CERTAIN ABNORMALITIES IN MILLETS INDUCED BY X-RAYS

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IRRADIATION with X-rays has been much resorted to by many workers in genetics and plant breeding in order to induce genetic variability. It has been the common experience of almost all the workers that in the first generation, are produced a number of mutations which are usually recessives and at the same time many of them may take the shape of abnormalities rarely met with in natural populations. Mutations more staid and of economic value have been obtained in the later generations. This method was used for the millets also and a few abnormalities were noted in the progenies of the X-rayed seeds of *Eleusine coracana* Gaertn. and *Pennisetum typhoides* S. & H. Since these abnormalities are the first of their kind reported in these millets a short account of them is given below.

I. E. coracana (Ragi)

The technique employed in the X-raying of the seeds of ragi (E.C. 593—Green—throughout, top curved, brown grained) was the same as for *P. typhoides* (Krishnaswamy and Ayyangar, 1941). The germination of the exposed seeds was slow and irregular. Many seedlings died even before the protrusion of the seedling leaves. A number of albino seedlings occurred. These were slightly yellower than the usual albinos met with in the normal populations. The incidence of the albinos and the number of survivors were as follows:

Treatments	No. of seeds	No. of albinos	No. of survivors
A. 1 hour	200	38	84
B. 2 hours	200	18	7
C. 3 ,, ...	200	..	..
Control	200	..	170

Thus as in the case of *P. typhoideum*, here also two hours exposure proved to be just sublethal and three hours lethal. Some of the albinos in treatment

A, later produced a green shoot and grew into mature normal plants. Out of the 91 X_1 plants 9 were semi-sterile and 4 had gappy panicles (Krishnaswamy, 1939). The gappiness in two plants was nearly 2 in. in length.

(*a*) *White banded leaves* (Fig. 1):

In two cultures of the X_2 generation some of the seedlings showed an irregular albino zone in the leaves. When the seedlings were only two leaved the latter showed constrictions of the margins at the albino zones. The next three leaves showed definite green and white zones alternating. The white bands ran in patches across the whole width of the blade. The mature leaves, however, were completely green. In the X_2 generation the total number of normal to banded seedlings was 483 greens to 148 banded. In the succeeding generations no white banded seedlings appeared in the progenies of a number of green selections, while they appeared in the progenies of all the white banded selections (total of 5 families Pure green 784: white banded 1443).

White banded seedlings (Zebra) have been reported in Maize (Eyster, 1934). Four kinds of Zebra-striping zb_1, zb_2, zb_3 and zb_4 are described. The banding in ragi is similar to the zb_2 and zb_4, manifesting in the seedling stages and disappearing in the mature plants. In Maize they are simple recessives. In the progenies of an artificial cross in *Rice*, Ramiah and Ramanujam (1936) found similar striped seedlings. In this case, however, the striped seedlings bred pure and behaved as simple recessives. Cross banded seedlings have occurred in the natural populations of *Sorghum sudanense* (Ayyangar and Ponnaiya, 1939), inherited as simple recessives.

Albinism has been reported in Ragi (Ayyangar and Krishna Rao, 1931) as caused by a pair of duplicate factors. In these segregations, however, the heterozygous dominants are not distinguishable from the homozygous one, *i.e.*, normal green and the homozygous recessives lived till the reserve food material in the seeds was exhausted. In the present case the white banded seedlings have always segregated into green and white banded seedlings, while the greens have bred true. This behaviour is obviously due to the heterozygosity of the white banded seedlings. The banded seedlings come to flower a week later than the homozygous greens probably as a result of heterosis. The inheritance of this character is being further followed.

