LINKAGE-STUDIES IN PISUM. III

by

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(Wageningen, Holland [1])

CONTENTS

I. INTRODUCTION

It is extremely difficult to combine into one theory the results of different investigators on linkage-relations in *Pisum*. Two genes, independent according to the one, are found to be linked by another. Much variation in percentages of crossing-over occurs. Several cases of about 50 % crossing-over — resulting in phenotypic independence — have come to our knowledge. The use of different parental lines and lack of uniformity in symbols make it hard to judge whether or not a

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[1] Presently: Buitenzorg, Java.

gene used in a certain study is identical with a gene occurring in other material.

No wonder that attempts to combine the data of different authors into one general conclusion fail to yield satisfactory results. Lots more of experimental work must be done, before we can form an opinion on the validity of the *Drosophila* principles in *Pisum*. For the present this work must be done in one group of genes which will leave no doubt with regard to the identity of factors. Furthermore, all possible relations two by two must be studied, since incompleteness does not allow to draw final conclusions.

In "Linkage-Studies I and II" an attempt was made to study the interrelations between fourteen genes according to the above two principles. Five indepedent genes in addition to four linkage-groups were found, whereas the number of bivalent chromosomes is only seven. Since a possibility of two linkages with about 50 % crossing-over between two of the independent genes was left, these results were not considered to form final proof of disharmony between the number of linkage-groups and the number of chromosomes.

The relations of two more genes to the above fourteen are now known. The general conclusion is similar as formerly arrived at, namely nine independent genes or groups of linked genes. Some relations, however, were found to be different from what was supposed before.

II. MATERIALS AND METHODS
§ 1. *The genes*

The following fourteen genes were studied before:
- (1) A : colored flower (recessive: white flower).
- (2) B : purple flower (rec.: pink).
- (3) D^w : double leaf-axil-spot. (Of the two recessive allelomorphs which are known, D occurs in the present material, standing for single axil-spot).
- (4) Fa : normal stem (rec.: fasciated).
- (5) G^b : green pod (rec.: yellow pod).
- (6) P : membrane in the pod-wall (rec.: no membrane).
- (7) V : strong membrane in the pod-wall (rec.: thin membrane in the presence of P).
- (8) Pl : black hilum (rec.: not black).

(9) M : marbled seed-coat (rec.: not marbled).

(10) F : stippled seed-coat (rec.: not stippled).

(11) I : yellow cotyledon (rec.: green).

(12) Le : long internode (rec.: short).

(13) $\widetilde{W}_2^b$: glaucous stem and foliage (rec.: emerald).

(14) S : seeds free in the ripe pod (rec.: seeds adhering "chenille"-like).

To these fourteen genes are added in the present study:

(15) $\underset{\smile}{Tl}$: tendrilled leaves (rec.: acacia).

(16) $\widetilde{K}$: normal wings (rec.: keeled wings).

$\underset{\smile}{Tl}$ was first described by VILMORIN (12) in 1910 and since occurred in several studies. PELLEW and SVERDRUP (9) were the first to study K which gene has not yet been present in the material of other investigators. Genes B, D^w, M and F are only active in the presence of A, while V only acts in the presence of P.

A striking cooperation exists between A and B on the one side and K on the other side. PELLEW and SVERDRUP (9, p. 127) already hinted at this cooperation, while SVERDRUP (11, p. 225 and plate XVII) went into more details. She states: "The wings more or less take on the colour of the keel, giving a much paler appearance to the whole flower". A somewhat different explanation seems to be more evident, however. In keeled winged purple or pink flowers the most conspicuous part of the wings, in which in normal forms the typical pigment develops, is almost completely reduced. Consequently the color genes do not find the substratum where they can act and no pigment is formed. This explanation fits perfectly well in GOLDSCHMIDT's theory on the action of genes (1, see especially pp. 112-113). Classification after flower-color in keeled-winged forms is easily done by inspecting the color of the standards.

§ 2. *The parents and the crosses*

Genes $\underset{\smile}{tl}$ and k were brought in my material in a line which I obtained through the kindness of miss C. PELLEW. It was unnamed originally and I indicated it as "Keeled Acacia". The other parental lines are the same as those used before. The genotypes — simply expressed in single symbols — are:

1-2-56-1   : A B D^w ja Gp P v pl m F I Le W^b_2 S Tl K
P. thebaicum   : A b D Fa Gp P V Pl M f I Le W^b_2 S Tl K
Pois à cosse jaune: a B D^w Fa gp p V pl m F I Le W^2_b S Tl K
Pois à brochettes : a B D^w Fa Gp P V pl m F i le w^b s Tl K
Keeled Acacia   : A b D ja Gp P V pl M f I Le W^b_2 S tl k

The new crosses, with the genes involved in each of them, are:

Cross 42. 1-2-56-1   × K. Acac.: B-D^w-V-M-F_Tl-K.
Cross 43. K. Acac. × P. thebaicum : Fa-Pl-Tl-K.
Cross 44. K. Acac. × P. à c. jaune : A-B-D^w-Fa-Gp-P-M-F-Tl-K.
Cross 45. K. Acac. × P. à broch. : A-B-D^w-Fa-M-F-I-Le-W^b_2-S-Tl-K.

The numbers of F_2-individuals are given in the following table:

cross-number	sown	succumbed	% succumbed	germ plants	full grown plants
42	1064	10	0.9	1054	1033
43	1089	61	5.6	1028	1017
44	372	4	1.1	368	355
45	1065	10	0.9	1055	1038

The F_2 of cross 43 was sown two weeks before the F_2 of cross 45 and four weeks earlier than the F_2's of crosses 42 and 44. This might account for the relatively bad germination of 43. Unfortunately the number of individuals in 44 is considerably smaller than in the other F_2's. This is caused by a relatively bad succeeding of the crossings, so that the number of F_1-plants was already small. This is nothing but accidental, since the same crossing succeeded well next year. Another factor which reduced the number of seeds produced by the F_1-plants, is the inherited dominant abortion (18) which occurs in cross 44, but which will not be discussed in the present paper, since its relation to Pl in still unknown and our information about it is consequently incomplete. The number of individuals for either B, D^w, M or F and for the relations involving these is about $^3/_4$ of the total number when A also segregates, because in the $^1/_4$ part which is aa, named genes cannot demonstrate their action.

§ 3. *Growing methods, notes, calculations*

The treatment of the material was exactly the same as in former studies (15, 16). As stated above, the sowing-time was varied in the different F_2's in order to obtain different flowering-times. The F_2's which were expected to blossom relatively early, were sown first, those expected to flower rather late, were sown later. This prevented too great an accumulation of work during the flowering-period. No classification difficulties were met with, except perhaps sometimes the differentiation between normal and fasciated stem (cp. p. 10). Summarizing tables of the total F_2-results were only prepared for crosses 42 and 43; they are given as appendix to this paper [1]). When the number of genes studied in a certain cross exceeds seven — as in crosses 44 and 45 — a summarizing F_2-table gets too complicated. In these cases the mono- and bifactorial segregations are made up immediately from the field-notes.

Two types of calculations are involved in linkage-studies. The first is the calculation of expectations in case of independence. When these expectations do not fit the observations, linkage is evident and the crossing-over-percentage must be determined. KAPPERT's method (6) of calculating the most probable expectation in case of independence has been very useful in former studies and is again used in the present material. As a rule, a larger value than 3 for actual deviation divided by mean error of expectation indicates linkage. Several methods are proposed for the determination of the percentage of crossing-over from F_2-material. It is quite natural that I prefer my own method (13) which reveals the gametic ratio $p : q : r : s$ [2]) from the following equations, in which (AB), (Ab), (aB) and (ab) are the phenotypic F_2-groups and n is the number of F_2-individuals:

$$s = \sqrt{(ab)}$$
$$r = \sqrt{(ab) + (aB)} - s$$
$$q = \sqrt{(ab) + (Ab)} - s$$
$$p = \sqrt{n} - (q + r + s)$$

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1) The order of the genes in the summarizing tables is different from the order in the text; this is due to the order of observation which is different from the historical arrangement in the text.

