



# **Inheritance of colours and pod characters in *Phaseolus vulgaris* L.**

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Inheritance  
of colours and pod characters  
in *Phaseolus vulgaris* L.

DOOR

R. PRAKKEN



'S-GRAVENHAGE  
MARTINUS NIJHOFF  
1934

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INHERITANCE OF COLOURS AND POD CHARACTERS IN  
PHASEOLUS VULGARIS L.

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Inheritance  
of colours and pod characters  
in *Phaseolus vulgaris* L.

PROEFSCHRIFT

TER VERKRIJGING VAN DEN GRAAD VAN DOCTOR IN DE WIS- EN NATUURKUNDE AAN DE RIJKS-UNIVERSITEIT TE UTRECHT OP GEZAG VAN DEN RECTOR-MAGNIFICUS DR. C. W. STARBUSMANN, HOOGLEERAAR IN DE FACULTEIT DER RECHTSGELEERDHEID, VOLGENS BESLUIT VAN DEN SENAAAT DER UNIVERSITEIT TEGEN DE BEDENKINGEN VAN DE FACULTEIT TE VERDEDIGEN OP MAANDAG 2 JULI 1934 DES NAMIDDAGS TE VIER UUR

DOOR

ROELOF PRAKKEN

GEBOREN TE ENTER



'S-GRAVENHAGE  
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1934

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*AAN DE NAGEDACHTENIS  
VAN MIJN OUDERS*



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## INTRODUCTION

The parent plants used in this investigation are the french beans „Fijne tros” and „Wagenaar”.

„Fijne tros” is a rather late, whiteflowering, white-seeded pole bean, with non-parchmented, nearly stringless pods.

„Wagenaar” is an early bush bean, very pale rose-flowering and yellow-seeded; the pod is semi-parchmented and provided with an extremely strong string.

The main intention was to investigate the inheritance of the strength of the string. Besides other characters were investigated. As the segregation for seedcoat colour was rather intricate, its discussion takes up most of the space in this work. Length of stem and linkage relations will not be dealt with in this publication.

In 1930 I had at my disposal 48  $F_2$  plants, of which in 1931 and 1932 I grew the  $F_3$  and  $F_4$  progeny. Their analysis led to provisional results. In the same year 1930 I repeated the cross myself. The three  $F_1$  plants (Fijne tros  $\times$  Wagenaar) resulting from this cross formed the material for more extensive investigations.

These  $F_1$  plants of 1931 (and those of '32) were on a large scale self-fertilized and backcrossed by the two parent plants. The castration of *Phaseolus* flowers is difficult to perform and even with accurate control of the stigma some pollen grains might be overlooked. I therefore castrated the flower buds already one or two days before they would have opened; one day after the castration they were pollinated after renewed close examination of the stigma. Among hundreds of backcross plants not a single individual has been found which was apparently due to self-fertilization of the  $F_1$  mother plant. The discussion of the inheritance of seedcoat colours is mainly based upon the backcross with Wagenaar.

## CHAPTER I

### STEM, FLOWER AND SEEDCOAT COLOURS

#### § 1. *Introduction*

Many factors for seedcoat colour have as yet been determined by the various investigators. It is, however, very difficult to find the connection between their investigations. In the first place the description of the colour types is often superficial. Secondly the greater part of the crosses contain rather few of the very numerous colours. And finally the connection between stem, flower and seedcoat colours has nearly always been neglected. After the analysis work of LAMPRECHT, the situation has become much more favourable, because we have now the disposal of a very accurately described material, which has been analysed for many factors.

It is for the following reasons that I venture to add the analysis of the cross *Fijne tros* × *Wagenaar* to the extensive material already known:

1. The analysis concerns seedcoat colour in connection with stem and flower colour.
2. The number of factors involved is rather great.
3. Backcrosses serve as a test for the factorial scheme.
4. The making of linkage investigations.

Points 1 and 2 make the comparability with earlier investigations fairly great. Therefore I have tried to limit the introduction of new factor symbols as much as possible although I am aware that only definite crosses could give certainty about supposed identity of factors.



§ 2. *Present state of the factorial analysis of the seedcoat colour.*

The factors for seedcoat colour as yet known may be classified as follows:

- a. Groundfactor.
- b. Complementary factors.
- c. Modifying factors.

a. *Groundfactor.*

This factor must be homozygous dominant or heterozygous for the seedcoat to be able to show colour. If the groundfactor, which I call P (SHULL, 1907b, p. 829) is recessive, the seedcoat and as a rule the flower too, are white. KOOIMAN (1931, p. 331) speaks of *ground- or ferment factor*, LAMPRECHT (1933, p. 313) of a *fundamental gene*.

b. *Complementary factors.*

The groundfactor alone does not produce colour. Colour only appears, if, besides the groundfactor P, there is at least one dominant „complementary” factor. Each of the complementary factors produces (in cooperation with the groundfactor P) a definite, mostly very pale seedcoat colour. More complementary factors together generally give a darker colour. This was for the first time analysed by KOOIMAN (1920), who adopted in the analysis of his cross between a yellow brown and a white race a groundfactor (A) and three complementary factors, his „*chromogenous factors*” B, C and D. LAMPRECHT was the first to give complete certainty about the existence of the two types of factors by crossing two coloured-seeded races, which gave in the F<sub>2</sub>-generation  $\frac{1}{16}$  white-seeded plants. As yet LAMPRECHT has described six complementary factors or „*colour genes*”.

The consequences of these relations are:

1. White-seeded are all p-plants and also those P-plants in which all complementary factors are recessive.
2. If one or more complementary factors are homozygous dominant, the ratio white-seeded: coloured-seeded can only be 1 : 3 (Pp-plants).
3. If the groundfactor is homozygous dominant and none of the

complementary factors are homozygous dominant, the proportion of white-seeded plants is  $\frac{1}{4^n}$ , in which formula  $n$  is the number of heterozygous complementary factors.

4. If the groundfactor is heterozygous and again none of the complementary factors are homozygous dominant, the proportion of white-seeded plants is  $\frac{1}{4} + \frac{1}{4^n} \times \frac{3}{4}$ .

### c. Modifying factors.

They only influence the colours produced by cooperation between groundfactor and complementary factors. The influence of such modifying factors (KOOIMAN 1931, p. 346: „intensifiers” E and F) may be rather general, but in other cases it is restricted to definite factor combinations.

These relations between ground-, complementary and modifying factors may be the cause of very intricate cryptomeric, epi- and hypostatic phenomena.

Here I have to mention some unexpected and as yet unexplained results of LAMPRECHT (1934*b*, p. 205). In his cross no. 38 between two coloured-seeded races, white-seeded plants appeared in the  $F_2$ , in spite of the fact that both parents possessed the complementary factor C; and in cross 33 a good many more white ones appeared than was to be expected according to the groundfactor-complementary factors assumption. One of the parents in both crosses was the partly coloured („teilarbig”) race L 29. According to LAMPRECHT „verbleibt da vorläufig wohl nur die Annahme, dass es eine oder gewisse „Kombinationen von Genen für Teilfarbigkeit gibt, bei denen die „Ganze Testa ungefärbt verbleibt.”

