Tropical Agricultural Research Vol. 3 1991

Apical Development Stages and Identification of Potential Yield Loss Periods of Lowland Rice

N. Senanayake and S.K. De Datta[1]

Rice Research Station,
Ambalantota.

ABSTRACT. An experiment was conducted at the Agronomy department, International Rice Research Institute, Philippines, during the 1987/88 wet season to identify the apical, development stages of IR50 and IR42 from germination to maturity.

Thirteen morphologically different panicle development stages of rice were identified up to the development stage of floral organs. Neck node differentiation of IR50 was observed at G.S. 1.8 (35 DAS) and of IR42 at G.S. 1.10 (49 DAS), whereas visual panicle initiation of IR50 was observed at G.S. 1.9 (42 DAS) and of IR42 at G.S. 1.11 (64 DAS). Panicle and spikelet differentiation of IR50 was observed at 4–7 and 11–15 days respectively and those of IR42 at 11–15 and 13–16 days respectively.

Potential grain yield was observed at maximum spikelet differentiation stage at G.S. 1.12, 39–41, in IR50 and IR42 at G.S. 1.13, 37. Potential yield loss occurs in two stages, pre flowering and post flowering spikelet abortion. The potential yield loss as determined conventionally was 37% for IR50 and 18% for IR42. However the actual potential grain yield loss for IR50 and IR42 was 44% and 54% respectively.

INTRODUCTION

Rice, the staple food of 40% of the world population, has an area of production second only to wheat. Rice provides more calories than any other temperate cereal (De Datta, 1981). In temperate cereals grain density is the strong determinant of yield (Stokes, *et. al.*, 1985) because

---

1 Dept. of Agronomy, International Rice Research Institute, Los Banos. Laguna, Philippines.

of considerable variation in grain size (Thorne, 1965). Rice grain size, however varies less because the rice grain is enclosed in an inflexible lemma and palea, and thus is determined as early as 5 days before anthesis (Matsushima, 1957). Thus panicle density and grains per panicle assume greater significance in rice yields.

Mature rice panicles have large numbers of unfilled spikelets which may be due to spikelet abortion or inadequate assimilate supply. Often, inputs in rice are in short supply. Timeliness of inputs is important to obtain maximum benefits.

The floral organ in rice is a determinate inflorescence bearing primary and secondary branches (occasionally tertiary branches) that terminate in spikelets. The spikelet contains a single hermaphrodite flower with six stamens and an ovule (De Datta, 1981). Arber (1934) showed that rice spikelet consists of two rudimentary glumes, two sterile lemma, functional lemma and palea enclosing six stamens and a single ovule. The two lodicules are borne between the lemma and the whorl of stamens.

The development stages of wheat (Bonnet, 1936; Tottman, 1977; Kirby and Appleyard, 1984), barley (Bonnet, 1935; Kirby, 1977) and oat (Bonnet, 1937) have already been described. The reproductive development of rice is similar to that of oat, differing only in the sequence of changes.

Noguchi (1929) who first reported on rice panicle development, observed that rice panicle primordia protruberences appear asymmetrically on the apical dome. Hitherto, a number of studies are being conducted on rice apical development using binocular microscope. A most detailed study (Matsushima, 1961), which included 21 development stages, used the paraffin sectioning method under binocular microscope. Moncur (1979) first described the three dimensional description of rice panicle development using the scanning electron microscope.

In this study, apical development stages of IR50 was investigated up to floral organ development using an electron microscope. This paper reports the apical development and identification of grain yield loss of IR50 and IR42.

MATERIALS AND METHODS

IR50 and IR42 rice cultivars were grown under greenhouse conditions in pots containing 10 kg oven-dried soil during 1987/88 wet season. Plants were fertilized with 120 kg N, 60 kg P and 60 kg K/ha. : 2/3 N and total P and K were applied basally and 1/3 N applied 7 days before visual panicle initiation. Eight seedlings were planted per pot. Eighteen plants were sampled weekly during vegetative and maturity stages. During the reproductive stage plants were sampled at 2-3 day intervals.

Morphological growth of plants was identified using the Zadoks growth scale (Zadoks, *et. al.*, 1974). Apical development was monitored by dissecting the plants under the binocular microscope, using techniques described by Kirby and Appleyard (1984) for temperate cereals. As the mature leaf sheaths of rice are much harder, they, were removed by splitting the sheath in to two along the midrib. Young leaf sheaths are tender and easily damaged. These were removed carefully under the microscope using a dissecting needle. The development stage of the exposed growing point (apical dome) was identified and selected for observation under the scanning electron microscope.

Sample preparation for the scanning electron microscope

Selected rice apices with a thin piece of stem below were cut and fixed in 3% glutaraldehyde in 0.025 M phosphate buffer for 4 hours (O'Brien, *et. al.*, 1973). After fixation, samples were rinsed 3-4 times in 0.025 M phosphate buffer and dehydrated using alcohol series. The dehydration series consisted of 50, 70, 80, 90, 100% and absolute ethyl alcohol, and was immersed for 5, 5, 10, 10, 15 and 60 minutes respectively. After dehydration, samples were transferred to absolute acetone and subjected to critical point drying at 1200 psi at 36-38 C using liquid carbon dioxide. Samples were then mounted on stubs using silver paint and was coated with metal gold in sputter coater at 1.4 Kv 16-18 mA for 2 minutes. Coated samples were transferred to the scanning electron microscope chamber for observation and photographing.

RESULTS

During vegetative development of IR50, which lasted for about 35 DAS, 7 laminated leaves were fully developed (Growth Stage G.S. 1.7, Table 1). During vegetative development, the apical dome remained very small (0.10 mm) and initiated 12 leaf primordia. In contrast, vegetative development of IR42 lasted 49 days during which period 10 laminated leaves fully emerged. The apical dome during vegetative development remained very small (0.10 mm) as in IR50 and initiated 14 leaf primordia. The axillary primordia of both varieties gave rise to the primary tillers. The vegetative apex of IR50 consisted of the apical dome which is enclosed by several leaf primordia (Figure 1).

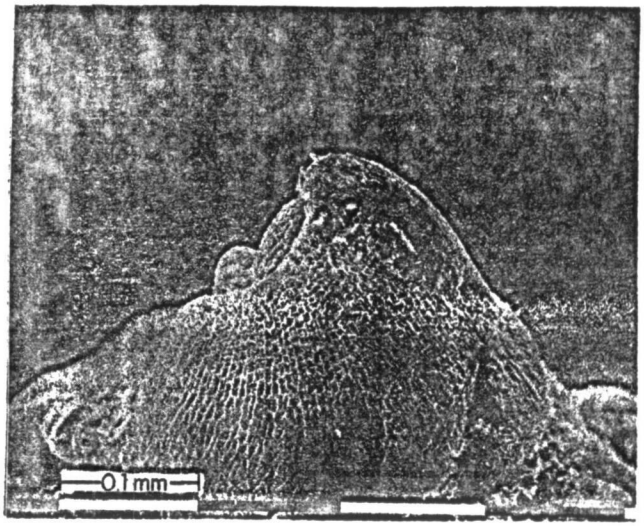
As the apex became reproductive, the apical dome was enclosed by the flag leaf primordia and it increased in length and width. During the reproductive development of IR50, which lasted for 18 days (Table 1), the apical dome length increase from 0.10 mm to 103.50 mm, and four leaves fully emerged.

The reproductive development stages are listed in Table 2. The reproductive phase of IR50 started after 35 DAS (G.S. 1.7) and was divided in to 13 morphologically different stages before panicle emergence. Reproductive development can be broadly divided in to two phases. The first phase includes the formation of panicle structures, the primary and secondary branches, which are the major determinants of potential grain number. The second phase involves the initiation and development of spikelet primordia on these primary and secondary branches.

Panicle development

Initiation of the panicle base, referred to as the neck node, was the foremost stage of panicle differentiation (Figure 2). The neck node produce a thin bract encircling the apical dome, and hairy growth which in combination with other bract hairs covered and protected the developing dome.

