

**Pisum-Crosses IV; The Genetics of Wax**  
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**INTRODUCTION.**

In Pisum-Crosses II (16<sup>1)</sup>, pp. 339—341) two genes were described as the basis of the character „wax”. These genes are *Bl* and *W* and their action is such that *Bl Bl W W* represents the normal glaucous type with „much” wax, *Bl Bl w w* means „little” wax and either *bl bl W W* or *bl bl w w* stand for total absence of wax, the extreme emerald type. In the same publication it was stated that two more classes than „much”, „little” and „no” wax could be distinguished and that new crosses were made to study these characteristics. This work, consisting of the study of 28 crosses with a total of over 10.000 F<sub>2</sub> individuals, is finished now and will be reported in the present paper. The results are in full agreement with the hypothesis, advanced in 1927 (17).

Instead of wax the term „bloom” is also used in English literature. This seems to be confusing, however, since it has been translated in German by „Blüte”. Therefore the term wax will be used exclusively.

**MATERIALS AND METHODS.**

As parental types, lines of the following varieties were used: *a*, Emereva; *b*, Johnson's British Empire; *c*, Pois à brochettes; *d*, Smaragd Reuzen; *e*, Sutton's Emerald Gem; *f*, Belle de Châtenay; *g*, Vlijmsche Krombek; *h*, Haarsteegsche or Express. Thruout this paper the parental lines will be represented by the letters *a*, *b*, . . . . . *h*; in some cases, however, also the varietal names will be indicated in abbreviated form, namely „Em.” for Emereva, „J.'s Br. Emp.” for Johnson's British Empire, „P. à br.” for Pois à brochettes, „Sm. R.” for Smaragd Reuzen, „S.'s Em. G.” for Sutton's Emerald Gem, „Chât.” for Belle de Châtenay, „Vl. Kr.” for Vlijmsche Krombek, and „H.” for Haarsteegsche.

The normal glaucous type, as found in most Pisum forms, is *h*. The others are „emerald”, but there are 4 types of emerald, depending on the amount of wax. Lines *a*, *b* and *c* were sent to me by Mr. A. MEUNISSIER at Verrières-le-Buisson; *b* is absolutely wax-free, *a* and *c* have some wax, just as *f* which I originally obtained from Prof. A. M. SPRENGER at Wageningen. The types *a*, *c* and *f* are called the „little wax” types. Lines *d*, *e* and *g* were obtained from Mr. A. R. ZWAAN at Voorburg—the Hague; *e* possesses an amount of wax which is in between nothing and

<sup>1)</sup> Reference is made by bracketed figures to „Literature Cited” on p. 12.

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little; it has some wax, but „extremely little”. On the other hand *d* and *g* have decidedly more wax than little, but yet are emeralds; so these two lines are „in between little and much”.

It is convenient to indicate the different types by the class-number 4, 3, 2, 1 and 0 according to the relative amount of wax. Two genotypes of class 2 were found which are called 2<sup>a</sup> and 2<sup>b</sup>. Table 1 summarizes the phenotypes of the parental lines.

TABLE 1.  
THE PHENOTYPES OF THE PARENTAL LINES.

Class	Amount of wax	Parental line
4	much	<i>h</i> (H.)
3	between much and little	<i>d</i> (Sm. R.), <i>g</i> (Vl. Kr.)
2 <sup>a</sup>	little	<i>a</i> (Em.)
2 <sup>b</sup>	little	<i>c</i> (P. à br.), <i>f</i> (Chât.)
1	extremely little	<i>e</i> (S.'s Em. G.)
0	nothing	<i>b</i> (J.'s Br. Emp.)

The differentiation of the 5 classes has taken 3 years of observation. After having learned to see the differences, practically no classification-difficulties were met with. Special attention should be paid to the amount of wax on the stem; sometimes the young pod may reveal typical characteristics, but the foliage does not demonstrate typical differences. The best time for taking notes is the week after blossoming has started; it is a good procedure to observe the wax on the internode below the node which bears the first inflorescence.

It should be kept in mind that it is not possible to determine the actual amount of wax. Comparing reveals relative differences and all classifications were made by comparing the F<sub>2</sub>-individuals with the parental types and with the F<sub>1</sub>. In the more complicated F<sub>2</sub>'s the classification of the first 25 or 30 plants took two or three times as long as of the next 25 or 30. When a reclassification was made, a perfect agreement between the different observations was always obtained.

The crosses are indicated by simply putting the parental symbols side by side: *ab*, *ac*, etc. Three of the crosses have already been mentioned in earlier publications, where numbers were used to symbolize the crosses. These are cross 9 (15, pp. 12—13) which is *fh*, crosses 25 and 37 (16, pp. 339—340) which are *bc* and *bf* respectively. The two letters, symbolizing a cross, are always put in alphabetic order. In some of them, however, the mother is not the first mentioned, but the second; these crosses are *bg*, *cg*, *df* and *eg*. The F<sub>1</sub>'s are numbered e.g. *ab*-1, *ab*-2, etc.; the F<sub>2</sub>'s are called e.g. *ab*-1-1, *ab*-1-2, ..... *ab*-2-1, ..... etc.

The usual methods of growing were followed. In most of the cases it was not necessary to give the plants a support like chicken-wire, because they could be cleared away at a rather early stage of development. The nature of the characters makes it possible to grow two generations a year under Dutch climatic conditions. However, since mildew may interfere with an easy observation of the wax-character, fall-sown material was only used to make supplementary observations.

Calculation-methods used will be discussed in the following chapters.

