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MORPHOLOGICAL CHANGES IN RICE PANICLE DEVELOPMENT

A review of literature

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MORPHOLOGICAL CHANGES IN RICE PANICLE DEVELOPMENT. A review of literature[1]

ABSTRACT

Knowledge of the stages in panicle development is important in various cultural practices such as in topdressing N fertilizer, producing hybrid rice seed, and sampling panicles for anther culture. In earlier studies, panicle development was observed with dissecting microscopes. This resulted in some misinterpretation because the tridimensional features of the panicle primordium were not observed. The rice panicle primordium is covered with thick bract hairs, making it difficult to observe. The scanning electron microscope (SEM) produced clearer pictures of the stages of panicle development and clarified problems obscured in earlier reports.

The panicle is a modified racemose branching inflorescence consisting of the panicle axis and primary branches. It extends from the neck node to the degenerated growing point. As many as three secondary branches form on the lower part of each primary branch. The secondary branches usually have three spikelets.

The first sign of panicle initiation is the appearance of the first-bract primordium. The order of branch primordium development differs from that of spikelet primordium development. The differentiation and development of primary and secondary branch primordia is acropetal while the sequence of primary or secondary branch development is basipetal.

Within any branch, the sequence of spikelet primordia development is acropetal except the topmost spikelet which develops the fastest. The sequence of flowering on a panicle is generally basipetal.

Flowering and grain filling follow the same order. The upper branches dominate the lower ones. The topmost and lowest spikelets in each branch are dominating. Going up the branch, the metabolic dominance seems to decrease, hence the second spikelet from the top is the most dominated. The dominant spikelets produce heavier grains and have less chance of sterility.

Pollen grain development has been used to identify the stage of panicle development. Various stages were reported as a result of difference in methods used to observe pollen development. Spikelet development on a panicle is not synchronous, therefore, the most representative spikelet — the III-2 spikelet — should be used. The auricle distance is the most widely used indirect method of showing the development of the pollen grain.

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MORPHOLOGICAL CHANGES IN RICE PANICLE DEVELOPMENT. A review of literature

In intensive high-input rice cultivation various patterns of cultural management have evolved from the experiences of rice technicians and farmers. In these management practices, such as topdressing of nitrogen, a knowledge of tiller growth and panicle development is very important.

In producing hybrid rice seeds, detailed knowledge of panicle development is necessary to predict if the flowering peak of the male and female parents can be synchronized. In gametocide-induced male sterility, information on panicle development is needed to time the chemical treatment to produce male-sterile plants. In tissue and anther culture, knowing the stage of development helps in sampling the young panicle.

Noguchi (28) first reported rice panicle development as observed with a dissecting binocular microscope. He compared growth of panicle primordia in nine species of Gramineae and verified that primary protuberances on their panicle primordia differentiate acropetally and symmetrically against an axis plane but asymmetrically only in rice panicle primordia. Bonnett (4, 5, 6, 7, 8) and others further clarified characteristics of panicle (spike) development of other cereal crops. Compared with other cereals, panicle development of rice is unique. Rice has the shortest reproductive apical cone among the cereal crops and its panicle primordium is covered with many thick bract hairs until the rapid elongation stage. These make it difficult to correctly observe the morphological changes.

Studies on the developmental process of the rice panicle by the paraffin sectioning method have been reported (2, 10, 19, 22, 23, 24, 31, 32, 42). Matsushima and Manaka (24) gave excellent detailed descriptions and illustrations. However, with paraffin sectioning it is difficult to note the tridimensional features because the panicle primordia differentiate asymmetrically. Therefore, errors or misinterpretations may appear in these descriptions.

Studies on panicle development using the dissecting microscope have also been made (1, 14, 15, 18, 20, 33, 34, 35, 36, 37, 39, 45). Ting et al (37) reported panicle development in detail, but the photographs (35) lack the tridimensional effect. Publications of Kawahara's group (14, 15) have clearer photographs describing the morphological differences between first-bract primordium and flag-leaf primordium. However, because of the limitations of the depth of field in photographs taken under the dissecting microscope, the three-dimensional appearance of the young panicle is not sufficiently sharp. Thus, some morphological changes in panicle development are still unclear.

Moncur (25) was the first to present scanning electron micrographs of young panicle primordia. Later, Zee (43) and Zee and Xu (44) showed panicle development in more detail. With the scanning electron microscope (SEM), a clear picture of the natural concave-convex appearance of various stages of panicle primordia can be obtained. The high resolution of the SEM could clarify problems obscured in previous reports or those not yet resolved.

GENERAL PANICLE MORPHOLOGY

The rice panicle is a modified racemose branching inflorescence. The panicle starts from the neck node or first bract but not from the flag leaf or any branch or spikelet (Fig. 1).

The panicle is a terminal inflorescence at the topmost internode of the culm. The topmost internode is a peduncle.

A panicle consists of the panicle axis and primary branches. The panicle axis extends from the first bract (neck node) to the degenerated growing point.

Generally up to three secondary branches form on the lower part of each primary branch; and approximately six spikelets form on the upper part of each primary branch. The secondary branches usually have three spikelets.

A spikelet is borne on top of a pedicel. Pedicels arise from the nodes of the primary or secondary branches.

Primary branches arise from the nodes of the panicle axis and secondary branches arise from the nodes of primary branches. On all these nodes, white hairs known as bract hairs grow out from bracts during panicle primordium development. The bract hairs can be seen until they dry up after heading.