2) Symbols $p \ldots r$ are used here to avoid confusion, since $a \ldots d$ which were used before (13), are used in the trifactorial ratio further on.

As a check we have:

(AB) $= p^2 + 2\,pq + 2\,pr + 2\,ps + 2\,qr$

The calculation of interference is sometimes a very helpful means to determine whether linkage is present between three genes. For this purpose we should know the trifactorial gametic ratio which is also necessary for the calculation of the percentage of double crossing-over. A similar method as the one described above for a bifactorial ratio may be used.

From an F_2-checkerboard with a gametic ratio $a : b : c : \ldots : h$ we read:

$$
\begin{aligned}
(ABC) &= a^2 + 2\,ab + 2\,ac + 2\,ad + 2\,ae + 2\,af + 2\,ag + \\
&\quad + 2\,ah + 2\,bc + 2\,be + 2\,bg + 2\,ce + 2\,cf + 2\,de \quad (1)\\
(ABc) &= b^2 + 2\,bd + 2\,bf + 2\,bh + 2\,df \ldots \ldots \ldots (2)\\
(AbC) &= c^2 + 2\,cd + 2\,cg + 2\,ch + 2\,dg \ldots \ldots \ldots (3)\\
(Abc) &= d^2 + 2\,dh \ldots \ldots \ldots \ldots \ldots (4)\\
(aBC) &= e^2 + 2\,ef + 2\,eg + 2\,eh + 2\,fg \ldots \ldots \ldots (5)\\
(aBc) &= f^2 + 2\,fh \ldots \ldots \ldots \ldots \ldots (6)\\
(abC) &= g^2 + 2\,gh \ldots \ldots \ldots \ldots \ldots (7)\\
(abc) &= h^2 \ldots \ldots \ldots \ldots \ldots (8)
\end{aligned}
$$

Furthermore:

$$n^2 = (a + b + c + d + e + f + g + h)^2 \ldots \ldots \ldots (9)$$

The solution proceeds by substituting the value for h from (8) respectively in (7), (6) and (4) which reveals g, f and d. Next e, c and b are found from (5), (3) and (2) and a follows from (9). Equation (1) is used as a check.

This calculation is rather laborious. It is much simpler to calculate separately the three bifactorial gametic series:

$$
\begin{aligned}
AB &: Ab : aB : ab \ldots \ldots \ldots \ldots \ldots \text{(I)}\\
AC &: Ac : aC : ac \ldots \ldots \ldots \ldots \ldots \text{(II)}\\
BC &: Bc : bC : bc \ldots \ldots \ldots \ldots \ldots \text{(III)}
\end{aligned}
$$

If, again, $a : b : c : \ldots : h$ is the trifactorial gametic ratio, we can substitute:

$$
\begin{aligned}
\text{for (I)} &\quad (a + b) : (c + d) : (e + f) : (g + h)\\
\text{for (II)} &\quad (a + c) : (b + d) : (e + g) : (f + h)\\
\text{for (III)} &\quad (a + e) : (b + f) : (c + g) : (d + h)
\end{aligned}
$$

Consequently the above 12 values $(a + b)$, $(c + d)$ etc. are known, but the values for $a, b \ldots, h$ cannot be determined, since some of the twelve equations are dependent. Fortunately h is easily deter-

mined from (8) as $h = \sqrt{(abc)}$ and simple substitutions reveal a, b, etc. If, for instance, $h = 5$, we know d from the value for $d + h$, we know c from $c + d$ etc.

Of course, the above methods do not give but approximate indications, since the total number of gametes, being $\sqrt{n}$, is small even in an F_2 with very large numbers. But when back-crossing is hard to be done, as in peas, an approximate indication is preferable to no indication at all.

III. EXPERIMENTAL RESULTS AND CONCLUSIONS

§ 1. *The monofactorial F_2-segregations*

In the tabulation of the monofactorial F_2-segregations, the theoretical expectation is printed in parentheses. Furthermore, actual deviation divided by mean error is indicated as c.

(1) *A*.   Cross 44.   269   :   86
                           (266.25) :   (88.75)
                           c=0.3

         Cross 45.   791   : 247
                      (778.5) : (259.5)
                      c=0.9

(2) *B*.   Cross 42.   772   : 261
                          (774.75) : (258.25)
                          c=0.2

         Cross 44.   208   :   61
                      (201.75) :   (67.25)
                      c=0.9

         Cross 45.   605   : 186
                      (593.25) : (197.75)
                      c=0.9

(3) *Dʷ*. Cross 42.   758   : 275
                          (774.75) : (258.25)
                          c=1.2

         Cross 44.   201   :   68
                      (201.75) :   (67.25)
                      c=0.1

Cross 45.   603   :   188
             (593.25) : (197.75)
             c=0.8

(4) *Fa.*   Cross 43.   813   :   204
             (762.75) : (254.25)
             c=3.6

             Cross 44.   267   :   88
             (266.25) :   (88.75)
             c=0.1

             Cross 45.   803   :   235
             (778.5)   : (259.5)
             c=1.8

(5) *Gp.*   Cross 44.   278   :   77
             (266.25) :   (88.75)
             c=1.4

(6) *P.*   Cross 44.   268   :   87
             (266.25) :   (88.75)
             c=0.2

(7) *V.*   Cross 42.   806   :   227
             (774.75) : (258.25)
             c=2.2

(8) *Pl.*   Cross 43.   739   :   278
             (762.75) : (254.25)
             c=1.7

(9) *M.*   Cross 42.   762   :   271
             (774.75) : (258.25)
             c=0.9

             Cross 44.   208   :   61
             (201.75) :   (67.25)
             c=0.9

             Cross 45.   617   :   174
             (593.25) : (197.75)
             c=1.9

(10) *F.*   Cross 42.   787   :   246
             (774.75) : (258.25)
             c=0.9

                   Cross 44.   206   :   63
                                (201.75) : (67.25)
                                c=0.6

                   Cross 45.   609   : 182
                                (593.25) : (197.75)
                                c=1.3

(11) *I.*   Cross 45.   772   : 266
                                (778.5) : (259.5)
                                c=0.5

(12) *Le.*   Cross 45.   768   : 270
                                (778.5) : (259.5)
                                c=0.7

(13) W_2^b.   Cross 45.   786   : 252
                                (778.5) : (259.5)
                                c=0.6

(14) *S.*   Cross 45.   787   : 251
                                (778.5) : (259.5)
                                c=0.6

(15) *Tl.*   Cross 42.   788   : 245
                                (774.75) : (258.25)
                                c=0.9

                   Cross 43.   781   : 236
                                (762.75) : (254.25)
                                c=1.3

                   Cross 44.   260   :   95
                                (266.25) : (88.75)
                                c=0.8

                   Cross 45.   772   : 266
                                (778.5) : (259.5)
                                c=0.5

(16) *K.*   Cross 42.   780   : 253
                                (774.75) : (258.25)
                                c=0.4

                   Cross 43.   739   : 278
                                (762.75) : (254.25)
                                c=1.7

Cross 44.   268   :   87
             (266.25) :   (88.75)
             c=0.2

Cross 45.   803   :   235
             (778.5) : (259.5)
             c=1.8

The only value for c which is too large — accepting c=3.0 as an extreme chance variation — is in the case of Fa in cross 43. Since sometimes the fasciation of the stem is modified so as to make it hardly distinguishable from normal stems, classification-mistakes may account for this large deviation.