### § 3. The cross *Fijne tros* × *Wagenaar*

The investigation of an  $F_2$  (*Wagenaar* × *Fijne tros*) consisting of 48 plants and their  $F_3$  and  $F_4$  offspring (1930—1932) induced me to the provisional adoption of a factorial scheme. For the analysis to be given here I will, however, use the more extensive material, viz.  $F_1$ ,  $F_2$ ,  $F_3$  and backcrosses with their progeny of the years 1931—1933. The provisional scheme was wholly confirmed by this analysis.

In this section colour names and factor symbols are used without ample explanation. The accurate description of the colour types and the justification of the choice of symbols will be given in the following sections. The colour numbers refer to the folding scheme table 31 and to the colour description in § 5.

*a. Description of the parent plants and  $F_1$*

The Fijne tros race is white-seeded and white-flowering. Hypocotyl, cotyledons and stems are green without any trace of anthocyanin. Only at the base of the full grown pod very small violet spots occur.

The Wagenaar race has a yellowish seedcoat, shading (especially at the ventral side) sometimes to canary yellow; the hilumring (cf. fig. 1) is yellow brown; around the hilumring is a narrow violet corona. Cf. the colour description of no. 3 in § 5. Its flower colour is a very pale pink or lilac rose (Repertoire de Couleurs par R. OBERTHÜR 130, 1, 132, 1 and paler). At the base of the standard and wings the colour is somewhat darker (Rep. de Couleurs 187, 1, pale light lilac). Hypocotyl and cotyledons are partly covered with a rose anthocyanin colour (Rep. de Couleurs between

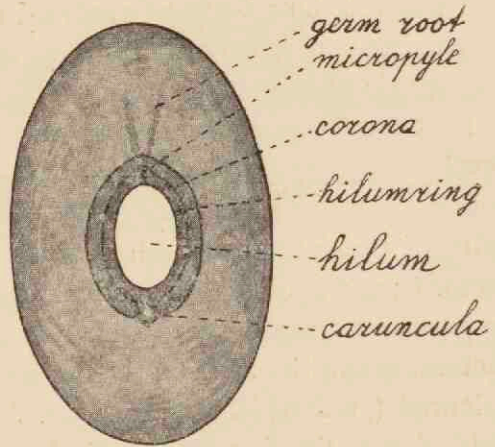


FIG. 1. Ventral side of a bean.

150, 3—4 and 118, 3; RIDGWAY, Color Standards, Plate XIII, 1' c). This cotyledon colour is brightest immediately after germination and vanishes about three days later. The anthocyanin colour of the hypocotyl appears about ten days after germination. The full grown pod is spotted with the same rose colour.

All  $F_1$  plants have a black mottled seedcoat (fig. 2). Their flower colour is a light violet; the wings a little more reddish than Rep. de Couleurs 195, 1 (Violet Mauve); the standard 189, 2 (Bishops violet). Hypocotyl and cotyledons are partly covered with a very

conspicuous dark blue violet anthocyanin colour (Rep. de Couleurs between 199, 4 and 190, 4, often much darker; the paler

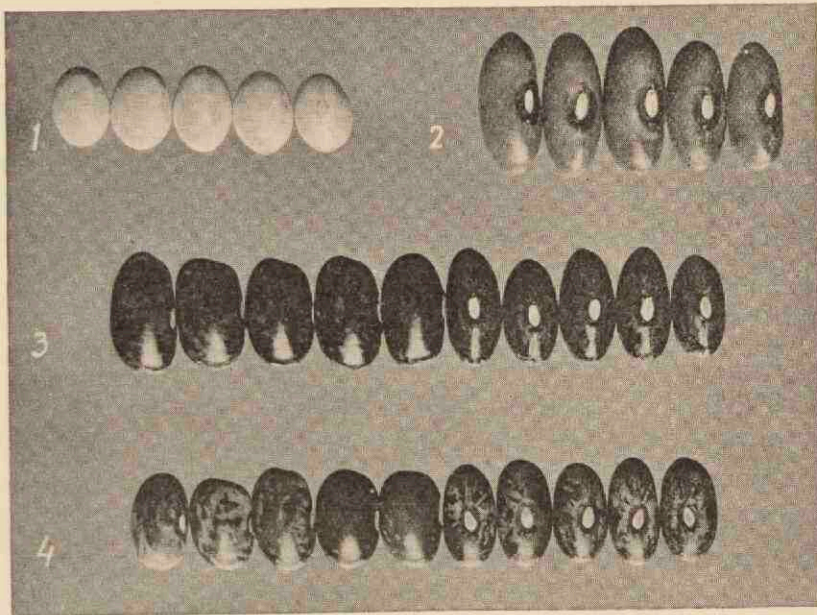


FIG. 2.

1. Fijne tros (white): pp JJ Sh Sh (or Sh sh)  $\widehat{cM} \widehat{cM}$  GG BB VV.
2. Wagenaar (yellowish): PP JJ Sh Sh  $\widehat{Cm} \widehat{Cm}$  gg bb vv.
3. F<sub>1</sub> (black mottled): Pp JJ Sh Sh (and Sh sh)  $\widehat{Cm} \widehat{cM}$  Gg Bb Vv.
4. Dull black mottled F<sub>2</sub> plant with nearly colourless background (of family 55-2): P J sh  $\widehat{Cm} \widehat{cM}$  G B V.

colours 195, 4; RIDGWAY, Color Standards Pl. XLIV, between 69'' i and 65'' m). The stem is green, except for narrow violet spots at the nodes; the full grown pod is dark blue violet spotted.

Henceforward I will use the following indications:

	Stem colour	Flower colour
Fijne tros . . . . .	green	white
Wagenaar . . . . .	rose	pale rose
F <sub>1</sub> . . . . .	violet	violet-1.

*b. Segregation for stem and flower colour*

As to stem and flower colour in all generations only the following three plant types occur:

1. Green stem, white flower (white seedcoat).
2. Rose stem, pale rose flower (coloured seedcoat).
3. Violet stem, violet flower (coloured seedcoat).

As to the violet flower colour, in  $F_2$  the violet-1  $F_1$  colour appears, but also darker types. Moreover some flowers are a little more reddish violet. The darker colours range between Rep. de Couleurs 189, 2—3 (Bishops violet) and 180, 1—2 (Reddish violet). I tried to distinguish between the paler  $F_1$  colour (violet-1) and darker colours (violet-2 and 3), but a sharp discrimination was impossible. The  $F_3$  and  $F_4$  generations, however, have shown that the violet-1  $F_2$  plants nearly always segregate into violet and pale rose, consequently are heterozygous; violet-2 and 3 plants do not segregate the pale rose type and therefore are homozygous.

The extension of the violet stem colour in the  $F_2$  plants was extremely variable: sometimes only the cotyledons and hypocotyl showed small spots, whereas in other cases nearly the whole plant was violet.

The rose hypocotyl and cotyledon colour was not always found. With a view to investigating whether or not this rose colour may be totally lacking in pale rose flowering plants, I planted 1600 seeds of  $F_1$  plants in flowerpots and examined the young plants twice closely, viz. about 2 days (cotyledons) and 10 days (hypocotyl) after their germination. Then I planted the green seedlings in the field and inspected the plants later on as to flower colour. It will be seen (table 1) that out of 262 rose plants only one had not been recognized by cotyledon or hypocotyl colour.