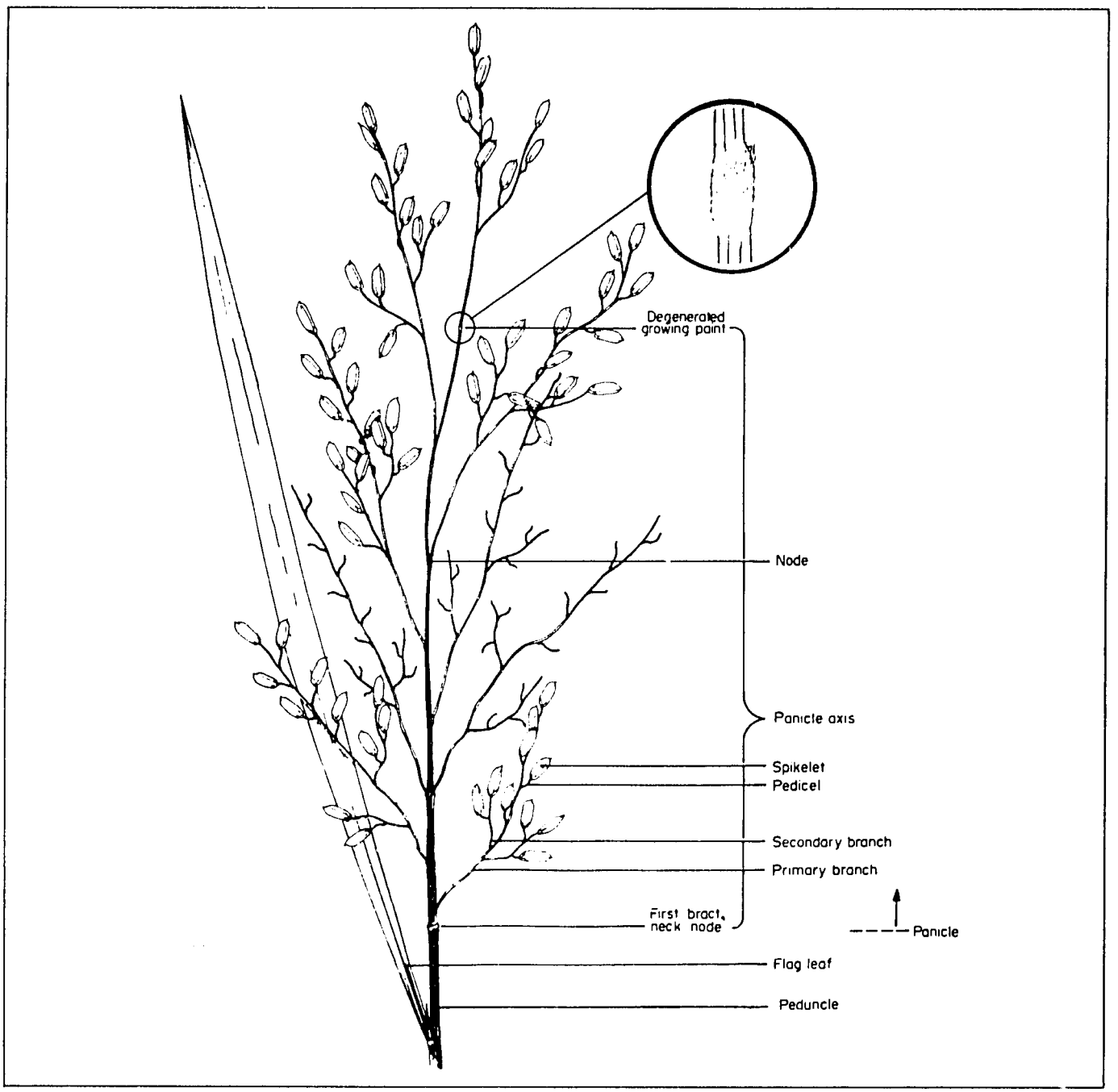
TERMS TO DESCRIBE MORPHOLOGICAL CHANGES

Apical cone — the portion of a vegetative shoot apex above the topmost leaf primordium. It is a dome which grows upward and widens before a new foliar plastochron begins (11).

Reproductive apical cone — the portion of the shoot apex above the first-bract primordium at the beginning of the reproductive phase. Its area gradually diminishes as the bracts and primary branch primordia differentiate successively from it. Finally only a small tip remains and does not differentiate anymore; this tip will be the degenerated growing point.

Morphogenetically, the primary branch results from the cell division of the outer layers of the apical corpus (31). The core of the reproductive apical cone links all primary branches. After elongation this core appears as the panicle axis and the tip of the reproductive apical cone is the degenerated growing point (Fig. 2).

(Primary branch primordium) differentiation — implies the *appearance* of the primary branch primordium. (The



1. Component parts of a panicle.

same term is used for secondary branch primordium and spikelet primordium.)

(Primary branch primordium) development — refers to the *growth* of the primordium, i.e., the primordia of all parts arising from it differentiate. For example, primary branch primordium development refers to the appearance of the secondary protuberances of this primary branch primordium; spikelet primordium development refers to the gradual appearance of the sterile lemmas, lemma, palea, stamen, and pistil primordia, etc.

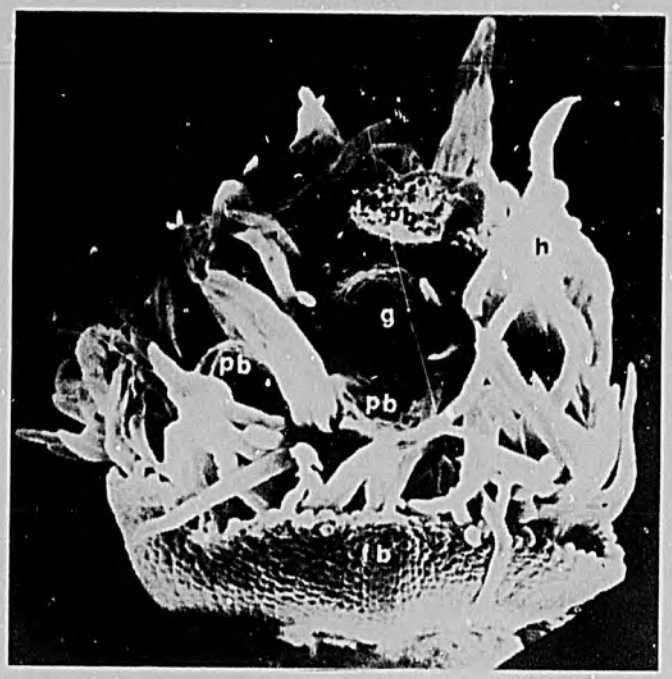
Sequence of spikelet primordia development — refers to which spikelet primordium within the same branch primordium develops first, which one follows, and so on.