§ 2. *The bifactorial segregations*

As in earlier studies, the factorial relations are published in the following way. At the left of the vertical line the four phenotypic F_2-classes are given on the first row and the corresponding expected values in case of independence are given on the second row in parentheses. At the right of the vertical line the ratio of sum of outer terms to sum of inner terms of the four class ratios at the left are given. These ratios indicate sum of parental types to sum of recombinations, or as the case is the reverse. Again, c is actual deviation divided by mean error of the two class ratio.

Gametic ratios are only given in case of linkage and in some more cases which have to be especially discussed in the following paragraph. In case of a 9 : 3 : 4 expectation, namely in those relations involving A and a gene depending in its action on presence of A (either B, Dw, M or F), only the first two terms can be used in deciding whether or not linkage is present. Independence is then indicated by agreement of the first two terms with a 3 : 1 expectation.

The way of numbering the 120 possible relations between the 16 genes will seem illogical at first sight, but will be comprehensible from a historical point of view. The relations which already occurred in Linkage-Studies I or II are namely numbered as they were before. This means for instance that relation A-F is 9, that A-I is 46 and that A-Tl is 92. When all the relations were studied in one year, these numbers would have been 9, 10 and 14.

(1) A-B.   208   :   61
    Cross 44.   (201.75) : (67.25)
    (A b × a B) c=0.9
     Cross 45.   605   :   186
    (A b × a B) (593.25) : (197.75)
                    c=1.0

(2) A-D^w.   201   :   68
    Cross 44.   (201.75) : (67.25)
    (A D × a Dᵂ) c=0.1
     Cross 45.   603   :   188
    (A D × a Dᵂ) (593.25) : (197.75)
                    c=0.8

(3) A-Fa.   198   :   71   :   69 :   17   215 : 140
    Cross 44.   (202) : (67) : (65) : (21)   (223) : (132)
    (A fa × a Fa)   c=0.9
    Cross 45.   605   :   186 :   198 :   49   654 : 384
    (A fa × a Fa) (612) : (179) : (191) : (56)   (668) : (370)
                                                        c=0.9

(4) A-Gp.   209   :   60   :   69 :   17   226 : 129
    Cross 44.   (211) : (58) : (67) : (19)   (230) : (125)
    (A Gp × a gp)   c=0.4

(5) A-P.   206   :   63   :   62 :   24   230 : 125
    Cross 44.   (203) : (66) : (65) : (21)   (224) : (131)
    (A P × a p)   c=0.7

(8) A-M.   208   :   61
    Cross 44.   (201.75) : (67.25)
    (A M × a m) c=0.9
     Cross 45.   617   :   174
    (A M × a m) (593.25) : (197.75)
                    c=1.9

(9) A-F.
    Cross 44.   206   :   63
    (A f × a F) (201.75) : (67.25)
                    c=0.6
    Cross 45.   609   :   182
    (A f × a F) (593.25) : (197.75)
                    c=1.3

(10) *B-Dw.*

Cross 42.	586	:	186	:	172	:	89	675	:	358
(B Dw × b D)	(566)	:	(206)	:	(192)	:	(69)	(635)	:	(398)

c=2.5

Cross 44.	152	:	56	:	49	:	12	164	:	105
(b D × B Dw)	(155)	:	(53)	:	(46)	:	(15)	(170)	:	(99)

c=0.8

Cross 45.	458	:	147	:	145	:	41	499	:	292
(b D × B Dw)	(461)	:	(144)	:	(142)	:	(44)	(505)	:	(286)

c=0.4

(11) *B-Fa.*

Cross 44.	154	:	54	:	44	:	17	171	:	98
(b fa × B Fa)	(153)	:	(55)	:	(45)	:	(16)	(169)	:	(100)

c=0.3

Cross 45.	463	:	142	:	142	:	44	507	:	284
(b fa × B Fa)	(463)	:	(142)	:	(142)	:	(44)	(507)	:	(284)

c=0.0

(12) *B-Gp.*

Cross 44.	159	:	49	:	50	:	11	170	:	99
(b Gp × B gp)	(162)	:	(46)	:	(47)	:	(14)	(176)	:	(93)

c=0.8

(13) *B-P.*

Cross 44.	160	:	48	:	46	:	15	175	:	94
(b P × B p)	(159)	:	(49)	:	(47)	:	(14)	(173)	:	(96)

c=0.3

(14) *B-V.*

Cross 42.	587	:	185	:	219	:	42	629	:	404
(B v × b V)	(602)	:	(170)	:	(204)	:	(57)	(659)	:	(374)

c=1.9

(16) *B-M.*

Cross 42.	572	:	200	:	190	:	71	643	:	390
(B m × b M)	(570)	:	(202)	:	(192)	:	(69)	(639)	:	(394)

c=0.3

Gametic ratio is 8.0 : 8.0 : 7.7 : 8.4; cross-ing-over is 51.1 %

Cross 44.	154	:	54	:	54	:	7	161	:	108
(b M × B m)	(161)	:	(47)	:	(47)	:	(14)	(175)	:	(94)

c=1.8

Gametic ratio is 3.4 : 5.2 : 5.2 : 2.6; cross-ing-over is 36.6 %

Cross 45.   471 : 134 : 146 : 40   511 : 280

(b M × B m)   (472) : (133) : (145) : (41)   (513) : (278)

                                                 c=0.2

Gametic ratio is 7.6 : 6.9 : 7.3 : 6.3; cross-
ing-over is 49.5 %

(17) B-F.   724 : 48 : 63 : 198   922 : 111

    Cross 42.   (588) : (184) : (199) : (62)   650 : 383

(B F × b f)   c=17.4

Gametic ratio is 14.4 : 1.6 : 2.1 : 14.1; cross-
ing-over is 11.5 %

    Cross 44.   197 : 11 :   9 : 52   249 : 20

(b f × BF)   (159) : (49) : (47) : (14)   (173) : (96)

                                                 c=9.7

Gametic ratio is 7.9 : 0.7 : 0.6 ; 7.2; cross-
ing-over is 7.9 %

    Cross 45.   545 : 60 : 64 : 122   667 : 124

(b f × B F)   (466) : (139) : (143) : (43) (509) : (282)

                                                 c=11.7

Gametic ratio is 12.0 : 2.5 : 2.6 : 11.0; cross-
ing-over is 18.3 %

(18) D^w-Fa.   152 : 49 : 46 : 22   174 : 95

    Cross 44.   '148) : (53) : (50) : (18)   (166) : (103)

(D fa × D^w Fa)   c=1.0

    Cross 45.   474 : 129 : 131 : 57   531 : 260

(D fa × D^w Fa) (461) : (142) : (144) : (44) (505) : (286)

                                                 c=1.9

(19) D^w-Gp.   159 : 42 : 50 : 18   177 : 92

    Cross 44.   (156) : (45) : (53) : (15)   (171) : (98)

(DGp × D^wgp)   c=0.8

(20) D^w-P.   161 : 40 : 45 : 23   184 : 85

    Cross 44.   (154) : (47) : (52) : (16)   (170) : (99)

(D P × D^w p)   c=1.8

(21) D^w-V.   598 : 160 : 208 : 67   665 : 368

    Cross 42.   (591) : (167) : (215) : (60)   (651) : (382)

(D^w v × D V)   c=0.9

(23) *Dw-M.*   560 : 198 : 202 : 73   633 : 400
    Cross 42.   (559) : (199) : (203) : (72)   (631) : (402)
  (Dw m × DM)   c=0.1
    Cross 44.   159 : 42 : 49 : 19   178 : 91
  (DM × Dwm) (155) : (46) : (53) : (15)   (170) : (99)
                                            c=1.0
    Cross 45.   466 : 137 : 151 : 37   503 : 288
  (D M × Dw m) (470) : (133) : (147) : (41)   (511) : (280)
                                            c=0.6

