# A provisional map of the yellow chromosome of *Pharbitis Nil*

by

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With 1 Text-figure

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The yellow linkage group was established in 1928 (IMAI 1929). At that time this group was known as containing only two genes, yellow and dusky. Two years later, it developed in this way: "The yellow linkage group is composed of five genes, yellow (y), dusky (dy), light-1 (lt 1), deformed (de) and speckled-reduced (sp-r). The frequency of recombination for y and dy is 1·0 per cent, . . . . . Light-1 is linked rather closely with y and dy. Speckled-reduced is linked with y at about 28·5 per cent of recombination, and y with de at about 15 per cent of recombination" (IMAI 1931 b). The genes constituting the yellow linkage group are regarded as arranged in the yellow chromosome. Owing to the incomplete knowledge with regard to their linkage relations, the drawing of the chromosome map of this group was not attempted as yet; and in this paper is presented a provisional map of the chromosome. By a recent investigation, IMAI (1933) adds a new gene bushy (bs) to this linkage group. The description of the characters of the genes is referred to IMAI's publication (1930).

MIYAZAWA (1918) first pointed out the dependent segregation of yellow and dusky, and later the recombination frequency was calculated to be 1·0 per cent by IMAI (1925). The calculation was made from the $F_2$ and $F_3$ data obtained by crossing normal with yellow dusky, which will give a coupling segregation. In Table 1 are shown their available data obtained by the writers recently, including those given by IMAI (1925).

Table 1. $F_2$ of cross, normal × yellow dusky

| Cross | + | y | dy | y dy | Total |
|---|---|---|---|---|---|
| IMAI's data | 2873 | 20 | 18 | 867 | 3778 |
| L25 × YK | 193 | 0 | 1 | 61 | 255 |
| T32W × YK | 166 | 3 | 4 | 66 | 239 |
| 410 × YKS | 131 | 1 | 1 | 27 | 160 |
| YK × RF | 711 | 5 | 4 | 241 | 961 |
| YK × 455 | 234 | 2 | 1 | 76 | 313 |
| YK × 9T | 304 | 2 | 2 | 94 | 402 |
| Total | 4612 | 33 | 31 | 1432 | 6108 |

From the available coupling data the recombination frequency is calculated to be 1·1 per cent. Conducting backcross experiments, the writers, however, obtained a more reliable figure. Table 2 contains those data recorded last summer.

Table 2. Backcross, (normal × yellow dusky) × yellow dusky

| Backcross | + | y | dy | y dy | Total |
|---|---|---|---|---|---|
| (410 × YK) × YK | 54 | 0 | 0 | 51 | 105 |
| YK × (L25 × YK) | 275 | 4 | 4 | 223 | 506 |
| (L25 × YK) × YK | 47 | 1 | 0 | 74 | 122 |
| Total | 376 | 5 | 4 | 348 | 733 |

The data represent the gametic distribution of the linked assortment, and the estimation of recombination frequency can be made directly from the observed numbers. Thus the recombination percentage for y and dy is determined to be 1·3, which is the most reliable figure at present. The data segregating yellow and light-1 were given by IMAI (1931 a). In Table 3, they are listed including new data.

Table 3. $F_2$ of cross, yellow × ligth-1

| Cross | + | y | lt1 | y lt1 | Total |
|---|---|---|---|---|---|
| 421 × 430[1] | 93 | 45 | 31 | 1 | 170 |
| 422 × 435[2] | 94 | 45 | 34 | 0 | 173 |
| L25 × YK | 150 | 61 | 44 | 0 | 255 |
| Total | 337 | 151 | 109 | 1 | 598 |

[1] Segregation occured into $y^i$: y: $y^i$ lt1: y lt1, and [2] into + : $y^i$: lt1: $y^i$ lt1.

On account of the deficit of light-1 segregates, the calculation is made from the observed numbers of classes lt 1 : y lt 1, giving 9·6 per cent of recombination. Owing to repulsion, the recombination frequency obtained is not very reliable, only indicating a rough value. For the relation between dusky and light-1 we have the data indicated in Table 4.