THE START OF THE REPRODUCTIVE PHASE

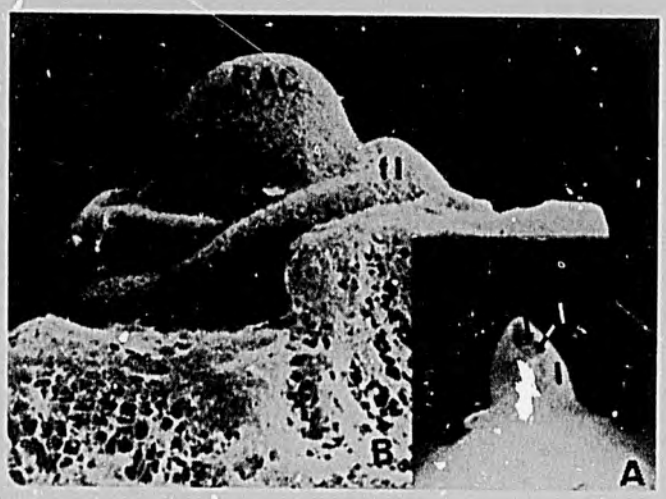
The reproductive phase starts from panicle initiation. The first signal of panicle initiation is the appearance of the first-bract primordium on the shoot apex of a stem.

Vegetative and reproductive apexes differ morphologically as follows: The apex is vegetative if the preceding leaf primordium is taller than the apical cone when the youngest leaf primordium is differentiating (Fig. 3). The apex is reproductive if when the first-bract primordium appears, the flag-leaf primordium is not as tall as the reproductive apical cone (15, modified).

This distinction does not resolve the main problem: by the



2. Degenerated growing point (g).
fb = first bract
pb = primary branch primordium (some of them removed)
h = bract hairs

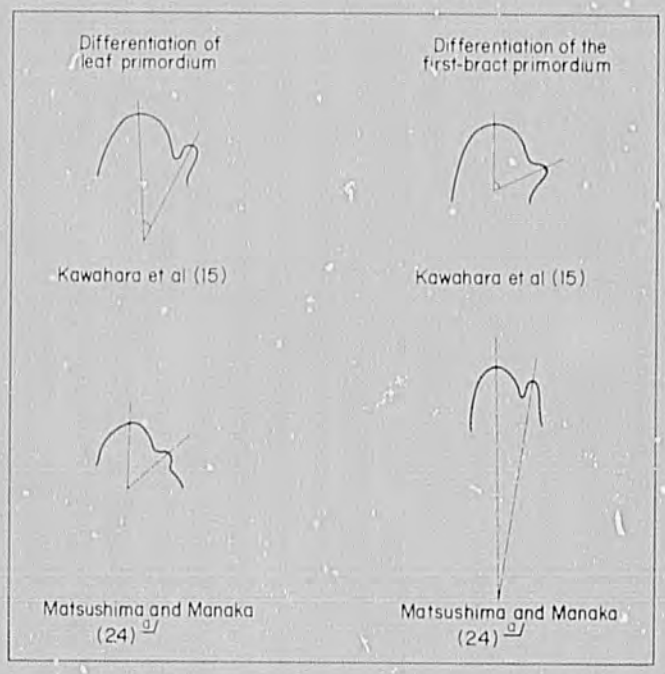


3. Vegetative and reproductive apices.

Vegetative apex (A)
l = leaf primordium; black arrow points the apical cone

Reproductive apex (B)* – first bract appearing
fl = flag leaf primordium
fb = first-bract primordium
RAC = reproductive apical cone
*(Moncur [25], modified)

4. Difference between leaf and first-bract primordia (Kawahara et al [15], modified).
Black arrow points to leaf primordium
fb = first-bract primordium
(cultivar: Tonewase).



5. Difference between protuberant angles of a leaf and the first-bract primordia.
[a]Mirror image of the original figure with the angles added for easy comparison.

time the flag-leaf primordium grows up to the tip of the reproductive apical cone, the reproductive apex will look like the vegetative apex.

Kawahara et al (14) pointed out that when the uppermost leaf primordium covers the shoot apex, the first-bract primordium grows to considerable magnitude and is distinguishable (Fig. 4). They also pointed out that the first-bract primordium appears to take a more obtuse angle to the shoot axis than the leaf primordium. But this evidence for the first-bract primordium is opposite that of Matsushima (23) (Fig. 5).

In identifying the first bract, Kawahara et al (14) and Matsushima and Manaka (24) did not check if the number of leaves of the plant dissected coincided with that of the other plants at flowering stage. It is difficult to determine which conclusion is correct.

Ling et al (20) used the criterion of Kawahara et al (15) to check first-bract primordium differentiation stage and kept some plants for leaf counting at flowering stage. But the result was not reported. Because plants of any rice variety in the same plot will have variation in leaf number (38), no convincing conclusion appears.

Some papers reported that the apical cone slightly elongates. If the ratio of the height and diameter of the apex is >1, then reproductive phase starts. Actually, unlike the spike primordium of wheat, all clear pictures of rice panicle primordia have proved that this conclusion is not correct.

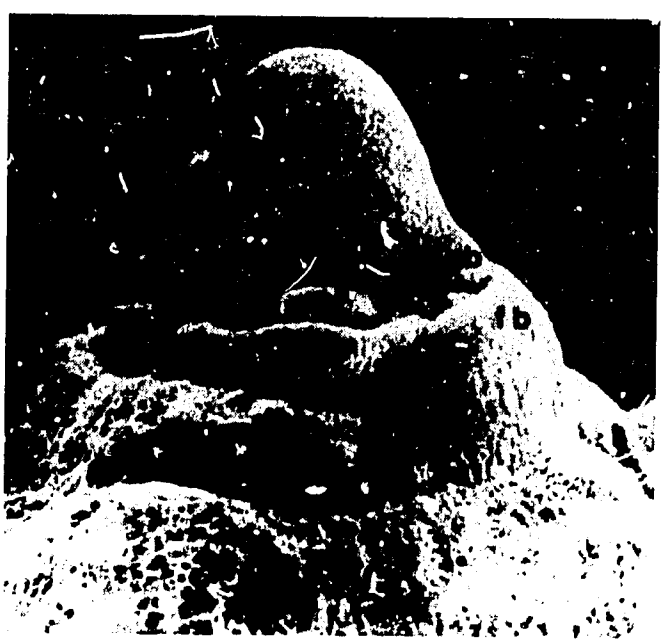
MORPHOLOGICAL CHANGE IN PANICLE FORMATION

The first-bract primordium appearing on a shoot apex signals the start of the reproductive phase.

Bract and primary branch primordia differentiation. The first-bract primordium makes a circle surrounding the panicle primordium base (Fig. 6). Subsequent bract primordia cover an arc of less than 180°. Bracts subtend corresponding primary branch primordia. The upper bract primordia are right below and do not seem to subtend their primary branch primordia (Fig. 7).