(24) *Dw-F.*   585 : 173 : 202 : 73   658 : 375
    Cross 42.   (577) : (181) : (210) : (65)   (642) : (391)
  (Dw F × D f)   c=1.0
    Cross 44.   152 : 49 : 54 : 14   166 : 103
  (D f × Dw F) (154) : (47) : (52) : (16)   (170) : (99)
                                            c=0.5
    Cross 45.   467 : 136 : 142 : 46   513 : 278
  (D f × Dw F) (464) : (139) : (145) : (43)   (507) : (284)
                                            c=0.4

Gametic ratio is 7.7 : 6.7 : 6.9 : 6.8; cross-ing-over is 48.4 %

(25) *Fa-Gp.*   206 : 61 : 72 : 16   222 : 133
    Cross 44.   (209) : (58) : (69) : (19)   (228) : (127)
  (fa Gp × Fa gp)   c=0.7

(26) *Fa-P.*   206 : 61 : 62 : 26   232 : 123
    Cross 44.   (202) : (65) : (66) : (22)   (224) : (131)
  (fa P × Fa p)   c=0.9

(28) *Fa-Pl.*   586 : 227 : 153 : 51   637 : 380
    Cross 43.   (591) : (222) : (148) : (56)   (647) : (370)
  (fa pl × Fa Pl)   c=0.6

(29) *Fa-M.*   155 : 43 : 53 : 18   173 : 96
    Cross 44.   (153) : (45) : (55) : (16)   (169) : (100)
  (fa M × Fa m)   c=0.5
    Cross 45.   465 : 140 : 152 : 34   499 : 292
  (fa M × Fa m) (472) : (133) : (145) : (41)   (513) : (278)
                                            c=1.0

(30) *Fa-F.*   155 : 43 : 51 : 20   175 : 94
      Cross 44.   (152) : (46) : (54) : (17)   (169) : (100)
      (fa f × Fa F)   c=0.8

      Cross 45.   478 : 127 : 131 : 55   533 : 258
      (fa f × Fa F) (466) : (139) : (143) : (43) (509) : (282)
                                                  c=1.8

(31) *Gp-P.*   209 : 69 : 59 : 18   227 : 128
      Cross 44.   (210) : (68) : (58) : (19)   (229) : (126)
      (Gp P × gp p)   c=0.2

(34) *Gp-M.*   158 : 51 : 50 : 10   168 : 101
      Cross 44.   (162) : (47) : (43) : (14)   (176) : (93)
      (GpM × gp m)·   c=1.0

(35) *Gp-F.*   160 : 49 : 46 : 14   174 : 95
      Cross 44.   (160) : (49) : (46) : (14)   (174) : (95)
      (Gp f × gp F)   c=0.0

(38) *P-M.*   161 : 45 : 47 : 16   177 : 92
      Cross 44.   (159) : (47) : (49) : (14)   (173) : (96)
      (P M × p m)   c=0.5

(39) *P-F.*   159 : 47 : 47 : 16   175 : 94
      Cross 44.   (158) : (48) : (48) : (15)   (173) : (96)
      (P f × p F)   c=0.3

(41) *V-M.*   596 : 210 : 166 : 61   657 : 376
      Cross 42.   (595) : (211) : (167) : (60) (655) : (378)
      (v m × V M)   c=0.1

(42) *V-F.*   604 : 202 : 183 : 44   648 : 385
      Cross 42.   (614) : (192) : (173) : (54) (668) : (365)
      (v F × V f)   c=1.3

(45) *M-F.*   544 : 218 : 243 : 28   572 : 461
      Cross 42.   (581) : (181) : (206) : (65) (646) : (387)
      (m F × M f)   c=4.7
      Gametic ratio is 5.3 : 10.4 : 11.2 : 5.3; cross-
      ing-over is 32.9 %

      Cross 44.   150 : 58 : 56 : 5   155 : 114
      (M f × m F) (159) : (49) : (47) : (14) (173) : (96)
                                                  c=2.3

Gametic ratio is 2.9 : 5.7 : 5.6 : 2.2; cross-
ing-over is 31.1 %

Cross 45.   456 : 161 : 153 : 21   477 : 314

(M f × m F) (475) : (142) : (134) : (40)   515 : 276

                                          $c = 2.8$

Gametic ratio is 6.0 : 8.9 : 8.6 : 4.6; cross-
ing-over is 37.6 %

(46) *A-I.*   589 : 202 : 183 : 64   653 : 385

     Cross 45.   (588) : (203) : (184) : (63)   (651) : (387)

     (A I × a i) $c = 0.1$

(47) *A-Le.*   580 : 211 : 188 : 59   639 : 399

     Cross 45.   (585) : (206) : (183) : (64)   (649) : (389)

     (A Le × a le) $c = 0.6$

(48) *A-W_2^b.*   604 : 187 : 182 : 65   669 : 369

     Cross 45.   (599) : (192) : (187) : (60)   (659) : (379)

     (A W_2^b × a w^b) $c = 0.6$

(49) *A-S.*   602 : 189 : 185 : 62   664 : 374

     Cross 45.   (600) : (191) : (187) : (60)   (660) : (378)

     (A S × a s) $c = 0.1$

(50) *B-I.*   447 : 158 : 142 : 44   491 : 300

     Cross 45.   (450) : (155) : (138) : (48)   (498) : (293)

     (b I × B i) $c = 0.5$

(51) *B-Le.*   431 : 174 : 149 : 37   468 : 323

     Cross 45.   (444) : (161) : (136) : (50)   (494) : (297)

     (b Le × B le) $c = 1.9$

(52) *B-W_2^b.*   462 : 143 : 142 : 44   506 : 285

     Cross 45.   (462) : (143) : (142) : (44)   (506) : (285)

     (b W_2^b × B w^b) $c = 0.0$

(53) *B-S.*   460 : 145 : 142 : 44   504 : 287

     Cross 45.   (460) : (145) : (142) : (44)   (504) : (287)

     (b S × B s) $c = 0.0$

(54) *Dw-I.*   446 : 157 : 143 : 45   491 : 300

     Cross 45.   (449) : (154) : (140) : (48)   (497) : (294)

     (D I × Dw i) $c = 0.4$

(55) *Dw-Le.*   473 : 130 : 107 : 81   554 : 237

    Cross 45.   (442) : (161) : (138) : (50)   (492) : (299)

    (D Le × Dw le)   c=4.6

Gametic ratio is 8.9 : 5.5 : 4.7 : 9.0; cross-
ing-over is 63.6 %

(56) *Dw-W$^b_2$.*   467 : 136 : 137 : 51   518 : 273

    Cross 45.   (460) : (142) : (144) : (45)   (505) : (286)

    (D W$^b_2$ × Dw w^b)   c=1.0

(57) *Dw-S.*   465 : 138 : 137 : 51   516 : 275

    Cross 45.   (459) : (144) : (143) : (45)   (504) : (287)

    (D S × Dw s)   c=0.9

(58) *Fa-I.*   593 : 210 : 179 : 56   649 : 389

    Cross 45.   (598) : (206) : (174) : (60)   (658) : (380)

    (fa I × Fa i)   c=0.6

(59) *Fa-Le.*   598 : 205 : 170 : 65   663 : 375

    Cross 45.   (594) : (209) : (174) : (61)   (655) : (383)

    (fa Le × Fa le)   c=0.5

(60) *Fa-W$^b_2$.*   610 : 193 : 176 : 59   669 : 369

    Cross 45.   (608) : (195) : (178) : (57)   (665) : (373)