During the next development stage, apical dome produced a number of primary branches in the axils of each bract acropetally (Figure 3) and these appeared as a bunch of apices. This is an important panicle



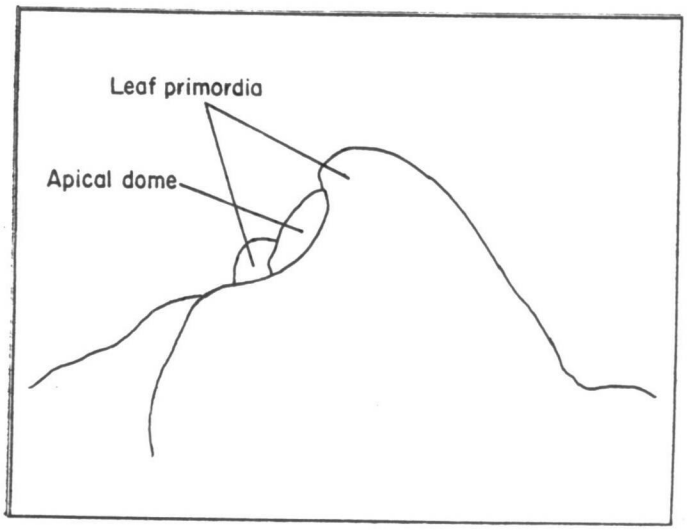
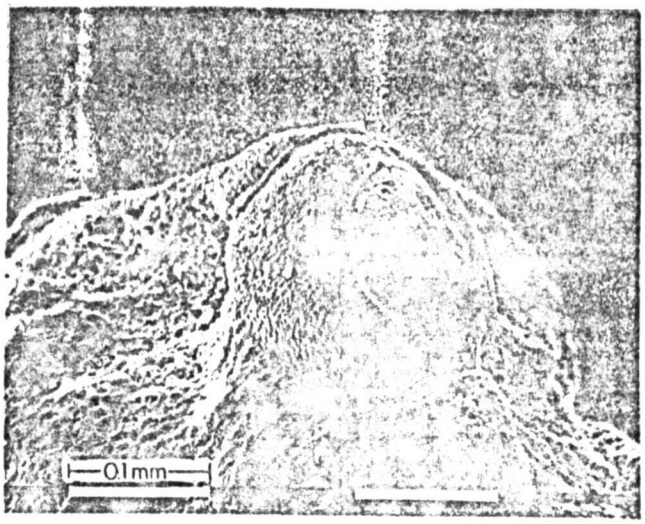


Fig. 1. Vegetative shoot apex of IR50 at growth stage 17 (35 DAS).



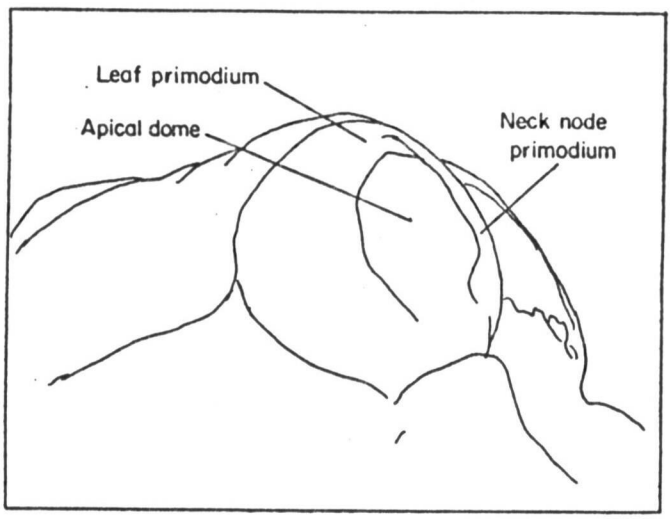


Fig. 2. Differentiation of the 'neck node' of IR50 at growth stage 18 (35-39 DAS).

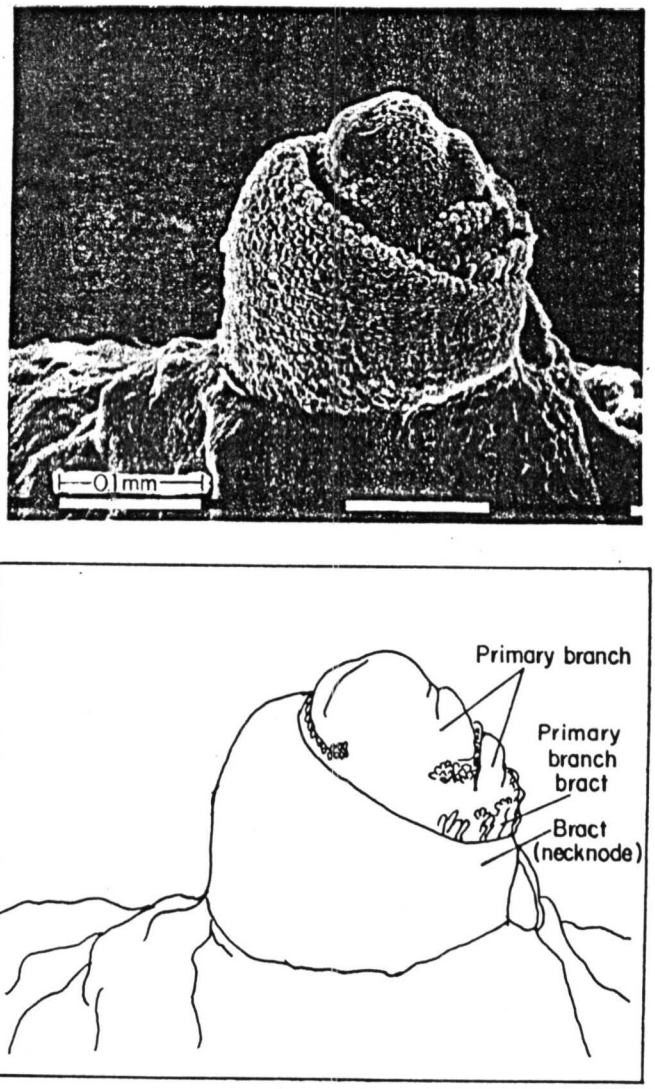
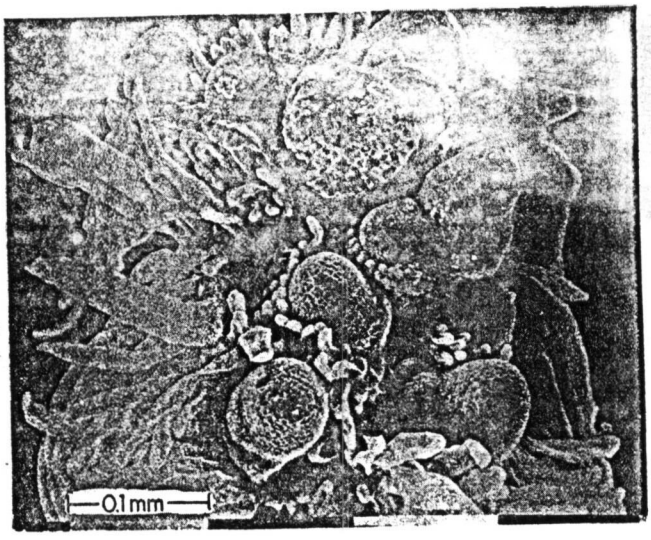


Fig. 3. Differentiation of the primary branch primodia of IR50 at growth stage 19 (37-42 DAS).

Table 1. Morphological growth and apical development of IR50.

