

LINKAGE STUDIES IN PHARBITIS NIL. IV

by

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With 2 textfigures

In the last publication of this series of investigation, IMAI (1933) described 70 loci that were situated in 12 chromosomes of *Pharbitis Nil*, the haploid chromosome number of which however is 15. Recently the writers determined the loci of 3 genes, white-2b, dwarf, and Globose in certain chromosomes and gene side-reduced was found to be independent of duskish. HAGIWARA (1930) reported linkage of side-reduced and duskish; but, according to the writers' observations, the segregation is quite independent, so that side-reduced is excluded from the linkage group. White-2b constitutes a set of triple allelomorphs with normal and flecked of the contracted linkage group. In her recent crossing experiments, YASUI (1934) found that pollen-sterile (*ps*), a new gene resulting in sterility of the microspores, is closely linked with dusky. Therefore the number of loci apportioned in 12 chromosomes is 72 at present, the list of the loci being as follows:

1. Variegated L.G. ¹⁾ (8 loci) variegated (*v*), crumpled-1 (*cI*), Blown-1 (*BI*), fasciated-3 (*f3*), brown (*br*), faded (*fd*), couple (*cu*), male-sterile-1 (*msI*).
2. Cordate L. G. (9 loci) cordate (*co*), feathered (*fe*), Globose (*Gb*), semi-contracted (*sc*), precocious (*pc*), palmate (*pl*), crêpe (*cp*), Restricted (*Rt*), bobbed-1 (*bbI*).
3. Yellow L. G. (8 loci) deformed (*de*), yellow (*y*), dusky (*dy*),

¹⁾ „L. G.” is an abbreviation of „linkage group”.

- pollen-sterile (*ps*), light-1 (*ltI*), speckled-reduced (*sp-r*), maple (*m*), bushy (*bs*).
4. Acuminate L. G. (4 loci) acuminate (*ac*), Margined-2 (*Mr2*), magenta (*mg*), Blizzard-1 (*BzI*).
 5. Contracted L. G. (11 loci) Rayed (*Ry*), cream (*cr*), shrubby (*sh*), interaxil-green (*ig*), contracted (*ct*), Margined-1 (*MrI*), white-2b (*w2b*), tube-white-1 (*twI*), intense-1 (*iI*), Margined-reduced (*Mr-r*), lilliputian (*lp*).
 6. Speckled L. G. (5 loci) speckled (*sp*), white-1 (*wI*), Margined-fluctuated (*Mr-f*), Striated (*Sa*), tube-white-2 (*tw2*).
 7. Delicate L. C. (3 loci) . . . delicate (*dl*), crumpled-2 (*c2*), dwarf (*dw*).
 8. Pear L. G. (9 loci) pear (*p*), fasciated-1 (*fI*), fasciated-2 (*f2*), Blown-2 (*B2*), intense-2 (*i2*), chestnut (*cn*), striped-2 (*st2*), light-2 (*lt2*), Margined-3 (*Mr3*).
 9. Duplicated L. G. (6 loci) duplicated (*dp*), striped-1 (*stI*), Dilute (*D*), white-2a (*w2a*), dragonfly (*dg*), extended (*e*).
 10. Retracted L. G. (3 loci) retracted (*r*), foliate (*fo*), dragonfly-suppressed (*dg-s*).
 11. Dusky L. G. (4 loci) dusky (*dk*), Blizzard-2 (*Bz2*), criss-crossed (*cs*), purple (*pr*).
 12. Polymorphic L. G. (2 loci) polymorphic (*py*), bobbed-2 (*bb2*).

In the following pages, the writers attempt to present linkage data for three genes that determined their loci, together with some related results. No detailed account of linkage studies of this plant will be given here (cf. IMAI 1933).

THE LOCUS OF DWARF

Dwarf (*dw*), which is one of the oldest mutants, is transmitted as a simple recessive to normal. This form is found to be linked with delicate (*dl*) of the delicate linkage group, as will be seen from table I.

