoptile. A secondary lateral originating in the axil of a prophyll is indicated by 0. For example: after tillering a bud 1/4/0 may be found, i.e. the bud in the prophyll of the tiller in the axil of the 4th leaf of the main stem.

Identification of the leaves and laterals of young plants is not difficult, if the coleoptile or the bladeless first leaf is still present. During development, these leaves die off. After some experience it was possible to recognize groups of tillers belonging to a lateral of the first order, which could be torn away from the main stem, leaving only a small scar. The main stem deprived of all laterals of the first order with their tillers shows the scutellum at the pointed, somewhat curved base, even when maturity is reached.

5. Results.

5.1. *The fruit.* Much attention has been paid to the different parts of the grain except to the embryo. The short stem not only bears the

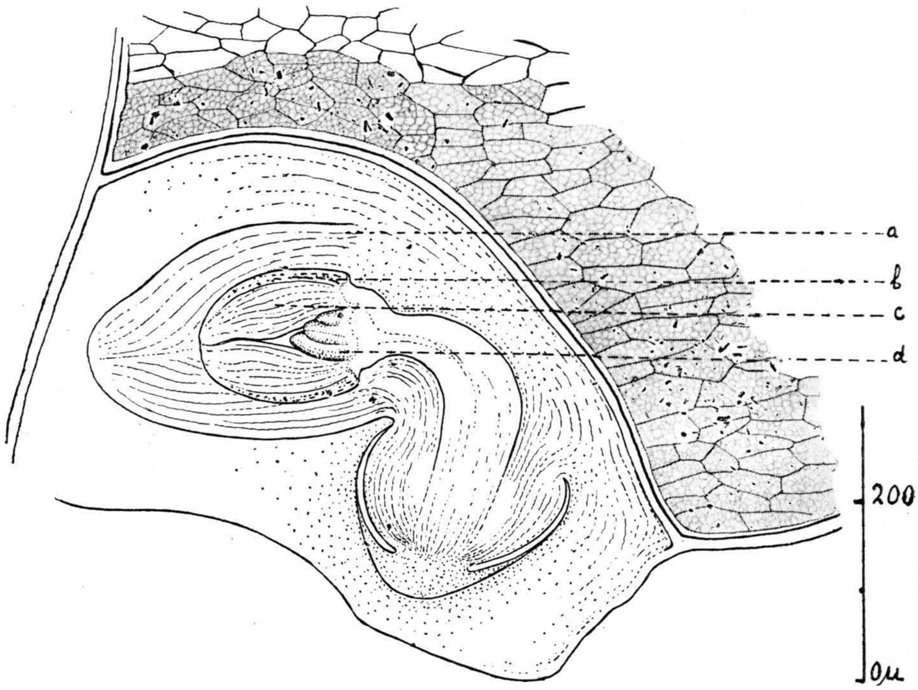

Fig. 2. Embryo of the Untung-variety after 24 h. soaking. *a:* coleoptile; *b–d:* 1st, 2nd and 3rd leaf.

scutellum and the epiblast, but the closed coleoptile covers three leaf primordia, a fact observed by CHI TUNG YUNG [9]. The second primordium is so tightly enclosed by the first that the two can hardly be distinguished (fig. 2). The third primordium is of the same height as the growing point: 0,080 mm. The three leaves can be detected a fortnight after flowering, at which time the grain is still immature.

5.2. *Germination.* After one day of exposure on wet filter paper, the swollen margins of the scutellum and the epiblast penetrate through the wall of the third glume, forming a cuplike cavity in which the tip of the plumule can be seen (fig. 3). The function of the hair-like epidermis cells