(*b*) *Foliation of the panicle* (Figs. 2 and 3):

In another culture out of 374 plants, 8 were noted to have produced no panicles, while the rest had them. Instead of the normal panicle a leafy bunch appeared in these eight plants. Except for this the plants were not vegetatively in any way different from the others. These abnormal panicles were borne on five main rachii corresponding to the five spikes. In the individual bunches each was seen to have five leafy structures corresponding to the two glumes and three lemmas. Of course only a few basal spikelets had developed into such leafy growths, while the rest had been suppressed. When examined for any pathogenic organism, it was found to be quite normal and healthy.

These bunches were found producing roots and when transplanted each grew into a large plant and again produced the abnormal panicles. The foliated panicles tended to become shorter in length and those formed on the secondary and tertiary branches, especially showed tendencies of reversion to the normal glume-like appearance. In some extreme cases of reversion to original type the panicles had become stumpy with almost normal glumes. In these the flowers contained much reduced ovary and stamens.

Similar foliations of the entire or a portion of the ears have been noted in large populations of Rye (Kostoff, 1940), Maize (Reeves and Stuvert, 1940), Sorghum (Karper, 1936; Ayyangar and Sankara Ayyar). In these plants also the separated plantlings produced new adult plants. This phenomenon has been adduced to be due to environmental influence in all the above cases and in some easily reversible.* In the natural populations of ragi also these mutations were noted in one particular strain (E.C. 3517 – 3 plants in 200,000).

It is interesting that this same effect has been produced by X-rays and in one of the X_3 progenies of this lot the same kinds of plants were again met with (out of a total population of 103, 5 were with ears completely foliated and 6 with main ears alone abnormal, partially foliated and partially fertile), indicating that this could be heritable also (probably involving 3 factors giving a 63 : 1 ratio).

(*c*) *Truncated panicles* (Fig. 4):

In this type the peduncle becomes much broadened and the individual spikes are reduced in length. The spikes appear as though the top 1/3 had been cut off to a level. The number of spikelets is reduced and they are branched. Partial sterility occurs. This type has bred true.

II. Pennisetum typhoides Stapf. & Hubbard (*Cumbu*)

(*a*) *Weak midribbed plants* (Fig. 5):

Amongst the X_2 progeny one culture was found segregating for plants with well-developed midribs and plants with weak or no midrib. In normal plants the blade develops a midrib which keeps the leaf supported more or less horizontally. When the midrib is not developed or is weak, on the other hand, the leaves droop and hang down. A slight amount of midrib tissue may be developed towards the base of the leaf blade. The midribless plants are completely sterile. The proportion of normal plants to the weak midribbed was 150 : 27. This ratio is much nearer to 13 : 3 (143·8 : 33·2) than to 3 : 1 (132·75 : 44·25). In the X_3 generation again the weak midrib plants were far in defect of the expected ratio. Cumbu being a protogynous plant, it is difficult to prevent contamination and this naturally much disturbs the ratio. In *S. sudanense* (*l.c.*) similar weak midribbed plants have been recorded, with a proportion of 3 normal to 1 weak midribbed plants. The inheritance of this character in cumbu is further being studied.

(*b*) *Male sterile* (Fig. 6):

Male sterility was induced in one progeny as a result of X-raying. The anthers were white in colour and produced very little pollen. They were shrivelled and did not become pendant as in the normal ears, so that they presented a characteristic appearance. The counts on X_2 and X_3 progenies gave 112 male fertile plants to 35 male sterile plants (expected on 3 : 1–110·25 and 36·75 respectively). The gene M_s is a simple dominant to m_s (male sterile).

(*c*) *Gappy panicles* (Fig. 7):

Normally the panicles bear the spikelets continuous from the base to the tip. The spikelets are arranged in close and consecutive whorls on the main axis. In the gappy panicles this consecutiveness is broken by zones completely bereft of all spikelets, and thus exposing the main axis here and there. Several grades of this type of sterility are shown in the figure. The gappy character (g_p) behaves as a simple recessive to the normal one (G_p) (159 normal panicles : 55 gappy ones. Ca. on 3 : 1 = 160·5 : 53·5). In *E. coracana* (Krishnaswamy, *l.c.*) a monogenic segregation with the normal condition dominant was obtained in one family. However, the progenies of several other crosses effected between Normal and Gappy panicled plants gave a series of intermediates and when quantitatively considered it was estimated that at least 3 factors were involved. The gappiness in ragi appeared at a definite place and lent inself to quantitative determination. In cumbu, on the other hand, there is no definiteness as to the place of incidence of the gappiness.