TABLE I. F_2 FROM THE CROSS OF DELICATE WITH DWARF

Cross	Normal	Delicate	Dwarf	Delicate dwarf	Total
SM \times KD	50	25	26	0	101

On selfing 15 normal F_2 , the writers raised F_3 as shown in table II.

TABLE II. F_3 SHOWING LINKAGE BETWEEN DELICATE AND DWARF

Num. of pedigrees	Normal	Delicate	Dwarf	Delicate dwarf	Total
2	115	35	—	—	150
2	198	—	60	—	258
10	878	320	318	23	1539
1	153	26	29	24	232

Of these pedigrees, 2 segregated into normal and delicate, and another 2 into normal and dwarf, in both cases monogenically, while the remainder, except 1 which was in coupling segregation, showed digenic repulsion. The recombination frequency is 31.6 per cent from the repulsion data and 30.3 per cent from the coupling, the latter figure being more reliable.

THE LOCUS OF WHITE-2B

White-2b (*w2b*) is one of the genes that manifest white flowers. In table III are presented data showing linkage between white-2b and contracted.

TABLE III. F_2 FROM THE CROSS OF WHITE-2B WITH CONTRACTED

Cross	Normal	White-2b	Contracted	White-2b contracted	Total
G202 × KD2	56	38	28	0	122

The segregation was repulsion, giving no double recessives. On selfing 11 normal F_2 , the writers obtained the data of table IV.

TABLE IV. F_3 SHOWING LINKAGE BETWEEN WHITE-2B AND CONTRACTED

Num. of pedigrees	Normal	White-2b	Contracted	White-2b contracted	Total
11	547	249	244	0	1040

All the pedigrees so far tested were segregated in repulsion scheme, and since they gave no double recessives, the recombination fre-

quency for white-2b and contracted cannot be calculated at present. Gene white-2b is allelomorphic to normal and flecked, and the repulsion data for flecked and contracted also gave no double recessives. However, flecked is linked with Margined-1 of the contracted linkage group in 1.2 per cent of recombination (IMAI 1931).

THE COMPLEXITY OF GLOBOSE

Globose (*Gb*) is a leaf form that is less commonly found in our gardens. The leaves are roundish and their lobes not much conspicuous (Fig. 1). The flowers (Fig. 2) are larger compared with the normal, frequently having more than five rays.

Globose acts as an incomplete dominant in inheritance. The F_1 hybrids

obtained by crossing Globose with normal bore leaves intermediate in form (hetero-formed) and large flowers. In F_2 the segregation occurred as shown in table V.

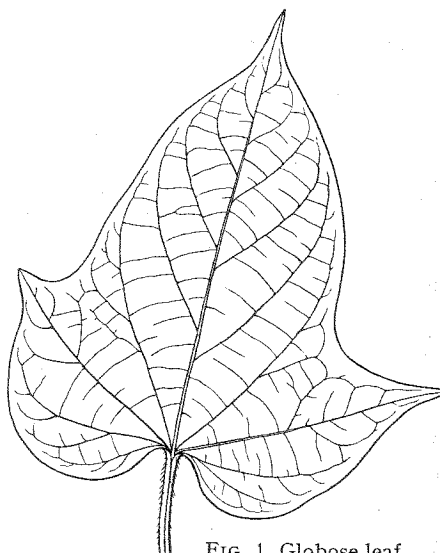


FIG. 1. Globose leaf.

TABLE V. F_2 FROM THE CROSS OF GLOBOSE WITH NORMAL

Cross	Normal	Hetero-formed	Globose	No-lobe Globose	Total
ID × 1906	84	164	78	20	346
1906 × L	4	10	4	1	19
1906 × G	38	56	26	4	124
1906 × 1919	40	93	31	9	173
Total	166	323	139	34	662
Expected	165.5	331.0	134.5	31.0	662
(Ratio)	(16)	(32)	(13)	(3)	(64)