#### EXPERIMENTAL RESULTS.

The detailed experimental results are put together in appendix I on p. 14 and are summarized in table 2 on p. 4. In the appendix the crosses are put in the same order as in column 2 of table 2. Of course, when no segregation in  $F_2$  took place, the crosses are not treated in the appendix. This is the case for *dg* and *cf*. With regard to the crosses of the type class 4  $\times$  class 4, the results in the table refer to a number of crosses, partly published in earlier papers, partly unpublished. The crosses *bc*, *bf* and *fh* were treated before, as was mentioned above. Yet they are included in the appendix in a somewhat different form, for completeness' sake.  $F_2$ 's of *ah* were studied in 1927 and 1928. The 1927 results were not quite satisfactory; the deviation from expectation was fairly large. In 1928 better results were obtained. In this year the deviations ran in opposite direction as in 1927, so that there is no reason to suspect the monofactorial character of this cross.

As to the comparison between observed numbers and calculated ones, the standard error from expectation was used when the  $F_2$  was composed of two classes. In these cases the value of *c*, as mentioned in the appendix, indicates actual deviation divided by standard deviation. When *c* is not larger than 3, the deviations are within the limits expected in random sampling. Harris (5) has pointed to the fact that the use of probable errors — consequently also of standard deviations — is not correct when the population is composed of more than two classes. For these cases he introduced PEARSON'S goodness of fit method which is as follows. If *o*, *o'* . . . . are observed and *c*, *c'* . . . . are the corresponding calculated values,  $\chi^2$  is determined from the formula

$$\chi^2 = \sum \frac{(o-c)^2}{c}$$

To this value for  $\chi^2$  corresponds a certain value *P* which indicates the chance that a worse agreement between observation

and calculation is obtained than in the experiment in question. Of course, the smaller  $\chi^2$  and the larger P is, the better is the agreement. According to FISHER (2, p. 79), it is strongly indicated that the hypothesis fails to account for the whole of facts, when P is below 0.02; he draws a conventional live at 0.05 and considers that lower values indicate a real discrepancy.

The values of P were determined with the aid of FISHER's table of  $\chi^2$  (2, pp. 98—99). As seen in the appendix the lowest value obtained is 0.21 both in cross *bg* and in cross *ce*, so that there is a good agreement between observation and calculation in all crosses.

In the appendix theoretical expectations are put in parentheses.

The results of the crosses of the types  $4 \times 3$ ,  $3 \times 2^b$ ,  $2^a \times 1$  tend to demonstrate in the simplest way that a distinct limit between classes 4 and 3, 3 and 2, 2 and 1 exists. The same is true for classes 1 and 0, when we consider the latter two classes of the  $F_2$  of cross *be*, representing the  $1 \times 0$  combination.

TABLE 2.

## SUMMARIZED RESULTS FROM THE CROSSES.

Combination of parent-types, expressed as class-numbers.	Crosses. *)	Class-number of $F_1$ .	Type of $F_2$ -segregation.	Total number of $F_2$ -plants.	Years of study.
$4 \times 4$	several	4	no segregation	> 26000	1922—1928
$4 \times 3$	<i>dh, gh</i>	4	3 : 1	1045	1927
$4 \times 2^a$	<i>ah</i>	4	3 : 1	819	1927, 1928
$4 \times 2^b$	<i>ch, fh</i>	4	3 : 1	994 **)	1922, 1927
$4 \times 1$	<i>eh</i>	4	3 : 1	252	1927
$4 \times 0$	<i>bh</i>	4	3 : 1	305	1927
$3 \times 3$	<i>dg</i>	3	no segregation	515	1927
$3 \times 2^a$	<i>ad, ag</i>	4	9 : 3 : 4	243	1925
$3 \times 2^b$	<i>cd, cg, df, fg</i>	3	3 : 1	806	1928
$3 \times 1$	<i>de, eg</i>	4	9 : 3 : 4	515	1928
$3 \times 0$	<i>bd, bg</i>	4	9 : 3 : 4	384	1928
$2^a \times 2^b$	<i>ac, af</i>	4	9 : 7	1124	1927
$2^a \times 1$	<i>ae</i>	2	3 : 1	455	1927
$2^a \times 0$	<i>ab</i>	4	9 : 3 : 4	329	1928
$2^b \times 2^b$	<i>cf</i>	2	no segregation	464	1927
$2^b \times 1$	<i>ce, ef</i>	4	9 : 3 : 4	592	1925, 1928
$2^b \times 0$	<i>bc, bf</i>	4	9 : 3 : 4	609 **)	1925
$1 \times 0$	<i>be</i>	4	9 : 3 : 4	278	1928

\*) *a* = Emereva; *b* = Johnson's British Empire; *c* = Pois à brochettes; *d* = Smaragd Reuzen; *e* = Sutton's Emerald Gem; *f* = Châtenay; *g* = Vlijmsche Krombek; *h* = Haarsteegsche.

\*\*) included similar  $F_2$ -groups.

## INTERPRETATION.

As an explanation of the experimental results I offer the hypothesis that the different types, as mentioned in table 1, be represented by the following genetic formulae:

Class 4, line <i>h</i> (H.):	<i>Bl</i>	<i>Bl</i>	$W_2^a$	$W_2^a$	$W_2^b$	$W_2^b$
Class 3, lines <i>d</i> (Sm. R.), <i>g</i> (Vl. Kr.):	<i>Bl</i>	<i>Bl</i>	$W_2^a$	$W_2^a$	$W_1^b$	$W_1^b$
Class 2b, lines <i>c</i> (P. à br.), <i>f</i> (Chât):	<i>Bl</i>	<i>Bl</i>	$W_2^a$	$W_2^a$	$w^b$	$w^b$
Class 2a, line <i>a</i> (Em.):	<i>Bl</i>	<i>Bl</i>	$W_1^a$	$W_1^a$	$W_2^b$	$W_2^b$
Class 1, line <i>e</i> (S's Em. G.):	<i>Bl</i>	<i>Bl</i>	$w^a$	$w^a$	$W_2^b$	$W_2^b$
Class 0, line <i>b</i> (J's Br. Emp.):	<i>bl</i>	<i>bl</i>	$W_2^a$	$W_2^a$	$W_2^b$	$W_2^b$

*Bl* is groundfactor and its presence is prerequisite for the action of the other factors. The gene, formerly called *W*, is split into two genes, called  $W^a$  and  $W^b$ , each of which consists of three multiple allelomorphs, indicated as  $W_2^a - W_1^a - w^a$ , resp. as  $W_2^b - W_1^b - w^b$ . The dominance runs in the given order. It is the easiest way to pronounce the letter-indices before the number-indices, e.g.  $W_2^a$  is pronounced:  $W - a - 2$ , etc. The use of single letters is impossible, because the Pisum-alphabet is long exhausted.

