THREE CASES OF DEFICIENCY IN CHROMOSOME 9 OF ZEA MAYS

BY HARRIET B. CREIGHTON

BOTANY DEPARTMENT, CORNELL UNIVERSITY

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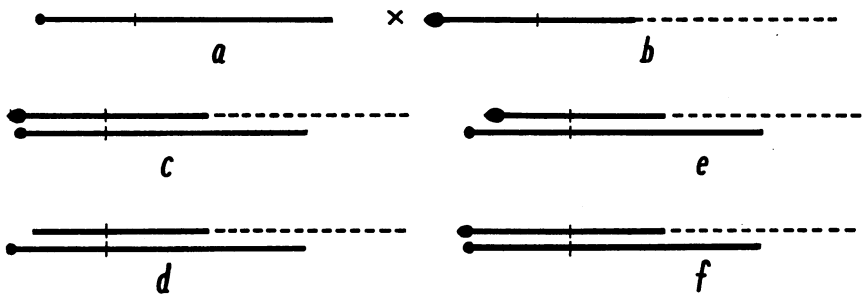
The purpose of the present investigation was to locate by means of x-ray induced deficiencies the regional position of the genes yg_2 (yellow-green), *C* (colored aleurone), *sh* (shrunken endosperm) and *wx* (waxy endosperm) in chromosome 9 of *Zea mays*. Cytogenetic evidence has already shown that all four of these genes are in the short arm of the chromosome, that yg_2 is nearest the end and that *wx* is nearest the spindle fibre insertion region.[1,2,3,4,5] In the present study only the position of yg_2 has been determined with any precision, but several points of interest with respect to deletions and deficiencies have arisen. It is with these and the three cases of Yg_2 deficiency in which they appeared that this report deals. One of the deficiencies is small and does not affect the functioning of either the male or the female gametes which possess it. Another shows that a truly terminal deletion can occur. All three give evidence of the position of yg_2.

A stock of maize was used which was homozygous for a large terminal knob on the end of the short arm of a modified chromosome 9 (text figure 1*b*).[1,6] The stock was also homozygous for the dominant allelomorphs of the genes Yg_2, *C*, *Sh* and *Wx*. Pollen from such plants was irradiated and applied to the silks of plants possessing allelomorphs of the above genes (yg_2, *c*, *sh* and *wx*) and a medium-sized knob on the end of the short arm of the normal or "standard" chromosome 9 (text figure 1*a*). The colored, non-shrunken, non-waxy kernels (*C c*, *Sh sh*, *Wx wx*) which were produced by this cross were grown and, as was expected, most of the individuals were normal green ($Yg_2\ yg_2$). A few were yellow-green, indicating a loss or an inactivation of the dominant allelomorph, Yg_2. These plants were examined cytologically.

Examinations were made of the mid-prophase (pachytene) of the first meiotic mitosis in the microsporocytes by the aceto-carmine method. In the normal F_1 plants the synapsis of the short arm of the standard chromosome 9 with that of the modified chromosome 9 brings the medium-sized terminal knob opposite the base of the large one. Since the large knob is approximately five times the size of the smaller one, it protrudes some distance beyond its homologue (text figure 1*c*). The heteromorphism of the knobs, however, in no way affects their close synapsis nor the synapsis of the terminal portion of the short arms.

Deficiency 9-1.—When the microsporocytes of *DF* 9-1 (*DF* for deficiency,

the plant or the chromosome as indicated by the context; 9 for chromosome 9; 1 for the first deficiency reported for that chromosome) were examined it was found that the distal part of the short arm of the modified chromosome 9 was lacking (text figure 1*d*). About one-quarter of its length was lost as determined by measurements of camera lucida drawings of several figures. Synapsis of the short arms from the spindle fibre insertion regions to the point of deletion was regular in most cases. Sometimes there was a lack of association of the last few chromomeres of the deficient chromosome with their homologues on the standard chromosome. Beyond the point of deletion the standard chromosome was frequently more or less folded back on itself. In order to make it as nearly certain as



TEXT FIGURE 1

a. Diagram of chromosome 9 of *Zea mays*, possessing a medium-sized knob on the end of the short arm. Spindle fibre insertion region indicated by cross bar.
b. Diagram of modified chromosome 9 with large knob on end of its short arm.
c. Diagram of normal F_1 from cross of the two chromosomes shown in (*a*) and (*b*).
d. Diagram of an exceptional F_1, Deficiency 9-1, showing loss of the terminal portion of modified chromosome 9.
e. Diagram of Deficiency 9-2 showing loss of an internal segment near the end of the short arm of modified chromosome 9.
f. Diagram of Deficiency 9-3 showing deletion of part of the large knob and a small part of the short arm of modified chromosome 9.