    (fa W$^b_2$ × Fa w^b)   c=0.3

(61) *Fa-S.*   611 : 192 : 176 : 59   670 : 368

    Cross 45.   (609) : (194) : (178) : (57)   (666) : (372)

    (fa S × Fa s)   c=0.3

(78) *M-I.*   459 : 158 : 130 : 44   503 : 288

    Cross 45.   (459) : (158) : (130) : (44)   (503) : (288)

    (M I × m i)   c=0.0

(79) *M-Le.*   458 : 159 : 122 : 52   510 : 281

    Cross 45.   (452) : (165) : (128) : (46)   (498) : (293)

    (M Le × m le)   c=0.9

(80) *M-W$^b_2$.*   472 : 145 : 132 : 42   514 : 277

    Cross 45.   (471) : (146) : (133) : (41)   (512) : (279)

    (M W$^b_2$ × m u^b)   c=0.2

(81) *M-S.*   473 : 144 : 129 : 45   518 : 273

    Cross 45.   (470) : (147) : (132) : (42)   (512) : (279)

    (M S × m s)   c=0.4

(82) *F-I.*   454 : 155 : 135 : 47   501 : 290
  Cross 45.   (454) : (156) : (135) : (46)   (500) : (291)
  (f I × F i)   c=0.1

(83) *F-Le.*   468 : 141 : 112 : 70   538 : 253
  Cross 45.   (447) : (162) : (133) : (49)   (496) : (295)
  (f Le × F le)   c=3.1
  Gametic ratio is 8.5 : 6.1 : 5.1 : 8.4; cross-
  ing-over is 60.1 %

(84) $F\text{-}W_2^b.$ 450 : 159 : 154 : 28   478 : 313
  Cross 45.   (465) : (144) : (139) : (43)   (508) : (283)
  (f W_2^b × F w^b)   c=2.2

(85) *F-S.*   448 : 161 : 154 : 28   476 : 315
  Cross 45.   (464) : (146) : (138) : (43)   (507) : (284)
  (f S × F s)   c=2.3

(86) *I-Le.*   575 : 197 : 193 : 73   648 : 390
  Cross 45.   (571) : (201) : (197) : (69)   (640) : (398)
  (I Le × i le)   c=0.5

(87) $I\text{-}W_2^b.$ 594 : 178 : 192 : 74   668 : 370
  Cross 45.   (585) : (187) : (201) : (65)   (650) : (388)
  (I W_2^b × i w^b)   c=1.2

(88) *I-S.*   596 : 176 : 191 : 75   671 : 367
  Cross 45.   (586) : (187) : (201) : (64)   (650) : (388)
  (I S × i s)   c=1.3

89) $Le\text{-}W_2^b.$ 592 : 176 : 194 : 76   668 : 370
  Cross 45.   (582) : (186) : (204) : (66)   (648) : (390)
  (Le W_2^b × le w^b)   c=1.3

(90) *Le-S.*   596 : 172 : 191 : 79   675 : 363
  Cross 45.   (582) : (186) : (205) : (65)   (647) : (391)
  (Le S × le s)   c=1.8

(91) $W_2^b\text{-}S.$ 782 :   4 :   5 : 247   1029 :   9
  Cross 45.   (596) : (190) : (191) : (61)   (657) : (381)
  (W_2^b S × w^b s)   c=24.0
  Gametic ratio is 16.2 : 0.1 : 0.2 : 15.7; cross-
  ing-over is 0.8 %

(92) *A-Tl.*   199 : 70 : 61 : 25   224 : 131

     Cross 44.   (197) : (72) : (63) : (23)   (220) : (135)

   (A tl × a Tl)   c=0.2

     Cross 45.   587 : 204 : 185 : 62   649 : 389

   (A tl × a Tl)   (588) : (203) : (184) : (63)   (651) : (387)

                                                  c=0.1

(93) *A-K.*   204 : 65 : 64 : 22   226 : 129

     Cross 44.   (203) : (66) : (65) : (21)   (224) : (131)

   (A k × a K)   c=0.2

     Cross 45.   615 : 176 : 188 : 59   674 : 364

   (A k × a K)   (612) : (179) : (191) : (56)   (668) : (370)

                                                  c=0.4

(94) *B-Tl.*   591 : 181 : 197 : 64   655 : 378

     Cross 42.   (589) : (183) : (199) : (62)   (651) : (382)

   (B Tl × b tl)   c=0.2

     Cross 44.   154 : 54 : 45 : 16   170 : 99

   (b tl × B Tl)   (154) : (54) : (45) : (16)   (170) : (99)

                                                  c=0.0

     Cross 45.   450 : 155 : 137 : 49   499 : 292

   (b tl × B Tl)   (449) : (156) : (138) : (48)   (497) : (294)

                                                  c=0.1

(95) *B-K.*   575 : 197 : 205 : 56   631 : 402

     Cross 42.   (583) : (189) : (197) : (64)   (647) : (386)

   (B K × b k)   c=1.0

     Cross 44.   159 : 49 : 45 : 16   175 : 94

   (b k × B K)   (158) : (50) : (46) : (15)   (173) : (96)

                                                  c=0.3

     Cross 45.   474 : 131 : 141 : 45   519 : 272

   (b k × B K)   (470) : (135) : (145) : (41)   (511) : (280)

                                                  c=0.6

(96) *Dw-Tl.*   594 : 164 : 194 : 81   675 : 358

     Cross 42.   (578) : (180) : (210) : (65)   (643) : (390)

   (Dw Tl × D tl)   c=2.0

     Cross 44.   154 : 47 : 45 : 23   177 : 92

   (D tl × Dw Tl)   (149) : (52) : (50) : (18)   (167) : (102)

                                                  c=1.3

Cross 45.　454 : 149 : 133 : 55　　509 : 282
(*D tl* × *Dʷ Tl*)　(447) : (155) : (140) : (49)　(496) : (295)
　　　　　　　　　　　　　　　　　　c=1.0

(97) *Dʷ-K.*　584 : 174 : 196 : 79　　663 : 370
　Cross 42.　(572) : (186) : (208) : (67)　(639) : (394)
(*Dʷ K* × *D k*)　　　　　　　　　　　c=1.5
　Cross 44.　156 : 45 : 48 : 20　　176 : 93
(*D k* × *Dʷ K*)　(152) : (49) : (52) : (16)　(168) : (101)
　　　　　　　　　　　　　　　　　　c=1.0

　Cross 45.　458 : 145 : 157 : 31　　489 : 302
(*D k* × *Dʷ K*)　(469) : (134) : (146) : (42)　(511) : (280)
　　　　　　　　　　　　　　　　　　c=1.6

(98) *Fa-Tl.*　619 : 194 : 162 : 42　　661 : 356
　Cross 43.　(624) : (189) : (157) : (47)　(671) : (346)
(*fa tl* × *Fa Tl*)　　　　　　　　　　c=0.7
　Cross 44.　199 : 68 : 61 : 27　　226 : 129
(*fa tl* × *Fa Tl*)　(196) : (71) : (64) : (24)　(220) : (135)
　　　　　　　　　　　　　　　　　　c=0.7

　Cross 45.　586 : 217 : 186 : 49　　635 : 403
(*fa tl* × *Fa Tl*)　(598) : (206) : (174) : (60)　(658) : (380)
　　　　　　　　　　　　　　　　　　c=1.5

(99) *Fa-K.*　594 : 219 : 145 : 59　　653 : 364
　Cross 43.　(591) : (222) : (148) : (56)　(647) : (370)
(*fa k* × *Fa K*)　　　　　　　　　　　c=0.4
　Cross 44.　206 : 61 : 62 : 26　　232 : 123
(*fa k* × *Fa K*)　(202) : (65) : (66) : (22)　(224) : (131)
　　　　　　　　　　　　　　　　　　c=0.9