Researchers have reported a "number of bracts increasing stage" or a "panicle primordium elongating stage" before the primary branch primordium differentiation stage. Under the dissecting microscope, a panicle primordium with a few slightly projecting annular protuberances can be seen occasionally. In other cereal crops, e.g., wheat spike primordium, there is an elongating spike primordium stage before a double ridges stage (equivalent to primary branch primordium stage of rice panicle). From the SEM picture, it seems that bracts and their corresponding primary branch primordia arise simultaneously (Fig. 7). So, it is not possible to have a stage specifically for "number of bracts increasing stage." This should be ascertained under the SEM.

As the primary branch primordia arise acropetally, the reproductive apical cone becomes smaller (Fig. 7) while the primary branch primordia enlarge. The size of the bract primordia does not change much. Subsequently, bract hairs appear (Fig. 8). The reproductive apical cone becomes difficult to see. The number of primary branch primordia is fixed and primary branch primordia start to elongate.



6. Primary branch primordia appearing (Moncur [25], modified).

fb = first-bract primordium
b = bract primordium
pb = primary branch primordium

7. Primary branch primordia appearing (Moncur [26], modified)

fb = first-bract primordium
b = bract primordium
pb = primary branch primordium

8. Primary branch primordia starting to elongate (Moncur [26], modified).

fb = first-bract primordium
b = bract primordium
pb = primary branch primordium
h = bract hairs

Secondary branch primordium and spikelet primordium differentiation. On all primary branch primordia, their secondary protuberances, i.e., secondary branch primordia and spikelet primordia, arise acropetally (Fig. 9, 10).

Generally, on every primary branch primordium the topmost 5-6 secondary protuberances are spikelet primordia while the lowest 2-3 secondary protuberances are secondary branch primordia.

Spikelet primordium development. The topmost spikelet primordium of the topmost primary branch primordium starts differentiating the glume primordia first (Fig. 11-4).

On every spikelet primordium, the following primordia appear in acropetal sequence: two glume primordia, then two sterile lemma primordia, followed by lemma primordium and finally palea primordium (Fig. 11-3, 11-5, 11-6). Figures 11-1 and 11-2 show the visible panicle primordium stage and Figure 11-7 shows the top view of Figure 11-6.

Floret primordium development is also in acropetal succession. After the palea primordium appears, the stamen primordia (spherical swellings) arise simultaneously in a whorl slightly below the spikelet primordium apex (Fig. 12). The tip of the spikelet primordium apex becomes a pistil primordium. This dome-shaped primordium is bigger than the stamen primordia surrounding it. The lodicule primordia appear between the palea and stamen primordia.

As palea and lemma primordia elongate, the floret is closed and stamen and pistil primordia cannot be seen anymore (Fig. 13). From then on the outer appearance of the panicle changes little — it only elongates and expands. Important changes take place in the anther and ovary. Usually the pollen grain developmental process is used to indicate the progress of panicle development, as discussed later.

INTERPRETATIONS IN DESCRIBING CHANGES

1. The sequence of branch and spikelet primordium development is commonly described as opposite that of their differentiation, i.e., the later a primordium differentiates, the earlier it begins to develop (31, 37).

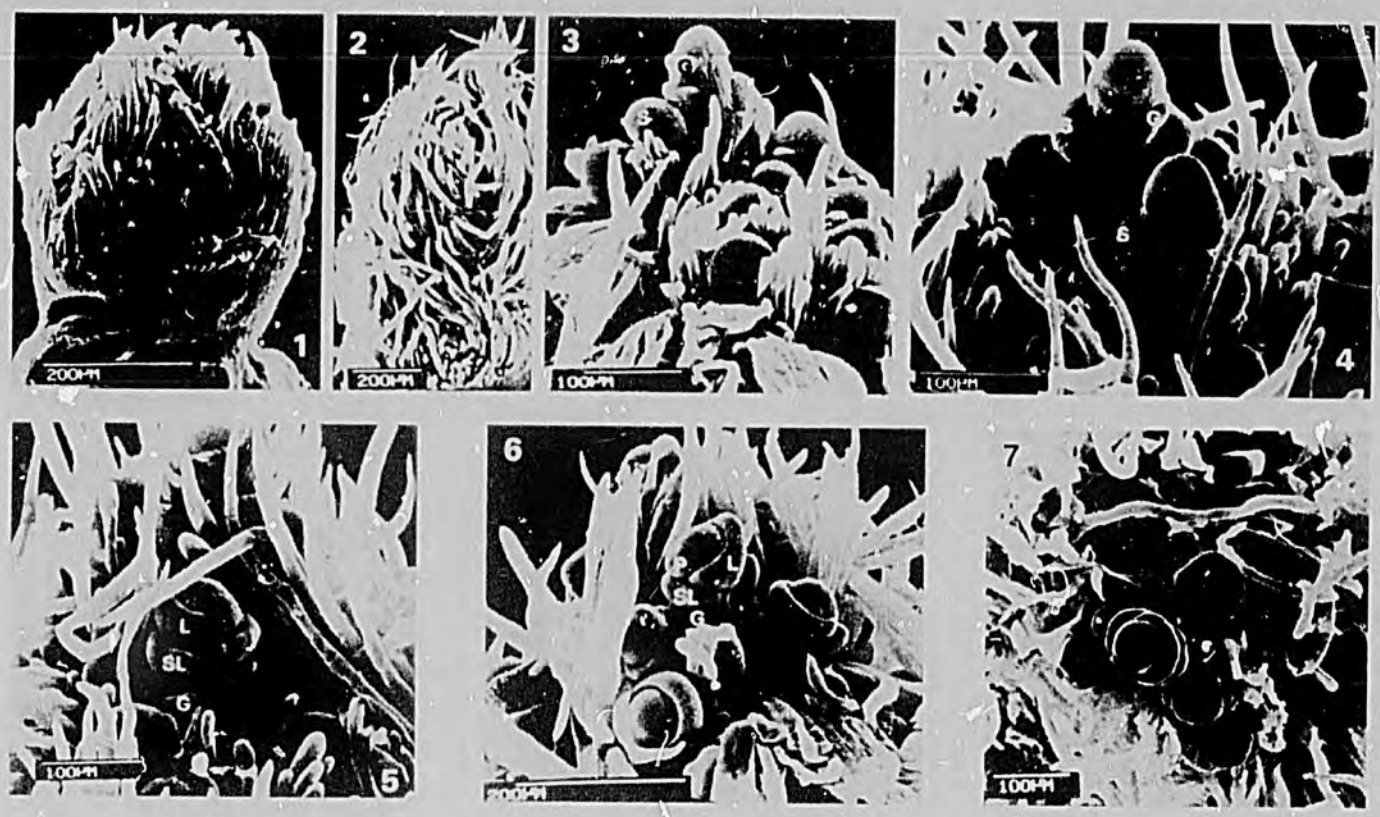
As mentioned above, the differentiation of panicle branch and spikelet primordium is in acropetal succession. According to this interpretation, both branch and spikelet primordia should develop in basipetal succession, meaning that the upper spikelet should have more advanced growth than the lower one. This is not completely true because with two adjacent spikelets on a primary or secondary branch, the lower one always flowers earlier except the topmost spikelet (Fig. 14).