The numbers of the three plant types green, rose and violet approach the bifactorial 4 : 3 : 9 ratio, but there is a considerable shortage of rose. The  $F_2$  families in table 2 show the same marked shortage of rose plants, together with a surplus of violet ones ( $D/m = 2.59$ ). The tables 1 and 2 together give:

	white flower	pale rose flower	violet flower	total
Observed . . . . .	816	540	1876	3232
Expected ratio 4 : 3 : 9 . .	808	606	1818	3232
D/m . . . . .	0.32	2.97	2.06	

That is too few rose plants, too many violet ones (D/m still less than three, but very high!). The two factors involved are the „ground factor” P (SHULL, 1907*b*, p. 829) and a „violet factor” which I call V (LAMPRECHT, 1932*a*, p. 177; JOHANNSEN, 1926 p. 443). Both races have a complementary factor J (LAMPRECHT, 1932*a*, p. 176) in common, as will be shown later on.

Fijne tros is: pp VV (JJ).

Wagenaar is: PP vv (JJ).

F<sub>1</sub> is: Pp Vv (JJ).

F<sub>2</sub> consists of 4 white flowering p plants, 3 pale rose flowering Pv plants and 9 violet flowering PV ones. Of these 9 PV plants 6 are Vv (violet-1) and 3 are VV (violet-2 and 3); according to table 2 actually found 567 violet-1 and 283 violet-2 and 3.

The backcrosses of F<sub>1</sub> with the parent plants agree with the bifactorial scheme for stem and flower colour.

Fijne tros × F<sub>1</sub> (pp VV × Pp Vv) gave the expected 1 : 1 ratio:

	white	violet-1 and 2	total
Observed . . . . .	81	78	159
Expected 1 : 1 . . . . .	79.50	79.50	
D/m . . . . .	0.24		

The reciprocal cross, F<sub>1</sub> × Fijne tros gave 6 white and 4 violet. In both crosses not a single rose plant occurred.

Wagenaar × F<sub>1</sub> (PP vv × Pp Vv) gave:

	pale rose	violet-1	total
Observed . . . . .	42	40	82
Expected 1 : 1 . . . . .	41	41	
D/m . . . . .	0.22		

Therefore no trace of certation! Neither white flowering plants nor violet-2 or 3 ones were found.

The reciprocal cross,  $F_1 \times$  Wagenaar, showed a marked deficiency of rose plants:

	pale rose	violet-1	total
Observed . . .	96	124	220
Expected 1 : 1 .	110	110	
D/m . . . . .	1.88		

The segregation for the factors P and V in the  $F_3$  families is shown by tables 3—7. Table 3 contains the progeny of homozygous  $F_2$  plants. The flower colour of all PP VV  $F_2$  plants was violet-2; in their  $F_3$  only violet-2 (and 3) occurred.

Table 4 of Pp vv plants; the agreement with the 1 : 3 ratio is quite satisfactory:

	white	pale rose	total
Observed . . .	75	229	304
Expected 1 : 3 .	76	228	
D/m . . . . .	0.13		

Table 5 of Pp VV plants. One of the  $F_2$  mother plants was classified as violet-1, three as violet-1—2 and five as violet-2. In the  $F_3$  progeny the flower colour violet-1 was not found. All families together gave:

	white	violet	total
Observed . . .	64	187	251
Expected 1 : 3 .	62.75	188.25	
D/m . . . . .	0.18		

Table 6 of PP Vv plants. Nearly all  $F_2$  mother plants were noted as violet-1. The figures point to a clear monofactorial segregation.

There is no evidence of a possibly weaker constitution of rose PP vv plants as compared with violet PP Vv and PP VV ones.

	pale rose	violet	total
Observed . . .	88	264	352
Expected 1 : 3 .	88	264	
D/m . . . . .	0.00		

The progeny of double heterozygous Pp Vv plants (table 7) showed very surprising results! In most of the families the number of rose plants is considerably lower than the expected  $\frac{3}{16}$ . Only in 7 families out of 41 it is  $\frac{3}{16}$  or a little more. Summarizing the families, we obtain very high D/m values:

	white	pale rose	violet	total
Observed . . . .	297	166	751	1214
Expected 4 : 3 : 9	303.50	227.62	682.88	
D/m . . . . .	0.43	4.53	3.94	

The percentage pale rose flowering plants is 13.67 instead of 18.75. In order to determine possible differences between Pp Vv plants (as to the number of rose plants in their progeny), I made (spring 1934) a second sowing of those families, which contained the lowest and the highest percentages of the rose plant type. Tables 8 and 9 show the results. The percentages of rose plants in the second sowings of both groups are nearly the same: 15.32 and 15.42. Therefore I conclude that the shortage of rose plants is a general characteristic of the F<sub>2</sub> and of probably all F<sub>3</sub> families of Pp Vv mother plants.

These „irregularities” are up to now unexplained. The segregation for stem and flower colour served as a foundation for the analysis of the seedcoat colour. The results I arrived at concerning the inheritance of seedcoat colour have not given me any indication as to the cause of the irregularities.



Of the 88  $F_2$  plants of which the progeny has been tabulated, there appeared to be (tables 3—7) 27 PP plants and 61 Pp ones (the expected ratio 1 : 2 is 29.3 and 58.7).

c. Seedcoat colour in the backcross  $F_1$  with  
Wagenaar

In all tables the columns for the seedcoat colours are found under the heading of the three stem and flower colour types, since with each of them specific seedcoat colours correspond, i.e. the factors P and V for stem and flower colour are just as well factors for seedcoat colour.

As the Vv plants can only be distinguished from the VV ones by the flower colour and not by the seedcoat colour, only the three plant types

green stem (white flower),  
rose stem (pale rose flower) and  
violet stem (violet-1, 2 or 3 flower)

are used in the tables.

The backcross  $F_1 \times$  Wagenaar ( $Pp Vv \times PP vv$ ) and the reciprocal one contain among the rose v plants 4 seedcoat colour types, which show a strongly marked difference. They are called:

yellowish (the Wagenaar-colour),  
orange (yellow brown),  
greenish brown and  
brown.

Among the violet V plants only 2 seedcoat colour types can be easily distinguished, viz.:

violet and  
black.

The violets are partly pure violet, partly rather brown violet. As I could not yet distinguish these two violet types at the time when I analysed the first backcrosses, I have taken them together as violet.

In each colour class there occur (table 10) about as many plants with mottled as with selfcoloured seeds; the dark pattern of the mottled seeds has the same colour as the selfcoloured ones. In each colour class, except for the pale yellowish, the mottled seeds are easy to discover.

It appears (bottom rows of table 10) that the numbers of the six

colour types are in accordance with the ratio 1 : 1 : 1 : 1 : 2 : 2.

	ob- served	expected	D/m
yellowish . . .	38	37.75	0.04
orange . . . .	31	37.75	1.17
greenish brown	28	37.75	1.69
brown . . . .	41	37.75	0.56
violet . . . .	90	75.50	1.93
black . . . .	74	75.50	0.20

It seems to be (leaving for the present the mottling out of consideration) a trifactorial backcross, the Wagenaar race (yellowish) being recessive for each of these three factors. One of the three is of course the factor V. The other two factors must be responsible for the four seedcoat colour types among rose plants. The difference between violet and black seedcoat must depend upon one of these two factors, whereas the influence of the other one is inconspicuous in the violet class (brown violet and pure violet) and hardly or not at all perceptible in the black colour class (the black of some plants is a very dark chrome green, cf. p. 199 and p. 210).