Zadoks growth stage (G.S.)	Development stage	Days after sowing		Apical dome length (mm)
		Range	Average	
11 – 17	Vegetative	0 – 35	35.0	0.10
18	Neck node differentiation	35 – 39	37.0	0.13
19	Primary branch differentiation	37 – 42	39.5	0.19
19	Secondary branch differentiation	39 – 42	40.0	0.38
19	Rudimentary glume differentiation	42 – 44	43.0	1.17
1.10	Sterile lemma differentiation	42 – 44	43.0	1.69
1.10	Fertile lemma differentiation	42 – 48	45.0	2.43
1.10	Palea differentiation	44 – 48	46.0	3.17
1.11	Stamen initials differentiation	46 – 48	47.0	13.98
1.11, 37	Stigma initials differentiation	48 – 50	49.0	23.70
1.12,43	Spikelet development	53	53.0	103.50

development stage as it primarily determines the potential spikelet number. The stem, which remained less than 1 cm before neck node differentiation, started to elongate. Each of these primary branches produced secondary branch primordia first and lately spikelet primordia (Figure 4). Each distal end then differentiated into a spikelet. Each of, secondary branches also produced 3 – 5 spikelet primordia, coinciding with the spikelet primordia production by the primary branch. At this stage, the apical dome was covered with hairy outgrowth and appeared as a fluffy mass of about 1 mm long (visual panicle initiation).



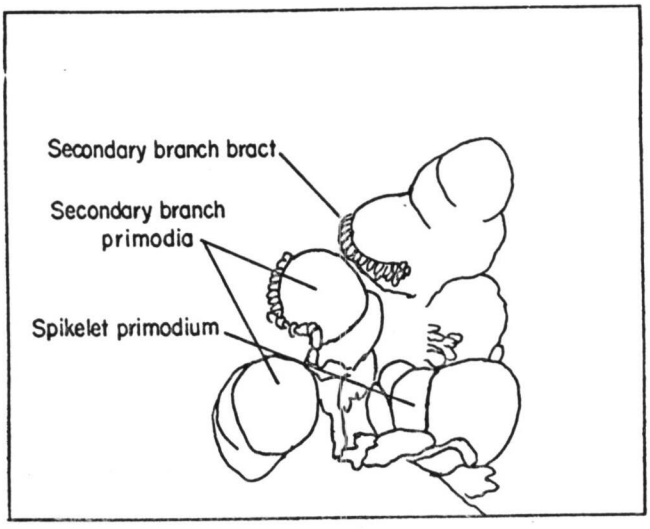


Fig. 4. Differentiation of the secondary branch primodia and spikelet primodia of IR50 at growth stage 19 (39-42 DAS).

Table 2. Development stages of the rice apex.

Development stage	Description	Figure No.
Vegetative	Short apical dome enclosed by leaf primordia, 0.10 mm height	1
Neck node	Differentiation of the panicle base	2
Primary branch	Acropetal development of number of apices from the apical dome	3
Secondary branch	Differentiation from the basal region of primary branches, 3 – 5 in number	4
Rudimentary glume 1	Initiation of the spikelet base remains small	5
Rudimentary glume 2		6
Sterile lemma 1	Formation of initials which remain	7
Sterile lemma 2		8
Fertile lemma	Formation of lemma initials	9
Palea initial	Formation of palea initials	10
Stamen initial Awn initial	Formation of six stamen initials Formation of awn initial at the distal end of lemma	11
Lodicule development	Development of 2 lodicules between stamens and lemma	12
Stigma initial	Formation of 2 stigma initials from the short style on the ovule	13

Spikelet development

The first spikelet development stage was the initiation of rudimentary glumes (Figures 5, 6) which remained small and obscure with further development. There are two glumes that differentiated one after the other on either side. This formed a smooth base for the development of other floral parts. The sterile lemmas were the next to differentiate one above each glume and these remained thin and small (Figures 7, 8). The sterile lemmas persisted even after the grain

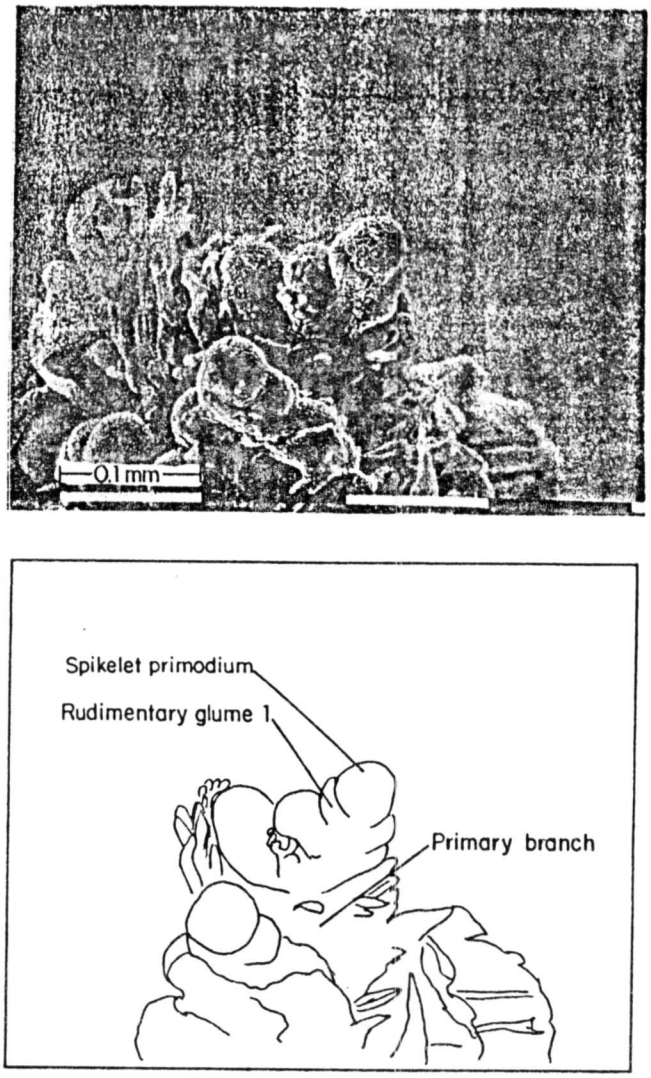
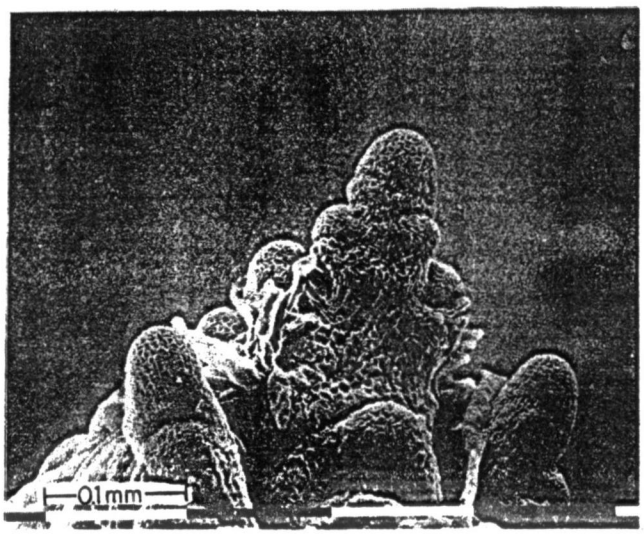


Fig. 5. Differentiation of the rudimentary glume 1 of spikelet of IR50 at growth stage 1.10 (42-44 DAS).