2. A different description was reported by a group in China (9). Spikelet primordia (from a secondary branch primordium or directly from the same primary branch primordium) differentiate and develop in the same order (24), i.e., the lowest spikelet primordium appears and develops first, so flowering order is from bottom to top on a branch.

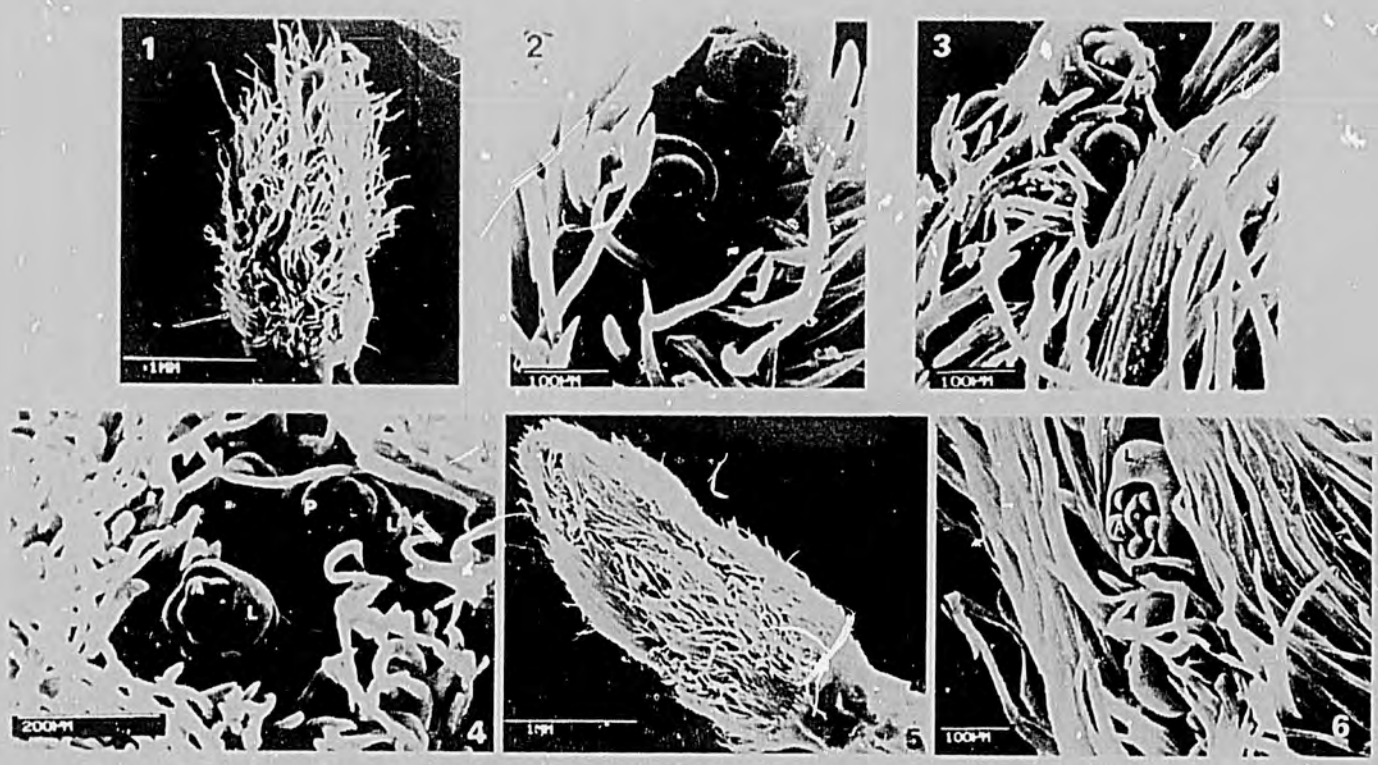
9. Secondary branch primordia appearing.
b = bract primordium
pb = primary branch primordium
sb = secondary branch primordium

10. Secondary protuberances increasing (Moneur [26], modified).
pb = primary branch primordium
Secondary protuberances:
sb = secondary branch primordium
s = spikelet primordium