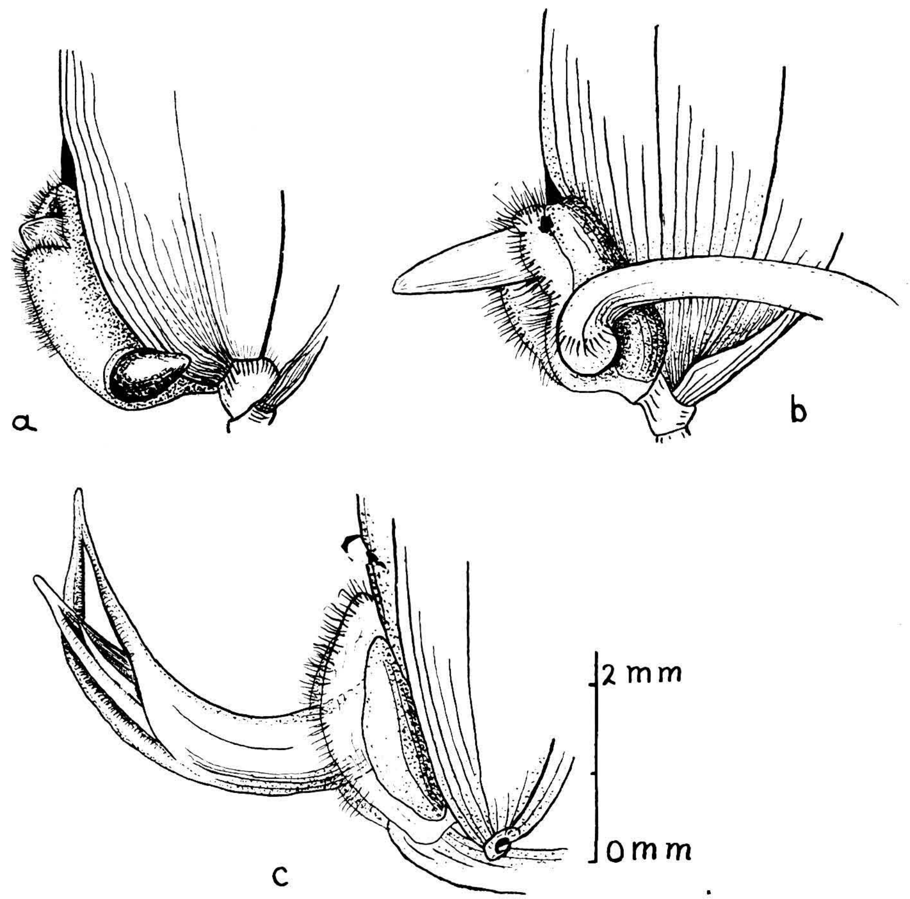

Fig. 3. *a–c:* development of the root and the plumule after 24 h. soaking and respectively 1, 2 and 3 days germinating. In *c* the coleoptile is split open by the 1st and 2nd leaf.

of the margins may be to retain water and to prevent dessication of the germinating grain, (JULIANO and ALDAMA [16]). On the other hand the hairs, retaining air if submerged, may protect the embryo against oxygen deficiency, which causes abnormal germination (VALETON [41]; JONES [15]).

5.3. *The development of the leaves in the first vegetative period.* At the second day after germination the coleoptile, the first and the second primordia elongate rapidly, the third primordium only to a small extent (fig. 4). A 4th primordium, which forms a wall with a higher and a lower side is developed at the growing point. The highest part, opposite the midrib of the preceding leaf elongates till it reaches the height of the growing point. By lateral growth the margins overlap each other, enclosing the growing point. CHI TUNG YUNG [9], who probably employed longitudinal sections, described this process, but overlooked the lateral growth.