All results from crossing are readily explained by the above hypothesis, as is seen from a comparison between the actual results and the expectation, built up from the formulae.

The existence of a triple allelomorphic set  $W_2^a - W_1^a - w^a$  is proved by the results of the crosses  $4 \times 2^a$ ,  $4 \times 1$  and  $2^a \times 1$  which all three segregate in  $F_2$  according to a (3) : (1) scheme. The same is true for the existence of the multiple set  $W_2^b - W_1^b - w^b$ , when we consider the crosses  $4 \times 3$ ,  $4 \times 2^b$  and  $3 \times 2^b$ .

Several combinations have not been found as originally existing lines, but must have occurred as segregates. Combination  $Bl W_1^a W_1^b$  — using single letters for simplicity's sake — has split up from crosses *ad* and *ag* and, according to the  $F_2$ -composition, must represent class 2. Proceeding in this way, we arrive at the results composed in table 3.

TABLE 3.

THE POSSIBLE FACTOR-COMBINATIONS AND THEIR  
PHENOTYPIC EXPRESSION.

Combination.			Expression.	Source from which expected.
(1) <i>Bl</i>	$W_2^a$	$W_2^b$	class 4	original line <i>h</i>
(2) <i>Bl</i>	$W_2^a$	$W_1^b$	class 3	original lines <i>d, g</i>
(3) <i>Bl</i>	$W_2^a$	$w^b$		original lines <i>c, f</i>
(4) <i>Bl</i>	$W_1^a$	$W_2^b$	class 2	original line <i>a</i>
(5) <i>Bl</i>	$W_1^a$	$W_1^b$		crosses <i>ad, ag</i>
(6) <i>Bl</i>	$W_1^a$	$w^b$		crosses <i>ac, af</i>
(7) <i>Bl</i>	$w^a$	$W_2^b$		original line <i>e</i>
(8) <i>Bl</i>	$w^a$	$W_1^b$	class 1	crosses <i>de, eg</i>
(9) <i>Bl</i>	$w^a$	$w^b$		crosses <i>ce, ef</i>
(10) <i>bl</i>	$W_2^a$	$W_2^b$		original line <i>b</i>
(11) <i>bl</i>	$W_2^a$	$W_1^b$		crosses <i>bd, bg</i>
(12) <i>bl</i>	$W_2^a$	$w^b$	class 0	crosses <i>bc, bf</i>
(13) <i>bl</i>	$W_1^a$	$W_2^b$		cross <i>ab</i>
(14) <i>bl</i>	$w^a$	$W_2^b$		cross <i>be</i>
(15) <i>bl</i>	$W_1^a$	$W_1^b$		
(16) <i>bl</i>	$W_1^a$	$w^b$		
(17) <i>bl</i>	$w^a$	$W_1^b$	not expected	
(18) <i>bl</i>	$w^a$	$w^b$		

From this table we can draw some conclusions regarding the action of the factors. Combinations (10) up to (14) show that presence of *Bl* is necessary for  $W^a$  and  $W^b$  to express themselves, because they have no effect in *Bl*'s absence. Combinations (7) up to (9) indicate that *Bl* in itself gives the effect of class 1. That there is no difference in the expression of (7), (8) and (9) suggests that either  $W_2^b$  or  $W_1^b$  do not act in the absence of  $W_2^a$  or  $W_1^a$ .

At first it looks rather puzzling that the four combinations (3) up to (6) all represent the phenotypic class 2. We might suppose that very delicate phenotypic differences occur, but that they are too small to be observed. A more satisfactory hypothesis,

however, is the following. The similar phenotypic expression of (4), (5) and (6) suggests that  $W_2^b$  and  $W_1^b$  do not influence the effect already brought about by  $Bl + W_1^a$ , or, in other words that only  $Bl + W_2^a$  are composite groundfactor for  $W_2^b$  and for  $W_1^b$ , but that  $Bl + W_1^a$  are not. Furthermore comparison of (3) and (6) — which have a similar effect — with (1) and (2) makes it evident that the only difference between  $W_2^a$  and  $W_1^a$  is that  $W_2^a$  is influenced by  $W_2^b$  or  $W_1^b$  in the presence of  $Bl$ , but that  $W_1^a$  is not.

Summarizing we arrive at the following positive action of the factors:

- $Bl$  : groundfactor for wax, in itself giving extremely little wax, class 1.
- $W_2^a$  : together with  $Bl$ , but without  $W_2^b$  and  $W_1^b$ , gives class 2.
- $W_1^a$  : allelomorphous to  $W_2^a$  and acting as  $W_2^a$ , but not influenced by  $W_2^b$  or  $W_1^b$ .
- $W_2^b$  : together with  $Bl + W_2^a$  gives class 4.
- $W_1^b$  : together with  $Bl + W_2^a$  gives class 3, allelomorphous to  $W_2^b$ .

When we give the numerical value of 1 to the action of  $Bl$  and also to the action of  $W_2^a$  and  $W_1^a$ , of 2 to  $W_2^b$  and of 1 to  $W_1^b$ , the different factorial combinations get exactly the numerical value of the class which they represent, when we add the actions of all factors in a certain combination and when we keep in mind the mutual influence of the factors. Combination (1) e.g. gives  $1 + 1 + 2 = 4$ ; (2) gives  $1 + 1 + 1 = 3$ ; (3) gives  $1 + 1 + 0 = 2$ ; (4), (5) and (6) also give  $1 + 1 + 0 = 2$ , because  $W_2^b$  and  $W_1^b$  are supposed not to give any effect in these combinations, and so on. Of course this is merely a suggestion how the factors might work quantitatively which has no real value.