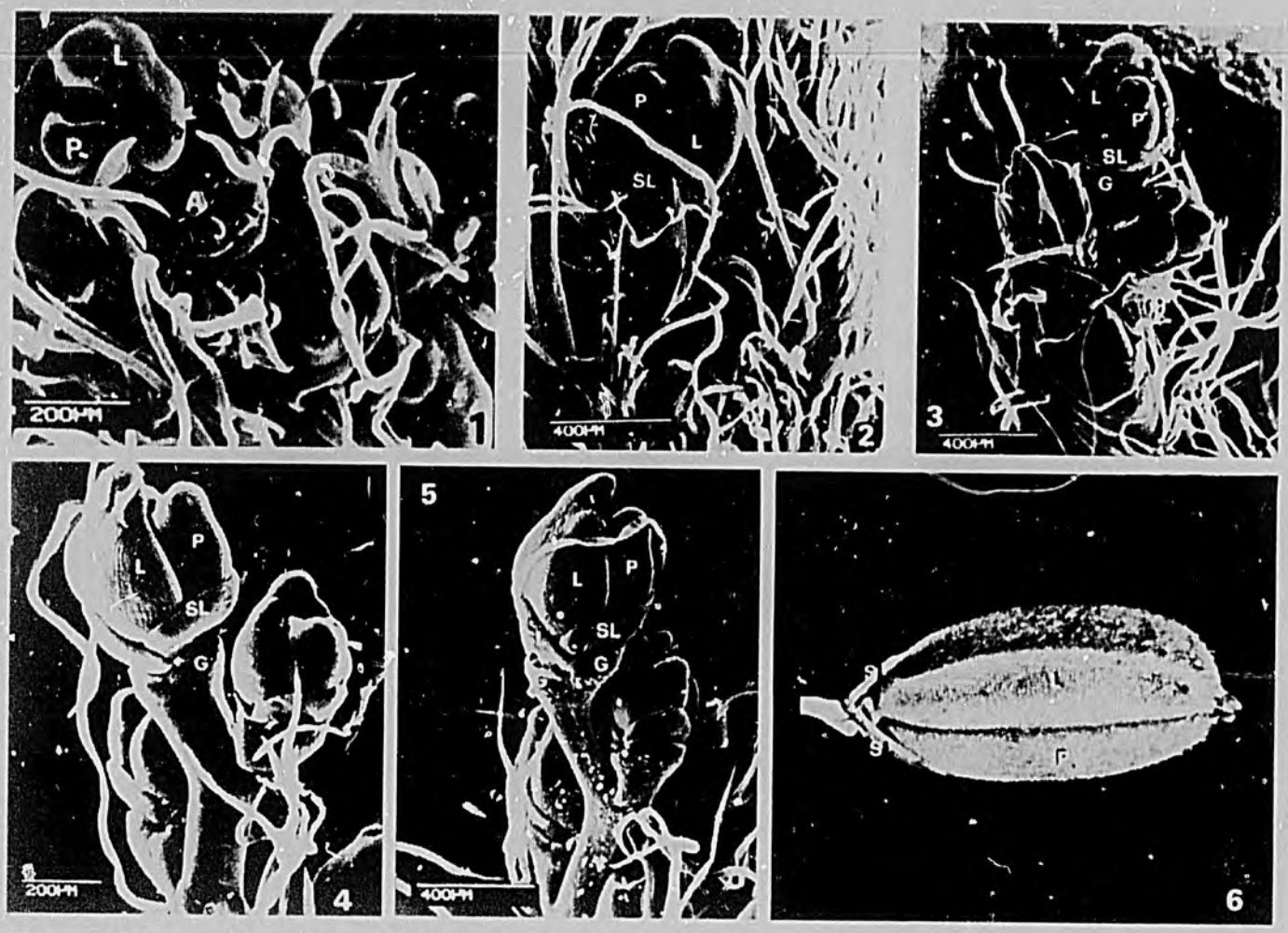
In this interpretation, the topmost spikelet primordium develops last (differentiates its glume primordium and the like), because it appears last on any branch primordium. Figure 10 shows that although the secondary protuberances on the base of the branch primordia are very clear, the



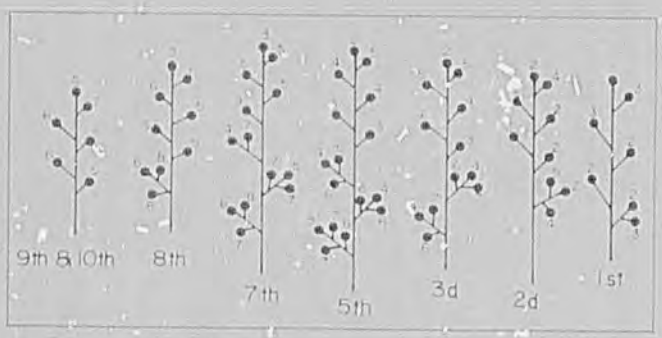
11. Young panicle primordium (nos. 1 and 2) and spikelet primordium development (nos. 3 to 7) showing glume, lemma, and palea primordia. G = glume primordium (in picture 3, G = sterile lemma primordium), S = spikelet primordium, L = lemma primordium, SL = sterile lemma primordium, P = palea. Source: (44).



12. Panicle primordium covered with bract hairs (nos. 1 and 5) and spikelet primordium development (nos. 2, 3, 4, and 6) showing stamen and pistil primordia. L = lemma primordium, P = palea primordium, A = stamen primordium, O = pistil primordium. Source: (44).



13. Spikelet formation (44). G = glume primordium, SL = sterile lemma primordium, P = palea primordium, L = lemma primordium, S = spikelet primordium.



14. Flowering date of spikelets on primary branches of a panicle (Typical primary branches shown, Variety: Nangken 58) (Zhejiang Agricultural University et al [46], modified).

topmost spikelet primordium has not yet appeared because the differentiation of secondary protuberances is still proceeding. Subsequently, the topmost spikelet primordium is the first to have its glume primordium differentiated (Fig. 11-1). Thus, this interpretation is not completely correct.

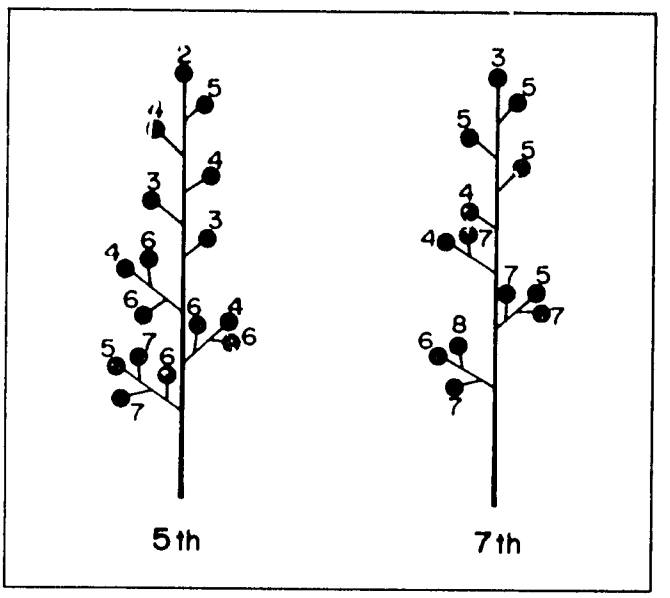
3. Observations were made to clarify these conflicting descriptions. Results show that the order of branch primordium development differs from that of spikelet primordium development. Two kinds of order should be distinguished.