Table 4. $F_2$ of cross, dusky × light-1

| Cross | + | dy | lt 1 | dy lt 1 | Total |
|---|---|---|---|---|---|
| L25 × YK | 149 | 62 | 44 | 0 | 255 |

The segregation is also of repulsion of rather high intensity, and contains no double recessives. With these facts, the three genes, yellow, dusky and light-1, are linked each other rather closely; so that they are considered as grouping their loci in the chromosome with rather a short distance.

The linked segregation for yellow and deformed was shown by the data, which were some of $F_2$ from the cross of yellow by normal heterozygous for deformed (Imai 1931a). Thirty-seven normal $F_2$ were selfed, and their progeny was examined, the summary of the observations being shown in Table 5.

Table 5. $F_3$ from $F_2$ having constitution, y +/+ de

| No. of families | + | y | de | y de | Total |
|---|---|---|---|---|---|
| 10 | 1076 | 298 | — | — | 1374 |
| 5 | 637 | — | 164 | — | 801 |
| 22 | 1840 | 739 | 656 | 30 | 3265 |

Owing to repulsion with about 15 per cent recombination, no homozygous families were observed in this examination. All families segregating for y and de were of repulsion and there were observed no coupling pedigrees. In Table 6 are collected available data for linkage of y and de.

Table 6. Available data of linkage for yellow and deformed

| Origin | + | y | de | y de | Total |
|---|---|---|---|---|---|
| Previous $F_2$ | 431 | 217 | 128 | 3 | 779 |
| New $F_2$ | 277 | 121 | 48 | 2 | 448 |
| $F_3$ | 1840 | 739 | 656 | 30 | 3265 |
| Total | 2548 | 1077 | 832 | 35 | 4492 |

As the result of the low viability of deformed, a great deficit of its segregates was observed. Calculating on the basis of the observed numbers of the classes de and y, the recombination frequency is 20·1 per cent. The relation of deformed to dusky is found by the data in Table 7.

Table 7. $F_2$ from $F_1$ having constitution, dy +/+ de

| Cross | + | dy | de | dy de | Total |
|---|---|---|---|---|---|
| T32 W × YK | 136 | 68 | 33 | 2 | 239 |

The recombination frequency for dy and de is 23·9 per cent[1]. The data from which this figure is obtained are rather small in number and we cannot attach much importance to it. However, if we compare it (23·9 %) with that (20·1 %) for y and de, the former is a little more than the latter. This shows, if reliable, the fact that the locus de is situated nearer to y than dy, the order of arrangement in the chromosome being de—y—dy. The difference 3·8 (= 23·9-20·1) may correspond to the recombination (1·3) of y and dy. The linkage between lt 1 and de is indicated by the data in Table 8.

Table 8. $F_2$ from $F_1$ having constitution, lt 1 +/+ de

| Cross | + | lt 1 | de | lt 1 de | Total |
|---|---|---|---|---|---|
| T30 × L25 | 147 | 47 | 14 | 1 | 209 |

The recombination frequency is 25·8 per cent. From this figure, if reliable, the order of the linear arrangement of the genes in the chromosome may be de—y—dy—lt 1.

Speckled-reduced is a modifier working on speckled. The recombination frequency of y and sp-r was 28·5 per cent. The data from which the calculation was made were 124 +: 51 y: 57 sp-r: 5 y sp-r, all having the gene speckled (Imai 1931a, Table 13). New data showing the same segregation are presented in Table 9.

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[1] Owing to the low viability of deformed, the calculation is made on the basis of the observed numbers of the two de classes, as previously made. The same method is appliced to those data given in Tables 8, 14 and 15. In Tables 14 and 15, the deficit, however, occurs in the willow segregates.