(*d*) *Forked panicles* (Fig. 8):

The panicle normally is cylindric and tapering only at the apex. The apex may be sometimes short and blunt or it may prolong much attenuated bearing a few vertically disposed, adpressed spikelets. Sometimes it is found to branch and the branching or forking may extend downwards beyond the middle of the panicle. Such panicles often appear as twin panicles. Both of them are completely fertile and give the same degree of grain setting. Rarely it might fork once more giving three branches. This phenomenon is very commonly observed in normal populations occurring on stray plants. Further the forking may not appear in all the panicles in a plant. In one of the X_2 families, however, a greater proportion of the plants with forked panicles was observed. The incidence was from rudimentary to almost complete twinning. Counts taken in this progeny gave 75 with all panicles normal and 36 with forked panicles suggesting a single factor difference. This phenomenon is being further studied.

(e) *Goose-necking of peduncles* (Fig. 9):

Goose-necked peduncles have been recorded in *Sorghum* (Ayyangar and Ponnaiya, 1941), where they are of very common occurrence. In *Pennisetum* this feature is a very rare phenomenon. Segregations were observed in X_3 progenies for this character. The counts gave (total of two families) normal 36 : goose-necked 18, indicating a single factor difference while in another family 47 goose-necked to 33 normal panicles were counted. The behaviour requires further pursuit.

(f) *Tip sterility* (Fig. 10):

In one of the X_2 progenies plants were met with in which the panicles were short but stout and the central axis was seen protruding beyond the panicle. In normal panicles this is fertile and the axis is not seen naked beyond the apex of the panicles. Shorter lengths of sterile axis are found at the apex, probably facilitating the emergence of the panicles. In the present case, however, the sterile portion measured about 5·1 cm. The analysis of the population gave 54 normal panicles and 32 tip-sterile ones (ratio agrees with 9 : 7 than with 3 : 1), indicating interaction of complementary factors.

(g) *Chlorophyll deficienceis — (i) Albinism*:

Albino seedlings were met with in only a few of the X_2 and X_3 cultures. In a few families of X_3 yellow seedlings also occurred. The incidence of this character has already been reported in natural populations (Ayyangar and Harihara Ayyar, 1935; Ayyangar, 1934). Both single factor and duplicate factor segregations were met with. Apart from these albino seedlings sectorial chimera (Fig. 11) expressed as partially albinotic occurred. Cases of albino striping, partly green and partly white leaved, were also met with.

In one case a thin white line was noted just within the margin running the whole length of the leaf. Very rarely streaks of white appeared in the middle.

(ii) *Golden yellow plants.*—A few plants were met with which were golden yellow in colour. This colour was most prominent in the mechanical tissues especially round the veins so that the midrib, the internode, the peduncle, bristles and glumes showed the colour predominantly. Thirteen genotypically different types of golden plants have been reported in Maize (Eyster, *l.c.*). The plants are fertile. The behaviour of this character is being further studied.

(*h*) *Suppression of leaf-blade* (Fig. 12):

The normal cumbu plant has fairly large wavy leaves. Types were found in which the blade was reduced equally on either side of the midrib, while the midrib itself was normal. In one instance the blade was suppressed on only one side of the midrib while on the other side it was normal. On the suppressed side just a flange along the midrib was all that was left of the blade. It appeared as though the two blades had rolled themselves on each other.

In one plant the panicle was found completely modified into a tubular leafy growth (Fig. 13). In another plant at the base of the peduncles was a bunch of leafy growth arranged fan-like and from this arose as a branch a long peduncle at the end of which was a normal panicle (Fig. 14).