possible that the part deleted was a terminal and not an internal segment of the arm careful study was made of the end of the deficient chromosome for some evidence of knob material. If an internal deletion had occurred, it would be expected that the knob would be visible at the end of the deficient chromosome (see *DF* 9-2). Since this knob can be partitioned in x-ray treatment (*DF* 9-3) it might be represented by only a small chromomere-like part. As no knob was discerned, it is highly probable that the deletion was truly terminal. It might be pointed out that in previously reported deletions (*Drosophila*, *Zea*, etc.) the lack of any distinctive morphological appearance of the end of the chromosome has made it impossible to decide whether a terminal segment or an internal segment near the end had been deleted. In fact, there has been no critical evidence for the occur-

rence of terminal deletions. Studies of chromosome morphology at diakinesis or metaphase or the detection of the loss of the terminal genes of a linkage group cannot substitute for a knowledge of the changes in the minute morphology of the prophase chromosomes in such a question.

The plant designated as *DF* 9-1, although partly yellow-green, had some normally colored regions. This means that the deletion did not occur in the male nucleus nor the first embryonic division but happened at some later stage in the development of the embryo. Only the tissue which was derived from one of the daughters of the cell in which the deletion occurred showed the recessive character. The proportion of the plant body which was produced by this sector diminished as the plant grew. Half of the first and second leaves, a stripe on the third, fourth and fifth leaves, and no part of the succeeding leaves were yellow-green. Only one branch of the tassel gave any evidence of deficiency. Since all of it was used for cytological examination, no pollen was available for genetic study of the extent of the deficiency (that is, whether *C*, *Sh* or *Wx* were lost with *Yg*). No kernels developed to maturity, their failure probably being due to seasonal conditions.

Deficiency 9-2.—The plant designated as *DF* 9-2 was found to have an internal deletion in the short arm of the modified chromosome 9. About a third of the arm was lost but the large knob was still present (text figure 1*e*). Near the spindle fibre insertion region synapsis was regular, but in the more distal regions near the large knob asynapsis was frequent. Sometimes the medium-sized knob was associated with the large one, necessitating a bulging or folding back of the standard chromosome to accommodate for the difference in the lengths of the two chromosomes. From the configurations observed it is clear that the part deleted was near the end of the short arm close to the terminal knob.

It has been pointed out previously that a distinction between the deletion of the terminal region of a chromosome and a deletion of an internal segment near the end of a chromosome may not be possible from studies of synaptic behavior alone, but may require the presence of distinctive terminal morphological features.[7] In the cases described above the difference in the synaptic configurations might have been sufficient to make a decision possible, but in each case a relatively large segment was deleted. The presence of the knobs, however, facilitated the solution and made it more decisive. It seems clear that in many cases of small deletions (see *DF* 9-3) only terminal visible markers will render the distinction possible.

The plant called *DF* 9-2 was completely yellow-green and was nearly as vigorous as a homozygous recessive yellow-green plant. It shed no pollen, however, nor were any silks exserted. Again it was impossible to determine whether any of the marked genes were lost with Yg_2.

Deficiency 9-3.—The third case of Yg_2 deficiency was a plant fully as vigorous as a homozygous recessive yellow-green individual. Examination of the microsporocytes showed that a very small internal deletion had occurred (text figure 1*e*). The evidence for this is that the terminal knob on the modified chromosome 9 was slightly smaller than the normal large knob. The synapsis of the short arm of chromosome 9 with the modified 9 was complete and regular. The association of the ends of the chromosomes in diplotene was normal, showing none of the precocious opening out which is often evidence of lack of complete homology. At diakinesis the configurations were entirely normal. Thus, from observations alone it would seem that the deletion included only a part of the knob. However, it seems more probable that a small portion of the arm of the chromosome was deleted also. If only a part of the knob were lost, then the locus of yg_2 must be in the knob, unless simultaneous deletion and gene mutation or inactivation are assumed. That the locus is not in the knob is evident from the fact that crossing-over can occur between the knob[4] and the gene and from the fact that in *DF* 9-2 there was no apparent diminution of the size of the large knob concurrent with the loss of Yg_2. Hence, although it is possible that Yg_2 mutated to the recessive form coincident with the deletion it is also reasonable to infer that the deletion included some of the adjacent chromatin carrying the locus of Yg_2 with part of the knob. This, in agreement with other data, places the locus of the gene yg_2 very near to the end of the short arm of chromosome 9.