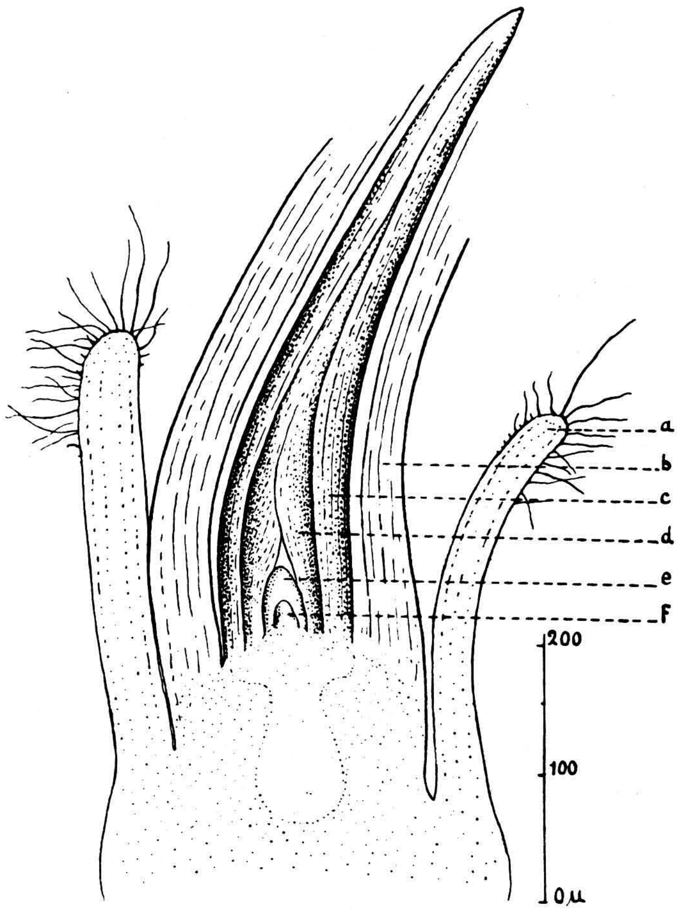

Fig. 4. Longitudinal section through the plumule of a 2 days-old plant of the Untung-variety. *a:* epiblast; *b:* coleoptile; *c–e:* 1st, 2nd and 3rd leaf; *f:* 4th primordium, covering the growing point.

At the 3rd day the coleoptile is split open by the horny point of the first leaf. This leaf and the second one elongate simultaneously. The sheaths of all leaves reach maturity after the blades, all parts arising from meristematic cells at the base of the primordium.

At the 6th day the coleoptile and the first leaf have reached maturity, the second leaf has nearly stopped elongating, the 3rd leaf just enters the grand period of growth, the 4th leaf has hardly reached 1 mm, and a 5th primordium appears (fig. 5). 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.

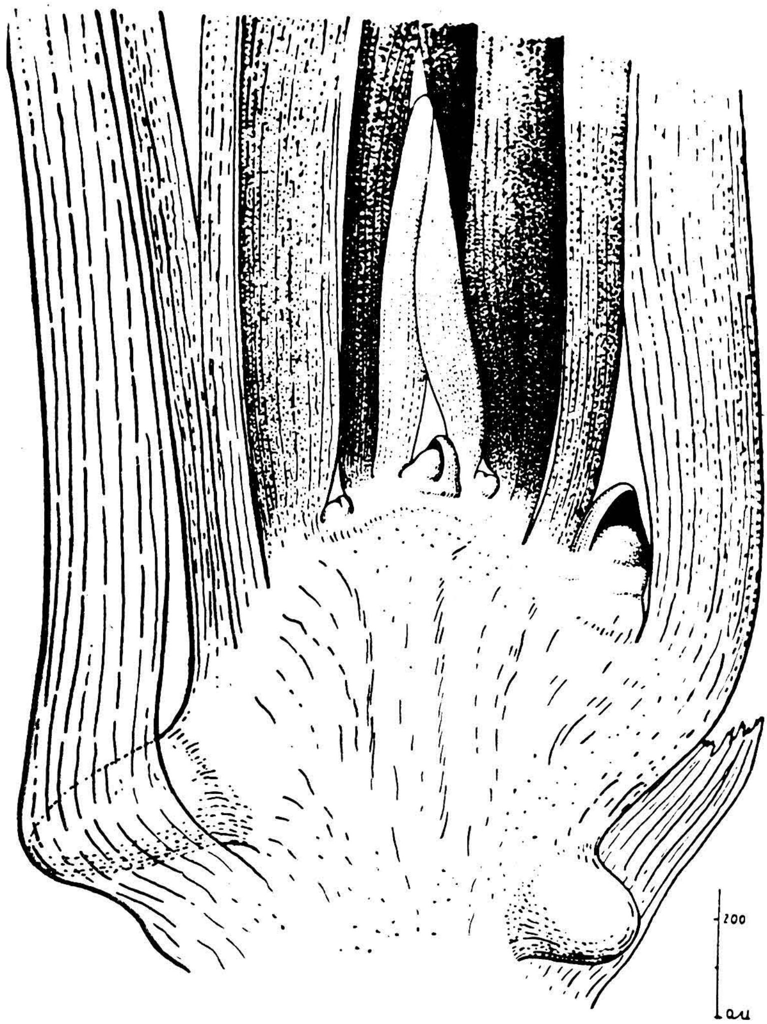

Fig. 5. Longitudinal section of a 6 days old seedling of the Untung-variety. The growing point is surrounded by the 5th leaf, axillary buds are developed. Adventitious roots piercing through the coleoptile.