Apart from the few abnormalities noted above, mutations of economic value such as early maturity and differences in panicle shapes in ragi and length and thickness of panicles, size of grains and leaf size in cumbu were also noted.

Mutations affecting the chlorophyll characters are the most common and those of the panicles come next. Least affected are the growth forms and the vegetative characters. Male sterility occurred in a number of cases in the X_2 generations in ragi, while in cumbu it was rare.

Grain colour in ragi is determined by three factors (S, B_1 and B_2). SB_1B_2 is a purple plant with brown grain. A factor D deepens the effects of the brown factors (Ayyangar *et al.*, 1931). Under the present heavy dose of X-rays no mutations occurred for grain colour in any of the numerous progenies examined.

The panicle shapes in ragi, though also determined by three factors (Q, E_1 and E_2; Ayyangar *et al.*, 1932) easily mutated, giving incurved, fisty and open panicles, while the glume lengths (three factors—Gl_1, Gl_2 and

Gl_3; Ayyangar and Warier, 1936) gave in only a few cases longer glumes in the X_1, but reverted to the normal condition in the X_2 itself.

In *D. melanogaster* it has been found that "different genes have different mutation rates and consequently different degrees of stability as regards those factors which produce "spontaneous" mutations. The X-ray work with *drosophila*, *antirrhinum* and Maize shows that the frequency of induced changes is also different for different genes. Different allelomorphs of the same genes may also show different degrees of stability in X-ray experiments (Timoféeff-Ressovsky, 1934). Thus in ragi the brown factors and the glume-length factors appear to be more stable than either panicle shape or chlorophyll factors.

The number of recognisable mutants was greater in cumbu than in ragi. Cumbu threw out mutations in all directions. Ragi is a tetraploid species, while cumbu is diploid. Stadler (1929) from his experiments on *Avena*, and *Trictícum* obtained a high rate of mutations in the diploid species and to a lesser degree in the tetraploid, while he obtained no mutations at all in the hexaploid species. Timoféeff-Ressovsky (*l.c.*) concludes from Stadler's data "in polyploid species most of the genes are present in double (or triple) number so that most of the recessive mutations cannot manifest themselves even in homozygous conditions as they are covered by the normal allelomorphs present in the other homologous chromosomes........the doubling of the set of chromosomes can mask the detection of mutations." Further he mentions that mutations become difficult of observation due (i) "Karyotypic masking" due to doubling of chromosomes, (ii) "Genotypic masking" due to specific suppressors, and (iii) "Phenotypic masking". Stadler (1936) gives "the characteristic effects which may be expected in polyploid species as (1) a reduction in the apparent frequency of gene mutations, due to the presence of duplicate genes, (2) a reduction in the frequency of induced partial sterility due to the survival of deficient gametophytes, (3) the appearance of variations due to the phenotypic effects of the deficiencies and duplications which have been transmitted because of polyploidy, (4) the appearance of apparent recessive mutations, due to the loss of segments bearing a dominant gene which is present in only one set of chromosomes". It is possible that these causes have contributed to a fewer number of mutants being thrown out in ragi.

Summary

1. Some of the recessive abnormalities induced by X-rays in *E. coracana* Gaertn. and *Pennisetum typhoides* S. & H. are described.

2. In *E. coracana* are described a chlorophyll deficiency in which the first two or three leaves are green and white banded, but the mature plant is fully green and two mutations effecting the panicle. In *P. typhoides* have been noted gappiness, tip-sterility, forking and goose-necking in the panicle, male-sterility, and weak-midribbed leaves all behaving as recessives.

3. While some of the plant characters in both these millets mutated easily, others showed no tendency to mutate. Thus in *E. coracana* the panicle shapes and chlorophyll factors mutated while the grain colour, length of glume and growth factors did not give any mutations, while in *P. typhoides* the greatest number of mutations were observed in the chlorophyll and panicle characters.