Furthermore the similar effect of  $W_2^a$  and  $W_1^a$  combined with the fact that only  $W_2^a$  is influenced by other genes which do not influence  $W_1^a$ , is suggestive for supposing analogy with two stereo-isomeric chemical substances, of which only one is acted upon by a certain enzym. We might, therefore, consider the difference between  $W_2^a$  and  $W_1^a$  as a support for KARCZAG'S recent theory on the nature of the gene (8a).

#### THE INTERRELATION OF FACTORS $R$ AND $I$ TO $Bl$ , $W^a$ AND $W^b$ .

Besides the wax-genes the two genes for cotyledon-shape and cotyledon-color demonstrated their action by segregation in the

material studied. *R* means a smooth surface and *r* means a wrinkled surface of the cotyledons, while *I* represents yellow and *i* stands for green. The interrelations of *R* and *I* to the wax genes were studied.

With regard to the study of linkage relations, multiple allelomorphs must of course be considered as represented by one and the same locus in a chromosome. Therefore  $W_2^a$ ,  $W_1^a$  and  $w^a$ , just as  $W_2^b$ ,  $W_1^b$  and  $w^b$  represent one locus.

The detailed results of the interrelations  $R-BI$ ,  $R-W^a$ ,  $R-W^b$ ,  $I-BI$ ,  $I-W^a$  and  $I-W^b$  are given in appendix II on p. 26. The bifactorial segregations of the different crosses — indicated in the first column of the tables — are kept separate. Immediately below the row of totals the expectation is mentioned, printed in brackets. The meaning of the numbers behind the semi-colons and the method of calculation of the expectations need some further discussion.

Expectations are calculated according to KAPPERT's method which was cursorily indicated in a 1924 publication (6, pp. 5—6) and worked out in more detailed form in 1927 (8). The principle of this method is as follows. A bifactorial segregation is composed of two monofactorial segregations which theoretically split according to a 3 : 1 scheme. The bifactorial expectation is then calculated as  $(3 \times 3) : (3 \times 1) : (1 \times 3) : (1 \times 1) = 9 : 3 : 3 : 1$ . If now the monofactorial segregations show deviations from a 3 : 1 scheme — which they almost always do — the expectation is no longer 9 : 3 : 3 : 1. If one of the monofactorial segregations is 2.5 : 1.5 instead of 3 : 1, and if the other is 3 : 1, the expectation is  $(2.5 \times 3) : (2.5 \times 1) : (1.5 \times 3) : (1.5 \times 1) = 7.5 : 2.5 : 4.5 : 1.5$ . Or, in general terms, if the one monofactorial segregation is  $p : q$  and the other one is  $r : s$ , the theoretical bifactorial expectation in case of independence is  $\frac{pr}{n} : \frac{ps}{n} : \frac{qr}{n} : \frac{qs}{n}$ , wherein  $n = p + q = r + s$ .

Dividing the terms by  $n$  is necessary in order to get the same total of the expectation as of the actual numbers. A simple calculation shows that the deviations from expectation must be equally large in the four classes, but that the first and the fourth run in opposite direction as the second and the third.

If the two outer terms and the two inner terms are added, both of actual and of theoretical numbers, the ratio of original combinations to recombinations is obtained. The numbers behind the semi-colons in the tables indicate this ratio and  $c$  is the actual deviation divided by the standard deviation of this two class ratio.

The values for  $c$  vary from 0.2 to 1.2, so that there is no reason



to suspect the independence in any of the cases and to surmise linkage. No indications of linkage were obtained between  $Bl-W^a-W^b$ , as the results from the foregoing chapter show, for the expectations were calculated for independent factors. Consequently we must conclude that  $R-I-Bl-W^a-W^b$  form a group of 5 independent factors, unless some of them are linked with percentages of crossing-over of about 50 %.

#### DISCUSSION.

The genetics of wax is far more complicated indeed than one would suppose it to be when starting the research. Besides a groundfactor two sets of three multiple allelomorphic genes influence the wax character, so that it is determined by 5 positive genes which mutually influence each other in their action in a rather complicated way.

It is remarkable that all 4 different emerald types studied show a one-factor difference with glaucous. This would suggest that the emeralds have arisen from the phylogenetically probably older glaucous type by simple point mutations.

When we compare the results, described in the foregoing part of this paper, with the results of other workers, we find a difficulty in the fact that most of them did not distinguish between different emerald types. The monofactorial difference between glaucous and emerald with dominance of glaucous, as found by VILMORIN (14), perhaps by TSCHERMAK (12, p. 180) — his numbers are small and not absolutely convincing —, by HAMMARLUND (4, p. 107) and by DE HAAN (3, p. 495—496), is in agreement with my results, but it is impossible to say which factor-pair was involved in their crosses.

VILMORIN (13, 14) found a two-factor difference between different emeralds. My crosses  $ab$  (Em.  $\times$  J.'s Br. Emp.) and  $ac$  (Em.  $\times$  P. à br.) are exactly the same as VILMORIN's and confirm his results. I only distinguished between different emerald types in the  $F_2$  of cross  $ab$  and found a (9) : (3) : (4) segregation, whereas VILMORIN had obtained a (9) : (7) segregation.

Recently SVERDRUP (10, p. 225, 227) mentioned the existence of two emeralds. One of her types is probably the same as my parental line  $c$  and the other one is perhaps identical with my line  $a$ . This is not to be said with absolute certainty however. The (9) : (7)  $F_2$ -segregation which SVERDRUP obtained (10, p. 250) is in agreement with my results. Therefore it may be that her factor-pairs are identical with  $W_2^a-W_1^a$  and  $W_2^b-w^b$ , as occurring in my cross  $ac$ .