Table 9. $F_2$ of cross, yellow (speckled) × speckled-reduced (speckled)

| Cross | + | y | sp-r | y sp-r | Total |
|---|---|---|---|---|---|
| 410 × YKS | 87 | 24 | 45 | 4 | 160 |

On account of the simultaneous segregation of one or more modifiers affecting the quantity of spots on the corollas, nearly continuous gradations occurred in the speckled flowers. Those with the smallest quantity of spots have a close connection with speckled-reduced flowers having the largest quantity of spots. On this condition, the discrimination of speckled and speckled-reduced segregates is difficult at times. The data listed in Table 9 and also in the following tables were taken with such a handicap, which may result in unbalanced distribution of the segregates. Therefore, the recombination frequency is calculated on the basis of the observed numbers of the two sp-r classes, giving 28·6 per cent[1], which is practically the same with the figure formerly calculated. The same cross showed also the linked segregation of dy and sp-r, the data of which are indicated in Table 10.

Table 10. $F_2$ of cross, dusky (speckled) × speckled-reduced (speckled)

| Cross | + | dy | sp-r | dy sp-r | Total |
|---|---|---|---|---|---|
| 410 × YKS | 86 | 25 | 46 | 3 | 160 |

The recombination frequency is 24·8 per cent, presenting probably a proof for the relative loci of dy and y in the chromosome, or y—dy—lt 1—sp-r. Crosses were made between speckled speckled-reduced and normal heterozygous for deformed; and in some of $F_2$, a trihybrid segregation occurred. The first observation was made at the seedling stage, the results obtained being shown in Table 11.

Table 11. $F_2$ seedlings from $F_1$ having constitution, + sp sp-r / de + +

| Cross | + | sp | de | de sp | Total |
|---|---|---|---|---|---|
| T32a × 410 | 114 | 27 | 31 | 7 | 179 |
| T32b × 410 | 112 | 45 | 25 | 10 | 192 |
| T32c × 410 | 198 | 60 | 40 | 16 | 314 |
| Total | 424 | 132 | 96 | 33 | 685 |

[1] The same method is applied to the case of Table 10.

In these crosses, the majority of green-stemmed seedlings had no spots on their hypocotyls, only a few of them being speckled. This fact seems to have some connections with the occurrence of modifiers affecting the quantity of the speckles of the flower. Therefore we had no clue to distinguish sp and sp sp-r segregates at their seedling stage, and we were obliged to grow further the green-stemmed seedlings for this purpose. In summer a second observation was made on their flowers, the actual data being shown in Table 12.

Table 12. Later observation on green-stemmed seedlings from Table 11

| | sp | sp sp-r | de sp | de sp sp-r | Total |
|---|---|---|---|---|---|
| Observed | 94 | 36 | 8 | 4 | 142 |

Although the data are much incomplete for several reasons, they show roughly an independent relation between de and sp-r. The locus sp-r is considered to be situated on the other side of de in the chromosome, the order of arrangement being de—y—dy—lt 1—sp-r. In this arrangement, the relation of sp-r and de is expected to be nearly independent, as actually the case was.

Maple (m) was known to be independent of the genes of the known ten linkage groups, including y and dy of the yellow linkage group; therefore it was regarded as to constitute another linkage group (Imai 1931b). In a recent observation[1], however, m shows linkage with y, dy and other genes of the yellow linkage group, and maple is now determined to be gathered under this group. Hagiwara's data (1932) also include linkage of y and m. In Table 13 are collected the results indicating linkage between y and m.

Table 13. $F_2$ of cross, yellow × maple

| Cross | + | y | m | y m | Total |
|---|---|---|---|---|---|
| ML × H70 | 73 | 26 | 27 | 2 | 128 |
| ML × YK | 180 | 82 | 80 | 8 | 350 |
| D110 × W315 | 118 | 50 | 51 | 2 | 221 |
| Total | 371 | 158 | 158 | 12 | 699 |

[1] The former data were rather fragmental.

The frequency of recombination for y and m is 28·1 per cent. The maple locus includes another recessive variant willow ($m^w$). Willow, therefore, is expected also to be linked with y. Table 14 contains data showing this relation.