$$\chi^2 = 0.636 \quad P_b = 0.729$$

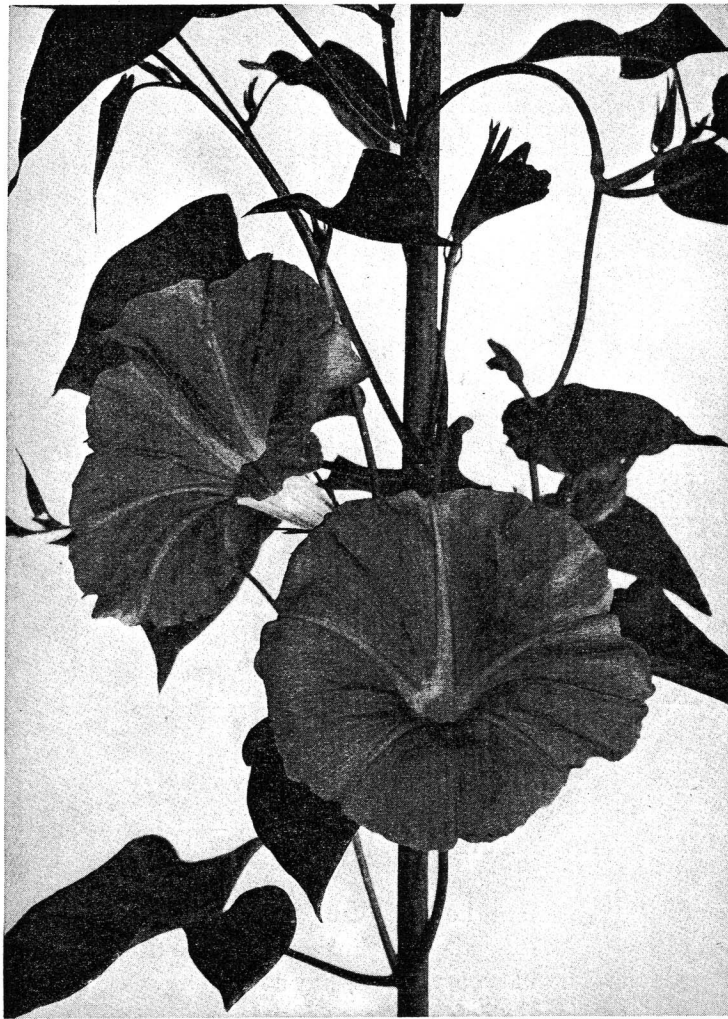


FIG. 2. Globose

To account for the results, the following new genes may be registered.

No-lobe (*nl*) recessive; working on Globose results in nearly lobeless leaves. The laminae of no-lobe Globose are oblong in shape and sometimes have unobscured lobes.

No-lobe-suppressed (*nl-s*) recessive; working on a no-lobe Globose compound, produces normal Globose by suppressing the manifestation of gene no-lobe.

By homozygous combinations of these genes with Globose, the following leaf forms are manifested:

Normal +; *nl*; *nl-s*; *nl nl-s*.
 Globose *Gb*; *Gb nl-s*; *Gb nl nl-s*.
 No-lobe Globose *Gb nl*.

The matings shown in table V are supposed to be *Gb nl nl-s* × +++; and in F₂, we should expect segregation into 16 normal: 32 hetero-formed: 13 Globose: 3 no-lobe Globose, the theoretical number calculated from this agreeing with the data of table V.

When Globose is crossed with cordate (*co*) the resulting F₁ hybrids bear leaves of a form intermediate between both parents, or Globose without side lobes. The recorded F₂ data are shown in table VI.

TABLE VI. F₂ FROM THE CROSS OF GLOBOSE WITH CORDATE

Cross	Normal	Hetero-formed	Globose	Globose without lobes	Cordate	Total
190 × 928	0	3	70	180	84	337
YK × 1906	0	6	88	251	108	453
455 × 1906	0	3	38	119	42	202
Total	0	12	196	550	234	992

The matings shown in the above table are supposed to be + *Gb nl nl-s* × *co* +++. Owing to close linkage between *Gb* and *co*, the segregation is somewhat complicated, only a few hetero-formed leaves having been obtained. Before discussing this subject, the F₃ data will be collected in table VII.