The blade and the sheath of a preceding leaf has to reach maturity before the next leaf primordium can enter the grand growing period. 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.

Every 3 or 5 days another leaf has reached maturity and a new primordium is initiated (fig. 6). This applies in the Untung- as well as in the Baok-variety for the earlier stage of development. The leaf production rate seems to be rather independent of variety and of environmental

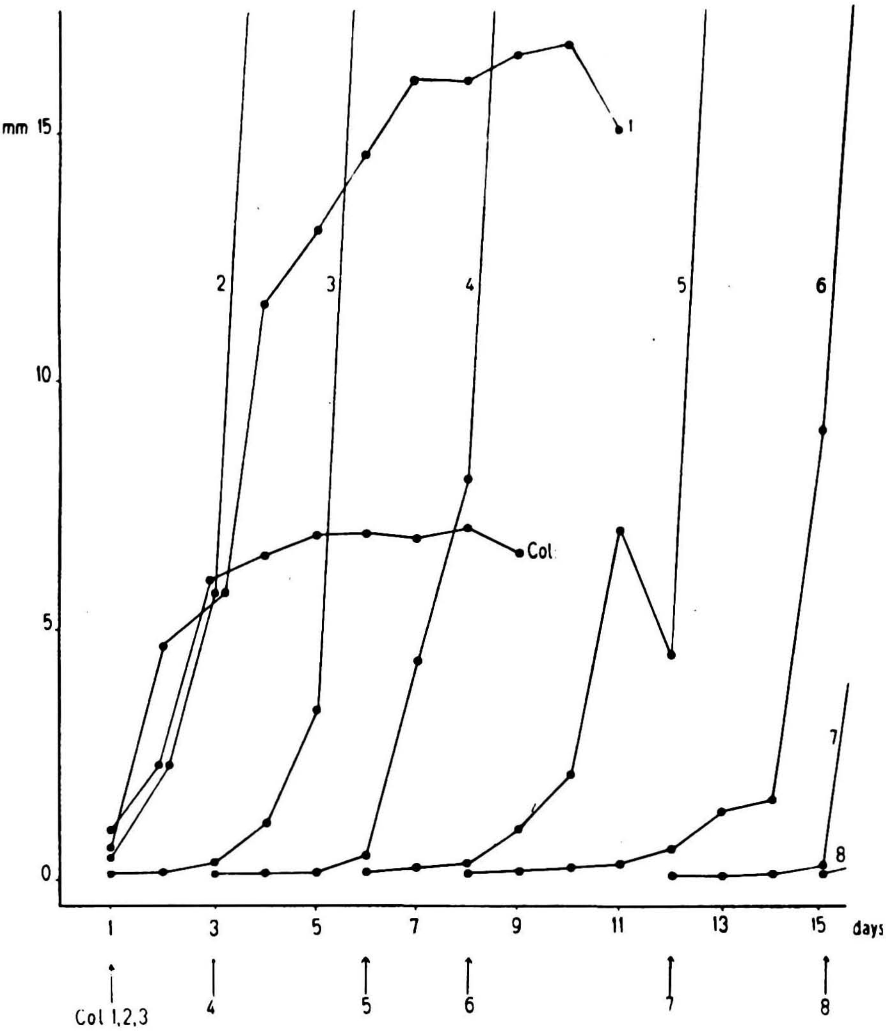

Fig. 6. Parts of the growing curves of the first 7 leaves. ↑ time of initiation of a leaf with its number; col: coleoptile. The coleoptile and the leaves 1, 2 and 3 are present in the embryo.

conditions up to the 4th or 6th week. The same phenomenon has been observed by PURVIS and GREGORY in rye [32].

In the later stages the successive leaves reach greater lengths; a younger one has to wait for 7, 8 or even more days before the preceding one has reached maturity and elongation can start. Elongation in the Baok-variety proceeds much more slowly than in the Untung-variety. In the latter the rate of elongation depends on daylength.

Though the lengths of the blades vary, the sheaths are of increasing lengths, that of the highest or flag-leaf is longest of all. It is leathery, with a very smooth interior surface, which facilitates the emergence of the mature panicle. Transplanting and other disturbances influence the lengths of blades and sheaths of plants grown in the field.