First, after the degenerated growing point appears, all primary branch primordia start to develop in acropetal succession. But the topmost and upper ones seem to grow slightly faster than the lower ones (Fig. 15).

For the secondary branch primordia on the same primary branch primordium, the later a secondary branch primordium differentiates, the earlier it begins to develop (17, 24). Thus, the upper secondary branch primordium develops earlier and flowers earlier (Fig. 16). Combining these two aspects (primary and secondary branch primordia) would result in flowering on a panicle generally from top to bottom.

Second, spikelet primordia differentiate and develop in acropetal succession except the topmost spikelet primordium which differentiates (appears) last but develops first. After the topmost spikelet primordium starts developing, the uppermost secondary branch primordium and the lowest spikelet primordium start to develop. This effect of the topmost spikelet is similar to the effect of the degenerated growing point on the whole panicle primordium development. On any branch primordium the sequence of spikelet primordia development and flowering is the topmost spikelet first, followed by bottom spikelet, then going up in succession (Fig. 17, 18).

15. Primary branch primordium development. pb = primary branch primordium, sp = secondary protuberance, g = degenerated growing point.



16. Flowering date of spikelets on the fifth and seventh primary branches of a panicle, Nongken 58 variety (From Zhejiang Agricultural University et al [46], modified).

Summary of panicle primordium differentiation and development:

For branch primordium

Primary branch primordium

differentiation: acropetal

development: acropetal

sequence of primary branch primordia development: basipetal

Secondary branch primordium

differentiation: acropetal

development: acropetal

sequence of secondary branch primordia development: basipetal

Thus, sequence of flowering on a panicle is generally basipetal.

For spikelet primordium

differentiation: acropetal

development: acropetal

sequence of spikelet primordia development: acropetal, except the topmost spikelet which is the fastest to develop on that branch primordium.

Thus, within any branch, the sequence of flowering is acropetal except the topmost spikelet which is the first to flower.

FLOWERING ORDER RESULTING FROM PANICLE PRIMORDIUM DEVELOPMENT

For primary branch primordia (PBP): After the degenerated growing point appears, the topmost and upper PBP grow faster than the lower ones (Fig. 14).

For secondary branch primordia (SBP) on the same PBP: After the topmost spikelet primordium starts to develop, the uppermost SBP develops first, the second follows, then the third, going down (Fig. 16).

Thus, sequence of flowering on a panicle is generally basipetal.

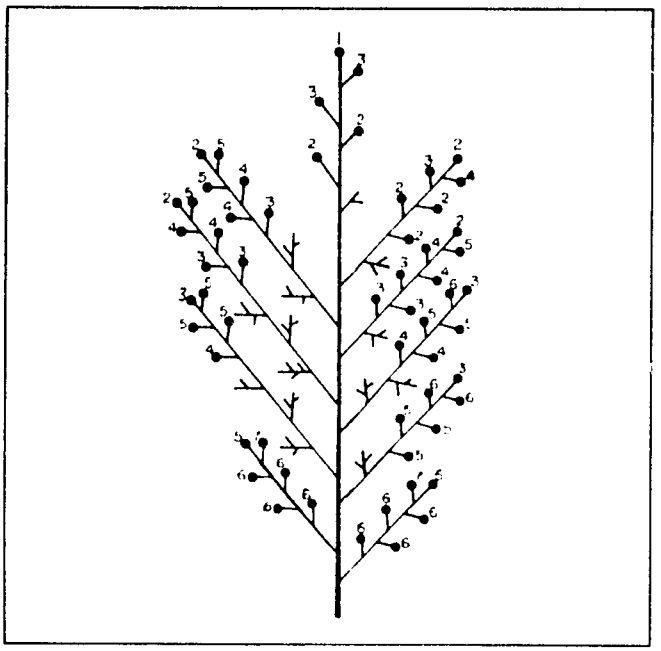
For spikelet primordia on any PBP or SBP: After the topmost spikelet primordium starts to develop, the lowest SP follows, and then going up in succession (Fig. 17, 18).

Thus, within any branch, the sequence of flowering is acropetal, except the topmost spikelet which is the first to flower.

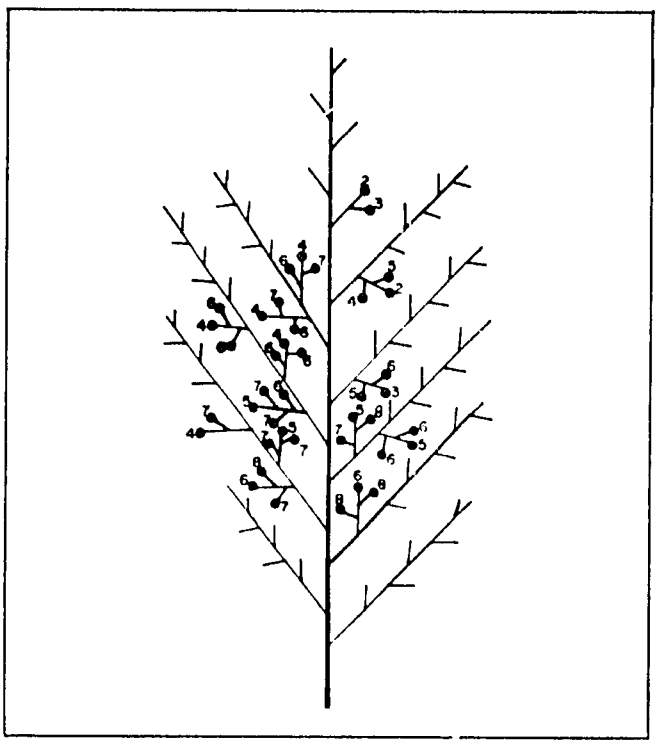
Flowering and grain filling follow the same order. During grain filling the upper branches dominate the lower ones. With spikelets, the topmost and lowest spikelets of each branch are dominating: going up the branch, the metabolic dominance seems to decrease, thus, the second spikelet from the top is the most dominated. The dominating spikelets seem to produce larger, heavier grain and have higher success in hybridization and less chance of sterility and abortion than the dominated spikelets. All of these deserve further study.