The progeny of the selfcoloured backcross plants exactly confirmed the trifactorial conception. All plants must be recessive or heterozygous concerning the three factors involved. As to the groundfactor, part of the backcross plants appeared to be PP, the other part Pp. As I have not found any indication of linkage between P and those three factors, I have counted together the coloured-seeded offspring of PP and Pp plants and left the white-seeded offspring out of consideration. The signification of the homozygous dominant factors JJ and Sh Sh and of the linked factors  $\widehat{CM} \widehat{CM}$  in the formulae of the genotypes in tables 11—18 will be explained later.

Selfcoloured yellowish (table 11) does not segregate (except white).

Selfcoloured orange (table 12) segregates into:

	observed	expected 1 : 3	D/m
yellowish . . .	1	4	1.73
orange . . . .	15	12	

This „orange factor” I call G (LAMPRECHT 1932a, p. 177; LUNDBERG and ÅKERMAN 1917).

Selfcoloured greenish brown (table 13) segregates into:

	observed	expected 1 : 3	D/m
yellowish . . . . .	6	5	0.50
greenish brown . . . . .	14	15	

This „greenish brown factor” I call B (LAMPRECHT 1932a, p. 177; JOHANNSEN 1926 p. 443).

The constitution of the diverse backcross plants for the factors G, B and V is:

yellowish:	gg bb vv (no. 3; Wagenaar colour).
orange:	Gg bb vv. (no. 9)
greenish brown:	gg Bb vv. (no. 15)
brown:	Gg Bb vv. (no. 21)
violet:	gg bb Vv. (no. 6)
brown violet:	Gg bb Vv. (no. 12)
black:	gg Bb Vv (no. 18) and Gg Bb Vv. (no. 24)

Selfcoloured brown (Gg Bb vv; table 14) segregates into:

	formula	ob- served	expected 1 : 3 : 3 : 9	D/m
yellowish . . .	g b v	4	7.44	1.30
orange . . . . .	G b v	25	22.31	0.64
greenish brown	g B v	24	22.31	0.40
brown . . . . .	G B v	66	66.94	0.17

Family 491 does not segregate yellowish and orange, but this family is very small.

Selfcoloured violet (gg bb Vv; table 15) segregates into:

	formula	ob- served	expected 1 : 3	D/m
yellowish . . .	g b v	16	15	0.30
violet . . . . .	g b V	44	45	

Selfcoloured brown violet (Gg bb Vv; table 16) segregates into:

	formula	observed	expected 1:3:3:9	D/m
yellowish. . .	g b v	1	1.63	0.51
orange . . . .	G b v	1	4.87	1.90
violet . . . .	g b V	4	4.87	0.44
brown violet .	G b V	20	14.63	2.12

Selfcoloured black (gg Bb Vv; table 17) segregates into:

	formula	observed	expected	D/m
yellowish. . .	g b v	3	3.37	0.21
greenish brown	g B v	10	10.13	0.05
violet . . . .	g b V	16	10.13	2.05
black . . . . .	g B V	25	30.37	1.47

These black-seeded mother plants were recessive for the factor *g*. Their colour was somewhat greenish black and in family 513 I found among the „black” offspring 4 plants with a blackish chrome green seedcoat colour. In some other families too these greenish black seeds appeared, but as a rule they did not show a strongly marked difference with the pure black ones (cf. p. 199 and p. 210).

One selfcoloured black backcross plant (table 18) segregates according to all three factors and therefore is Gg Bb Vv:

	formula	observed	expected 1:3:3:9:12:36
yellowish	g b v	1	0.31
orange . . . . .	G b v	0	0.94
greenish brown .	g B v	0	0.94
brown . . . . .	G B v	3	2.81
violet . . . . .	g b V and G b V	4	3.75
black . . . . .	g B V and G B V	12	11.25

The colourtypes dealt with above could always be nicely discriminated (except for violet and brown violet). As to the factors ascertained up to now, the parent plants have the following constitution:

Fijne tros: pp GG BB VV.

Wagenaar: PP gg bb vv.

#### d. The analysis of $F_2$

Cf. the upper half of the folding scheme table 31.

The analysis of the backcross with Wagenaar has been treated before that of the  $F_2$  generation, because in the backcross and its progeny all the six main colourtypes (or seven, if violet and brown-violet are separated) could be nicely discriminated and complete certainty could be obtained as to the influence of the factors G, B and V. The mottling I left out of consideration.

The mottling I have to deal with is the so-called ever-segregating-mottling, i.e. mottled plants never breed true, but they always segregate into mottled and selfcoloured in the ratio 1 : 1.

In all  $F_2$  families together I found:

463 mottled-seeded plants and

465 selfcoloured ones.

It was already shown by SHAW and NORTON (1918), KOOIMAN (1920) and especially by LAMPRECHT (1932a) that every mottled plant of this type always segregates into mottled plants and two selfcoloured types. One selfcoloured type corresponds with the „background colour” of the mottled seed, the second with its „dark pattern colour.” The ratio between the three colour types is always:

1 background colour,

2 mottled,

1 dark pattern colour.

KOOIMAN and LAMPRECHT therefore suppose that this mottling depends upon the heterozygous state of their (complementary) factor B, resp. C:

background colour type cc (resp. bb);

mottled seeds Cc (resp. Bb);

dark pattern colour type CC (resp. BB).

My view of this type of mottling is that it is due to a factor M for mottling which only works in connection with the dominant factor

C (= B of KOOIMAN), i.e. M locally suppresses the action of C; these two factors are absolutely (or nearly absolutely; cf. p. 227) linked. The outcome of this view will be dealt with in § 7 on mottling.

According to this view one parent must be  $\widehat{cM} \widehat{cM}$ , the other  $\widehat{Cm} \widehat{Cm}$ ;  $F_1$   $\widehat{Cm} \widehat{cM}$ , i.e. mottled. Segregation in  $F_2$ :

1  $\widehat{cM} \widehat{cM}$ : background colour type,

2  $\widehat{Cm} \widehat{cM}$ : mottled,

1  $\widehat{Cm} \widehat{Cm}$ : dark pattern colour type.

Which parent was  $\widehat{Cm} \widehat{Cm}$ , which  $\widehat{cM} \widehat{cM}$ ?

It has been mentioned above that in the backcross of  $F_1$  with Wagenaar in each of the colourclasses there occur about as many plants with mottled as with selfcoloured seeds. In all cases the latter colour is the dark pattern colour of the corresponding mottled seeds. (In the yellowish class the selfcoloured and mottled seeds could not be nicely discriminated). The numbers are (table 10):

	observed	expected	D/m	
yellowish (mottled + selfcol.) . . .	38	37.75	0.04	
orange {	mottled. . . . .	14	18.87	1.16
	selfcol. . . . .	17	18.87	0.45
greenish brown {	mottled. . . . .	15	18.87	0.92
	selfcol. . . . .	13	18.87	1.39
brown {	mottled. . . . .	19	18.87	0.03
	selfcol. . . . .	22	18.87	0.74
violet {	mottled . . . . .	50	37.75	2.12
	selfcol. . . . .	40	37.75	0.39
black {	mottled . . . . .	38	37.75	0.04
	selfcol. . . . .	36	37.75	0.30

Therefore:

Wagenaar is:  $PP \widehat{Cm} \widehat{Cm} gg bb vv$

Fijne tros is:  $pp \widehat{cM} \widehat{cM} GG BB VV$ .