4. *P. typhoides* threw out more mutations than *E. coracana* and this is adduced to the diploidy of the former and the tetraploidy of the latter.

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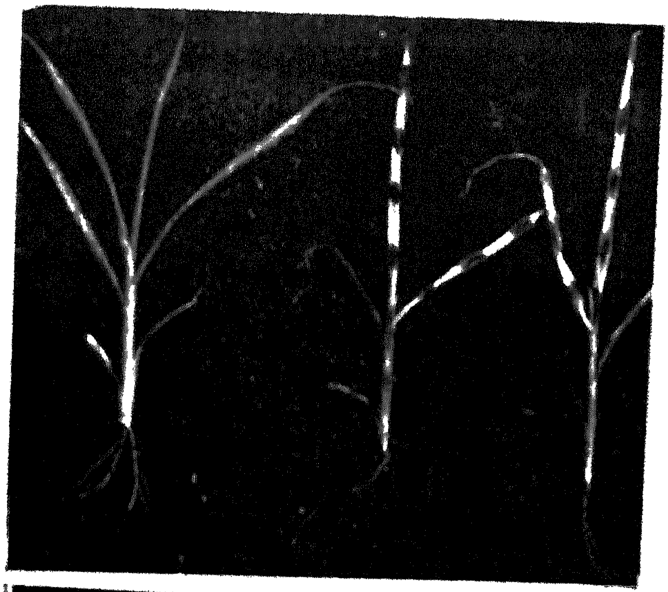


