

NOTES ON THE D-CHROMOSOME OF THE SWEET PEA

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(With Two Text-figures)

LINKAGE DATA

SOME data involving four pairs of characters in the D-chromosome of the sweet pea were given in an earlier number of this *Journal* (Punnett, 1932). In all cases the percentage of cross-overs was so high, ranging between 35 and 50 %, that it was not possible on the evidence collected to assign definite loci to the four genes concerned. At that time, however, a fifth factor had been discovered which was also located in this chromosome. This was the so-called "flake modifier" of which an account has already been given (Punnett, 1936). During the past few years experiments have been in progress relating this factor to the four earlier ones, and we are now in a position to provide a reasonably consistent map of this chromosome for further study. The five pairs of characters concerned are:

- D₁-d₁ ... Tendril-acacia leaves
- D₂-d₂ ... Bright-dull flower colour
- D₃-d₃ ... Presence and absence of flake modifier
- D₄-d₄ ... Hairy-glabrous (=smooth)
- D₅-d₅ ... Full-picotee flower pattern.

TABLE I

| | Coupling series | | | | Cross-over value | Repulsion series | | | | Cross-over value |
|-------------------------------|-----------------|-----|-----|-----|------------------|------------------|------|------|-----|------------------|
| | XY | Xy | xY | xy | | XY | Xy | xY | xy | |
| D ₁ D ₂ | 634 | 192 | 163 | 101 | 0.460 | 2263 | 809 | 882 | 124 | 0.370 |
| D ₁ D ₃ | 286 | 11 | 19 | 79 | 0.073 | 324 | 162 | 182 | — | — |
| D ₁ D ₄ | 3217 | 790 | 784 | 544 | 0.360 | 692 | 278 | 300 | 58 | 0.398 |
| D ₁ D ₅ | — | — | — | — | — | 3112 | 1126 | 1114 | 277 | 0.417 |
| D ₂ D ₃ | 992 | 273 | 265 | 124 | 0.425 | 296 | 97 | 88 | 20 | 0.448 |
| D ₂ D ₄ | 1580 | 482 | 421 | 148 | 0.480 | 1844 | 592 | 603 | 171 | 0.482 |
| D ₂ D ₅ | 1438 | 443 | 424 | 162 | 0.469 | 1337 | 465 | 415 | 128 | 0.483 |
| D ₃ D ₄ | 200 | 52 | 44 | 35 | 0.350 | — | — | — | — | — |
| D ₃ D ₅ | 373 | 112 | 103 | 42 | 0.457 | — | — | — | — | — |
| D ₄ D ₅ | 1076 | 298 | 283 | 188 | 0.381 | 2537 | 1003 | 993 | 131 | 0.340 |

So far as possible F_2 families of both the coupling and repulsion types have been raised for each combination of these five genes. The condensed

results are given in Table I and may be left to speak for themselves. From them has been constructed the map of the chromosome shown in Fig. 1. The cross-over values in the table have been calculated by Immer's method (1930), and where these differ on the coupling and repulsion sides the approximate mean between the two values has been made use of in constructing the map. The cytological bearing of these data is discussed by Dr C. D. Darlington in an Appendix to these notes.

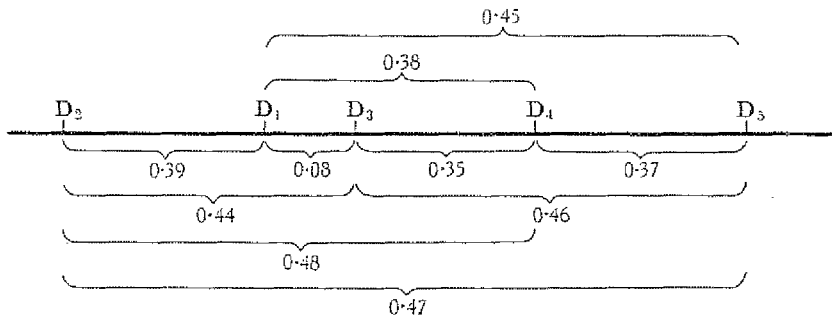


Fig. 1.