$F_1$  is:  $Pp \widehat{Cm} \widehat{cM} Gg Bb Vv$ .

And the backcross  $F_1 \times$  Wagenaar is  $\widehat{Cm} \widehat{cM} \times \widehat{Cm} \widehat{Cm}$ , resulting in

1  $\widehat{Cm} \widehat{Cm}$  (dark pattern colour) } in each colour type.  
 1  $\widehat{Cm} \widehat{cM}$  (mottled)

Other colour types than the six (or seven) types of the backcross  $F_1$  with Wagenaar did not occur in the  $F_2$  (except for one family which will be discussed sub *e*). I may conclude from this that both races in their genetical constitution only differed as to factors already discussed.

In the backcross with Wagenaar, however, in each „colour class” only two types occurred, whereas in  $F_2$  I could distinguish in each „colour class” the expected three types:  $\widehat{cM} \widehat{cM}$ ,  $\widehat{Cm} \widehat{cM}$  and  $\widehat{Cm} \widehat{Cm}$ .

In the 4 colour classes among the pale rose flowering *v* plants (yellowish, orange, gray-greenish brown and brown) the difference between the two selfcoloured types,  $\widehat{cM} \widehat{cM}$  and  $\widehat{Cm} \widehat{Cm}$  is not very conspicuous; the  $\widehat{cM} \widehat{cM}$  background colours generally are somewhat paler.

Especially in the yellowish class the difference between the three types is often so inconspicuous that in  $F_2$  (and some other families) all three colour types had to be counted together. Cf. the colour description of the nos. 1, 2 and 3 in § 5.

The mottled seeds in the orange colour class can always be clearly distinguished from the two selfcoloured types. Yet the discrimination between these two types is very difficult in some cases. Again I must refer to the description in § 5 (nos 7, 8 and 9).

Exactly the same applies to the brown colour class: mottled seeds easy to find, discrimination of the two selfcoloured types difficult. Cf. description of the nos 19, 20 and 21.

In the gray-greenish brown colour class there is a marked difference between the two selfcoloured types: the background colour  $\widehat{cM} \widehat{cM}$  is grayish brown, the dark pattern colour  $\widehat{Cm} \widehat{Cm}$  more greenish brown. See description of the nos 13, 14 and 15.

In the violet flowering *V* plants the mottling of the violet seeds and of the black ones is often very conspicuous and naturally the difference between the  $\widehat{cM} \widehat{cM}$  and  $\widehat{Cm} \widehat{Cm}$  colour types as well! The  $V \widehat{cM} \widehat{cM}$  background colour types are only partially tinged with violet or blue. These tinges are darkest at the ventral side (hilumring side) near the caruncula and the germ root; their extension and intensity are extremely variable for seeds of the same plant! The non-tinged parts have exactly the same

colour as the corresponding  $\widehat{cM} \widehat{cM}$  types among  $v$  plants: pale yellowish, pale orange, gray brown and brown.

The violet and bluish tinges of these 4  $V \widehat{cM} \widehat{cM}$  background colour types are not equally strong in all plants and in some plants even totally lacking. In the latter case the difference between the  $V \widehat{cM} \widehat{cM}$  colours and their corresponding  $v$  colour is hardly perceptible; the hilumring colour of the  $v$  types, however, is always brighter.

As to the lack of these violet and bluish tinges in  $V\widehat{cM} \widehat{cM}$  plants I have found indications that it depends upon the recessiveness of one factor, the heterozygous forms being intermediate; there is, however, no certainty about it, because of the extremely high variability of the tinges. The influence of this factor should be hardly or not at all perceptible in the other colour types.

For the description of these four variable background colours I may refer to the nos. 4, 10, 16 and 22.

The colours discussed so far and the factors involved in the segregation are to be found in the upper half of the folding scheme in table 31. The lower half of the scheme will be dealt with sub *e*).

Table 19 shows the numbers actually found in the  $F_2$  generations. For the expected ratio in 1024 plants cf. the scheme opposite the table. Under each „colour class” the three types belonging to it are found, each indicated by its colour number. It should be remarked that the nos. 16 and 22,  $V \widehat{cM} \widehat{cM}$  background colours, under the heading „black”, are not black at all! And that in the „violet”  $V \widehat{cM} \widehat{cM}$  background colour nos 4 and 10 the violet or bluish tinge may be totally lacking. — There is an entire agreement of all colour types with the theoretically expected numbers. There seems to be no linkage between the colour factors  $P, \widehat{Cm} (\widehat{cM}), G, B$  and  $V$ .

Table 20, derived from table 19, shows the  $F_2$  segregation (in coloured seeded plants) concerning the factors  $\widehat{Cm} (\widehat{cM}), G, B$  and  $V$ . The ratio mottled: selfcoloured is exactly 1 : 1 (463 and 465). The numbers in the column of the „total numbers coloured” very nearly approach the theoretically expected ratio 1 : 3 : 3 : 9 : 3 : 9 : 36 between the colour classes yellowish, orange, gray greenish brown, brown, „violet”, „brown violet” and „black”.

To conclude, I give (table 21) the monofactorial ratios in coloured-seeded plants for the factors  $G, B$  and  $V$ , again derived from table 19.



The numbers are:

	observed		expected 1 : 3		D/m
g — G:	150	408	139.50	418.50	1.02
b — B:	235	707	235.50	706.50	0.04
v — V:	235	707	235.50	706.50	0.04

As to the  $F_3$  I may point to table 22. This table and tables 22—27 of the progeny of mottled backcross plants of  $F_1$  with Wagenaar require no further discussion.

The backcross  $F_1 \times$  Fijne tros is in perfect agreement with the above analysis.

Fijne tros: pp (JJ Sh Sh)  $\widehat{cM} \widehat{cM}$  GG BB VV.

Wagenaar: PP (JJ Sh Sh)  $\widehat{Cm} \widehat{Cm}$  gg bb vv.

$F_1$  Pp (JJ Sh Sh)  $\widehat{Cm} \widehat{cM}$  Gg Bb Vv.

The backcross of  $F_1$  with Fijne tros therefore must be:

$\frac{1}{2}$  pp: white.

$\frac{1}{2}$  Pp (JJ Sh Sh) G B V:  $\left\{ \begin{array}{l} \frac{1}{4} \widehat{Cm} \widehat{cM}: \text{mottled black.} \\ \frac{1}{4} \widehat{cM} \widehat{cM}: \text{background colour of mottled} \\ \text{coloured} \\ \text{black, i.e. brown with (or without) bluish} \\ \text{tinge.} \end{array} \right.$

The numbers are:

	white	mottled black	brown with (or without) bluish tinge
Observed . . . . .	77	34	40
Expected 2 : 1 : 1	75.50	37.75	37.75
D/m . . . . .	0.22	0.70	0.42

#### e. The „shine” factor Sh

One of the three large  $F_2$  families in 1932 (55-2) showed the same colour types as the two other families (55-4 and 55-6), but also many additional ones: 55-2 segregated moreover for another factor, for which I use the new symbol Sh (derived from shine). The  $F_1$  plants 55-2 and 55-4 originated from the same cross; probably the Fijne tros parent plant will have been heterozygous for this factor.