5.4. *Bud development and tillering in the first vegetative period.* The future axillary bud originates as a group of meristematic cells between

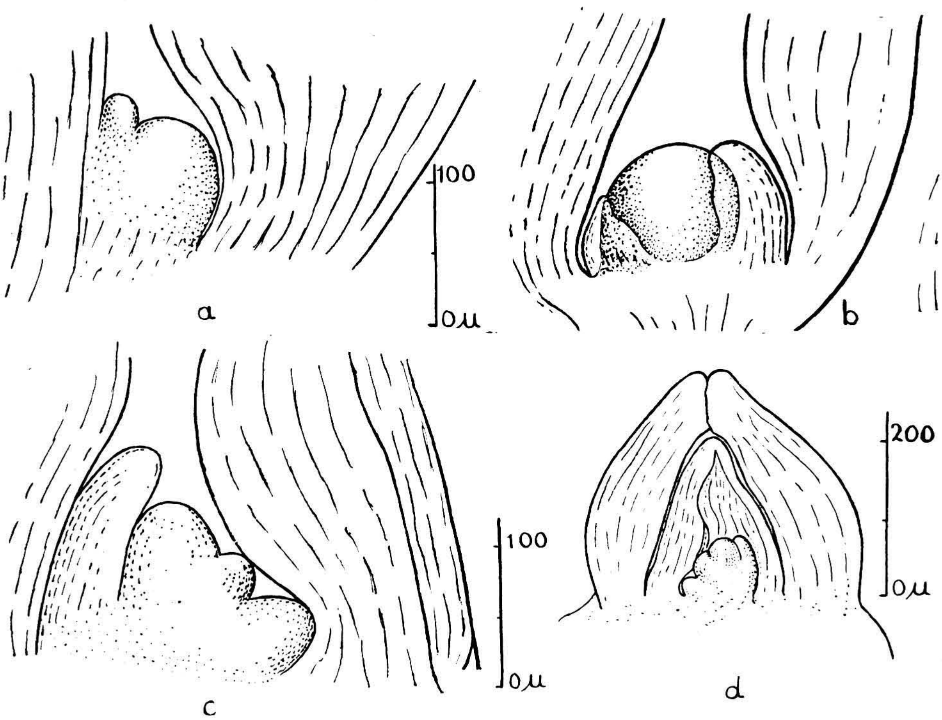

Fig. 7. Axillary buds. *a:* with primordium of the prophyll; *b:* with the prophyll developed; *c:* with prophyll and primordium of the 1st leaf; *d:* with prophyll and 2 leaf primordia.

the growing point and a newly formed leaf primordium; a seedling 6 days old showed 4 axillary buds (fig. 5). Each growing point is soon surrounded by the closed prophyll and underlying leaf initials (fig. 7 and 8). KUILMAN [21] as well as RAMIAH and NARISIMHAM [36] consider the moment an elongating bud appears above the ligule of the subtending leaf as the beginning of the process of tillering. In fact the moment at which bud elongation starts cannot be detected without dissecting the plant and even then it is difficult to say if a bud has entered the grand period of growth or not. Here it must be remarked that during the vegetative period the number of buds smaller than 4,5 mm increases rapidly. In all plants, however, only a few buds between 4,5 mm and about 60 mm could be detected and also the number of shoots developed out of the elongated buds is relatively small. Probably the buds, initiated at an increasing rate, grow slowly until they reach a length of about 4,5 mm, when they enter