　Cross 45.　622 : 181 : 181 : 54　　676 : 362
(*fa k* × *Fa K*)　(622) : (182) : (181) : (53)　(675) : (363)
　　　　　　　　　　　　　　　　　　c=0.1

(100) *Gp-Tl.*　204 : 74 : 56 : 21　　225 : 130
　Cross 44.　(204) : (74) : (57) : (20)　(224) : (131)
(*Gp tl* × *gp Tl*)　　　　　　　　　　c=0.1

(101) *Gp-K.*　207 : 71 : 61 : 16　　223 : 132
　Cross 44.　(210) : (68) : (58) : (19)　(229) : (126)
(*Gp k* × *gp K*)　　　　　　　　　　　c=0.7

(102) *P-Tl.*   196 : 72 : 64 : 23   219 : 136
      Cross 44.   (196) : (72) : (64) : (23)   (219) : (136)
      (P tl × p Tl)   c=0.0

(103) *P-K.*   205 : 63 : 63 : 24   229 : 126
      Cross 44.   (202) : (66) : (66) : (21)   (223) : (132)
      (P k × p K)   c=0.7

(104) *V-Tl.*   606 : 200 : 182 : 45   651 : 382
      Cross 42.   (615) : (191) : (173) : (54)   (669) : (364)
      (v Tl × V tl)   c=1.2

(105) *V-K.*   605 : 201 : 175 : 52   657 : 376
      Cross 42.   (609) : (197) : (171) : (56)   (665) : (368)
      (v K × V k)   c=0.5

(106) *Pl-Tl.*   565 : 174 : 216 : 62   627 : 390
      Cross 43.   (567) : (172) : (213) : (65)   (632) : (385)
      (pl tl × Pl Tl)   c=0.3

(107) *Pl-K.*   545 : 194 : 194 : 84   629 : 388
      Cross 43.   (537) : (202) : (202) : (76)   (613) : (404)
      (pl k × Pl K)   c=1.0

(108) *M-Tl.*   580 : 182 : 208 : 63   643 : 390
      Cross 42.   (581) : (181) : (207) : (64)   (645) : (388)
      (m Tl × M tl)   c=0.1
      Cross 44.   157 : 51 : 42 : 19   176 : 93
      (M tl × m Tl) (154) : (54) : (45) : (16) (170) : (99)
                                                    c=0.8

      Cross 45.   456 : 161 : 131 : 43   499 : 292
      (M tl × m Tl) (458) : (159) : (129) : (45) (503) : (288)
                                                    c=0.3

(109) *M-K.*   570 : 192 .: 210 : 61   631 : 402
      Cross 42.   (575) : (187) : (205) : (66)   (641) : (392)
      (m K × M k)   c=0.6
      Cross 44.   157 : 51 : 47 : 14   171 : 98
      (M k × m K) (158) : (50) : (46) : (15) (173) : (96)
                                                    c=0.3

      Cross 45.   484 : 133 : 131 : 43   527 : 264
      (M k × m K) (480) : (137) : (135) : (39) (519) : (272)
                                                    c=0.6

(110) *F-Tl.*   610 : 177 : 178 : 68   678 : 355
     Cross 42.   (600) : (187) : (188) : (58)   (658) : (375)
     (F Tl × f tl)   c=1.3
     Cross 44.   155 : 51 : 44 : 19   174 : 95
     (f tl × F Tl)   (152) : (54) : (47) : (16)   (168) : (101)
                                  c=0.8

     Cross 45.   454 : 155 : 133 : 49   503 : 288
     (f tl × F Tl)   (452) : (157) : (135) : (47)   (499) : (292)
                                  c=0.3

(111) *F-K.*   592 : 195 : 188 : 58   650 : 383
     Cross 42.   (594) : (193) : (186) : (60)   (654) : (379)
     (F K × f k)   c=0.3
     Cross 44.   153 : 53 : 51 : 12   165 : 104
     (f k × F K)   (156) : (50) : (48) : (15)   (171) : (98)
                                  c=0.8

     Cross 45.   492 : 117 : 123 : 59   551 : 240
     (f k × F K)   (474) : (136) : (141) : (40)   (514) : (277)
                                  c=2.8

(112) *I-Tl.*   580 : 192 : 192 : 74   654 : 384
     Cross 45.   (574) : (198) : (198) : (68)   (642) : (396)
     (I tl × i Tl)   c=0.8

(113) *I-K.*   590 : 182 : 213 : 53   643 : 395
     Cross 45.   (597) : (175) : (206) : (60)   (657) : (381)
     (I k × i K)   c=0.9

(114) *Le-Tl.*   572 : 196 : 200 : 70   642 : 396
     Cross 45.   (571) : (197) : (201) : (69)   (640) : (398)
     (Le tl × le Tl)   c=0.1

(115) *Le-K.*   585 : 183 : 218 : 52   637 : 401
     Cross 45.   (594) : (174) : (209) : (61)   (655) : (383)
     (Le k × le K)   c=1.2

(116) Wb_2-*Tl.*   587 : 199 : 185 : 67   654 : 384
     Cross 45.   (584) : (201) : (188) : (65)   (649) : (389)
     (Wb_2 tl × wb Tl)   c=0.3

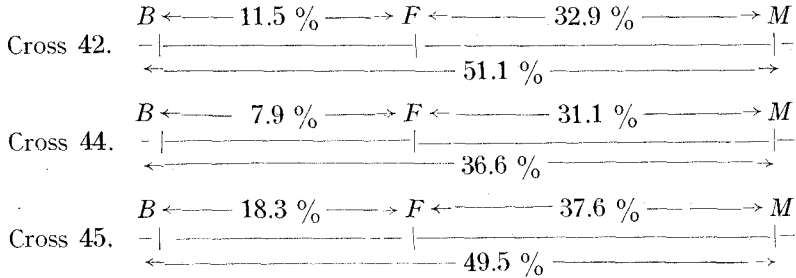(117) W_2^b-K.   555 : 231 : 248 : 4   559 : 479

    Cross 45.   (608) : (178) : (195) : (57)   (665) : (373)

    $(W_2^b\ k \times w^b\ K)$ c=6.9

Gametic ratio is 3.0 : 13.3 : 13.9 : 2.0; crossing-over is 15.6%

(118) S-Tl.   587 : 200 : 185 : 66   653 : 385

    Cross 45.   (585) : (202) : (187) : (64)   (649) : (389)

    $(S\ k\ \times\ s\ K)$ c=0.3

(119) S-K.   556 : 231 : 247 : 4   560 : 478

    Cross 45.   (609) : (178) : (194) : (57)   (666) : (372)

    $(S\ k\ \times\ s\ K)$ c=6.9

Gametic ratio is 3.1 : 13.3 : 13.8 : 2.0; crossing-over is 15.7 %

(120) Tl-K.   610 : 178 : 170 : 75   685 : 348

    Cross 42.   (595) : (193) : (185) : (60)   (655) : (378)

    $(Tl\ K\ \times\ tl\ k)$ c=1.9

    Cross 43.   560 : 221 : 179 : 57   617 : 400

    $(tl\ k\ \times\ Tl\ K)$ (568) : (213) : (171) : (65)   (633) : (384)

    c=1.0

    Cross 44.   195 : 65 : 73 : 22   217 : 138

    $(tl\ k\ \times\ Tl\ K)$ (196) : (64) : (72) : (23)   (219) : (136)

    c=0.2

    Cross 45.   595 : 177 : 208 : 58   653 : 385

    $(tl\ k\ \times\ Tl\ K)$ (597) : (175) : (206) : (60)   (657) : (381)

    c=0.3

§ 3. *Conclusions*

In discussing the conclusions which can be drawn from the factorial relations, we shall first treat those relations which were studied in "Linkage-Studies I or II" and occur again in the present material.