All colours discussed above were Sh; they are represented by the upper half of table 31, the sh types by the lower half.

a. All sh sh  $\widehat{Cm}\widehat{Cm}$  dark pattern colours (columns III and VI) are somewhat paler than the corresponding Sh Sh (or Sh sh) dark pattern colours and especially less shiny, often even dull or dead. Between the numbers 27 and 33 I could hitherto not sharply distinguish: both colours probably are of a pale yellow. The other colours may be indicated by the same colournames as the corresponding Sh types: dull greenish brown (39), dull brown (45), dull violet (30 and 36) and dull black (42 and 48). In some cases discrimination between the corresponding Sh and sh types is hardly feasible.

b. All sh sh  $\widehat{cM}\widehat{cM}$  background colour types (columns I and IV) have a yellow-brown hilumring, but for the rest their seedcoat is nearly colourless. For their indication I use the name „hilumring type”.

So the influence of the factors G, B and V upon these sh sh  $\widehat{cM}\widehat{cM}$  background colour types is hardly or not at all perceptible. The nos of column I (= v; nos 25, 31, 37 and 43) may be distinguished by their brighter hilumring colour from the nos 28, 34, 40 and 46 (= V) in column IV. Some plants of the latter have a gray greenish blue tinge near the caruncula and the germ root, but the tinged part is always extremely small, never extending over the greater part of the seedcoat as the violet or bluish tinge in the corresponding Sh colour nos 4, 10, 16 and 22.

c. The mottled sh sh  $\widehat{Cm}\widehat{cM}$  types of columns II and V naturally have a less shiny (dull) dark pattern colour and a nearly colourless background, by which they are clearly distinguishable from the corresponding Sh types in the upper half of the columns (cf. fig. 2, p. 183).

As to the actual numbers found in  $F_2$  family 55-2 I have to remark that in table 29 I combined different colour types, because there were some difficulties in the classification. As to the factors V and Sh there occurred among coloured-seeded plants:

	v sh	v Sh	V sh	V Sh	Total
Expected 1 : 3 : 3 : 9	7 9.6	22 28.9	42 28.9	83 86.6	154

The general shortage of pale rose-flowering *v* plants is high in this family. There are too many *V sh* plants.

Perhaps the numbers point to a weak linkage between the factors *V* and *sh*. The constitution of *Sh F<sub>2</sub>* plants suggests the same. According to their *F<sub>3</sub>* there appeared to be:

among 6 *v Sh F<sub>2</sub>* plants: 4 *Sh sh* and 2 *Sh Sh*.

among 12 *V Sh F<sub>2</sub>* plants: 11 *Sh sh* and only 1 *Sh Sh*.

In *F<sub>3</sub>* all *sh sh F<sub>2</sub>* plants bred true for this factor. The 15 segregating *F<sub>3</sub>* families (of *Sh sh F<sub>2</sub>* plants; table 30) gave among coloured-seeded plants 89 *sh* and 211 *Sh* (expected 75 and 225).

I never found clear indications of another segregation into white- and coloured-seeded but the 1 : 3 ratio. Even the most recessive colour number (hilumring type no. 25) is not white-seeded. I obtained this colour number, which is recessive for all the factors discussed (*sh*, *c*, *g*, *b*, *v*) in two *F<sub>3</sub>* families. Therefore, at least one complementary factor is homozygous dominant in all plants. This „hilumring factor” I called *J* (LAMPRECHT, 1932*a*, p. 176). This factor *J* is responsible for the fact that coloured seeds with colourless hilumring never occurred, although the complementary factor *C* (= *B* of KOOIMAN) produces with *P*, according to LAMPRECHT and KOOIMAN, a pale sulphurous or citrine yellow seedcoat with a colourless hilumring.

#### § 4. *The choice of symbols*

A long time I have hesitated before I could make up my mind concerning factor names and symbols. In the course of my investigations I used the following names, some of which indicate in a suitable way the general or most conspicuous influence of the dominant factor; other names have been chosen more arbitrarily with a view to their influence upon one definite recessive genotype.

Groundfactor . . . . .	<i>P</i>
Hilumring factor (homozygous dominant) . . . . .	<i>J</i>
Shine factor. . . . .	<i>Sh</i>
Factor pair for mottling . . . . .	$\widehat{Cm}$ ( <i>cM</i> )
Orange factor . . . . .	<i>G</i>
Gray-greenish brown factor . . . . .	<i>B</i>
Violet factor . . . . .	<i>V</i>

Had I to use new symbols now, derived e.g. from the names given above? I have not done so (except for Sh) but I have taken as far as possible symbols already used by other investigators, at the risk of the same symbol being used for different factors.

As a symbol for the groundfactor the letter P was first used (by SHULL, 1907 *b*, p. 829).

The letter M for mottling was used by SHULL (1908), EMERSON (1909*a*) and TSCHERMAK (1912). In my opinion the same factor M is involved in true-breeding and in ever-segregating mottling (cf. § 7).

The colours in the upper half of my scheme are the same or almost the same as the J colours described by LAMPRECHT.

His P J C colours:

Schamois . . . . .	P J C g b v.
Bister . . . . .	P J C G b v.
Münzbronze . . . . .	P J C g B v.
Mineralbraun, dunkel . . . . .	P J C G B v.
Veilchenviolett, dunkel . . . . .	P J C g b V.
Kastanienbraun . . . . .	P J C G b V.
Schwarz . . . . .	{ P J C g B V.
	{ P J C G B V.

correspond with my P J Sh  $\widehat{Cm}$  colours:

Yellowish . . . . .	P J Sh $\widehat{Cm}$ g b v (no. 3).
Orange . . . . .	P J Sh $\widehat{Cm}$ G b v (no. 9).
Greenish brown . . . . .	P J Sh $\widehat{Cm}$ g B v (no. 15).
Brown . . . . .	P J Sh $\widehat{Cm}$ G B v (no. 21).
Violet . . . . .	P J Sh $\widehat{Cm}$ g b V (no. 6).
Brown-violet . . . . .	P J Sh $\widehat{Cm}$ G b V (no. 12).
Black . . . . .	{ P J Sh $\widehat{Cm}$ g B V (no. 18).
	{ P J Sh $\widehat{Cm}$ G B V (no. 24).

Even LAMPRECHT's typical colour: Chromgrün-Schwarz: PP CC JJ gg Bb Vv was found in my material (cf. p. 189, p. 191 and p. 210).

I therefore used the same factor symbols J, C, G, B and V, supposing that my factors are identical with those of LAMPRECHT. In § 5 his colour descriptions are compared with my own. The main difference concerns the gray greenish brown colours depending on the factor B: my colours 13 and 15 are somewhat darker and more greyish than LAMPRECHT's corres-

ponding colours: „Havannabraun” and „Münzbronze”. My colour nos 4 and 16 (V c colours of column IV) are the only two J colours which up to now have not been described by LAMPRECHT. Their character (tinged with violet or blue; extremely variable) fits in very well with that of the V c colours „Ageratublau” (my no. 10) and „Graulich Indigo” (my no. 22) of LAMPRECHT.