MUTABILITY IN FLAKES

In connexion with this work there are a few points which call for special notice. The first of these concerns the constancy of the flaked form. Recent work by Imai and Iinuma (1938) showed that the red flaked variety "America" throws off an appreciable proportion of self-coloured and dark-flaked individuals, viz. about 3.5% of the former and about 3% of the latter. Their analysis further indicates that in the allelomorphous series G_1 , G_1' , g_1 (viz. self, flaked, white) G_1' may mutate to G_1 ; also that d_3 may mutate to D_3 . The occurrence of such mutational changes obviously introduces a disturbing element into the numerical ratios upon which depend the values of linkage determinations. Nevertheless I do not consider that these results of Imai & Iinuma affect my own data; for a notable difference in the material with which the Japanese observers worked and my own was that theirs consisted of reds and my own entirely of purples. And as Beale (1939) and his co-workers have recently shown these two colour classes are characterized by different anthocyanins, i.e. the reds by cyanidin and the purples by delphinidin. Certainly I have grown great numbers of flaked purples without encountering a single indubitable mutation.¹ It is possible that

¹ I gave a few cases of selfs and dark flakes arising in families of normal flakes in an earlier paper (1932) and I still regard these as more probably due to roguing by *Megachile* than to mutation; for I have had many long rows of purple flakes showing no darker form.

there may be a connexion between the nature of the anthocyanin involved and the occurrence of mutability. It would be interesting to test the point in other species where both flaking and different kinds of pigment are found.

MUTATION AT THE G_1 LOCUS

In their paper of 1938 Imai & Iinuma suggest the addition of a further allelomorph to the series G_1 , G_1' , g_1 . This is expressed as a very pale form, practically a white tinged with pink at the periphery of the petal. It occurred very rarely in their experiments and bred true. The authors denote it as g_1' , regarding it as a member of the above series coming between G_1' and g_1 ; but since no genetical work was carried out with it the attribution so assigned must at present remain doubtful.

During the course of my own work, however, I have come across a form which must clearly be regarded as due to an additional allelomorph of the G_1 locus. The circumstances under which it appeared were as follows. In 1936 I found myself short of the blue-flaked acacia type which I needed for certain combinations. At my request Dr Brieger, then at Merton, kindly sent me a few seeds of this form. When sown in 1936 I noticed that some of them were decidedly lighter than what I had come to regard as the normal blue flake. Others, however, were near the normal type and one of these crossed with a self-coloured purple ($D_3D_3G_1'G_1'$) gave five F_1 plants of which one was a dark flake (as expected) and the other four were of the light flake type, though rather darker than normal. The dark flake gave the expected F_2 result in 1938, there being only regular selfs, dark flakes and light flakes in the expected proportions. One of the lighter flakes was also grown on to F_2 and gave a quite different result (cf. Table II). Self-coloured plants were fewer than would have been expected, while the flakes ranged from a very pale up to a very dark form.

In 1936 one of the palest flakes received from Dr Brieger was back-crossed extensively with plants of an F_1 purple dark flake tendril carrying blue and acacia, i.e. $D_1d_1D_2d_2D_3d_3$ in composition. In 1937 ninety-eight plants were raised from this series of crosses. They were all flakes ranging from a dark-flake type, rather lighter than the normal dark flake, down to very light flakes. In 1938 families were raised from three plants of the darker type, which in appearance were very like the lighter type of F_1 mentioned above. The results were very similar in all four families and are given in Table II. The plants were graded into six different

classes, though the distinction between the darks and very darks on the one hand, and between the dark-lights and the lights was not always easy.

To explain these results I assume the existence of another allelomorph of the G_1 locus, viz. G_1'' , of which the action brings about less production of pigment than does G_1' , the gene for normal flaking. With D_3 , the flake modifier, G_1'' cannot give rise to the self-coloured form even though the plant be homozygous for D_3 . Also, plants of the constitution