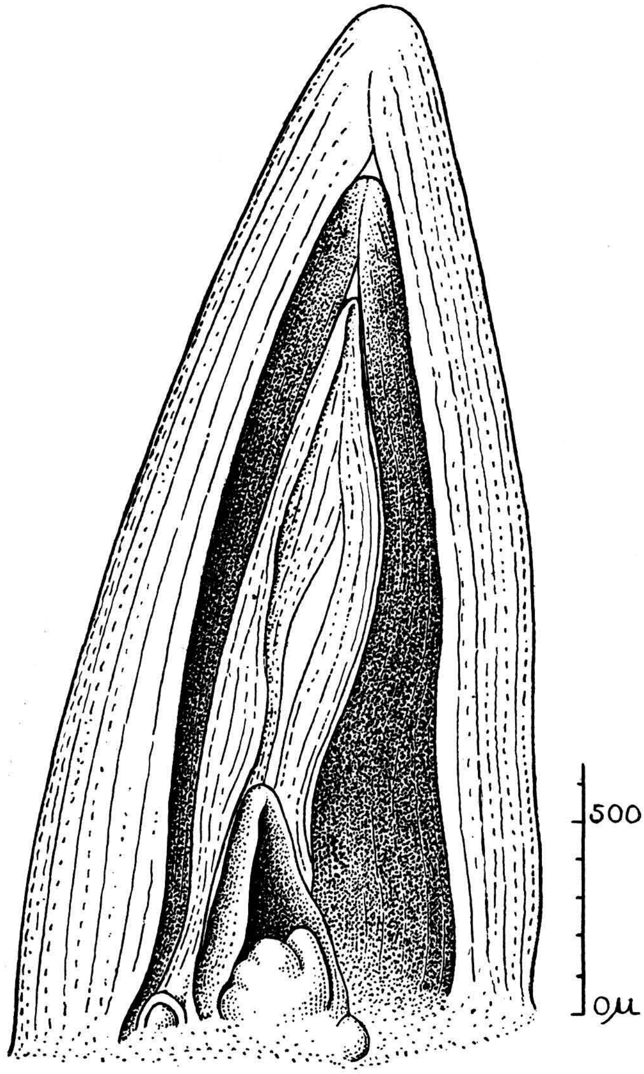

Fig. 8. Axillary bud 1/6 of a 27 days old plant of the Untung-variety, with 4 leaf primordia under the prophyll and the 5th leaf just visible.

the grand period of growth. They quickly pass the stages between 4,5 mm and 60 mm, which explains the small number of these elongating buds in each plant. After elongation the prophyll is split open by the first leaf and the bud can be considered as a shoot. The number of shoots increases only slowly. Fig. 9 shows the relation between the number of buds before the grand period of growth, the number of buds in this period and the number of shoots found in plants of the Baok-series from the 3rd till the 46th day.

In buds with a length of 3,5 mm to 4 mm 3 leaf primordia are found under the prophyll (table 1, 44 days). At the time a 4th primordium is split off, the prophyll starts elongating, immediately followed by the 1st

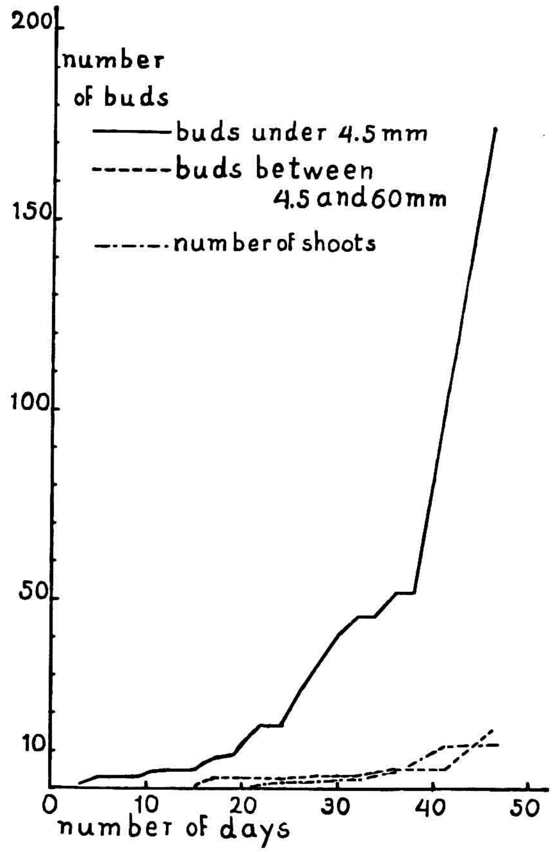

Fig. 9. Number of buds under 4,5 mm, number of elongating buds and number of shoots found during the first part of the vegetative period in the Baok-series.

leaf. The younger primordia are left behind, surrounding the growing point (table 1, 49 days). The development of the primordia of the buds is similar to those of the main stem.