According to the latter all these factors are complementary ones. I must emphasize here again that it was not possible for me to judge about the complementary or modifying character of the factors involved in my cross, because at least one complementary factor was homozygous dominant.

About the influence of his complementary factors J, C, G, B, V and R LAMPRECHT says (1933 p. 251): „Die verschiedenen Kombinationen der genannten sechs Gene verursachen meistens mehr oder weniger dunklere Töne als einer reinen Mischung der jedem dieser Gene (zusammen mit P) entsprechenden Farben zukommen würde. Hier bestehen in sofern keine bestimmten Regeln, als etwa dem Hinzukommen eines bestimmten Gens zu irgendwelchen anderen Kombinationen eine bestimmte Wirkung entsprechen sollte. Es kommt hierbei stets auf die Kombination in ihrer Gänze an, welche Farbe erzielt wird”.

I might, however, remark that we may speak of a „general” or „definite” influence of some factors, at least on groups characterized by definite genotypical constitutions.

Having adopted those symbols for the colours in the upper half of the scheme, I was obliged to take the new symbol Sh-sh to indicate the difference between the shiny colours on the one side and the hilmring type and dead colours on the other side. This factor Sh is supposed to be a modifying factor which is homozygous dominant in all LAMPRECHT's colours.

It is noteworthy that nearly all jj CC colours described up to now by LAMPRECHT are dead or dull colours. Cf. his description of „Steinfarbig” (1932c. p. 4), „Ambraweisz” (1933 p. 255), „Russgrün” (1933 p. 256) and „Mattmünzbronze” (1933 p. 257). In all these cases he mentions „mattes aussehen” oder „matte Oberfläche”. At first I was therefore inclined to ascribe my sh colours to the recessiveness of the factor J. Then I should be obliged to assume a complementary factor (other than J) which is homozygous dominant in all my plants and

causes, with P, my hilumring type no. 25, if all other factors involved in my cross are recessive.

The complementary factor D of KOOIMAN (1920, 1931) produced, if no further complementary factors were present, with P beans of the same appearance as my hilumring type (his „ecru”). Together with other complementary factors (B and C of KOOIMAN) it „makes the colours but slightly darker and more greyish” (TJEBBES 1931 p. 185).

If we suppose this factor D of KOOIMAN to be present together with J in my Wagenaar race, the latter should be of the constitution PPDD JJ  $\widehat{Cm}\widehat{Cm}$  gg bb vv. D, J and C are complementary factors, of which C (= B of KOOIMAN) without D and J produces (together with P) a pale sulphurous or citrine yellow seedcoat without coloured hilumring. D or J each cause (together with P) a very pale seedcoat colour with brown or yellow brown hilumring.

SIRKS (1922a, p. 110) however, crossed a „Wagenaar” line with a „Citroen” (lemon-coloured) bean, the latter „without or at most with a bluish navelring” (this „bluish navelring” apparently is a corona). The Wagenaar race is „immediately after harvesting „lemon-coloured with a brown navelring, but soon the lemoncolour „changes into greyish yellow and a year afterwards the seeds are „entirely yellowish-brown”. The colour of „Citroen” does not change. Cf. his col. Pl. II nos 18 and 22. The  $F_1$  is of the Wagenaar type. The  $F_2$  segregation is unifactorial: 30 „Citroen” and 99 „Wagenaar”. (The factor involved is according to SIRKS perhaps the same as D of KOOIMAN). I therefore left off ascribing to the Wagenaar-race the constitution PP DD JJ  $\widehat{Cm}\widehat{Cm}$  gg bb vv, because in that case in a cross of my Wagenaar race with „Citroen”, the type without a coloured hilumring would appear in  $F_2$  according to the bifactorial ratio 1:15, instead of the ratio 1:3 in the cross of SIRKS. Consequently I assumed all my plants to be JJ and for the unifactorial difference between „shiny” colours on the one side and „less shiny” colours together with „hilumring type” on the other side, the modifying factor Sh-sh was adopted.

The differences between „Citroen” and „Wagenaar” of SIRKS are nearly the same as those between the colours

„Geschwefeltes Weisz” . . . . . PC j g b v and  
 „Schamois” . . . . . PC J g b v

of LAMPRECHT. „Geschwefeltes weiss ist eine sehr konstante Farbe und verändert sich auch bei jahrelangem Aufbewahren nur wenig“. And „Schamois verändert sich beim Aufbewahren sehr schnell, es wird viel dunkler und der oben erwähnte, zuweilen stark kanariengelbe Ton verschwindet vollkommen“ (LAMPRECHT 1932a, p. 172).

This makes it all the more probable that we are right in identifying the factor D of SIRKS with the factor J of LAMPRECHT.

To conclude with the formulae of the races used in my cross are:

Fijne tros: pp JJ Sh Sh  $\widehat{cM} \widehat{cM}$  GG BB VV

(one parent plant: pp JJ Sh sh  $\widehat{cM} \widehat{cM}$  GG BB VV)

Wagenaar: PP JJ Sh Sh  $\widehat{Cm} \widehat{Cm}$  gg bb vv.

### § 5 Description of the seedcoat colours

These descriptions were made in December 1933 towards the end of the investigations. At that time I had kept a sample of seeds of each plant. In each of the colours described here a considerable variation is found, partly due to individual variation of seeds of one and the same plant, but no doubt for the other part depending on genetical differences (not the same as the factors described) between individuals belonging to the same type. Especially for the PJ Sh  $\widehat{cM} \widehat{cM}$  colour nos 4, 10, 16 and 22 the variation in the amount of the bluish or violet tinge is partly individual, partly genetic.

The Sh colours (1—24) of the upper half of the scheme (table 31) are first described. Between brackets the colour name of the corresponding type of LAMPRECHT is given. The colour types corresponding with my nos 4 and 16 have up to now not been described by him. For the colour description I have used:

1. R. RIDGWAY, Color Standards and Color Nomenclature (1912), referred to as C. S; and

2. R. OBERTHÜR, Repertoire de Couleurs (1905), referred to as R.C.

The order of description of the Sh colours is:

$\widehat{cM} \widehat{cM}$ : background colour type

$\widehat{Cm} \widehat{Cm}$ : the corresponding dark pattern colour type.

$\widehat{Cm} \widehat{cM}$ : the mottled type.

1. P J Sh  $\widehat{cM} \widehat{cM}$  g b v; pale yellowish.

(cf. LAMPRECHT: Rohseidengelb, 1932a, p. 172).

The common colour is C.S. Pl. XV 17'e (Light Buff — Warm Buff);

R.C. 66, 2—4 (Pale Ecu) or between this colour and 138,3 (Salmon flesh). The yellower shades are not always easily distinguishable from no. 3 (cf. LAMPRECHT 1932*a*, p. 172); they almost correspond with C. S. Pl. XXX 19"*e* (Cartridge Buff-Cream Buff); R.C. almost 36,2 (Maize Yellow). Hilum ring C.S. Pl. III 13 j (Xanthine Orange-Amber Brown); R.C. 318,2—328,3 (Rust red-Bistre).

In process of time this colour grows darker and darker. After 1 year: C.S. Pl. XXIX 16" b (Pinkish Cinnamon-Cinnamon Buff); R.C. 307,1—309,1 (Dark fawn-Buff.) After 2 years: C. S. Pl. XV 13' j (Tawny-Russet); R.C. 308,2 (Fawn).

