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## Shorter Articles and Reports: The Simultaneous Modification of Distinct Mendelian Factors

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## SHORTER ARTICLES AND REPORTS

### THE SIMULTANEOUS MODIFICATION OF DISTINCT MENDELIAN FACTORS

IN another paper<sup>1</sup> on the inheritance of a recurring somatic variation in variegated ears of maize, it was shown that the amount of red color developed in the pericarp of variegated seeds bears a definite relation to the development of color in the progeny of such seeds. The relation is such that the more color there is in the pericarp of the seeds planted the more likely are they to produce plants with wholly self-red ears and correspondingly the less likely to produce plants with variegated ears. Self-red ears thus produced behave just as if they were hybrids between self-red and variegated races or self-red and white races, the behavior in any given case depending upon whether the parent variegated ears were homozygous or heterozygous for variegated pericarp and whether they were self-pollinated or crossed with white.

To interpret these facts I have suggested that perhaps (1) a Mendelian factor for variegation,  $V$ , is changed to a self-color factor,  $S$ , in a somatic cell, (2) that all pericarp cells directly descended from this modified cell develop red color, and (3) that of the gametes arising from modified cells one half carry the  $S$  factor and one half the  $V$  factor.<sup>2</sup> Whether it ever happens that more than one half of such gametes carry  $S$  is unknown, but it is certain that a considerable part of them carry  $V$ . This is shown by the fact that self-red seeds from a variegated ear that has been cross-pollinated by white-eared maize produce a considerable percentage of variegated-eared plants. Evidently in such cases the duplex condition of the factors is changed to the simplex condition by the change of one  $V$  factor to an  $S$  factor, so that the zygotic formula  $VV$  becomes  $VS$ .

Now it often happens that a considerable patch of self-red grains occurs on an otherwise variegated ear. The cob immediately beneath such a patch is sometimes variegated, just like

<sup>1</sup> Not yet in print.

<sup>2</sup> This hypothesis was noted in my discussion of the possible origin of mutations in somatic cells. *AMERICAN NATURALIST*, 47: 375-377, 1913.

that beneath the variegated grains of the same ear, and sometimes self-red, the red cob spot corresponding exactly with the patch of red grains. Yet the wholly red ears arising from such self-red seeds invariably have wholly red cobs without respect to whether the parent seeds were from a red or variegated cob spot. It seems possible that in some cases the change from  $V$  to  $S$  occurs earlier in the life of the plant than in other cases. In some plants the change may, it seems possible, occur soon after the cob is laid down, in which case all the cells of the glumes as well as of the pericarp over a considerable area will be red. In other plants it appears that the change from  $V$  to  $S$  occurs independently in the rudiments of several grains, but not until after the glumes associated with them have been laid down. But in either case, it must be remembered, the red ears produced from such red seeds always have wholly red cobs as well as wholly red grains and cob and pericarp colors are coupled in all later generations. Evidently, whatever is responsible for the change from variegation to self-color always affects both cob and pericarp colors.

This would occasion no surprise if it were known that red cob color and red pericarp color are due to identical factors. But I have presented, in another place,<sup>3</sup> evidence that cob and pericarp colors are dependent upon distinct genetic factors which are either coupled or allelomorphous in inheritance. Even if it should be shown that the red color of the cob is due to identically the same pigment as the red color of the pericarp, it must nevertheless be assumed that there are distinct genetic factors that influence the distribution of this pigment. The factor  $S_c$  that has to do with the determination of self-pattern of cob color can hardly be the same as the factor  $S_p$  that has to do with the same pattern in the pericarp, for, if it were the same, a cross of a strain having variegated cob and variegated pericarp with a strain having self-red cob and colorless pericarp should produce progeny self-red in both cob and pericarp, whereas such a cross actually produces ears with self-red cobs and variegated pericarp. We are practically driven, therefore, to the conclusion that there must be distinct factors for self-color of the cob and self-color of the pericarp,  $S_c$  and  $S_p$ , respectively. It seems reasonable then to suppose that the same is true of the variegation pattern and that there are both  $V_c$  and  $V_p$  for variegated cob and variegated pericarp, respectively.

<sup>3</sup> Ann. Rpt. Nebr. Agr. Expt. Sta., 24: 59-90, 1911.

If this is true, we are confronted with the problem of explaining the apparently universal occurrence of self-red cobs in connection with self-red ears arising in  $F_1$  from variegated-eared parents. Why, in short, should  $V_c$  and  $V_p$ , if they are really distinct, always change together to  $S_c$  and  $S_p$ , whenever either one changes? This seems the more unaccountable when considered in connection with the fact that the change often, or perhaps always, affects only one of the two like (duplex) factors of a homozygous somatic cell, so that  $V_c V_p \cdot V_c V_p$  becomes  $S_c S_p \cdot V_c V_p$ .

In my former paper (*loc. cit.*) I accounted for perfect coupling of cob and pericarp factors in certain crosses by the assumption that the two factors were located in the same chromosome, and explained perfect allelomorphism of the same factors in other crosses by the assumption that the two factors were located in homologous chromosomes. This was on the further assumption that homologous chromosomes separate at the reduction division exactly at the plane of their union in synapsis. If in place of this last assumption, however, we accept Morgan's<sup>4</sup> suggestion, based upon cytological evidence presented by Janssens, that homologous chromosomes may become spirally twisted together in synapsis and that the plane of separation may not always coincide exactly with the plane of union, we must also accept his further suggestion that the linear position of factors within a chromosome has much to do with the degree of coupling and allelomorphism, "linkage." To me Morgan's hypothesis seems the most reasonable interpretation of the facts of partial coupling and "repulsion," and it also affords a satisfactory explanation of perfect coupling and allelomorphism.

In accordance with Morgan's hypothesis, we must suppose, not only that the factors  $V_c$  and  $V_p$  are located in the same chromosome as I had done before, but in addition that they are situated very close together in this chromosome, since their linkage seems to be perfect. Similarly we must suppose, not only that  $V_p$  and  $S_p$  are in homologous chromosomes, as I had previously done, but that they are in almost exactly homologous positions in these chromosomes, since their allelomorphism appears to be perfect. This second supposition follows of course as a corollary of the first one if  $S$  is produced through a modification of  $V$ .

Now we might suppose further that the two factors,  $V_p$  and

<sup>4</sup> *Science*, N. S., 34: 384, 1911.

$V_c$  are located side by side in the same chromosomes not only at the time of the reduction division but also in all nuclear divisions and even perhaps that they remain in fairly close proximity in the more diffused chromatin of the resting nucleus. Then if homologous chromosomes or their chromatin masses are not closely associated in somatic cells, it would seem possible that whatever causes the change of a  $V_p$  factor into an  $S_p$  factor might at the same time affect the  $V_c$  factor of the same chromosome changing it into an  $S_c$  factor, while the  $V_p$  and  $V_c$  factors of the homologous chromosome remain unchanged.

It is of course recognized that a rather formidable number of hypotheses, with subsidiary assumptions, have been marshalled here to account for what may be very simple phenomena, but, if they do not do too great violence to the known facts of cytology, we are justifiable in accepting them tentatively as an attempt at a consistent interpretation of what otherwise seem inconsistent genetic facts.

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