TABLE II

| Flower grade | Ex F_1 Fam. 28 | Ex back-cross | | | Total | Expectation |
|--------------|---------------------|---------------|---------|---------|-------|-------------|
| | | Fam. 32 | Fam. 35 | Fam. 36 | | |
| Self | 10 | 10 | 7 | 4 | 31 | 20.7 |
| Very dark | 18 | 9 | 8 | 7 | 42 | 41.4 |
| Dark | 11 | 16 | 12 | 4 | 43 | 62.1 |
| Dark-light | 20 | 23 | 17 | 13 | 73 | 52.8 |
| Light | 27 | 48 | 31 | 12 | 118 | 103.5 |
| Very light | 6 | 10 | 5 | 3 | 24 | 20.7 |

$D_3D_3G_1'G_1''$ are very dark flake instead of being self-coloured. The plant of the constitution $D_3d_3G_1'G_1''$ must be regarded as a "dark-light" similar to the F_1 parent of Fam. 28 and the back-cross parents of Fams. 32, 35 and 36. On this hypothesis such "dark-lights" should produce the four types of gamete D_3G_1' , D_3G_1'' , d_3G_1' , d_3G_1'' and give rise to families with six different grades ranging from self to very light flakes, and in the proportions shown in Fig. 2. Having regard to the fact

| | | | |
|-------------------------------------|------------------------------------|------------------------------------|------------------------------------|
| D_3G_1' D_3G_1' Self | D_3G_1' D_3G_1'' V. dark | D_3G_1' d_3G_1' Dark | D_3G_1' d_3G_1'' Dk.-lt. |
| D_3G_1'' D_3G_1'' V. dark | D_3G_1'' D_3G_1'' Dark | D_3G_1'' d_3G_1' Dk.-lt. | D_3G_1'' d_3G_1'' Lt. |
| d_3G_1' D_3G_1' Dark | d_3G_1' D_3G_1'' Dk.-lt. | d_3G_1' d_3G_1' Lt. | d_3G_1' d_3G_1'' Lt. |
| d_3G_1'' D_3G_1' Dk.-lt. | d_3G_1'' D_3G_1'' Lt. | d_3G_1'' d_3G_1' Lt. | d_3G_1'' d_3G_1'' V. lt. |

Fig. 2.

that some of the classes tend to run together, and are not easy to classify when only very few flowers are available, the hypothesis accords reasonably well with the data, and may be taken as rendering highly probable the existence of a fourth member in the allelomorph series at the locus of G_1 .

DEFICIENCY OF RECESSIVES

In a brief discussion of this question in 1932 I suggested that the general deficiency of recessives was more likely to be due to some inherent weakness than to specific semi-lethals. The following piece of evidence bears upon this point. In 1933 I had three large families from sister plants carrying smooth (d_4) and also white (g_1) as recessives, and from them were obtained in all 887 plants. From considerations of space they were sown rather closer than usual and germination was good. Due probably to their crowded condition they started to bloom rather late, and by 3 July barely one-quarter were in flower. The whites were pulled up and recorded as soon as they showed a flower, the remainder being left until 15 July by which time about one-half of the plants had flowered. Since the majority of those which had not flowered seemed unlikely to do so, most being very small and stunted, the rows were pulled and recorded. Those which had not flowered were determined without difficulty in respect of the hairy-glabrous pair (D_4-d_4). The distribution of hairy and glabrous plants in the flowered and unflowered plants respectively is shown in Table III.

TABLE III

| Fam. | Earlier | | Later | | Total | |
|-------|----------|--------|----------|--------|----------|--------|
| | Hairy | Smooth | Hairy | Smooth | Hairy | Smooth |
| 21 | 81 | 25 | 52 | 20 | 133 | 45 |
| 22 | 96 | 22 | 74 | 41 | 170 | 63 |
| 23 | 185 | 48 | 175 | 68 | 360 | 116 |
| | 362 | 95 | 301 | 129 | 663 | 224 |
| Ratio | 3.81 : 1 | | 2.33 : 1 | | 2.96 : 1 | |

There is an evident deficiency of recessive smooths among the earlier plants which flowered, but this is compensated for by a redundancy among the later ones which failed to do so, so that the ratio for the total number of plants is almost exactly the expected 3 : 1. Evidently the smooths germinate as well as the hairy but are rather slower in growth and consequently more affected by crowded conditions.

I have mentioned that the white-flowered plants were pulled up and recorded as soon as they came into flower. Table IV shows the distribution of hairy and smooth on the whites up to the date of record in each case.