All these colours correspond with those given by LAMPRECHT.

3. P J Sh  $\widehat{Cm}\widehat{Cm} g b v$ ; yellowish.

The „Wagenaar” race.

(cf. LAMPRECHT: Schamois, 1932*a*, p. 172).

For the Wagenaar race a difference in colour is characteristic between the hilum side and the opposite dorsal side of the seed. Dorsal side C.S. Pl. XXX 19" d (Cream Buff) but a shade paler, or Pl. XVI 19' d (Naples Yellow); R.C. 325, 1 (Shamois). Hilum side C.S. Pl. XVI 23' (Strontian Yellow); R.C. 17, 3—4 (Canary Yellow). The shamois and yellow are not sharply separated; transition colours occur. The canary yellow colour is very variable in its extension; sometimes it may be restricted to a very small spot close to the hilum ring. Hilum ring C.S. Pl. III between 13 k and 15 i (Amber Brown-Mars Yellow); R.C. 316, 3—4 (Mars Yellow) or 328,3 (Bistre).

This colour too grows rapidly darker. After 1 year dorsal side C.S. Pl. XXIX 17" a (Cinnamon Buff-Clay Colour), R.C. 325,4 (Shamois); hilum side between C.S. Pl. XXX 21" and Pl. XVI 23'. After 2 years dorsal side C. S. Pl. XXIX 15" k (Cinnamon-Sayal Brown); R.C. 309, 2—3 (Buff.).

The above description concerns the pure Wagenaar race. F<sub>2</sub>-individuals with the same P J Sh  $\widehat{Cm}\widehat{Cm} g b v$  constitution often show a less marked difference between the shamois and the canary yellow. — The Wagenaar race has a narrow violet corona (cf. fig. 1, p. 182), which in older seeds is gray brown.

2. P J Sh  $\widehat{Cm}c\widehat{M} g b v$ ; yellowish mottled, 3/1.

(cf. LAMPRECHT: Schamois/Rohseidengel b).

Dark pattern colour as number 3 on groundcolour as number 1;



henceforward indicated as mottled 3/1, analogous to LAMPRECHT's mode of indication. The mottling of no. 2 is often very difficult to distinguish! For this reason I was often obliged to take the colours 1, 2 and 3 together. Many investigators have probably overlooked this mottled type (MIYAKE c.s., 1930).

4. P J Sh  $\widehat{cM} \widehat{cM} g b V$ ; pale yellowish tinged with plumbago violet.

(LAMPRECHT: as yet not described).

Extremely variable colour, just as nos 10, 16 and 22; especially with respect to the extension of the violet tinge. This tinge may be more or less clouded and is always deepest at the ventral side near the caruncula. On the same plant there may occur seeds that are almost entirely deep gray violet and others almost without any bluish tinge. The colour without blue is C.S. Pl. XV 16' (Pale Ochraceous Buff-Light Buff); R.C. 66, 1—3 (Pale Ecu). The blue violet tinge is C.S. Pl. XLIX 53<sup>'''</sup> a—c, 57<sup>'''</sup> a—c and Pl. L 6<sup>'''</sup> a—c (Violet Plumbeous, Light Varley's Gray, Deep Plumbago Gray); in R.C. less accurately represented; 204, 2—3 (Violet blue) is the nearest colour, but too bright. Hilumring C.S. Pl. XV 15' i (Ochraceous Tawny) and paler; the darker types 13' i (Tawny); R.C. 324, 2—4 (Hazel), the darker colours less bright than 321,3 (Dead leaf).

6. P J Sh  $\widehat{Cm} \widehat{Cm} g b V$ ; violet.

(cf. LAMPRECHT: Veilchenviolet, 1932a, p. 174).

In its brightest shade a little darker than R.C. 192,4 (Violet purple); mostly much darker, with transition to 347,4 (Violet black); C.S. Pl. XI 61 n (Fluorite Violet-Black), Pl. XXV 61' m, 63' m, 65' m (Dark violet colours) and darker. Hilumring about the same colour, but the corona (cf. fig. 1) is nearly always paler and more brownish.

Paler types occur as well, especially on badly ripened plants. LAMPRECHT (1932a, p. 174) says about this colour: „Schlecht ausgereifte Samen zeigen so grosse Unterschiede in der Farbe, dass sie „ohne besondere Kenntnis der Verhältnisse in der Regel nicht zu „erkennen sind“. I could nearly always clearly distinguish the violet colour no. 6 from the black.

5. P J Sh  $\widehat{Cm} \widehat{cM} g b V$ ; violet mottled, 6/4.

(LAMPRECHT: so far not described).

Owing to the great variability in the extension of the violet tinge of background colour no. 4, the mottling of no. 5 is not always equally conspicuous.

7. P J Sh  $\widehat{cM} \widehat{cM} G b v$ ; pale orange.  
(cf. LAMPRECHT: Maisgelb, 1933 p. 256).

Palest colour C.S. Pl. IV 19 e (Maize Yellow-Buff Yellow); R.C. 326, 1 (and paler) with transition to 36,4 (Maize Yellow). Darker colours C.S. Pl. XV 16' (Yellow Ocher-Ochraceous Orange); R.C. 315,2—329,2 (Yell. Tan colour-Raw Siena). Hilumring C.S. Pl. III 13 j (Xanthine Orange-Amber Brown); R.C. 329,4 (Raw Siena).

The analogy with no. 9 (see below) is very great. The main differences are that no. 7 is paler, less deeply orange, less shiny and a little more reddish (also the hilumring) than no. 9. The intensity of this pale orange colour in the same plant is rather variable. My pale colours are a trifle less reddish than the Maize Yellow of LAMPRECHT.

9. P J Sh  $\widehat{Cm} \widehat{Cm} G b v$ ; orange.

(cf. LAMPRECHT: Bister, 1932a, p. 173; 1933 p. 256).

C.S. Pl. III 17 h (Cadmium Yellow-Raw Sienna); the darkest colour Pl. III 16 i. R.C. 314,1—329,1 (Ocre de Ru-Raw Sena); the darker colours 328,2 (Bistre). Hilumring C.S. Pl. IIIi15 i (Mars Yellow) and darker; R.C. 328, 3—4 (Bistre).

It is often very difficult to distinguish between no. 9 and no. 7, cf. above. It was only after a long time and on comparison with the no. 9 resulting from backcross  $F_1 \times$  Wagenaar, that I could distinguish the two colours rather clearly.

This colour (or about the same) has been indicated by different investigators as brown, yellow brown, orange or yellow.

8. P J Sh  $\widehat{Cm} \widehat{cM} G b v$ ; orange mottled, 9/7.

(cf. LAMPRECHT: Bister/Maisgelb).

As a rule the mottling is easy to discover. But sometimes, if the background-splashes are minute and the colour difference is inconspicuous, a very close inspection is necessary.

10. P J Sh  $\widehat{cM} \widehat{cM} G b V$ ; pale orange tinged with ageratum blue.

(cf. LAMPRECHT: Ageratumblau, 1933 p. 258).

Seeds of the same plant very variable as to the extension and intensity of the bluish tinge. Just as in no. 4 the bluish colour is deepest near the caruncula and germ root. The colour without bluish

tinge is C.S. