3. The relation between light variegated and medium variegated pericarp.

We presented data last year (News Letter 25, March 17, 1951) demonstrating that the difference between two distinct variegated pericarp phenotypes, light and medium, is attributable to a genetic element which assorts with both the VV (variegated) and WR (red cob white) gametes formed by VV/WR heterozygotes and, hence, is separate from the P locus at which the VV and WR genes reside. A tentative hypothesis was set up to account for the breeding evidence then available. A second locus was postulated which was termed Modulator, as descriptive of the regulatory effect exercised on the variegated phenotype by the Modulator alleles. *Mp_1* (Modulator-1), in conjunction with *VV* at the *P* locus, was assumed to condition light variegated pericarp. Substitution of Mp_2 for Mp_1 resulted in the medium variegated phenotype. It was suggested that Mp_1 and Mp_2 mutate to each other with relatively high frequency. The irregular ratios of light and medium variegated plants in certain families led to the further suggestion that still other Modulator alleles might occur, some of which were stable and others unstable.

Two additional bodies of data bearing on these relations are now available. The first was obtained by continuing into the second backcross generation the mating plan, described in last year's News Letter, whereby the *VV* gametes from *VV/WR* heterozygotes were evaluated with reference to the differential between light variegated and medium variegated. The second set of facts concerns the genotypes of the kernels in twin spots (adjacent light variegated and self colored areas on otherwise medium variegated ears).

Thirty families were grown in 1951 in the second backcross generation from medium variegated parent ears in the four respective series involving inbred lines 8, 22, 23 (red cob colorless pericarp) and 4Co63 (white cob colorless pericarp). These families gave the same kinds of distributions of light variegated, medium variegated, and self colored plants as had been observed in the corresponding first generation backcross families (News Letter 25), That is to say, most of the offspring were medium variegated, a few were light variegated, and a slightly higher proportion were self colored. Family 62-12, for example, contained 91.7% medium variegated, 3.7% light variegated, and 5.6% self colored ears. The proportions in the other families were of the same general order, although the data are clearly not homogeneous, even with a given backcross series.

The second generation backcross families from light variegated seed ears likewise corresponded to the first generation families from ears of this class.

According to the Modulator hypothesis, as formulated in last year's report, light variegated ears should have appeared in only one-half of the second generation backcross families from medium variegated ears, the assumption being that the remaining families would be homozygous for the stable Modulator allele derived from the inbred line used as the recurrent parent. Since all 30 second generation families grown from medium variegated seed ears contained both light and medium variegated individuals, the Modulator hypothesis, in its original form, is invalidated.

The fairly extensive first and second generation backcross data now available show that light variegated arises regularly from medium variegated with frequencies comparable to those with which the *VV* gene mutates to self color. The similarity in frequency with which the two genetically separable effects occur suggests that they are correlated phenomena, and may result from a single mutational event. The evidence from twin spots gives direct support to this view.

The proportion of self colored mutant areas, including five kernels or more, which were twinned with light variegated was determined on 1413 medium variegated second generation backcross *VV/WR* or *VV/WW* ears. One hundred five such self colored areas were found, of which 66% were twinned with light variegated.

An additional generation is needed to complete the progeny tests on the kernels in five pairs of twins which are being analyzed in detail. First generation data are now available, however, on the inheritance transmitted through the *VV* and *RR* (self color) gametes from these twins. The numbers of plants are small, but the results are in accord with the view that the light variegated component of a twin is genetically the same as light variegated occurring on the numerous entire ears of this class which have been tested in these stocks. The self colored kernels from twin spots, likewise, appear to carry the well known self colored (*RR*) allele at the *P* locus. The *WR* or *WW* segregates from the twin spot phenotypes remain to be assayed for their composition with reference to the differential between light and medium variegated.

The evidence, as far as it goes, suggests that variegated pericarp rests upon a genetic basis such that, when variegated mutates to the stable self colored condition, a differential may be established simultaneously elsewhere in the genome which, in the presence of the *VV* gene, distinguishes between the light variegated and medium variegated phenotypes. Further evidence, which cannot be summarized conveniently for this report, indicates that the differential in question may take different positions in the chromosome complement. The differential assorts as though it is linked with *P* in some plants and independent of this locus in other individuals.

The following revised hypothesis is consistent with the present evidence and provides a basis for further tests.

1. It is assumed that the unstable variegated (*VV*) allele is a modified form of the stable *RR* (self color) gene, the difference between them being that VV embodies a unitary element termed Modulator (*Mp*) which inhibits pigment formation. Mutation of *VV* to *RR* consists in the loss of *Mp* from the *P* locus.

2. Following removal from the P locus, Mp may become attached at one or another site elsewhere in the chromosome complement. Modulator thus situated, plus *VV*, gives the light variegated phenotype. *VV,* without Mp elsewhere in the genome, conditions the medium variegated phenotype.

3. The relatively few light variegated and self colored offspring of medium variegated plants are interpreted as newly arisen mutations many of which involve concurrent changes at the *P* locus and at a point elsewhere in the genome. The distribution of light and medium variegateds and self colored ears in families from light variegated parents is conditioned by such mutations and also the segregation of Modulator as a unit separate from the *P* locus.

4. The varying proportions of light and medium variegated offspring of light variegated plants are interpretable in terms of linkage or independence of Modulator relative to the P locus.

It is clear from the experimental evidence that Modulator cannot be interpreted in conventional genetic terms either in respect to origin or mechanism of transmission. Nor can a firmly supported explanation now be given on any other basis. The largely speculative hypothesis outlined above brings into relief the main features of the data and thus serves to indicate the directions in which the analysis may be continued.

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