The demonstration of the existence of multiple allelomorphism

in *Pisum* is not new. Ten years ago already WHITE (18) stated that height was determined by one set of 3 and another set of 4 factors which may be supposed to be multiple allelomorphs. WHITE did not mention this term himself, however, and his actual data are far too meagre to be convincing. Therefore BROTHERTON (1) must be considered to be the first who has clearly demonstrated the existence of three allelomorphs, namely in the case of stipule-shape. It is interesting to see that he found two allelomorphs, called  $x$  and  $x'$  which do not differ in their expression, but only in their stability. Doubtlessly there is analogy with the difference between  $W_2^a$  and  $W_1^a$  as discussed on p. 7. Both KAPPERT (7) and the TEDINS (11) found the leaf axil spot to be determined by three multiple allelomorphs in addition to a basic gene. Finally NEFF and WHITE (9) have found a series of three multiple allelomorphs, acting upon chlorophyll deficiencies.

The demonstration of two sets of three multiple allelomorphs in addition to a basic factor, interacting in a rather complicated but interesting way and determining the characteristic wax, as described in the present paper, is entirely new and offers a type of inheritance of a quantitative character, hitherto unreported in genetics, as far as I know.

#### SUMMARY.

1. A number of emerald varieties of *Pisum* were divided in 4 classes according to the relative amount of wax which they develop. Together with the glaucous type the classes are numbered 0, 1, 2, 3, 4, where 0 represents the total absence of wax — the extreme emerald — and 4 stands for the normal glaucous.
2. Between 8 lines all possible 28 crosses were studied which led to the result that besides a basic factor two series of three multiple allelomorphic factors influence the wax character.
3. The following action of the individual factors is evident:
  - $B1$  : groundfactor for wax, in itself giving extremely little wax, class 1. In the absence of  $B1$  class 0 is always brought about.
  - $W_2^a$  : together with  $B1$ , but without  $W_2^b$  and  $W_1^b$ , gives little wax, class 2.
  - $W_1^a$  : allelomorphic to  $W_2^a$  and acting as  $W_2^a$ , but not influenced by  $W_2^b$  or  $W_1^b$ .
  - $w^a$  : allelomorphic to  $W_2^a$  and  $W_1^a$ , no effect.

$W_2^b$ : together with  $Bl + W_2^a$  gives glaucous, class 4.

$W_1^b$ : together with  $Bl + W_2^a$  gives class 3; allelomorphous to  $W_2^b$ .

$w^b$ : allelomorphous to  $W_2^b$  and  $W_1^b$ , no effect.

4. Factors  $Bl$ ,  $W^a$  and  $W^b$ , together with  $R$  (cotyledon shape) and  $I$  (cotyledon color), represent a group of 5 independently inherited chromosome loci.

Wageningen, Oct. 29, 1928.

## LITERATURE CITED.

- (1) BROTHERTON, JR., WILBER: Further studies on the inheritance of „rogue” type in garden peas (*Pisum sativum* L.). (*J. agr. Res.* 24, 1923: 815—852.)
- (2) FISHER, R. A.: Statistical methods for research workers. Oliver and Boyd, Edinburgh and London, VII + 239 pp., 1925.
- (3) HAAN, H. DE: Length-factors in *Pisum*. (*Genetica* 9, 1927: 481—498.)
- (4) HAMMARLUND, C.: Zur Genetik, Biologie und Physiologie einiger Erysiphaceen. (*Hereditas* 6, 1925: 1—126.)
- (5) HARRIS, J. A.: A simple test of the goodness of fit of Mendelian ratios. (*Amer. Naturalist* 46, 1912: 741—745.)
- (6) KAPPERT, HANS: Über die Zahl der unabhängigen Merkmalsgruppen bei der Erbse. (*Zschr. ind. Abst. u. Vererb. L.* 36, 1924: 1—32.)
- (7) KAPPERT, H.: Über absolut gekoppelte Faktoren oder multiple Allelomorphe bei *Pisum*. (*Ber. D. Bot. Ges.* 43, 1925: 583—589.)
- (8) KAPPERT, H.: Über die Auswertung dihybrider Spaltungsreihen bei Koppelungsstudien. (*Zschr. ind. Abst. u. Vererb. L.* 44, 1927: 303—314.)
- (8a) KARCZAG, L.: Die Stereogene als Erbeinheiten. (*Zschr. ind. Abst. u. Vererb. L.* 48, 1928: 86—144.)
- (9) NEFF, DOROTHY I. and ORLAND E. WHITE: Inheritance studies in *Pisum* VI. Multiple allelomorphism and the inheritance of green and yellow foliage and pod color. (*Amer. J. Bot.* 14, 1927: 379—394.)
- (10) SVERDRUP, ASLAUG: Linkage and independent inheritance in *Pisum sativum*. (*J. Gen.* 17, 1927: 221—251.)
- (11) TEDIN, HANS and OLOF: Contributions to the genetics of *Pisum* IV: Leaf axil colour and grey spotting on the leaves. (*Hereditas* 7, 1925: 102—108.)
- (12) TSCHERMAK, ERICH VON: Bastardierungsversuche an Lebköjen, Erbsen und Bohnen mit Rücksicht auf die Faktorenlehre. (*Zschr. ind. Abst. u. Vererb. L.* 7, 1912: 81—234.)

- (13) VILMORIN, PH. DE: Recherches sur l'hérédité mendélienne. (C. R. Acad. Sc. Paris 1910—II: 548—551.)
- (14) VILMORIN, PH. DE: Etude sur le caractère „Adhérence des grains entre eux" chez le pois „chenille". (IV Conf. int. Génétique, Paris 1911: 368—372.)
- (15) WELLENSIEK, S. J.: Pisum-crosses I. (Genetica 7, 1925: 1—64.)
- (16) WELLENSIEK, S. J.: Pisum-crosses II. (Genetica 7, 1925: 337—364.)
- (17) WELLENSIEK, S. J.: Preliminary note on the genetics of wax in Pisum. (Amer. Naturalist 62, 1928: 94—96.)
- (18) WHITE, ORLAND E.: Inheritance studies in Pisum III. The inheritance of height in peas. (Mem. Torrey Bot. Club 17, 1918: 316—322; repr. as Contr. Brooklyn Bot. Garden No. 20.)

## APPENDIX I.

## THE WAX-SEGREGATIONS.

Cross *dh* (Sm. R. × H.): cl. 3 × cl. 4 → cl. 4 → cl. 4 : cl. 3 = (3) : (1)

	class 4	class 3
<i>dh</i> —1	100	48
2	31	10
3	86	24
4	132	49
	total F <sub>2</sub> 349	131
	(360)	(120)
	c = 1.1	

Cross *gh* (Vl. Kr. × H.): cl. 3 × cl. 4 → cl. 4 → cl. 4 : cl. 3 = (3) : (1)

	class 4	class 3
<i>gh</i> —1	102	45
2	107	33
3	39	12
4	172	55
	total F <sub>2</sub> 420	145
	(423.75)	(141.25)
	c = 0.4	

Cross *ah* (Em. × H.): cl. 2a × cl. 4 → cl. 4 → cl. 4: cl. 2 = (3): (1)

	class 4	class 2
<i>ah</i> -1	79	36
2	84	45
3	104	47
4	63	32
5	49	22
	<u>total F<sub>2</sub> (1927) 379</u>	<u>182</u>
	(420.75)	(140.25)
	c = 4.0	
<i>ah</i> -6	30	9
7	95	21
8	78	25
	<u>total F<sub>2</sub> (1928) 203</u>	<u>55</u>
	(193.5)	(64.5)
	c = 1.4	
	<u>total '27 and '28 582</u>	<u>237</u>
	(614.25)	(204.75)
	c = 2.6	

Cross *ch* (P. à br. × H.): cl. 2b × cl. 4 → cl. 4 → cl. 4: cl. 2 = (3): (1)

	class 4	class 2
<i>ch</i> -1	109	49
2	57	21
3	65	21
4	54	26
	<u>totaal F<sub>2</sub> 285</u>	<u>117</u>
	(301.5)	(100.5)
	c = 1.9	

Cross *fh* (Chât × H.): cl. 2b × cl. 4 → cl. 4 → cl. 4: cl. 2 = (3): (1)

	class 4	class 2
<i>fh</i> -1	45	15
2	44	17
3	18	6
4	23	7
5	23	3
6	3	3
7	23	1
8	35	7
9	14	3
10	22	12
11	27	18
	total $F_2$ 277	92
	(276.75)	(92.25)
	$c = 0.03$	
	total $F_3$ 445	147
	(444)	(148)
	$c = 0.1$	

Cross *eh* (S's Em. G. × H.): cl. 1 × cl. 4 → cl. 4 → cl. 4: cl. 1 = (3): (1)

	class 4	class 1
<i>eh</i> -1	61	20
2	48	19
3	80	24
	total $F_2$ 189	63
	(189)	(63)
	$c = 0.0$	



Cross *bh* (J.'s Br. Emp. × H.): cl. 0 × cl. 4 → cl. 4 → cl. 4 : cl. 0 = (3) : (1)

	class 4	class 0
<i>bh</i> —1	30	14
2	48	17
3	18	11
4	75	23
5	51	18
	total F <sub>1</sub> 222	83
	(228.75)	(76.25)
	c = 0.9	

Cross *ad* (Em. × Sm. R.): cl. 2a × cl. 3 → cl. 4 → cl. 4 : cl. 3 : cl. 2 = (9) : (3) : (4)

	class 4	class 3	class 2
<i>ad</i> —1	64	20	28
2	20	12	19
	total F <sub>1</sub> 84	32	47
	(92)	(30)	(41)
		$\chi^2 = 1.71$	$P = 0.44$

Cross *ag* (Em. × Vl. Kr.): cl. 2a × cl. 3 → cl. 4 → cl. 4 : cl. 3 : cl. 2 = (9) : (3) : (4)

	class 4	class 3	class 2
<i>ag</i> —1	46	16	18
	(45)	(15)	(20)
		$\chi^2 = 0.49$	$P = 0.81$

Cross *cd* (P à br. × Sm. R.): cl. 2b × cl. 3 → cl. 3 → cl. 3: cl. 2 = (3): (1)

	class 3	class 2
<i>cd</i> —1	16	9
2	29	10
3	34	12
4	28	5
5	17	7
	total F <sub>2</sub> 124	43
	(125. 25)	(41.75)
	c = 0.2	

Cross *cg* (P. à br. × Vl. Kr.): cl. 2b × cl. 3 → cl. 3 → cl. 3: cl. 2 = (3): (1)

	class 3	class 2
<i>cg</i> —1	45	18
2	60	21
3	74	22
	total F <sub>2</sub> 179	61
	(180)	(60)
	c = 0.1	

Cross *df* (Sm. R × Chât): cl. 3 × cl. 2b → cl. 3 → cl. 3: cl. 2 = (3): (1)

	class 3	class 2
<i>df</i> —1	18	6
2	15	2
3	21	3
4	13	5
5	18	3
6	6	4
7	17	13
	total F <sub>2</sub> 108	36
	(108)	(36)
	c = 0.0	

Cross *fg* (Chât. × Vl. Kr.): cl. 2b × cl. 3 → cl. 3 → cl. 3 : cl. 2 = (3) : (1)

	class 3	class 2
<i>fg</i> —1	18	3
2	55	22
3	46	20
4	61	30
	total $F_2$ 180	75
	(191.25)	(63.75)
	$c = 1.6$	