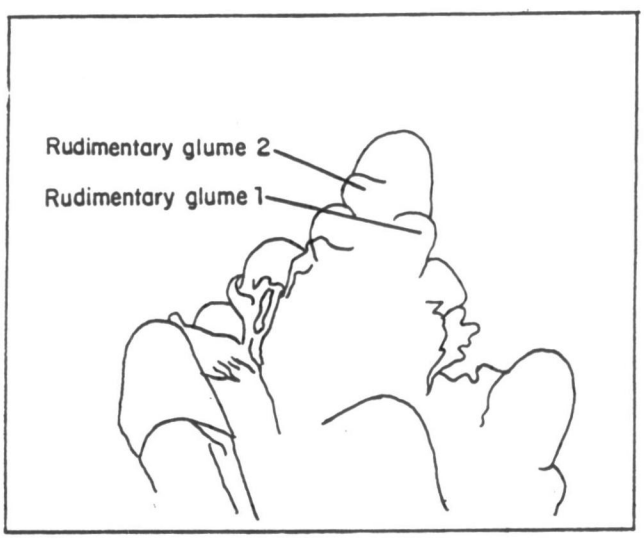
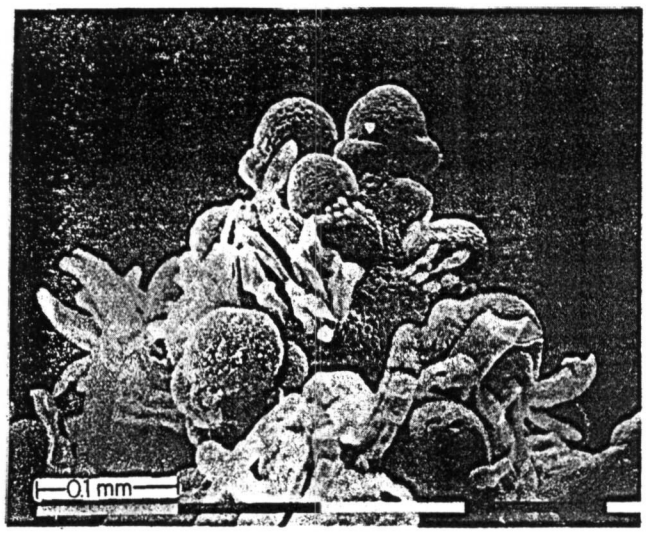


Fig. 6. Differentiation of the rudimentary glume 2 of spikelet of IR50 at growth stage 1.10 (42-44 DAS).



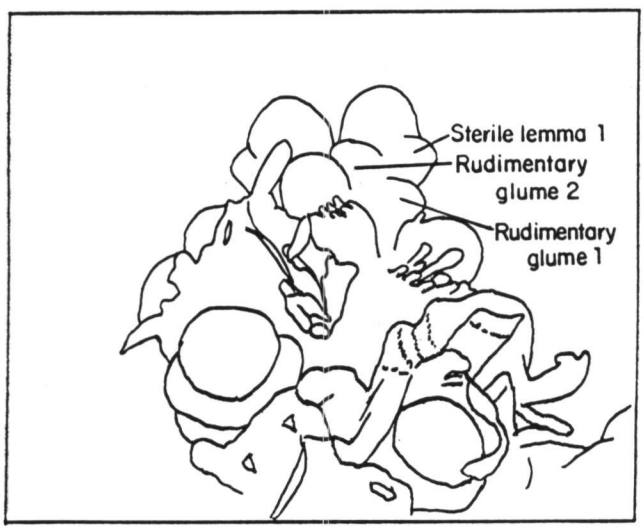
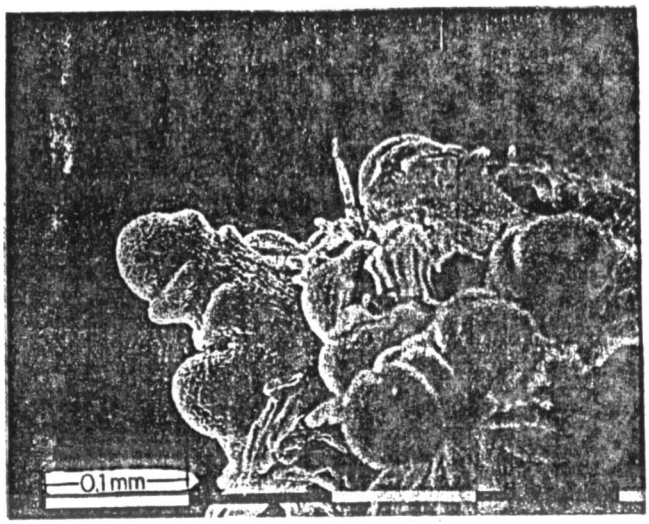


Fig. 7. Differentiation of the sterile lemma 1 of spikelet of IR50 at growth stage 1.10 (44 DAS).



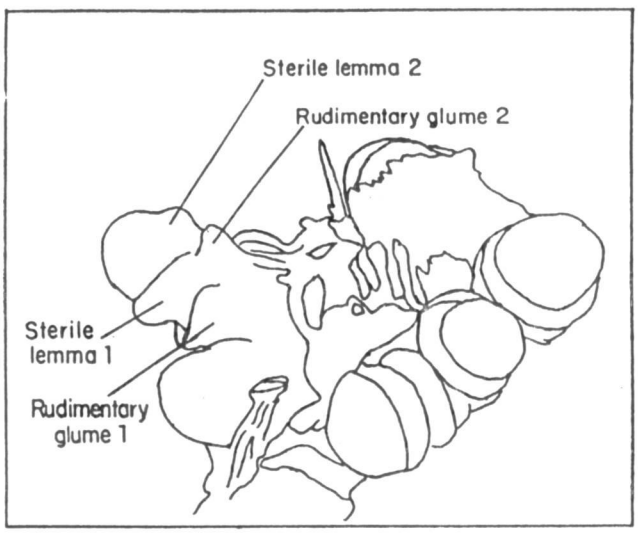


Fig. 8. Differentiation of the sterile lemma 2 of spikelet of IR50 at growth stage 1.10 (44 DAS).

matured on either side of the grain attached to the palea and fertile lemma.

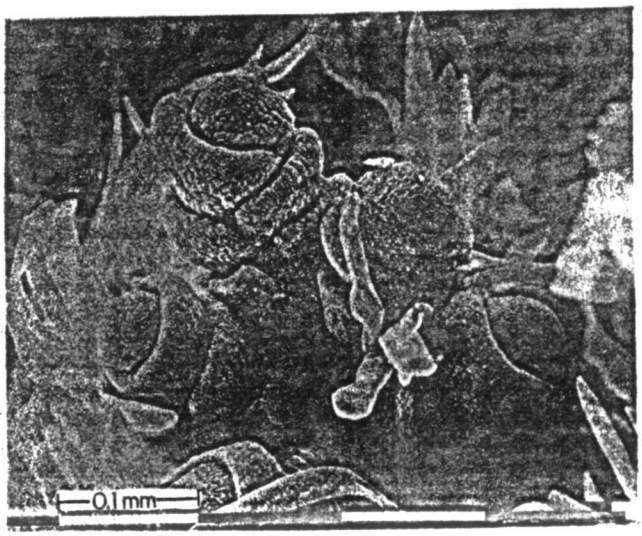
Five-nerved fertile lemma, the largest structure of the spikelet, differentiated (Figure 9) after the sterile lemma. This was initiated above the sterile lemma 1 and occupied 2/3 circumference of the developing floral parts. Palea (Figure 10), which is the smaller bract protecting the developing floral part, differentiated above the sterile lemma 2. During the next stage, the central apical dome of the developing spikelet initiated six stamens primordia around it (Figure 11). The development of stamens could be seen only by dissecting and removing the lemma or palea.

During the next development stage, the central dome developed to a pistil, the female reproductive organ. At the same time, two lodicule primordia were initiated between the whorl of stamens and the developing lemma (Figure 12). In the female reproductive organ, a single ovule was initiated and then a very short style and two stigma developed (Figure 13). Stigma initial developed further to form two hairy (plumose) stigmas positioned below the anther lobes. The panicle continued to grow to about 10 cm long when spikelet development was completed (Figure 14), and took another 11 days for anthesis to occur (Table 3).

Table 1 summarizes the apical growth and development of IR50 and the duration of each development stage. Panicle development took 4-7 days spikelet development was completed in 11 days.

Table 3 summarizes the IR50 growth and development from seeding to maturity, which took 90 days under greenhouse condition although its life span is 105 days. Visual panicle initiation was observed at G.S. 19 (42 DAS) and the neck node initiation at G.S. 18 (35 DAS). Leaf area per culm increased up to G.S. 55 (anthesis, 64 DAS) and was reduced thereafter. Leaf dry weight increased up to G.S. 37 (50 DAS), decreased, and then increased at harvest. Maximum spikelet number was obtained at G.S. 41 (53 DAS), spikelet number was reduced thereafter in two stages: before and after anthesis (Figure 15).