(1) T h e l i n k a g e-g r o u p *B-F-M*. It was concluded before that B, F and M are located in one chromosome in the given order and that the percentage of crossing-over for B-M is about 50 %, while also the linkage F-M is so weak that in some crosses it does not immediately demonstrate itself (cp. 15, pp. 457-460; 16, pp. 286-287). Similar conclusions can be drawn from the present material. B-M (relation 16) do not show any linkage, B-F (rel. 17) are clearly linked in all three

crosses 42, 44 and 45, while M-F (rel. 45) give a rather high value for c in all the crosses where they occurred which value however is too high only in cross 42. The following mapping would follow from the cross-ing-over percentages:

Cross 42.
$$B \longleftarrow 11.5\ \% \longrightarrow F \longleftarrow \text{———— } 32.9\ \% \text{ ————} \longrightarrow M$$
$$\longleftarrow \text{———— } 51.1\ \% \text{ ————} \longrightarrow$$

Cross 44.
$$B \longleftarrow 7.9\ \% \longrightarrow F \longleftarrow \text{———— } 31.1\ \% \text{ ————} \longrightarrow M$$
$$\longleftarrow \text{———— } 36.6\ \% \text{ ————} \longrightarrow$$

Cross 45.
$$B \longleftarrow 18.3\ \% \longrightarrow F \longleftarrow \text{———— } 37.6\ \% \text{ ————} \longrightarrow M$$
$$\longleftarrow \text{———— } 49.5\ \% \text{ ————} \longrightarrow$$

The percentages of double crossing-over were calculated to be resp. — 3.3 %, 1.2 % and 3.2 %. The following interference-relations were found:

				Cross 42	Cross 44	Cross 45
cr.-ov.	B-F	among	non cross-overs F-M	22.0%	9.7%	24.2%
,,	,,	,,	cross-overs ,,	— 9.9%	3.9%	8.5%
,,	F-M	,,	non cross-overs B-F	40.9%	32.4%	42.2%
,,	,,	,,	cross-overs ,,	— 28.4%	15.4%	17.5%
,,	B-M	,,	non cross-overs B-F	40.9%	32.4%	42.2%
,,	,,	,,	cross-overs ,,	128.4%	84.6%	82.5%
,,	,,	,,	non cross-overs F-M	22.0%	9.7%	24.2%
,,	,,	,,	cross-overs ,,	109.9%	96.1%	91.5%

Of course the negative values in cross 42, both for the percentage of double crossing-over and for some of the values in the above table make application of the calculation-method used questionable. Yet it is remarkable that in earlier material, entirely different from the material in cross 42, the same thing was found (16, p. 286). Moreover, the map for cross 42 makes us expect something like a negative crossing-over, since the value for B-M is larger than the sum of B-F and F-M.

I wish to draw the attention to a remarkable relation among the values in the interference-table. The sum of the values on the second

and eighth line is always 100 % and the same is true for those on the fourth and the sixth line. We can express this relation as follows: Crossing-over between F-M means 100 % crossing-over for B-F and B-M together. This is quite plausible, however, for crossing-over between F-M means 100 % crossing-over for B-M minus the double crossing-over; now this double crossing-over is the value for the crossing-over B-F among the cross-overs F-M. Consequently the above rule is a general one and again it is remarkable that the negative values in cross 42 confirm to this rule. This is the more remarkable since these values, according to the above, represent double cross-overs, so that in cross 42 all percentages of double crossing-over are negative.

If we put aside the questionable interference-relations in cross 42, the values for the other crosses indicate a distinct interference, from which we can conclude that B, F and M are located in one chromosome in the given order. As to the considerable variations in the percentages of crossing-over in the three crosses, we see that cross 44 has given the lowest values, while cross 45 gave the highest values and cross 42 is in between the other two; only the value for B-M in cross 45 is an exception. We may, therefore, suppose that the genotypes of the parents of the cross determine the rate of crossing-over in general, as was found by RASMUSSON (10) for other cases of linkage in *Pisum* and which, for the present material, was already demonstrated before (15, pp. 459-460).

(2) The linkage-group D^w-V-Le. Formerly D^w-Le (rel. 55) were found to be independent, c being 1.3 (16, p. 282). In cross 45 however, c=4.6 which indicates linkage. The crossing-over percentage is 63.6%. This is extremely high, but recently a similar value was found for two other genes in back-cross material (17). The extremely loose linkage is better comprehensible than the fact that the genes in question are independent in the one cross and linked in the other. However, more suchlike cases are known in *Pisum*. They may be explained either by variation in the crossing-over percentage, as especially worked out by RASMUSSON (10), or by chromosome-linkage, as was supposed by HÅKANSSON (2) for genes A and Gp in a certain cross of HAMMARLUND (3, 4, 5). The crossing-over for D^w-Le in the old material would have been 53.9 %, so that the variation from this value in 63.6 %, as occurring in the present material, is not very high

It is quite possible, therefore, that the genes Dw and Le, formerly supposed to be independent, are in reality linked, as was demonstrated above. Now V and Le were formerly found to be linked with 13.8 % crossing-over (16, p. 283), so that a linkage-group Dw-V-Le should occur. It is true that Dw-V (rel. 21) were found independent (confirmation of former results, see 15, p. 454), but we may have 50 % crossing-over. Consequently we may conclude that the existence of a linkage-group Dw-V-Le in which Dw-V show about 50 % crossing-over and Dw-Le over 60 %, is possible. Unfortunately the three genes did not occur in one cross, so that the interference-relations could not be studied. Therefore further confirmation is wanted, since also the possibility of chromosome-linkage remains. I am inclined to favor the hypothesis that linkage with variable crossing-over percentages is present, since extreme variations in the strength of linkages are quite common in *Pisum*. It is worth while noting that in the linkage-group Dw-V-Le almost identical values for the crossing-over percentages would occur as in the group Gp-N-Ss, recently described by the present author (17).

(3) T h e   r e l a t i o n F-Le. The value for c in relation 83 of cross 45 is just a little higher than the limit which is usually accepted for independent inheritance. Therefore we deal with a doubtful case. Some facts speak against linkage: In former material (16, p. 284) c=2.0 which indicates independence. As discussed above sub (1) F is linked to B and M; no indications of linkages B-Le (rel. 51) and M-Le (rel. 79) were obtained, however. At last, since Le is probably linked with Dw [as discussed sub (2)], there should be a linkage-group Dw-F-Le with crossing-over percentages of 48.4 % for Dw-F (rel. 24), of 60.1 % for F-Le (rel. 83) and of 63.6 % for Dw-Le (rel. 55) with a double crossing-over of 22.4 %. The interference-relations in this group are as follows:

| cr.-ov.	Dw-F	among	non cross-overs	F-Le	65.2 %
,,	,,	,,	cross-overs	,,	37.3 %
,,	F-Le	,,	non cross-overs	Dw-F	62.7 %
,,	,,	,,	cross-overs	,,	46.3 %
,,	Dw-Le	,,	non cross-overs	Dw-F	73.1 %
,,	,,	,,	cross-overs	,,	53.7 %
,,	,,	,,	non cross-overs	F-Le	65.2 %
,,	,,	,,	cross-overs	,,	62.7 %

The first and the second two cases might indicate location in one chromosome, the last four speak absolutely against it. All cases, however, are readily explained by assuming that D^w and Le on the one hand and F on the other hand are located in different chromosomes. Thus:

$$D^w \qquad\qquad\qquad\qquad Le \qquad\qquad\qquad\qquad F$$
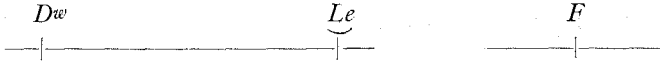
A similar reasoning as was held in Pïsum-Crosses III (14, pp. 234-236) makes us conclude that the above situation is quite plausible, when we keep in mind that the crossing-over percentage for D^w-Le is more than 50 %.