Cross *de* (Sm. R. × S.'s Em. G.): cl. 3 × cl. 1 → cl. 4 →  
cl. 4 : cl. 3 : cl. 1 = (9) : (3) : (4)

	class 4	class 3	class 1
<i>de</i> —1	34	12	16
2	8	5	4
3	15	4	6
	total $F_2$ 57	21	26
	(58.5)	(19.5)	(26)
		$\chi^2 = 0.15$	$P = 0.97$

Cross *eg* (S.'s Em. G. × Vl. Kr.): cl. 1 × cl. 3 → cl. 4 →  
cl. 4 : cl. 3 : cl. 1 = (9) : (3) : (4)

	class 4	class 3	class 1
<i>eg</i> —1	25	12	11
2	32	17	16
3	70	17	26
4	43	14	13
5	64	26	25
	total $F_2$ 234	86	91
	(231)	(77)	(103)
		$\chi^2 = 2.48$	$P = 0.29$

Cross *bd* (J's Br. Emp. × Sm. R.): cl. 0 × cl. 3 → cl. 4 →  
cl. 4 : cl. 3 : cl. 0 = (9) : (3) : (4)

	class 4	class 3	class 0
<i>bd</i> -1	4	2	2
2	4	4	5
3	9	0	4
4	12	2	5
	total $F_3$ 29	8	16
	(30)	(10)	(13)
		$\chi^2 = 1.43$	$P = 0.49$

Cross *bg* (J's Br. Emp. × Vl. Kr.): cl. 0 × cl. 3 → cl. 4 →  
cl. 4 : cl. 3 : cl. 0 = (9) : (3) : (4)

	class 4	class 3	class 0
<i>bg</i> -1	14	2	5
2	20	5	12
3	22	5	8
4	23	6	9
5	25	8	13
6	29	8	14
7	34	14	11
8	34	4	6
	total $F_3$ 201	52	78
	(186)	(62)	(83)
		$\chi^2 = 3.12$	$P = 0.21$

Cross *ac* (Em. × P. à br.): cl. 2a × cl. 2b → cl. 4 → cl. 4 : cl. 2 = (9) : (7)

	class 4	class 2
<i>ac</i> -1	63	39
2	88	62
3	67	49
4	58	50
5	96	68
	total F <sub>2</sub> 372	268
	(360)	(280)
	c = 1.0	

Cross *af* (Em. × Chât.): cl. 2a × cl. 2b → cl. 4 → cl. 4 : cl. 2 = (9) : (7)

	class 4	class 2
<i>af</i> -1	114	84
2	103	77
3	57	49
	total F <sub>2</sub> 274	210
	(272)	(212)
	c = 0.2	

Cross *ae* (Em. × S.'s Em. G.): cl. 2a × cl. 1 → cl. 2 → cl. 2 : cl. 1 = (3) : (1)

	class 2	class 1
<i>ae</i> -1	86	22
2	38	14
3	33	10
4	47	12
5	104	33
6	44	12
	total F <sub>2</sub> 352	103
	(341.25)	(113.75)
	c = 1.2	

Cross *ab* (Em. × J's Br. Emp.) : cl. 2a × cl. o → cl. 4 →  
cl. 4 : cl. 2 : cl. o = (9) : (3) : (4)

	class 4	class 2	class 0
<i>ab</i> -1	23	12	15
2	37	11	7
3	47	16	15
4	32	7	8
5	31	6	15
6	30	6	11
	total $F_2$ 200 (185)	58 (62)	71 (82)
		$\chi^2 = 2.94$	$P = 0.24$

Cross *ce* (P. à br. × S's Em. G.) : cl. 2b × cl. 1 → cl. 4 →  
cl. 4 : cl. 2 : cl. 1 = (9) : (3) : (4)

	class 4	class 2	class 1
<i>ce</i> -1	94	28	44
2	70	20	22
3	59	10	22
	total $F_2$ 223 (207)	58 (69)	88 (92)
		$\chi^2 = 3.19$	$P = 0.21$

Cross *ef* (S's Em. G. × Chât.) : cl. 1 × cl. 2b → cl. 4 →  
cl. 4 : cl. 2 : cl. 1 = (9) : (3) : (4)

	class 4	class 2	class 1
<i>ef</i> -1	69	16	31
2	32	13	16
3	27	5	14
	total $F_2$ 128 (125)	34 (42)	61 (56)
		$\chi^2 = 2.03$	$P = 0.38$

Cross *bc* (J's Br. Emp. × P. à br.): cl. 0 × cl. 2b → cl. 4 →  
cl. 4; cl. 2; cl. 0 = (9); (3); (4)

	class 4	class 2	class 0
<i>bc</i> -1	31	9	9
2	23	7	16
3	48	17	29
total F <sub>2</sub>	102	33	54
	(106)	(36)	(47)
		$\chi^2 = 1.44$	$P = 0.49$

### F<sub>3</sub> generation

#### 1) class 4 F<sub>2</sub>, segregating as F<sub>2</sub>

<i>bc</i> -1-7	15	5	7
<i>bc</i> -1-23	12	5	7
<i>bc</i> -1-30	19	7	10
<i>bc</i> -2-1	35	12	9
<i>bc</i> -2-35	27	7	14
<i>bc</i> -2-39	21	8	12
<i>bc</i> -3-13	8	4	7
total F <sub>3</sub>	137	48	66
	((141))	(47)	(63)
		$\chi^2 = 0.27$	$P = 0.88$

#### 2) class 4 F<sub>2</sub>, segregating cl. 4: cl. 2 = (3); (1)

	class 4	class 2
<i>bc</i> -1-1	10	7
<i>bc</i> -1-3	53	6
<i>bc</i> -1-47	17	11
<i>bc</i> -2-18	27	14
<i>bc</i> -2-42	35	5
<i>bc</i> -3-30	37	10
<i>bc</i> -3-84	34	8
total F <sub>3</sub>	213	61
	(205.5)	(68.5)
$c =$	1.0	