TABLE I

Lengths in mm of the primordia of buds in the vegetative and in the generative period

primordia present	length in mm of primordia of buds from plants of:			
	44 days	49 days	76 days	84 days
prophyll	3.600	4.000	3.600	4.000
1st leaf	3.270	2.700	3.200	2.000
2nd leaf	0.550	1.275	1.000	1.450
3rd leaf.	0.160	0.350	0.450	0.900
4th leaf.		split off	0.180	0.540
5th leaf.			split off	0.270
6th leaf.				split off

In the Untung-variety as a rule the axillary bud of the first leaf does not develop or it elongates slowly to an extent of only 1 or 2 mm. Its position just underneath the pointed stem base seems to be unfavourable. The bud 1/2 only develops occasionally (KUILMAN [21]), but by dissecting the plants it became evident that the rate of growth is low. If it becomes visible outwardly, it follows the younger bud 1/3, which has a somewhat higher rate of growth and appears about the 18th day. At approximately the same time the bud 1/4 emerges from the sheath of the fourth leaf, having a still higher rate of growth. Within a few days 1/2, 1/3 and 1/4 may all emerge. All other buds expand at the same rate as 1/4 and appear from now on at regular intervals of 3 or 5 days, the same interval as that between the maturity of two successive leaves. Actually there is no pause

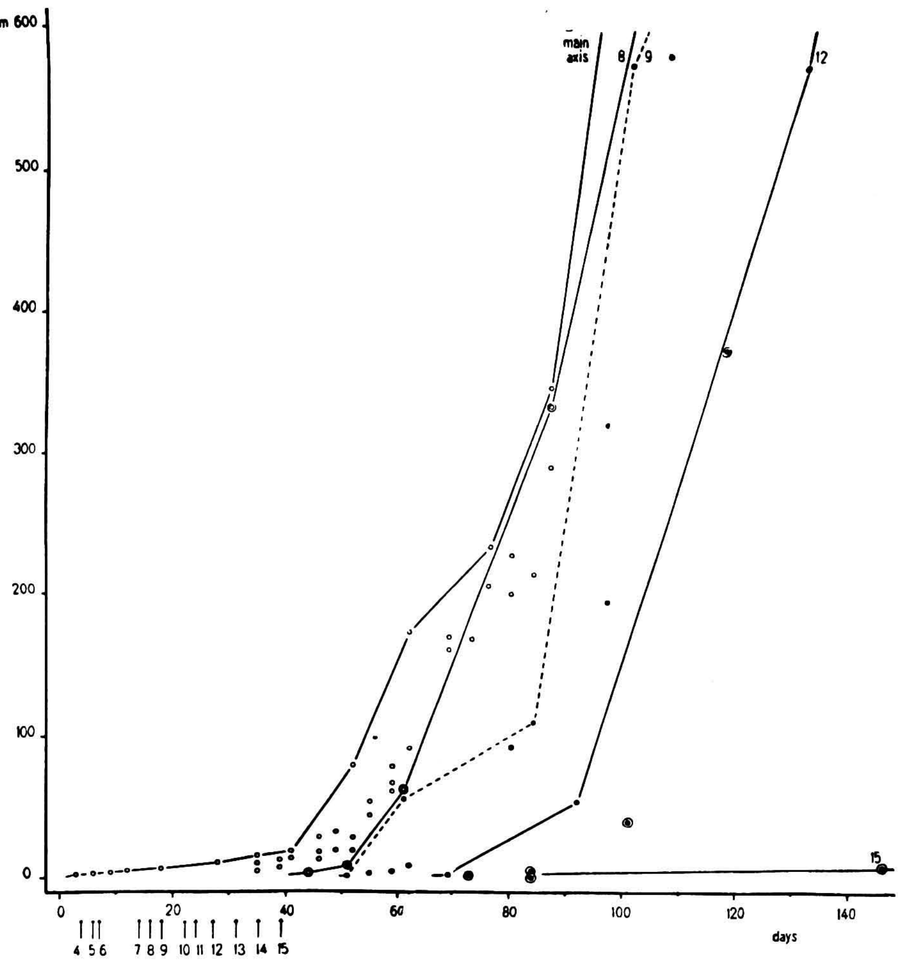

Fig. 10. Elongation of the main stem and its laterals of the July-series of the Untung-variety. Abcissa: number of days after germination. Ordinate: height in mm. ↑ time of initiation of the laterals with their number. -o- main stem; laterals: ○ 1/4–1/7; circle with circle = 1/8; --●-- 1/9; ● 1/10 and 1/11; –●– 1/12; circle with point = 1/13 and 1/14; line, circle with point, line = 1/15.

in the process of tillering at this early stage as has been asserted by KUILMAN [21], but only an increased rate of elongation (fig. 10). In the Baok-variety the buds 1/2, 1/3, 1/4 and the higher ones develop at equal rates (fig. 11), though on the whole more slowly than in the Untung-variety (KUILMAN [22]).