Table 4 summarizes the apical development of IR42 and indicates that IR42 panicle and spikelet development took 11-15 and 13-16 days, respectively, and took another 10 days for anthesis.



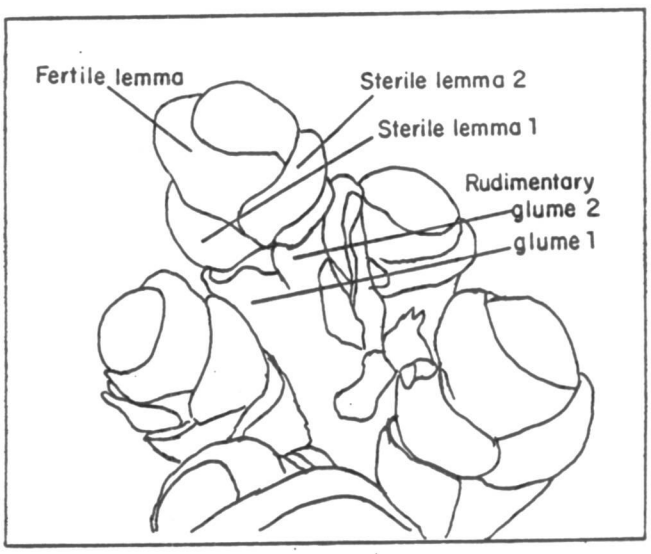
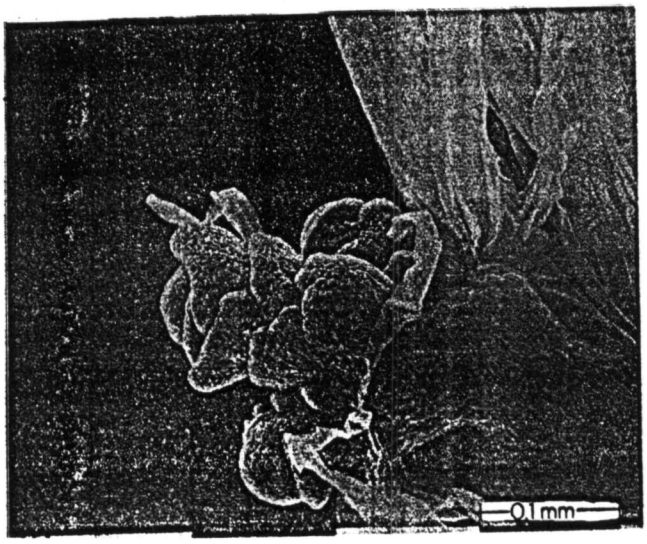


Fig. 9. Differentiation of the fertile lemma of spikelet of IR50 at growth stage 1.10 (42-48 DAS).



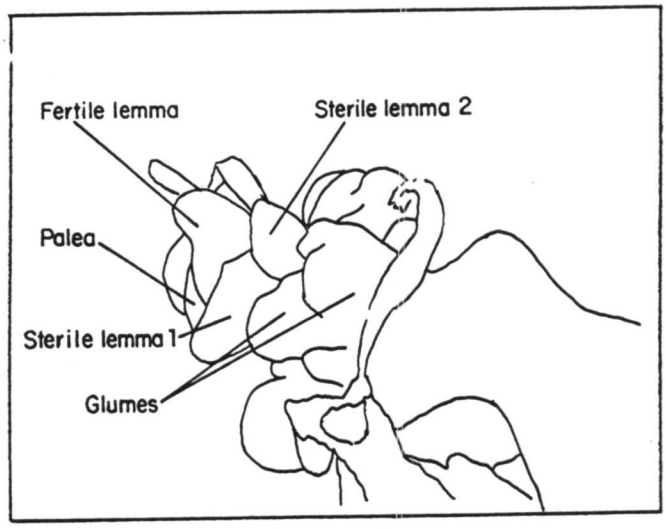
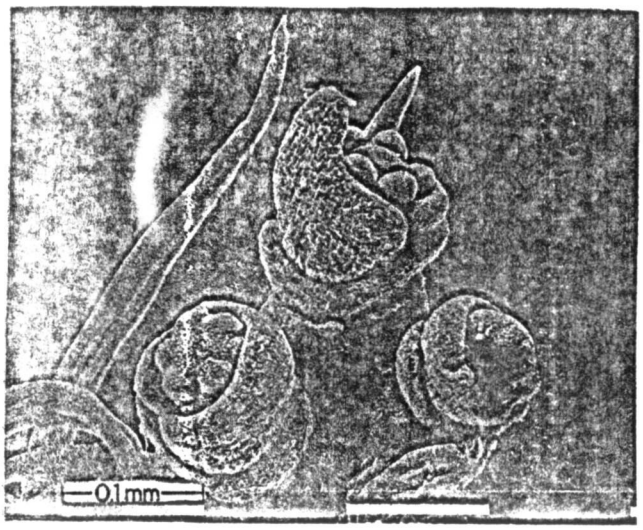


Fig. 10. Differentiation of the palea of the spikelet of IR50 at growth stage 1.10 (44-48 DAS).



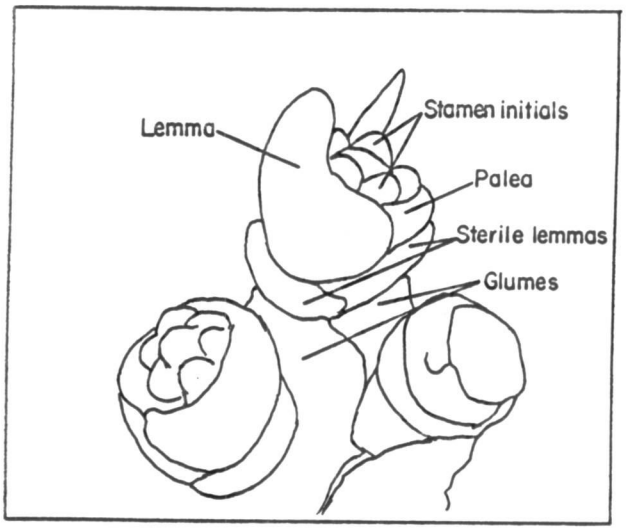


Fig. 11. Differentiation of the stamen initials of spikelet of IR50 at growth stage 1.11 (46-48 DAS).

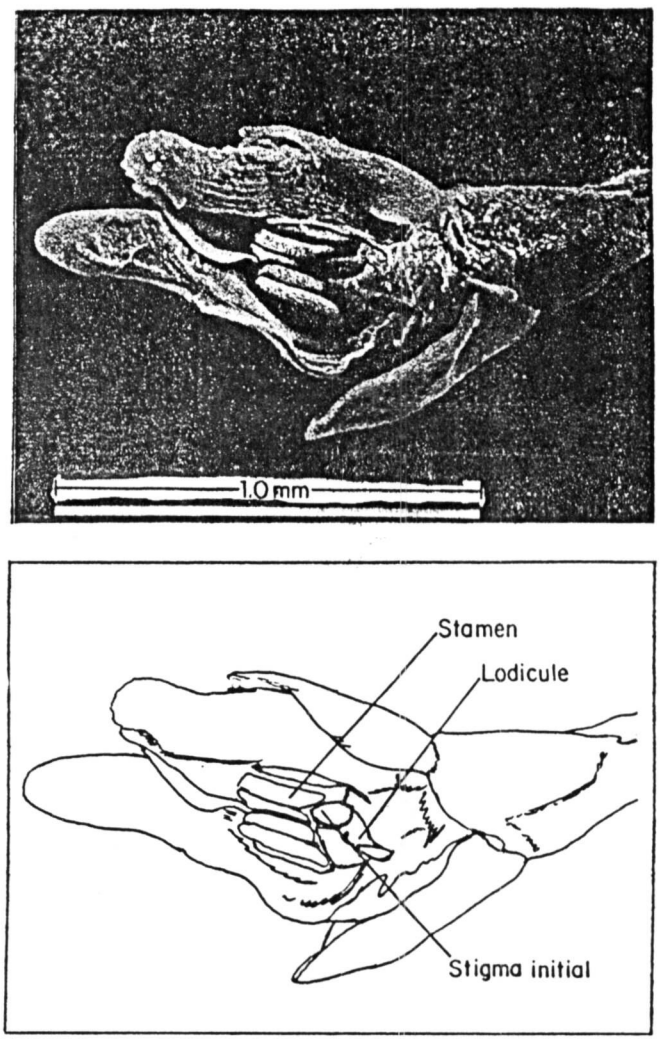


Fig. 12. Development of the lodicules of spikelet of IR50 at growth stage 1.11 (46-48 DAS).