FIG. 1


FIG. 4


FIG. 2

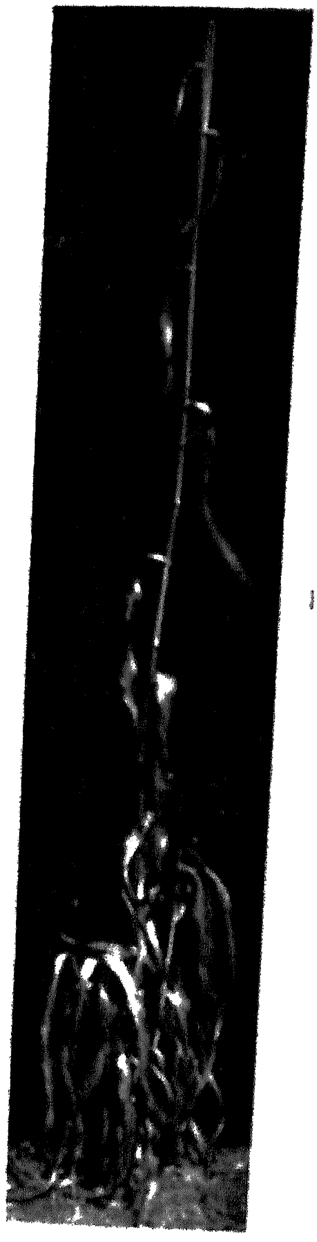


FIG. 5

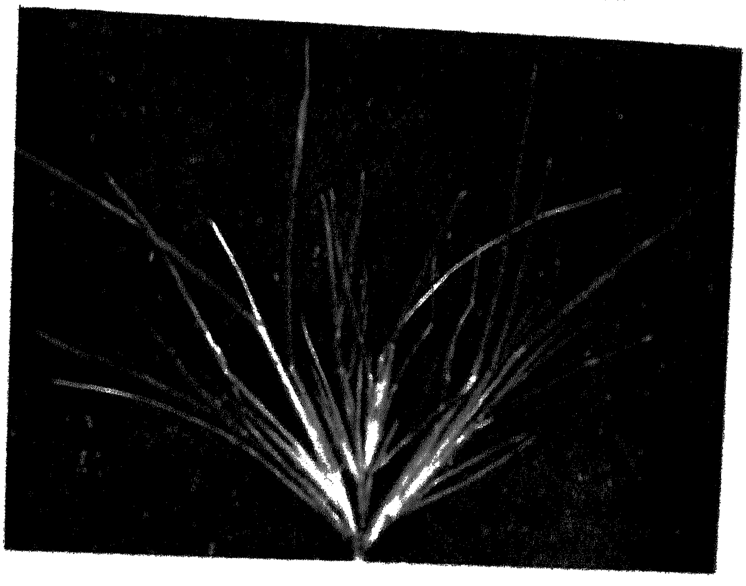


FIG. 3

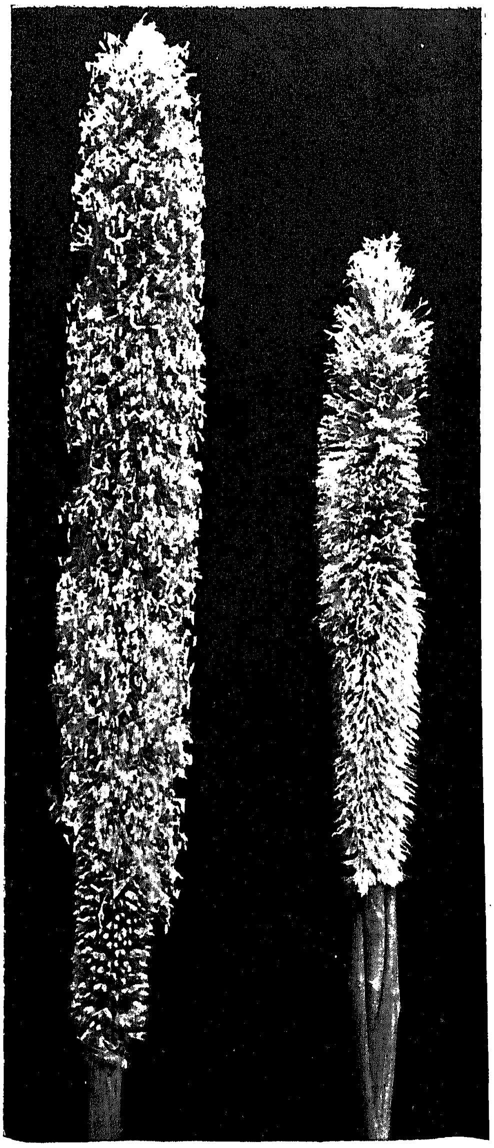


FIG. 6

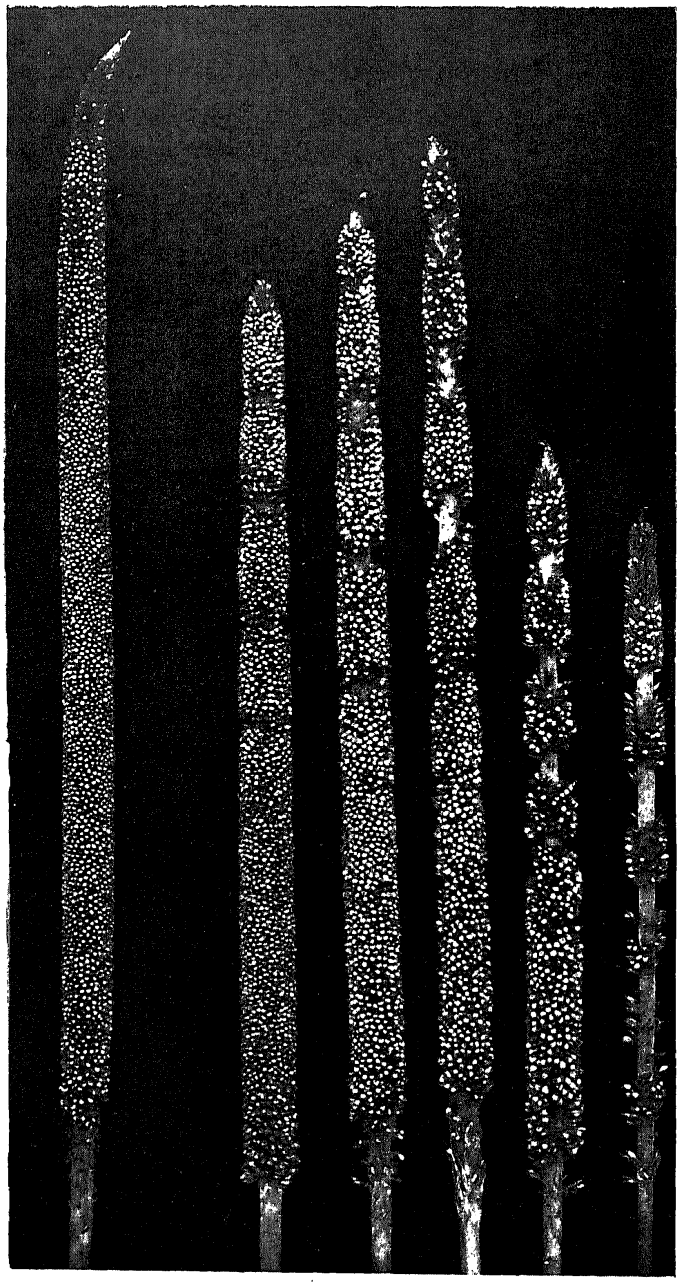


FIG. 7

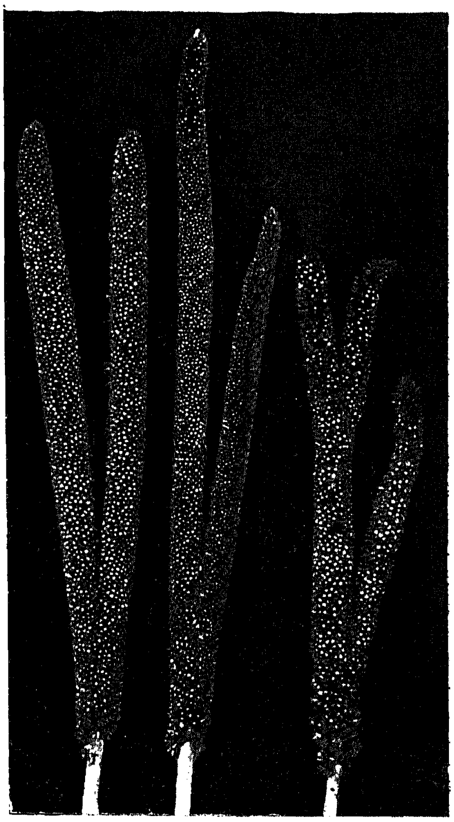


FIG. 8

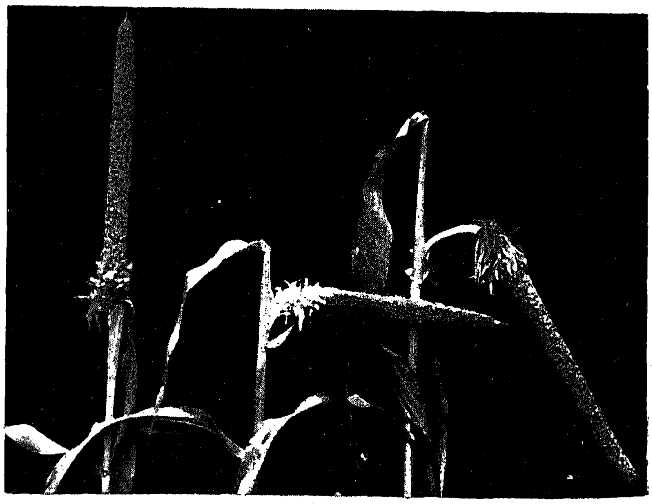
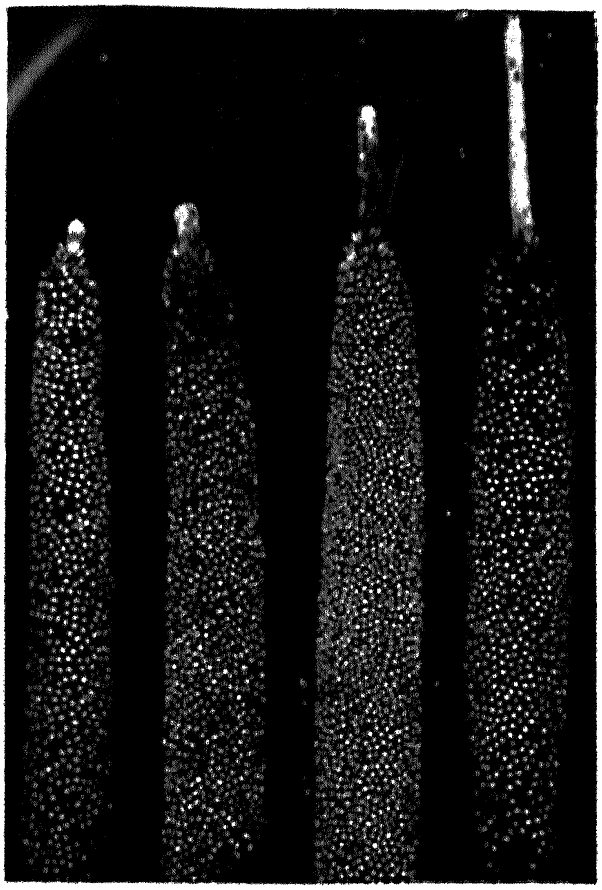


FIG. 9