The majority of genetical and cytological studies of plants have shown that haploid gametes or gametophytes lacking any part of their chromosome set are not functional. Recently there have been found some exceptions in which deficient gametes were viable.[8,9]

The first indication that the case here described was an exception came when it was found that there were equal proportions of *Wx* and *wx* pollen grains (in one count, 385 *Wx*: 381 *wx*). In this plant the deficient chromosome carried *Wx*. It had been thought that only a few, if any, *Wx* grains would be found, these being the ones possessing a chromosome which resulted from a crossover between the locus of *Wx* and the deletion. Such grains would have no deficiency. The *Wx* grains were of the same size as the others and equally well filled with food material. That they were equally viable and functional in competition with the non-deficient grains was shown by the fact that backcrosses to the multiple recessive gave no deficiency in the number of colored, non-shrunken, non-waxy kernels. There were 9 *C Sh Wx*, 3 *C Sh wx*, 1 *C sh wx*, 1 *c Sh Wx*, 6 *c sh Wx* and 16 *c sh wx* kernels. The reciprocal cross of the deficient plant by the multiple recessive showed that the female gametophytes and gametes possessing the deficient chromosome function to produce normal-sized, well-developed kernels. Here there were 47 *C Sh Wx*, 12 *C Sh wx*, 3 *C sh wx*, 5 *c Sh Wx*,

19 *c sh Wx* and 34 *c sh wx* kernels. Crossing-over between the loci of *C*, *Sh* and *Wx* occurred with a frequency equal to that found in normal material. When some of the colored, non-shrunken, non-waxy (*C c*, *Sh sh*, *Wx wx*) and colorless, shrunken, waxy (*c c*, *sh sh*, *wx wx*) kernels were grown, it was found that crossing-over had occurred in the region between the locus of *C* and the deficiency. All of the plants were yellow-green whether they possessed the gene yg_2 in the simplex (heterozygous for deficiency) or in the duplex condition (homozygous for the recessive). Counts of the pollen from the middle part of single anthers of plants heterozygous for the deficiency showed that there was no more abortion of pollen grains than is normal for maize. In one case 92 out of 1694 (5.4 per cent) were undeveloped. Pollen from one of the plants heterozygous for the deficiency and for the genes *C*, *Sh* and *Wx* was used in crosses to the multiple recessive stock the results agreeing with those obtained in the previous backcross (171 *C* : 165 *c*). It was possible to self-pollinate only one individual heterozygous for the deficiency. Unfortunately, it was homozygous for recessive *c*, *sh* and *wx*. This makes necessary a cytological examination of the plants from the kernels obtained for the presence of the diminished knob in the homozygous condition before it can be known whether a homozygous deficiency is viable.

[1] Burnham, C. R., *Proc. Nat. Acad. Sci.*, **16**, 269–277 (1930).
[2] McClintock, B., *Ibid.*, **17**, 485–491 (1931).
[3] Creighton, H. B., and McClintock, B., *Ibid.*, **17**, 491–497 (1931).
[4] Creighton, H. B., unpublished.
[5] Burnham, C. R., unpublished.
[6] McClintock, B., *Proc. Nat. Acad. Sci.*, **16**, 791–796 (1930).
[7] Idem, *Zeitschr. Zellforsch. Mikr. Anat.*, **19**, 192–237 (1933).
[8] Burnham, C. R., *Proc. Nat. Acad. Sci.*, **18**, 434–440 (1932).
[9] Stadler, L. J., *Mo. Expt. Sta. Res. Bull.*, 204 (1933).

NOTES ON INTENSITIES IN THE SPECTRUM O II

BY K. G. EMELEUS

DEPARTMENT OF PHYSICS, UNIVERSITY OF MICHIGAN

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Note on Intensities in the Spectrum O II.—When a discharge is studied in detail, anomalies are often encountered in the intensities of the spectra emitted which require for their elucidation rather full information about the electrical state of the emitting tube, but can in general be then referred to known atomic or molecular properties. In some cases, however, when the discharge parameters are adequately understood, known atomic properties are found insufficient to account for what is observed, and an