3) Class 4  $F_2$ , segregating cl. 4 : cl. 0 = (3) : (1)

	class 4	class 0
bc-1-4	42	10
bc-1-42	21	9
bc-2-17	38	10
bc-2-38	21	10
total $F_2$	122	39
	(120.75)	(40.25)
c =	0.2	

4) 1  $F_2$  class 4 kept constant

Consequently:

class 4 $F_2$	actual	expected	ratio
segregating as $F_2$	7	(8.5)	(4)
" cl. 4 : cl. 2 = (3) : (1)	7	(4.2)	(2)
" cl. 4 : cl. 0 = (3) : (1)	4	(4.2)	(2)
constant	1	(2.1)	(1)
		$\chi^2 = 2.78$	$P = 0.44$

5) Class 2  $F_2$ , segregating cl. 2 : cl. 0 = (3) : (1)

	class 2	class 0
bc-1-48	27	4
bc-2-30	43	16
bc-2-43	30	11
bc-3-67	35	6
bc-3-78	26	9
bc-3-80	20	6
total $F_2$	181	52
	(174.75)	(58.25)
c =	0.9	

6) 2  $F_2$ 's class 2 kept constant, consequently:

$$\text{class 2 } F_2 \text{ segregating : class 2 } F_2 \text{ constant} = \frac{6}{(5.3)} : \frac{2}{(2.7)}$$

$$c = 0.5$$

7) 12  $F_2$ 's class 0 kept constant.



Cross *bf* (J.'s Br. Emp. × Chât.) : cl. 0 × cl. 2b → cl. 4 →  
cl. 4 : cl. 2 : cl. 0 = (9) : (3) : (4)

	class 4	class 2	class 0
<i>bf</i> -1	48	16	19
2	19	8	12
3	25	9	11
	total F <sub>1</sub> 92	33	42
	(94)	(31)	(42)
		$\chi^2 = 0.18$	$P = 0.91$

Cross *be* (J.'s Br. Emp. × S.'s Em. G.) : cl. 0 × cl. 1 → cl. 4 →  
cl. 4 : cl. 1 : cl. 0 = (9) : (3) : (4)

	class 4	class 1	class 0
<i>be</i> -1	29	8	12
2	18	4	8
3	28	3	9
4	20	7	5
5	21	10	4
6	20	6	5
7	34	10	17
	total F <sub>1</sub> 170	48	60
	(157)	(52)	(69)
		$\chi^2 = 2.55$	$P = 0.29$

## APPENDIX II.

THE RELATIONS OF R AND I TO BI, W<sup>a</sup> AND W<sup>b</sup>*R—B<sub>l</sub>*

<i>ab</i>	194	:	48	:	64	:	23		
<i>bc</i>	112	:	42	:	23	:	12		
<i>be</i>	162	:	50	:	56	:	10		
<i>bf</i>	113	:	35	:	12	:	7		
<i>bg</i>	204	:	64	:	49	:	14		
<i>bh</i>	177	:	67	:	45	:	16		
total	962	:	306	:	249	:	82		
	(960)	:	(308)	:	(251)	:	(80)		
								1044	: 555
								(1040)	: (559)
								c =	0.2

*R—W<sup>a</sup>*

<i>ab</i>	147	:	47	:	53	:	11		
<i>be</i>	126	:	36	:	44	:	12		
<i>de</i>	60	:	18	:	18	:	8		
total	333	:	101	:	115	:	31		
	(335)	:	(99)	:	(113)	:	(33)		
								364	: 216
								(368)	: (212)
								c =	0.3

*R—W<sup>b</sup>*

<i>bc</i>	84	:	28	:	18	:	5		
<i>bf</i>	83	:	30	:	9	:	3		
<i>bg</i>	164	:	40	:	37	:	12		
<i>cd</i>	96	:	25	:	28	:	18		
<i>de</i>	45	:	15	:	12	:	6		
<i>df</i>	81	:	25	:	27	:	11		
<i>dh</i>	278	:	103	:	71	:	28		
total	831	:	266	:	202	:	83		
	(820)	:	(277)	:	(213)	:	(72)		
								914	: 468
								(892)	: (490)
								c =	1.2

*I—B<sup>l</sup>*

<i>ab</i>	210	:	59	:	48	:	12	
<i>bd</i>	25	:	8	:	12	:	8	
<i>be</i>	167	:	48	:	51	:	12	
<i>bg</i>	215	:	69	:	38	:	9	
total	617	:	184	:	149	:	41	658 : 333
	(620)	:	(182)	:	(146)	:	(43)	(663) : (328)

c = 0.3

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*I—W<sup>a</sup>*

<i>ab</i>	162	:	48	:	38	:	10	
<i>ad</i>	91	:	32	:	25	:	15	
<i>ah</i> (1927)	293	:	160	:	86	:	22	
<i>ah</i> (1928)	160	:	45	:	43	:	10	
<i>be</i>	129	:	38	:	41	:	10	
<i>ce</i>	205	:	62	:	76	:	26	
<i>de</i>	60	:	22	:	18	:	4	
<i>eh</i>	158	:	49	:	31	:	14	
total	1258	:	456	:	358	:	111	1369 : 814
	(1269)	:	(445)	:	(347)	:	(122)	(1391) : (792)

c = 1.0

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*I—W<sup>b</sup>*

<i>ad</i>	66	:	25	:	18	:	7	
<i>bd</i>	20	:	5	:	9	:	3	
<i>bg</i>	173	:	42	:	28	:	10	
<i>ce</i>	169	:	36	:	54	:	22	
<i>cg</i>	131	:	47	:	48	:	14	
<i>de</i>	45	:	15	:	12	:	6	
<i>df</i>	72	:	29	:	36	:	7	
<i>fh</i>	188	:	59	:	89	:	33	
<i>gh</i>	367	:	125	:	53	:	20	
total	1231	:	383	:	347	:	122	1353 : 730
	(1222)	:	(392)	:	(355)	:	(114)	(1336) : (747)

c = 0.8

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