It is evident that $R^F$ extracted from $R^{\text{rest}}$ heterozygotes regularly is paramutagenic, though weakly so when compared with $R^{\text{rest}}$. -- Douglas Brown

7. A test for genetic influence of endosperm on embryo.

Confirmation of Pissarev and Venogradova’s claim in which wheat plants of modified characteristics were produced by grafting mature wheat embryos onto rye endosperms has been reported by Muntzing. The alteration was expressed in this case by increased crossability of the “graft hybrid” to rye and was attributed to an incorporation into the embryo of substances from the endosperm upon germination. In a similar experiment with maize, Carangal (M.G.C.N.L.:32) observed no increase in the receptiveness of a dent sterile pop to dent pollen through such embryo-endosperm transplantation. He did note, however, a marked decrease in viability and seedling growth in the heterologous transplant -- pop embryo into dent endosperm -- over the corresponding homologous transplant -- pop embryo into pop endosperm. The question of whether or not there is any permanent heritable change resulting from the association of the embryo with genetically dissimilar endosperm was the subject of these experiments.

The method of attaining embryo-endosperm dissimilarity for these trials differs from those used previously. The crosses were designed such that these in which the egg and polar nuclei were fertilized by unlike sperm, i.e. heterofertilized, could be readily detected. In this manner the genetically deviant zygote and fusion nucleus of the endosperm can be juxtaposed at fertilization. Thus exchange of genetic material between the two tissues could occur either in the development of the caryopsis or during germination.

The first of two experiments involved recognition and subsequent study of plants arising from heterofertilized kernels produced by mating $r_{F}r_{F}$ females with $R^{\text{rest}}$ male parents. The colorless seeds from this mating were germinated and the seedlings were exposed to light. Those which failed to pigment were selected as the presumed heterofertilized class. The tassels of the resulting plants were examined for red sectors in order to ascertain whether or not the endosperm containing $R^F$ had evoked any change in the $r_{F}r_{F}$ embryo. The possibility that these green plants resulted from $r_{F}$ pollen contamination was excluded by verifying the presence of $R^F$ in the backcross of the mature plants to $r_{F}r_{F}$. Nine heterofertilized plants ($R^{\text{rest}}r_{F}$ embryo; $r_{F}r_{F}$ endosperm) were positively identified in this manner and all failed to show red tassel sectors.

In the second investigation mixed pollen from $R^{\text{rest}}F$ and $R^{\text{rest}}r_{F}$ plants was placed on $r_{F}r_{F}$ silks. The $r_{F}$ kernels from this mating were germinated, and the heterofertilized class identified by red seedlings ($R^{\text{rest}}$ conditions green seedlings and anthers). Seven such plants were testcrossed on $r_{F}r_{F}$ females. The $R^F$ expression in this case was indistinguishable from that resulting from similar testcrosses of plants grown from non-heterofertilized kernels ($R^{\text{rest}}r_{F}$ embryo; $r_{F}r_{F}$ endosperm). Furthermore the darkly motled kernels obtained in the above two sets of testcrosses are in sharp contrast to the near colorless, paramutant form of $R^F$ derived from $R^{\text{rest}}$.

These results support the view of autonomous development of the embryo irrespective of the endosperm genotype. There was no evidence for diffusion of substances bearing genetic potentialities from the endosperm to the embryo. Due to the infrequent occurrence of heterofertilization, the numbers of individuals observed in these studies were small. The need for obtaining a larger population is particularly important if one assumes that incorporation of any single genetic factor from the endosperm (e.g. the red anther component of $r_{F}$) occurs rarely if ever.
An expedient method for regular production of kernels with embryos and endosperms that are not concordant for a specified chromosome region is available in maize, but has not as yet been utilized. This procedure employs the use of A-B interchanges. It is well substantiated that in the case of such translocations the B segment undergoes non-disjunction at the second microspore division producing non-identical sperm nuclei. One nucleus is hyperploid, the other deficient for the arm of the A chromosome which is attached to the segment of the B possessing the centromere. The fertilization of the egg and polar nuclei by the unlike sperm nuclei would result in the requisite dissimilarity of embryo and endosperm.

-- Jerry Kermicle


In the initial report of a genetic analysis of red-light variegated twin mutations occurring in medium variegated pericarp, Brink and Nilan (Genetics 1952) demonstrated that the light variegated co-twin differs from medium variegated, not in the PyV allele present, but in the possession of Modulator (Mp) at a locus separate from P. The Modulator found in the light variegated sector was believed to be the one transposed from the P locus and lost from the red sector. The postulated absence of Mp from the red sector was not tested however, since a test, independent of a transposed Modulator (tr-Mp) effect on variegation, was not then available. In 1956 Brink (M.G.N.L.), using a "C - Ds" tester stock, reported the results of a test for Mp in the red sectors of eighteen twin mutations. He found, contrary to the Brink-Nilan hypothesis in its original form, that eleven red co-twins contained a tr-Mp somewhere in the genome while seven were lacking tr-Mp.

To date 70 clear cut twin mutations have been tested for the presence of Modulator in the red component using a "C - Ds" tester. Modulator has been found in 52 (74 percent) of the cases. It is thus clear that twin mutations fall into two distinct classes with respect to the presence or absence of tr-Mp in the red component, and that the class containing tr-Mp is decidedly more frequent.

In an attempt to explain twin mutations which contain tr-Mp in the red sector it is postulated that twin mutations result from a single transposition of Mp during the time of chromosome replication. Pft and its conjoined Mp replications at the P locus, producing two PftMp complexes, prior to replication of certain other portions of the chromosome. An Mp from one of the daughter PftMp complexes transposes to such an unreplicated site, and then replicates in phase with the chromosome in that region. The resulting daughter nuclei would then be of two genotypes: 1) Pft + tr-Mp, conditioning red pericarp, and 2) PftMp + tr-Mp, which gives rise to the light variegated phenotype. From this interpretation it is expected that tr-Mp would be situated at the same locus in the red and light variegated co-twins.

A three point backcross linkage analysis was employed to test the linkage relations of tr-Mp in the red and light sectors of a series of twin spots. The markers used were tr-Mp, P, and the breakage point of a reciprocal translocation. The reciprocal translocations utilized marked points both proximal (T1-2b, T1-5b) and distal (T1-7g) to P. A "C - Ds" tester stock was utilized to disclose the presence of tr-Mp in the non-variegated offspring resulting from the backcross mating.

Percent recombination between P and tr-Mp found in each of the co-twins of thirteen independent twin mutations is presented in Table 1. It is seen that the numerical values for the red and light variegated sectors of all but one twin (number 5) correspond well. Statistical analysis of the data (X² test of heterogeneity) indicates no greater variability for the values obtained for the linkage of P and tr-Mp than for the interval between P and the breakage point of the reciprocal translocations. The difference in values of P - tr-Mp found in each of the two sectors of twin number 5 is highly