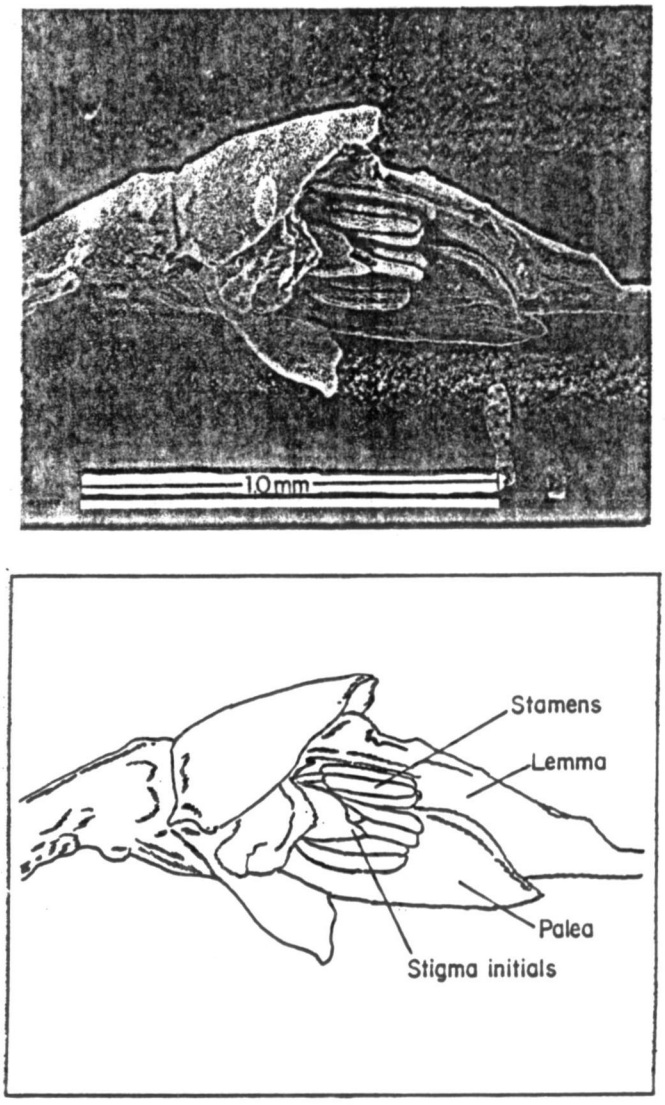
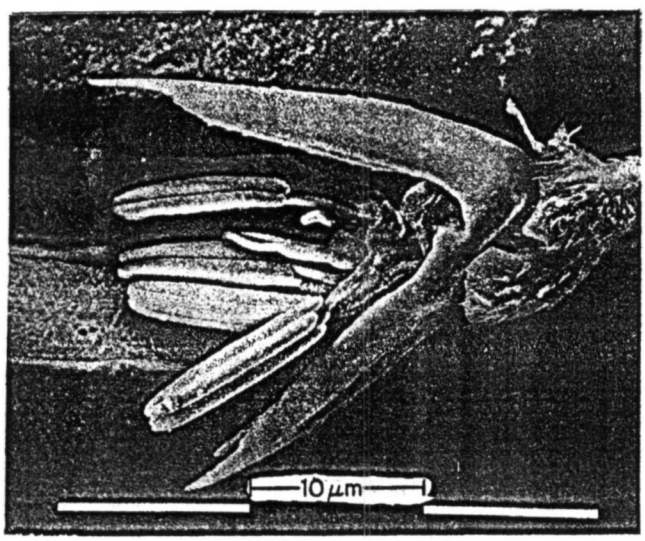


Fig. 13. Differentiation of the stigma initials of spikelet of IR50 at growth stage 37 (48-50 DAS).



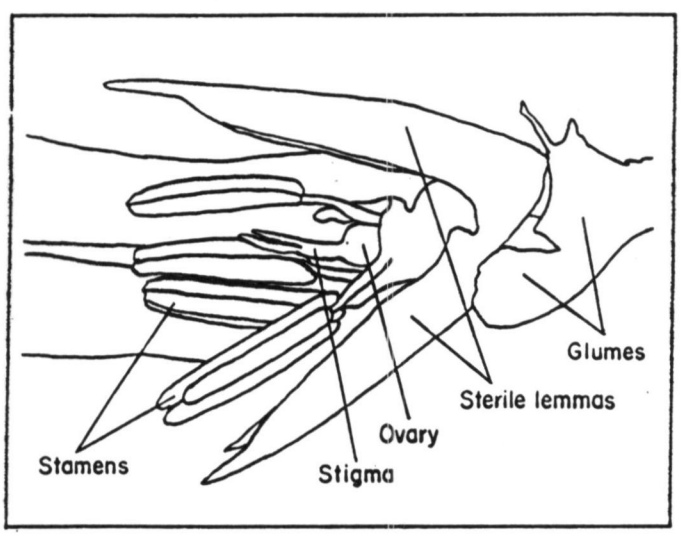


Fig. 14. Fully developed spikelet of IR50 at growth stage 41 (53 DAS).

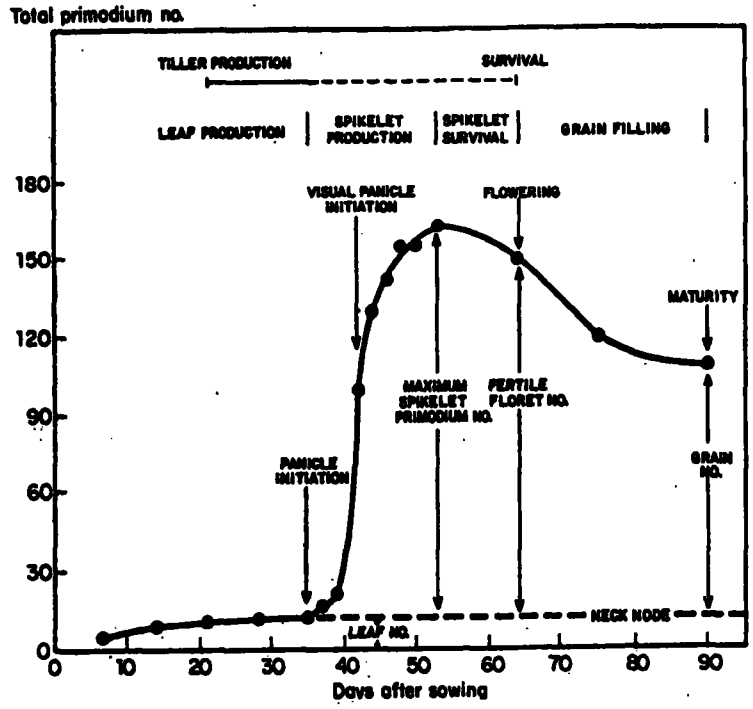


Fig. 15. Primodium production at different ages of IR50.

Table 3. Growth and development parameters at different ages of IR50.