TABLE IV

| | 3 July | 5 July | 7 July | 15 July |
|--------|--------|--------|--------|---------|
| Hairy | 31 | 55 | 76 | 109 |
| Smooth | 2 | 8 | 18 | 26 |

It will be noticed that the earliest flowered plants are almost all hairy, and that the proportion of smooths that come into flower gradually rises, until by 15 July it is not far short of the expected proportion of recessives.

SUMMARY

Linkage data are recorded for five pairs of characters in the D-chromosome of the sweet pea, and a provisional map of this chromosome is given.

Evidence is given for a fourth allelomorph in the series $G_1 \dots G_1' \dots g_1$.

Data are given for the hairy-glabrous pair (D_4-d_4) which bear upon the question of the deficiency of recessives so often noticeable in the sweet pea.

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*Appendix*CHIASMATA AND CROSSING-OVER IN THE
D-CHROMOSOME OF THE SWEET PEA

BY C. D. DARLINGTON

THE present data show that the greatest mapped length in the chromosomes of the sweet pea covers an uncorrected crossing-over distance of 119 units. Corrected for double crossing-over, this distance would be increased by 20 or 30%, according to the strength of interference. It thus approaches the greatest length previously mapped in a plant, that in the first chromosome of *Zea Mays* (128 units) where I have predicted (1934) a total length of 185 units from observed chiasma-frequencies.

It is therefore worth knowing how the breeding results compare with chiasma-frequencies in *Lathyrus*. On my theory of crossing-over, every chiasma results from a single act of crossing-over and every act of crossing-over gives rise to a single chiasma. The one is therefore individually or statistically predictable from the other. A mean chiasma-frequency of x for a given bivalent implies that this bivalent has a corrected or absolute total linkage map length of $50x$ crossing-over units.

In using this calculation to predict the limits of a linkage map we have to remember that the constancy of crossing-over for any given bivalent is subject to three conditions: (i) constant or indifferent genotypic control of chiasma frequency in the stocks used; (ii) constant or indifferent environmental conditions such as age and temperature; (iii) constant structural conditions in the particular chromosome, whether structurally homozygous or not. This last proviso is more important than might be expected. Chiasma-frequencies can usually be obtained on structurally homozygous material. Crossing-over frequencies cannot be obtained on such material where a position effect is the operative difference. The first two conditions, however, are likely to be the important ones in the present case.

Bearing in mind these reservations we can compare the chiasma and linkage data in *Lathyrus*. Stone's observations on the chromosomes, reported by Upcott (1937) can be used for predicting separate values for each chromosome in the following way. Stone recorded the chiasma-frequencies of the seven bivalents together, since they are not constantly distinguishable at meiosis, but he recorded their different lengths at mitosis. We may therefore assume that the total chiasma-frequency per nucleus (16.67) is, as usual, distributed among the seven chromosomes in proportion to their several lengths, thus:

| Chromosomes | Mitotic length | Proportionate Xma frequency | Units of crossing-over |
|----------------|-----------------|-----------------------------|------------------------|
| I and II | $8\mu \times 2$ | 2.96×2 | 148 |
| III, IV, V, VI | $6\mu \times 4$ | 2.22×4 | 111 |
| VII | $5\mu \times 1$ | 1.85×1 | 93 |
| Totals | 45μ | 16.67 | 833 |

It will be seen that a wide range in the mean chiasma-frequency of the individual bivalents is required. The possibility of such a range may be estimated by comparing the observed variance (0.8) with the value of the mean for all the bivalents in the nucleus (2.38). Data that I have recently collected show that this proportion of one-third would be high for homogeneous bivalents with low means in a non-hybrid diploid (cf. Haldane, 1931). A range in means of the different bivalents, such as I am assuming, is therefore to be expected from the meiotic as well as from the mitotic observations.

In a word, the linkage data show a minimum uncorrected map length of 118 units in one chromosome of the sweet pea and the chiasma data show a maximum absolute map length of 148 units in its longest chromosome. I conclude that, unless conditions or genotypes used at Cambridge

favour higher crossing-over than at Merton, the *D*-chromosome linkage must cover nearly the whole length of one of the two longest chromosomes.

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