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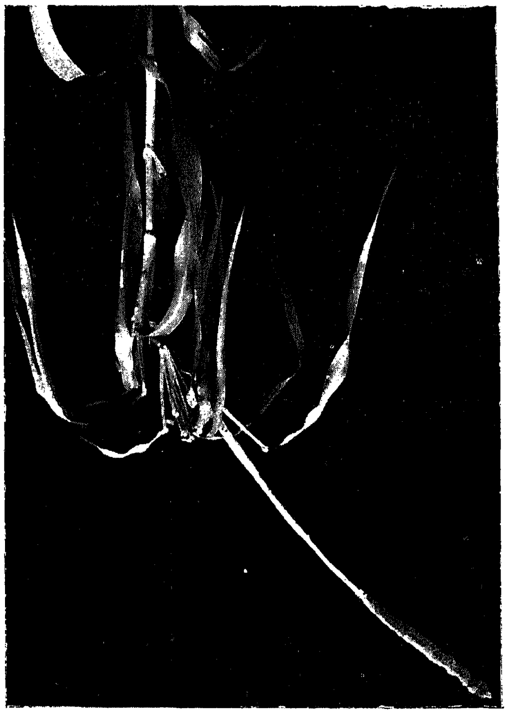

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EXPLANATION OF FIGURES

FIGS. 1-4. Ragi

Fig. 1. Green and banded seedlings. Fig. 2. Upper half of a plant with foliated panicles. Fig. 3. One of the branches separated out showing the modified glumes and lemmas and the roots at the base. Fig. 4. Truncated panicle.

FIGS. 5-14. Cumbu

Fig. 5. Weak-midribbed plant. Fig. 6. Normal (left) and sterile anthers (right). Fig. 7. Normal ear (left) and types of gappiness. Fig. 8. Forked panicles. Fig. 9. Normal and goose-necked panicles. Fig. 10. Types of tip-sterility. Fig. 11. Green and white striped plants. Fig. 12. Plant with leaf-blade suppressed. Fig. 13. Plant with panicle suppressed. Fig. 14. Partially foliated and partially normal panicle.