Crop age (DAS)[a]	Zadoks growth stage	Development stage	Primordia number	Apical dome/ panicle length (cm)	Culm length (cm)	Leaf dry weight/cm (cm)	Leaf area per culm (cm)
7	11,20	Vegetative	5	0.010	Very short	14.50	1.27
14	14,20	Vegetative	9	0.010	Very short	9.73	7.19
21	15,21	Vegetative	11	0.010	0.35	2.67	13.29
28	17,23	Vegetative	12	0.010	0.48	2.42	24.27
35	18,25	Neck node (N.N.) differentiation	13	0.013	0.72	1.96	38.43
37	19,27	N.N. – primary branch differentiation	16	0.019	0.96	2.41	41.05
39	19,28	Primary – secondary branch differentiation	22	0.038	1.51	2.48	46.46
42	19,28 31	Rudimen: glume – fertile lemma differentiation	99	0.117	2.89	2.26	69.11
44	1.10, 28,31	Rudimen: glume – stamen initial differentiation	129	0.169	3.83	2.76	59.72
46	1.10, 27,31	Fertile lemma – stamen development	141	0.317	4.57	2.19	74.68
48	1.11, 28,31	Fertile lemma – stigma initial differentiation	155	1.390	6.72	2.76	64.15
50	1.11, 27,32,37	Stigma initial – stigma development	156	2.370	8.62	2.97	75.12
53	1.12,27 32,39 – 41	Spikelet development complete	162	10.350	12.70	2.75	82.38
64	1.12,27 34,55	Flowering	149	22.700	41.35	2.68	105.48
75	1.12,27 34,85	Soft dough	119	22.000	50.06	2.43	92.83
90	1.12,25 34,92	Caryopsis hard (harvest)	108	22.200	67.55	4.01	42.60

[a]DAS = days after seeding.

Table 4. Morphological growth and apical development of IR42.

Zadoks growth stage (G.S.)	Development stage	Days after sowing		Apical dome length (mm)
		Range	Average	
11 – 19	Vegetative	0 – 49	49	0.10
1.10	Neck node differentiation	49 – 56	52	0.11
1.10	Primary branch differentiation	56 – 61	59	0.26
1.11	Secondary branch differentiation	56 – 64	60	0.53
1.11	Rudimentary glume differentiation	61 – 64	63	0.99
1.11	Sterile lemma differentiation	64	64	1.44
1.11	Fertile lemma differentiation	64 – 68	66	9.42
1.11	Palea differentiation	64 – 68	66	15.25
1.11	Stamen initials differentiation	64 – 74	69	17.13
1.13	Stigma initials differentiation	68 – 74	71	48.57
1.14	Spikelet development complete	74 – 77	76	167.90

Data presented in Table 5 indicate that growth and development of IR42 from seeding to maturity was completed in 120 days under greenhouse conditions, even though its normal duration was 138 days. Neck node initiation was observed at G.S. 1.10 (49 DAS) and visual panicle initiation G.S. 1.11 (64 DAS). Leaf dry weight increased up to G.S. 55 (87 DAS, anthesis), decreased and increased again at harvest while the leaf area increased up to G.S. 39 – 41 (77 DAS) then decreased thereafter. Spikelet number was reduced before and after anthesis (Figure 16).

DISCUSSION

Changes in the rice reproductive phase are complex and may be subject to a lot of misinterpretations. Other authors have indicated contrasting views regarding the initiation of the reproductive development of rice. For example Sircar and Sen (1950) indicated that there is no double ridge stage in rice unlike in wheat or barley. The growing apex, during its transition from vegetative to reproductive growth, elongated considerably at the top. Along the edges, groups of cells protruded to develop into branch rachids.

Matsushima (1961) indicated the initiation of the neck node primordia as the onset of reproductive development in rice. Moncur (1981), however, surmised that the appearance of a primary branch primodium in the axils of a bract marks the change from vegetative to reproductive phase.

In this paper, initiation of the neck node was considered to mark the onset of reproductive development. In reality, the neck node primordia differentiation was difficult to detect early because of its similarity to leaf primordia differentiation. However, if the exact number of leaves produced by a variety is known, this stage could be detected early.

Opposite views on the differences between leaf primordia initiation and neck node initiation, based on the angle produced by the developing primordia with the vertical axis of the apical dome, have been presented. For example, Matsushima and Manaka (1957) reported the idea that leaf primordia produces an obtuse angle with the vertical axis than the neck

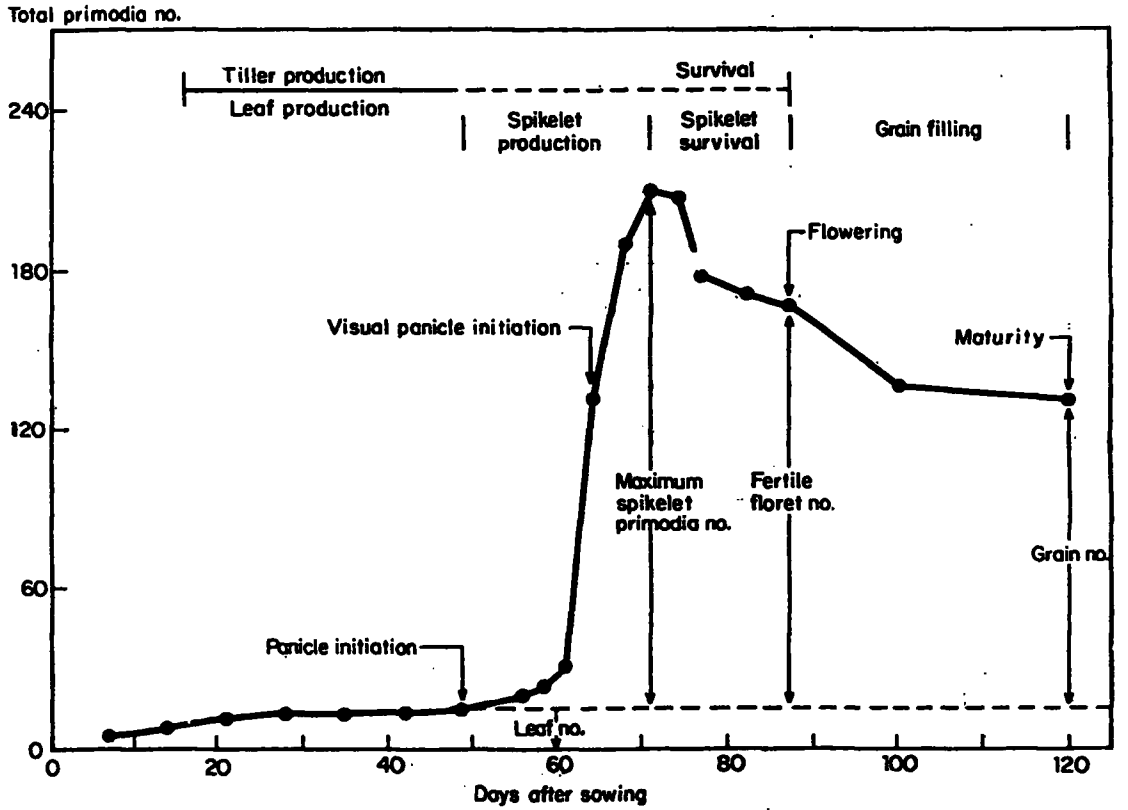


Fig. 16. Primodia production at different ages of IR42.

Table 5. Growth and development parameters at different growth stages of IR42.

Crop age (DAS)[a]	Zadoks growth stage	Development stage	Primordia number	Apical dome/ panicle length (mm)	Culm length (cm)	Leaf dry weight/cm^2 (mg)	Leaf area per culm (cm^2)
7	11,20	Vegetative	5	0.10	very short	2.64	0.89
42	19,24	Vegetative	14	0.10	0.77	2.16	111.21
49	1.10,25	Neck node differentiation	15	0.11	1.07	2.91	89.62
56	1.10, 24,31	Primary branch - differentiation	20	0.26	3.80	2.86	115.91
61	1.11, 26,31	Primary branch Secondary branch	32	0.53	4.75	3.30	108.43
64	1.11, 26,32	Rudimentary glume- stamen differentiation	135	1.44	8.10	2.97	130.43
74	1.13,24 33,37	Stamen development- complete spikelet	218	48.50	17.76	3.40	166.28
77	1.14,24 33,39-41	Spikelet development- complete	178	167.90	21.45	3.71	177.76
87	1.14,23, 35,56	Flowering	168	255.30	65.60	4.72	151.24
100	1.14,23 35,77	Late milk stage	146	254.30	70.30	4.13	83.02
120	1.14,23 35,92	Caryopsis hard (harvest)	142	256.10	71.92	4.76	23.66

[a]Days after sowing.

node primordia. Kahawara *et. al.*, (1968) indicated that the first bract primodium takes a more obtuse angle to the vertical axis than the leaf primordia. Our observation in IR50 supports the view of Kawahara *et. al.*, (1968).