TABLE VII. F₃ FROM CROSS, YK × 1906 ¹⁾

Character of F ₂	Num. of pedigrees	Normal	Hetero-formed	Globose	Globose without lobes	Cordate	Total
Hetero-formed	2	9	12	5	—	—	26
	1	4	6	1	3	—	14
	2	18	40	—	—	22	80
Globose	4	—	—	61	—	—	61
	3	—	—	27	9	—	36
Globose without lobes	4	—	—	—	49	—	49
	3	—	—	15	55	—	70
	4	0	0	32	74	31	137

The normal F₃ segregates that were derived from the hetero-formed pedigrees bred true to type in the subsequent F₄ generation. On account of the segregation of gene no-lobe-suppressed, lobeless Globose had either segregated out or had segregated from Globose.

Returning to the linkage between Globose and cordate, we calculate the recombination percentage, on the basis of the data given in table VI, to be 1.2.

Some backcrosses were made in several ways in order to verify the genic constitution of the Globose character and to determine the linkage value for Globose and cordate. When F₁, obtained by crossing Globose with normal, were backcrossed with normal, an equal number of normal and hetero-formed leaves were obtained, as expected. The data showing this are collected in table VIII.

TABLE VIII. BACKCROSS, (+ × Gb) × +

Backcross	Normal	Hetero-formed	Total
ID × (ID × 1906)]	52	59	111
(ID × 1906) × ID]	87	76	163
Total]	139	135	274

¹⁾ No pedigrees were propagated from cordate F₂.

Next, the same F_1 were backcrossed with Globose, the data being shown in table IX.

TABLE IX. BACKCROSS, $(+ \times Gb) \times Gb$

Backcross	Hetero-formed	Globose	Total
1906 \times (ID \times 1906) . . .	56	51	107
(ID \times 1906) \times 1906 . . .	25	29	54
Total	81	80	161

The results were simple and accorded with our expectations. The F_1 , obtained from the cross of Globose with cordate, were backcrossed with normal, the results being collected in table X.

TABLE X. BACKCROSS, $(co \times Gb) \times +$

Backcross	Normal	Hetero-formed	Globose	Total
(455 \times 1906) \times ID . .	2	51	1	54
(1906 \times YK) \times RL . .	1	42	1	44
RL \times (1906 \times YK) . .	5	205	4	214
Total	8	298	6	312

As these crosses correspond to $\frac{co +}{+ Gb} \times ++$, the normal and Glo-

bosc segregates are crossovers and the hetero-formed ones non-crossovers. The recombination is calculated directly on the basis of these segregates, the result being 4.5 per cent. Though this figure differs somewhat from the calculated from the F_2 data, it is more reliable on account of the results of backcrossing. Another backcross was made in such a way that similar F_1 were hybridized to cordate. Table XI contains the recorded data.

TABLE XI. BACKCROSS, $(co \times Gb) \times co$

Backcross	Hetero-formed	Globose	Cordate	Total
(455 + 1906) \times 455 . .	4	63	70	137
455 \times (455 \times 1906) . .	3	48	50	101
Total	7	111	120	238

Since the case corresponds to cross $\frac{co +}{+ Gb} \times co +$, the hetero-formed segregates are crossovers, the Globose non-crossovers, and the cordate a mixture of the two. From the ratio of the former two, the recombination is calculated and found to be 5.9 per cent, which is close to the previously estimated 4.5 per cent. When the calculation is made on the basis of their total numbers the result is 4.9 per cent, which is the most reliable figure at present.

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SUMMARY

So far the loci determined in *Pharbitis Nil* number 72, being located in 12 chromosomes. They include the two newly apportioned genes dwarf (*dw*) of the delicate linkage group and Globose (*Gb*) of the cordate linkage group. The recombination frequency is 30.3 per cent for dwarf and delicate and 4.9 per cent for Globose and cordate.

Globose is qualified by the two recessive genes, no-lobe (*nl*) and no-lobe-suppressed (*nl-s*).

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