Table 14

$F_2$ from $F_1$ having constitution, y + /+ $m^w$

| Cross | + | y | $m^w$ | y $m^w$ | Total |
|---|---|---|---|---|---|
| T32 W × YK[1] | 134 | 65 | 36 | 4 | 239 |
| YK × LW | 257 | 82 | 65 | 6 | 410 |
| Total | 391 | 147 | 101 | 10 | 649 |

Notwithstanding the fact that the low viability of willow gave a deficit of its segregates, the data show linkage between y and $m^w$ with 30·0 per cent of recombination, as expected. Nearly the same percentage of recombination was observed between dy and $m^w$, as indicated by the data in Table 15.

Table 15

$F_2$ from $F_1$ having constitution, dy +/+ $m^w$

| Cross | + | dy | $m^w$ | dy $m^w$ | Total |
|---|---|---|---|---|---|
| T32 W × YK | 133 | 66 | 36 | 4 | 239 |

The recombination frequency is 31·6 per cent. For the relation of willow to deformed, the writers obtained nearly an independent segregation, as presented by the data in Table 16.

The low viability of the recessives, especially the double recessive, results in an unbalanced distribution of the data. The segregation being nearly independent, the location of maple may be on the other side of deformed in the chromosome. On the same arm of the chromosome speckled-reduced is also situated. The distance of sp-r to y is 28·5[2]

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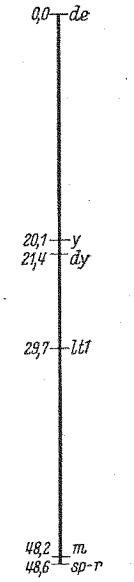
[1] The data were obtained by selfing $F_1$, having a constitution of y + / + $m^w$, which was given by crossing yellow with normal heterozygous for willow.

[2] This formerly calculated figure may be more reliable than the newly estimated one (28·6).

and that of m to the same is 28·1 [1], sp-r and m being expected to be arranged very closely in the chromosome.

Table 16. $F_2$ from $F_1$ having constitution de $m^w$ / + +

| Cross | + | de | $m^w$ | de $m^w$ | Total |
|---|---|---|---|---|---|
| T30a × 410 | 45 | 20 | 12 | 3 | 80 |
| T30 Wa × L25 | 65 | 17 | 17 | 3 | 102 |
| T30 Wa × YK | 53 | 28 | 16 | 2 | 99 |
| T30 Wb × L25 | 59 | 16 | 19 | 3 | 97 |
| T30 Wb × YK | 58 | 15 | 19 | 7 | 99 |
| T30 Wc × L25 | 28 | 11 | 6 | 2 | 47 |
| T30 Wd × L25 | 37 | 12 | 11 | 2 | 62 |
| T30 We × L25 | 39 | 12 | 8 | 2 | 61 |
| T32 W × YK | 164 | 35 | 40 | 0 | 239 |
| T32 Wa × 410 | 66 | 22 | 21 | 4 | 113 |
| T32 Wa × YK | 191 | 66 | 77 | 11 | 345 |
| T32 Wb × YK | 187 | 57 | 49 | 18 | 311 |
| Total | 992 | 311 | 295 | 57 | 1655 |



A provisional map of the yellow chromosome

## Conclusion

The linkage relations of the known six genes, deformed, yellow, dusky, light-1, speckled-reduced and maple, are as follows: The recombination percentage of de is **20·1** with y, 23·9 with dy, 25·8 with lt 1 and nearly independent of sp-r and m; y is linked with dy at **1·3** per cent of recombination, with lt 1 at **9·6**, with sp-r at **28·5** and with m at **28·1**; dy is linked with lt 1 rater closely, with sp-r at 24·8 and with m at 31·6. Adopting the figures written in gothic, a provisional map of the yellow chromosome may be drawn, as presented in the accompanying diagram, with the following loci: de (0), y (20·1), dy (21·4), lt 1 (29·7), m (48·2) and sp-r (48·6).

## Literature cited

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[1] This figure may be more reliable than 30·0.

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