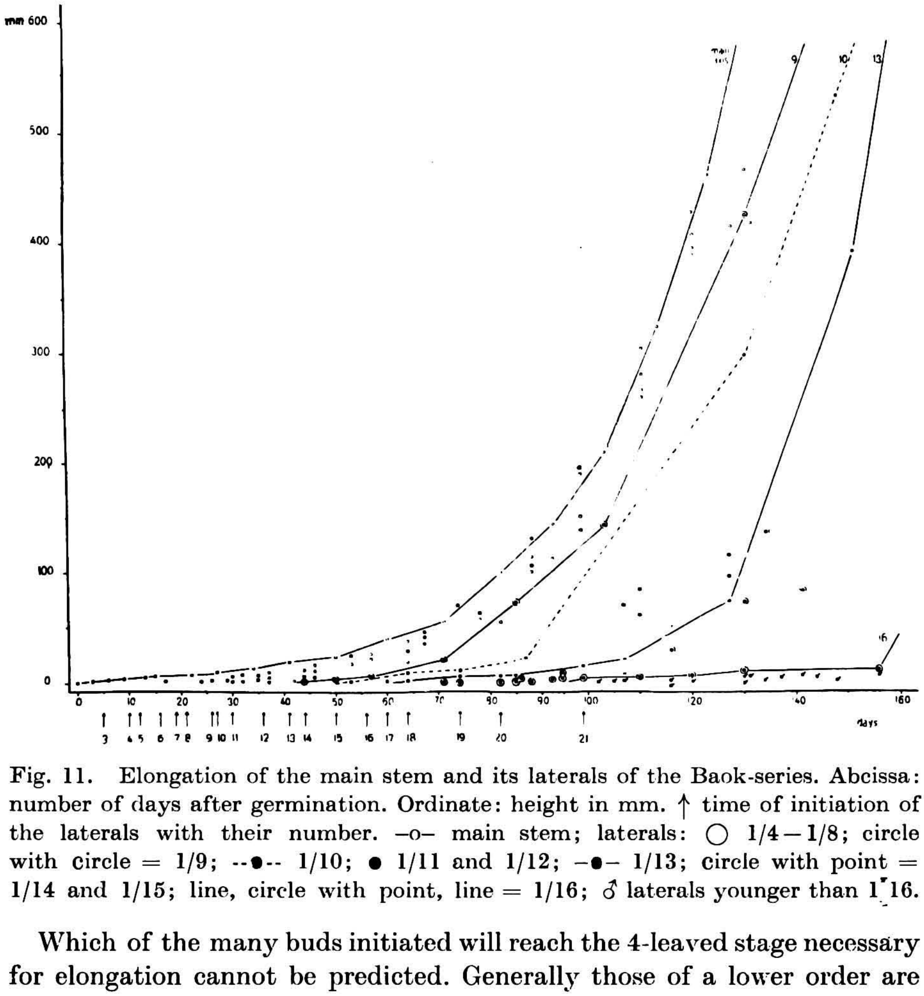

Fig. 11. Elongation of the main stem and its laterals of the Baok-series. Abcissa: number of days after germination. Ordinate: height in mm. ↑ time of initiation of the laterals with their number. –o– main stem; laterals: ○ 1/4 – 1/8; circle with circle = 1/9; --●-- 1/10; ● 1/11 and 1/12; –●– 1/13; circle with point = 1/14 and 1/15; line, circle with point, line = 1/16; ♂ laterals younger than 1/16.

Which of the many buds initiated will reach the 4-leaved stage necessary for elongation cannot be predicted. Generally those of a lower order are earlier in shooting than those of a higher order; those in the middle part of the stem have a better chance than those at the base or at the top. Environmental conditions are of great influence: the amount of nutrients, lodging, damage by insects may define the rate and the manner of tillering, unlike the rate of leaf initiation, which bears a constant character. In the vegetative period the ratio of the number of leaves and leaf initials to the number of shoots and axillary buds present at a particular moment may be an index of the degree of tillering. Plants of the same age grown in different soils showed a different index.

(To be continued in next number of "Proceedings")