No other relations which were already studied before, need special discussion, so that we can proceed to the new relations.

(4) T h e   l i n k a g e   g r o u p K-W^b_2-S. The linkages, found in cross 45 for W^b_2-S (rel. 91), W^b_2-K (rel. 117) and S-K (rel. 119) suggest the following localization:

$$K \longleftarrow \text{15.6 %} \longrightarrow W^b_2 \longleftarrow \text{0.8 %} \; S$$
$$\longleftarrow \text{15.7 %} \longrightarrow$$
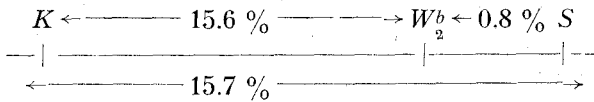
The order of W^b_2 and S, as supposed above, cannot be considered as final, since the difference in the crossing-overs K-W^b_2 and K-S is so extremely small. Calculation of the interference-relations cannot be expected to settle this question, since the cross-overs between W^b_2 and S are so few. Indeed, the calculated interference-relations are inconclusive and therefore will not be mentioned. Localization of K, W^b_2 and S in one chromosome cannot be doubted, but the exact order might also be: K, S, W^b_2.

(5) F i n a l   c o n c l u s i o n s. All relations, not yet disscused, were found to be independent. When we put linked genes between brackets and separate independent genes or groups of linked genes by a dash, we arrive at the following conclusions:

Cross 42: $[B, F, M]$-D^w-V-Tl-K
Cross 43: Fa-Pl-Tl-K
Cross 44: A-$[B, F, M]$-D^w-Fa-Gp-P-Tl-K
Cross 45: A-$[B, F, M]$-$[D^w,Le]$-Fa-I-$[K, W^b_2, S]$-Tl

The final conclusion of Linkage-Studies I and II (16, p. 287) was:

$$A\text{-}[B, F, M]\text{-}D^w\text{-}Fa\text{-}Gp\text{-}[P, Pl]\text{-}[V, Le]\text{-}I\text{-}[W_2^b, S]$$

When we keep in mind that D^w and V in cross 42 are evidently linked with about 50 % crossing-over which changes the last mentioned series by bringing D^w in the group $[V, Le]$, the total results are:

$$A\text{-}[B, F, M]\text{-}[D^w, V, Le]\text{-}Fa\text{-}Gp\text{-}[P, Pl]\text{-}I\text{-}[K, W_2^b, S]\text{-}Tl$$

The number of chromosomes is exceeded by two by the above number of nine independent groups or single genes.

IV. DISCUSSION

In so far as the relations 1 up to 91 were studied by other investigators, these results have been discussed in Linkage-Studies I and II (15, pp. 461-462; 16, pp. 288-290). Since then NILSSON (8, p. 263) obtained some evidence for independence of $V\text{-}I$ (rel. 70) or of $P\text{-}I$ (rel. 66); it cannot be said with certainty whether V or P is the gene in question. Anyhow do these results confirm my former conclusions (16, pp. 282-283).

Among my new relations 92 up to 120 the following were also studied by others. Tl on the one side and A, B, Fa, I and Le on the other side (relations 92, 94, 98, 112 and 114) were found to be independent by WHITE (19, pp. 175, 186-188). $W_2^b\text{-}Tl$ (rel. 116) and $S\text{-}Tl$ (rel. 118) occurred in MEUNISSIER's crosses (7, p. 317) and evidently were independent, although the numbers are small. PELLEW and SVERDRUP (9) found linkage with about 20 % crossing-over between $W_2^b\text{-}K$ (rel. 117), while K on the one side and A, B, Fa, I, Le and Tl on the other side (relations 93, 95, 99, 113, 115 and 120) were said to be independent.

SVERDRUP (11) gave more evidence for these statements and moreover found independence for the same relations as studied by WHITE and mentioned above. Once more I draw the attention to the independence of $D\text{-}Le$ (rel. 55), found by SVERDRUP, because these genes were linked in my present material and independent in my former crosses, as was discussed above. For the rest my results confirm those of the other *Pisum*-workers.

Not much need to be said about the disagreement between the

number of chromosomes and the number of independent genes or groups of linked genes, as occurring in my material. This question was fully discussed in "Linkage-Studies II" (16, pp. 289-290) and the present situation is essentially the same as in the earlier group of genes. It is true that Dw, formerly thought to belong to the "single genes", evidently was brought in the linkage-group V-Le, but Tl has taken its place as "single gene". Consequently four linkage-groups in addition to five independent single genes remain and also the possibility of two linkages with about 50 % crossing-over among the five single genes remains. This would reduce the number of independents to seven. New crosses, adding six more genes to the sixteen already studied, are being investigated and will perhaps settle this question.

V. SUMMARY

1. In former studies the relations between the fourteen genes A, B, Dw, Fa, Gp, P, V, Pl, M, F, I, Le, Wb_2, S were studied. In the present study two more genes were added to the above fourteen namely:

   Tl : tendrilled leaves; tl : "acacia"-leaves.
   K : normal wings; k : keeled wings.

2. Putting linked genes between brackets and separating independent genes or linkage-groups by a dash, the total results can be expressed as:

   A-$[B, F, M]$-$[Dw, V, Le]$-Fa-Gp-$[P, Pl]$-I-$[K, Wb_2, S]$-Tl

   Further confirmation is wanted with regard to the position of Dw in the second linkage-group.

3. The number of bivalent chromosomes is still exceeded by two by the number of independents, but two linkages with about 50 % crossing-over between two of the single genes might occur.

4. Methods for calculating trifactorial gametic ratios from given F_2 ratios were described on pp. 6—7.

to Professor Dr. J. A. HONING. During the ten years of my Pisum-work Prof. HONING gave me all possible facilities in his fields and laboratory, although I did not belong to his staff. Moreover I am indebted for his constant interest and critical remarks during the progress of the work.

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SUMMARIZED TOTAL F_2-RESULTS OF CROSS 43:

$fa\ tl\ k\ pl\ \times\ Fa\ Tl\ K\ Pl$

Phenotype	class	total	F_2-groups, originated from 1 F_1-plant each								
			1	2	3	4	5	6	7	8	9
Fa Tl K Pl	1	327	40	50	32	46	38	41	29	42	9
——— *K pl*	2	121	17	14	8	20	11	10	16	17	8
——— *k Pl*	3	116	12	17	12	18	14	12	11	17	3
——— *k pl*	4	55	6	9	5	5	4	7	10	7	2
Fa tl K Pl	5	108	16	16	8	17	10	9	16	13	3
——— *K pl*	6	38	5	3	4	8	3	4	7	3	1
——— *k Pl*	7	35	6	4	2	4	5	8	1	5	0
——— *k pl*	8	13	0	4	0	1	1	0	5	1	1
fa Tl K Pl	9	87	11	13	7	16	8	9	7	11	5
——— *K pl*	10	25	1	6	2	3	4	2	2	3	2
——— *k Pl*	11	35	6	3	3	6	4	2	3	5	3
——— *k pl*	12	15	1	2	1	4	1	0	4	2	0
fa tl K Pl	13	23	2	2	3	1	4	3	3	4	1
——— *K pl*	14	10	3	2	0	2	1	0	0	1	1
——— *k Pl*	15	8	3	1	1	1	0	0	1	1	0
——— *k pl*	16	1	0	1	0	0	0	0	0	0	0
	total	1017	129	147	88	152	108	107	115	132	39