NOTE ON THE ORIGIN OF TRIPLOIDY IN MAIZE[1]

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Triploid individuals arise sporadically in diploid populations of maize. It has been assumed that these triploids came from the fertilization of a diploid or unreduced egg with a haploid sperm because in other plants this has apparently been the usual manner of origin. Recently, however, triploidy in maize has occurred in another way. It would seem pertinent, therefore, to consider the different ways by which triploids have arisen.

Contribution of the diploid number of chromosomes by the female parent

A failure of the chromosomes to disjoin normally in the anaphase of the first meiotic division may result in the formation of a restitution nucleus containing the unreduced number of chromosomes. Beadle (1930) found triploid individuals in the cross of asynaptic maize by haploid pollen. The diploid eggs arose through non-disjunction of the entire chromosomal complement brought about by the lack of pairing of the homologous chromosomes. Diploid eggs in normal strains of maize have arisen, presumably, through some disturbance in the meiotic processes, but no critical proof of this has been reported.

Non-disjunction of the haploid chromosome set in any of the three somatic mitoses of the female gametophyte could give rise to an egg possessing the unreduced number of chromosomes. One case of this kind has been reported in maize (Rhoades, 1933).

Contribution of the diploid number of chromosomes by the male parent

The male parent could, theoretically, contribute the diploid number of chromosomes. The origin of triploidy in this manner, however, has not been previously reported.

In the summer of 1934 a triploid individual appeared in the writer's

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cultures in the progeny of a cross between two diploid genetic stocks. The female parent was homozygous for the gene glossy 1 ($\mathbf{gl_1}$), while the male parent was homozygous for the white sheath 3 ($\mathbf{ws_3}$) gene. Both of these factors are recessive. Glossy 1 is located in chromosome 7 and white sheath 3 in chromosome 2. Fortunately, this triploid plant was involved in several crosses with $\mathbf{gl_1}$ and $\mathbf{ws_3}$ plants, so a test of its genetic constitution was possible. In the cross of the triploid as the female parent by a male homozygous for $\mathbf{gl_1}$ there were 89 non-glossy to 20 glossy plants in the F_1 progeny. This ratio is extremely close to that expected from the progeny of a trisomic individual carrying two dominant and one recessive allelomorphs and indicates that the constitution of the triploid, as far as the $\mathbf{gl_1}$ locus was concerned, was $\mathbf{Gl_1Gl_1gl_1}$. In the crosses with the triploid used as the pollen parent on silks of plants homozygous for the $\mathbf{ws_3}$ gene the ensuing F_1 progeny consisted of 42 non-white sheath to 90 white sheath plants. These data suggest that the constitution of the triploid was the $\mathbf{Ws_3ws_3ws_3}$, since a 1 : 2 ratio is obtained from trisomic plants with one dominant and two recessive allelomorphs when used as pollen parents in a back-cross. As the triploid had only one recessive $\mathbf{gl_1}$ gene and two $\mathbf{ws_3}$ genes the conclusion that the diploid number of chromosomes was contributed by the male plant seems logical.

Contribution of the diploid number of chromosomes by the male parent could have been accomplished in one of three ways. The triploid individual could have arisen from the union of a haploid egg with a sperm from a diploid male gametophyte. The recent work of Randolph (1935) on reciprocal matings of diploid and tetraploid maize shows that diploid pollen usually is incompatible with diploid silks, although a viable embryo occasionally results. Sprague (1932) interpreted certain genetic data on hetero-fertilization as indicating that the egg and two polar nuclei of a single embryo-sac were fertilized by sperm from different male gametophytes. Sprague's assumption that more than one pollen tube could penetrate the embryo-sac was confirmed by the unpublished cytological observations of Virginia H. Rhoades who found that 11 per cent. of the embryo-sacs examined contained more than one pollen tube. In view of these facts there is the possibility that the triploid individual could have arisen from the simultaneous fusion of two haploid sperm nuclei with a haploid egg. There also is the possibility of non-disjunction of the haploid chromosome set of the generative nucleus during the formation of the male gametophyte. This would give a male gametophyte with a single diploid sperm nucleus and a haploid vegetative nucleus.

The compatibility of this type of male gametophyte on diploid silks is unknown. On this supposition the endosperm would need to be fertilized by a sperm from an additional pollen grain. The writer is inclined to believe the second explanation to be the more likely. Irrespective of the exact mechanism, however, the available data indicate that the diploid number of chromosomes was contributed by the male parent.

SUMMARY

Triploid individuals in maize occur through the fertilization of diploid or unreduced eggs by haploid sperm. The diploid eggs have arisen by complete non-disjunction of the entire chromosome set during meiosis or through non-disjunction during one of the three mitotic divisions of the female gametophyte. In either of these eventualities, however, the female gamete carried the diploid number of chromosomes.

Triploidy in maize is here shown to have arisen when the diploid number of chromosomes was contributed by the male parent.

REFERENCES

BEADLE, G. W. (1930). "Genetical and cytological studies of Mendelian asynapsis in *Zea mays*." *Mem. Cornell agric. Exp. Sta.* No. 129.

RANDOLPH, L. F. (1935). "Cytogenetics of tetraploid maize." *J. agric. Res.* **50**, 591–605.

RHOADES, M. M. (1933). "An experimental and theoretical study of chromatid crossing-over." *Genetics*, **18**, 535–55.

SPRAGUE, G. F. (1932). "The nature and extent of hetero-fertilization in maize." *Ibid.* **17**, 358–68.