USING POLLEN GRAIN DEVELOPMENT TO INDICATE PANICLE DEVELOPMENT

Using the growth stage of pollen grain to indicate the later part of panicle development is less complex than using the growth stage of the megaspore. Two classifications have been adopted extensively. The Matsushima and Manaka classification (24) has 6 stages: differentiating stage of pollen mother cells, reduction division stage, early stage of exine formation, exine formation stage, early ripe stage of pollen, and ripe stage of pollen. Another classification by Ting et al (37) divides the later part of panicle development into 4 stages: pollen mother cell formation stage, reduction stage of pollen mother cell, early ripe stage of pollen, and ripe stage of pollen.



17. Flowering date of spikelets on the primary branches of a panicle, Nongken 58 variety (From Zhejiang Agricultural University et al [46], modified).



18. Flowering date of spikelets on secondary branches of panicle, Nongken 58 variety (From Zhejiang Agricultural University et al [46], modified).

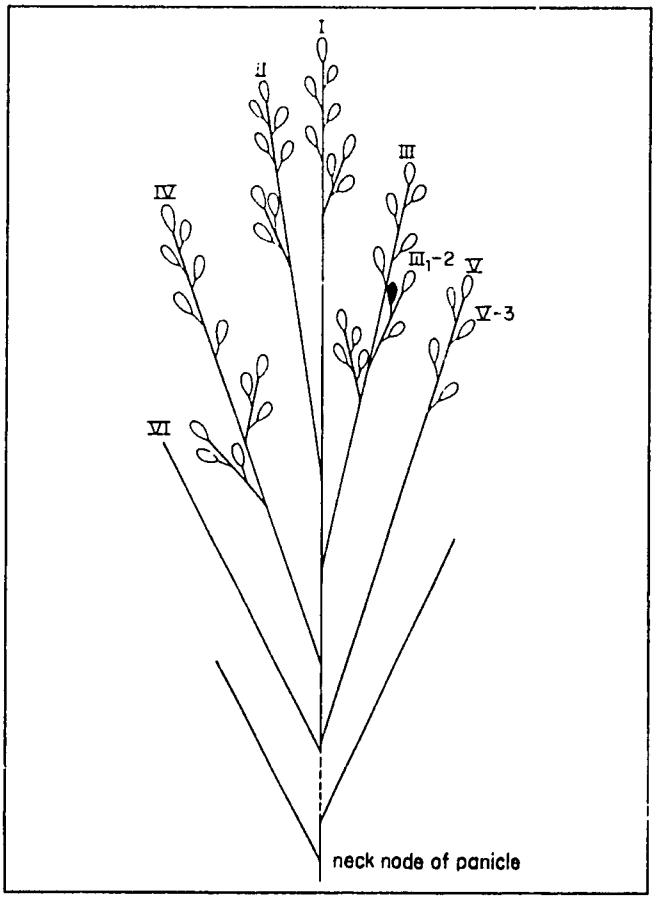
Kihara and Hirayoshi (16) reported in detail the morphological changes of pollen grain development from the pollen tetrad stage to maturity, with the first and second contraction and recovery stages. The illustrations have been widely used for more than 4 decades in describing pollen grain development (17, 21, 27, 29, 30) and panicle development (9, 23, 24).

Kihara and Hirayoshi (16) started their description at pollen tetrad, that is after pollen mother cell formation in the anthers. But scientists used to start earlier at pollen mother cell stage, that is before pollen tetrads.

Before the pollen grains mature, the first and second mitotic divisions occur (13, 16) and pollen grains are in the three-celled state at anthesis. The first division delimits the gamete and gametophyte generations while the second means the sperm nuclei are ready to fertilize. Knowing the timing of these divisions in days before heading (flowering) would help in sampling of anthers for tissue culture.

Satake (30) attempted to correct the first and second contraction and recovery stages of Kihara and Hirayoshi by using glutaraldehyde as a fixative with the paraffin sectioning method. However, other artifacts were obtained and were misunderstood as normal features of young microspores. Xu et al (41) obtained no contractions when microspores were checked with the fresh anther distilled water squash slide.

Anthers fixed in Carnoy's fluid squash slide can still be used in checking pollen grain development for identifying panicle development stage because nucleus behavior during meiosis is easier to see and the user is aware of the contraction of the microspores caused by the fixative.



19. Diagram of a panicle and the designation of spikelets.

The development of spikelets on a panicle is not synchronous: sometimes when the topmost spikelet is flowering, the second spikelet of the lowest secondary branch of the same panicle is in the pistil and stamen primordia formation stage. It takes about 15 days for all spikelets on a panicle to reach the same developmental stage. Therefore, the most representative spikelet should be used. Unpublished finding of Xu et al (41) shows that spikelet III-2 is the most representative spikelet (Fig. 19), representing 49-68% of the spikelets of a panicle in reduction division stage.

Of the indirect methods of showing the development of pollen grain, particularly for the reduction division stage, the auricle distance (AD) is most used. AD is the distance between flag leaf auricles and the auricles of the preceding leaf; negative value means the flag leaf auricles are below the preceding leaf auricles. When AD reaches about -3 to 0 cm, the panicle is in the reduction division stage (Table 1). But the conclusions that a panicle with a -10 cm AD begins to undergo reduction division stage and that a panicle with 9 cm AD is in the final period of reduction division stage (24) need further study.

Use of spikelet length is also not reliable because it can only approximate the growth stage (Table 1). Although the relationship between microspore development and spikelet length was reported in detail (12), division of substages of microspore development associated with spikelet length is poor and fails to show the developmental stages of the panicle.

Table 1. Indirect methods of showing reduction division (RD) stage of pollen grains.

Spikelet length			Auricle distance (cm)	Annotation	Source
Actual length (mm)	% of full length	Annotation			
3	45	Beginning of RD	-10	Beginning of RD	24
4	55-60	Active RD	0	Active RD	
6	80-90	End of RD	9	End of RD	
	50		-3 to 3	One early season variety	37
			-7 to 0	One late season variety	
2.5 -5.5			-3 to 0	One early season variety	40
			-7 to -3	One late variety	
2.45-5.35		Spikelet flowers on 1st day			3
3.45-4.65		Spikelet flowers on 4th day			
3.08-5.08		Spikelet flowers on 7th day			
2.8 -4.8	40-65	One sinica variety	-4 to 0		21
3.7 -5.6		One indica variety			
2.6 -5.7		Most of RD spikelets on their panicles (IR36)	-3 to 1.0	IR36	41
2.2, 6.1		Minimum and maximum limit			

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