LINKAGE WITH CROSSING-OVER BETWEEN RUBRICALYX BUDS AND OLD-GOLD FLOWER COLOR IN OENOTHERA[1]

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I had but recently published my paper[2] on the independence of old-gold flower color from characters produced by factors included in the first linkage group (including the factor for *rubricalyx* buds, R^h), when one of my cultures (25244) showed a close association between old-gold flower color and *rubricalyx* buds. For a moment I thought I had at last found a case of linkage between two hitherto independent linkage groups, which I assumed ought to be expected frequently if the physical basis of linkage were the cohesion of non-homologous chromosomes to form circles, as supposed by Cleland, Håkansson, Gates, Sheffield and others. When I looked into this case of seeming contradiction of the assumed independence of *rubricalyx* bud color and old-gold flower color, however, I found at once that the difficulty resolved itself into another instance of the mistaken conclusions we sometimes draw or imply when we express hereditary relationships in terms of phenotypic characters instead of genetic factors. It seems to me worthwhile, therefore, to describe this case here in order to help emphasize again the fact which has been so often stressed by leading genetical investigators for the past two decades, but which is often inadequately taken into account by the tyro, that characters are not the resultant of single genetic factors but the combined result of numerous genetic factors, and that when we speak of the gene "for" a given character we are using figurative language, as also when we adopt as a symbol for a given gene the initial letter of a correlative phenotypic characteristic.

The particular cross which gives occasion for this paper was made in 1924 when a plant of my pure strain of *Oe.* seg. *aurata* with green hypanthia and gold-center flowers was pollenated with pollen from an *Oe. rubricalyx nanella* with old-gold flowers.

The F_1 family (24188), grown in 1925, consisted of the expected uniform group of 178 tall *rubricalyx* with old-gold flowers. One of these F_1 plants was backcrossed to pure tall *aurata* and gave rise in 1926 to a family (25244) consisting of 78 old-gold *rubricalyx*, 4 old-gold with green hypanthia, 4 *aurata rubricalyx* and 65 *aurata* with green hypanthia. This strikingly typical cross-over ratio attracted immediate attention and steps were taken to test a number of the individuals by selfing and backcrossing to the double-recessive type. The results are assembled in table 1 and are consistent in support of the occurrence of strong but partial linkage between an old-gold factor and a *rubricalyx* factor. From the backcrosses between the heterozygotes and the double recessive the totals show 525 *rubricalyx* old-gold; 25 green-hypanthium old-gold; 18 *rubricalyx aurata* (gold-center); 346 green-hypanthium *aurata*, representing a cross-over ratio of 4.7 per cent.

A consideration of these results can leave no doubt of the validity of the conclusion that *rubricalyx* bud color and old-gold flower color show, in this material, linkage with crossing-over. What then is the explanation of the apparent discrepancy between these results and the previously reported evidence for the independent inheritance of these two characters? The key is to be found in the fact that old-gold flower color is not a simple, monogenic character, but a *compound* produced by the interaction of two factors, a dominant factor, S, the normal allele of the *sulfurea* factor, s, and a recessive factor, v, which has been called the *vetaurea* or old-gold factor. Since two factor pairs are concerned in the production of old-gold flower color, it is clear that there must be two types of crosses which

TABLE 1

PEDIGREE NUMBER	TYPE OF CROSS*	PLANTS SECURED *rubricalyx* OLD-GOLD	GREEN-HYPANTHIUM OLD-GOLD	*rubricalyx aurata*	GREEN-HYPANTHIUM *aurata*
26271	$A^R \times$ self	—	—	—	92
26279	$A^c \times$ self	—	—	45	19
26287	$A^c \times$ self	—	—	19	4
26272	$V^R \times$ self	—	29	—	—
26274	$V^c \times$ self	71	2	—	3
26280	$A^c \times A^R$	—	—	35	43
26288	$A^c \times A^R$	—	—	57	61
26273	$V^R \times A^R$	—	11	—	10
25244	$V^c \times A^R$	78	4	4	65
26275	$V^c \times A^R$	38	2	3	18
26276	$V^c \times A^R$	43	3	5	45
26277	$V^c \times A^R$	69	1	2	37
26278	$V^c \times A^R$	70	—	—	39
26285	$V^c \times A^R$	85	1	—	48
26286	$V^c \times A^R$	86	10	1	46
26289	$V^c \times A^R$	56	4	3	48
Totals of last eight		525	25	18	346

*A^R = *aurata* with green hypanthia.
A^c = *aurata rubricalyx.*
V^R = old-gold with green hypanthia.
V^c = old-gold *rubricalyx.*

can give rise to old-gold segregates: In the first of these, $SSVv \times$ self or the corresponding backcross $SSVv \times SSvv$, the old-gold flower-color plays the rôle of a recessive to the dominant wild-type yellow, while in the second type of cross $Ssvv \times$ self or $Ssvv \times ssvv$, the old-gold plays the rôle of dominant to the recessive gold-center. It will be noted that in the former type of cross it is the segregations of the Vv factors which determine the flower colors in the resulting progenies, while in the second type of cross it is the *Ss* factors whose segregations determine the flower colors of the families produced. The *Ss* factors are in linkage group I in which the *rubricalyx* factor is also included, while the *Vv* factors are in linkage-group III. It is clear, therefore, that independence between old-gold and *rubricalyx* can be observed whenever the *Vv* factors alone are segregating and the *SS* factors remain constant; whereas, a close linkage may be observed between old-gold and *rubricalyx*, or other first-chromosome factors, when it is the *Ss* pair that is segregating and the *vv* factors remain constant.

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[2] Shull, G. H., "'Old-Gold' Flower Color, the Second Case of Independent Inheritance in Oenothera," *Genetics*, **11**, 201–234 (1926).

A NEW PROOF OF THE LEFSCHETZ FORMULA ON INVARIANT POINTS

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1. The sum of the indices of the fixed points of a given transformation, which, since Brouwer's[1] first proofs of fixed point theorems, was the subject of many special investigations, has been completely determined for arbitrary transformations of arbitrary manifolds by Lefschetz.[2] His theory includes the fixed point formula as a special case of more general theorems on coincidences and multiply valued transformations, and he also makes the remark that it is possible to apply the same methods to certain transformations of an arbitrary complex.[3]

In the following there will be sketched a new proof of the fixed point formula. This proof holds for all complexes, under the assumption that the transformation is one-valued; the question whether it holds also for multiply-valued transformations will not be treated here. A paper with all details will be published in the *Mathematische Zeitschrift*.

2. *The Lefschetz formula.*—Let f be a one-valued continuous transformation of an n-complex C^n into itself and $\gamma_1^i, \gamma_2^i, \ldots, \gamma^i_{p^i}$ a fundamental set of i-cycles on C^n. Then there exists a system of homologies