The sequence of changes in rice panicle development was more complex than of other cereals. At any time, apical dome consisted of a number of development stages, even in the same primary branch. This posed problems in classifying the development stages. Kirby and Appleyard (1984) suggested that the development stage be identified by the most advanced stage of panicle structure. Accordingly, the terminal spikelet, which flower first in the panicle was considered in judging the development stage. However, our findings revealed that the first spikelet differentiated in the primary branch and the terminal spikelet of the last secondary branch differentiated were in a more advance development state. Therefore, it is not always true to consider the terminal spikelet as a guide.

Considering the rate of primordia production during the reproductive phase, the age difference between two adjacent spikelets was less than an hour (Table 3): increase in primordia number was 77 from 39th to 42nd day in IR50 and 103 from 61st to 64th day in IR42 (72 hrs). Therefore, these differences can be disregarded and the terminal spikelet considered as the most advanced spikelet. Based on the flowering order of spikelets in a panicle, flowering of the spikelet immediately below the terminal spikelet occurred on the 3rd day although the age difference was less than an hour. This suggests that other physiological control of spikelet development, probably an apical dominance, operates independently in each panicle branch. However, the overall flowering order which is basipetal was not affected since development was also basipetal.

Panicle development and spikelet development of IR50 lasted for 4 – 7 and 11 days, respectively (Table 1); and those of IR42 lasted for 11 – 15 and 13 – 16 days, respectively (Table 4). This differed from data obtained by Matsushima (1961) with 10 – 12 days for panicle development and 8 – 9 days for spikelet development. Differences in observations can be attributed to differences among varieties, particularly the age groups.

After obtaining the maximum spikelet number, the spikelet number decreased in two successions: a slight reduction before anthesis and a

larger one after anthesis in IR50 and vice versa in IR42. The crop was maintained well throughout. No stress occurred due to moisture, pest, and diseases. Therefore, the two reduction phases can be attributed to either insufficient fertilizer and/or inefficient fertilizer application timing or to inherent physiological deficiency of the variety.

Spikelet abortion in IR42 was higher before anthesis than that in IR50 (Figures 15 and 16). This is attributed to the time lag between physiological panicle initiation (49 DAS) and N top-dressing at 5 days before visual panicle initiation (60 DAS) of IR42. In IR50 physiological panicle initiation stage coincided with N top-dressing at 5 days before visual panicle initiation (35 DAS) and thus less spikelet abortion.

The post flowering spikelet abortion even under ideal conditions never fall below 15% (Yoshide, 1981) since it depends on a large number of biotic factors. This reduction in grain number hitherto is called the potential yield loss of rice and accordingly the potential yield of rice is considered as the number of fertile spikelet number at flowering.

This study revealed another period of loss of spikelets which occur before flowering stage of rice. Hitherto this period of spikelet loss was not considered and quantified, as the loss was not visible. Pre flowering spikelet abortion also depend on several factors both biotic and abiotic. Pre flowering spikelet abortion period extend from Maximum spikelet number stage (MSN) upto flowering but it could start even before MSN, at very early stages of spikelet differentiation, depending on the stress conditions experienced by the rice plant. Thus under ideal conditions the potential yield loss period extend from MSN stage up to harvest and not from fertile spikelet stage (flowering). Hence envisage a higher potential yield of present day varieties and a higher potential yield loss. Figure 15 and 16 shows that the actual potential yield loss of IR50 and IR42 was from 156-108 and (44%) hitherto considered for IR50 and IR42 was from 149-108 (37%) and 168-142 (18%) respectively. Lower difference of the actual and hitherto considered potential yield loss of IR50 could be attributed to the fact that N top dressing at 5-7 DBPI coincide with the physiological PI because of short growth duration of IR50.

Results suggest that, potential yield of modern rice cultivars and potential yield loss of varieties are much higher than hitherto quantified

and therefore input timing studies should consider the actual potential yield loss in order to increase the rice yield.

REFERENCES

Arber, A. (1934). Gramineae. Cambridge University Press. p. 580.

Bonnet, O.Y. (1935). The development of barley spike. J. Agric. Res. 51: 451 – 457.

..... (1936). The development of wheat spike. J. Agric. Res. 53: 445 – 451.

..... (1937). The development of oat panicle. J. Agric. Res. 54: 927 – 931.

De Datta, S.K. (1981). Principles and practices of rice production. John Wiley and Sons, New York. p. 681.

..... (1978). Fertilizer management for efficient use in wet – land rice soils. pp. 671 – 701. In International Rice Research Institute, Los Banos, Philippines.

Kawahara, H., Ota, T. and Chonan, N. (1968). Studies on morphogenesis in rice plants. 2. Observations on the differentiation of stem vascular bundles connecting with the formation of other organs and tissues. Scientific Report of the Faculty of Agriculture, Ibaraki University. 16: 7 – 14.

Kirby, E.J.M. (1977). The growth of the shoot apex and dome of barley during ear initiation. Ann. Bot. 41: 1297 – 1308.

..... and Appleyard, M. (1984). Cereal development guide, 2nd Ed. Arable Unit, National Agricultural Centre, Stoneleigh, Konilworth, Warwickshire, U.K. p. 95.

Matsushima, S. (1957). Analysis of development factors determining yield and yield prediction in lowland rice. Bull. Nat. Inst. Agric. Sci. Japan Series A – 5. pp. 1 – 271.

..... and Manaka, T. (1957). Development process of the young panicle of rice and its identification. Nogyo Gijutsu Kyokai. p. 57. (In Japanese).

..... (1961). Theory and techniques of rice cultivation, determination of yield and its application. Department of Agriculture, Kuala Lumpur, Malaya. p. 257.

Moncur, M.W. (1979). Scanning electron micrographs of rice primordia. Int. Rice Res. Newsl. 4(2): 22.

..... (1981). Floral initiation of field crops, an atlas of scanning electron micrographs, CSIRO, Canberra, Melbourne. p. 135.

Nogushi, Y. (1929). Studien uber, die entwicklung der infloreszenzen und der bluten bei getrendepflanzen. J. Coll. Agric. Tokyo Imp. Univ. 10(4): 247 – 303.

O'Brien, T.P., Kuo, J., Macully, M.E. and Zee, S.Y. (1973). Coagulant and non – coagulant fixation of plant cells. Aust. J. Biol. Sci. 26: 1231 – 1250.

Sircar, S.M. and Sen. S.P. (1950). Photoperiod induction and the development of growing apex in rice. Nature 165: 855.

Stokes, D.T., Naylor, R.E.L. and Mathews, S. (1985). The incorporation of tiller manipulation by chlormequat into winter barley production systems. pp. 535 – 541. In Proc., British Crop Protection Conference. Weeds, November 18 – 21, 1985, Brighton Metropole, Brighton, England.

Thorne, G.N. (1965). Physiological aspects of grain yield in cereals. pp. 88 – 105. *In*: The growth of cereals and grasses. Milthorpe, F.L. and Ivins, J.D. (Eds). Butterworths, London.

Tottman, D.R. (1977). The identification of growth stages in winter wheat with reference to the application of growth regulator herbicides. Ann. Applied Biol. 87: 213 – 224.

Zadoks, J.C., Chang, T.T. and Konzac, C.F. (1974). A decimal code for the growth stages of cereals. Weed Res. 14: 415 – 421.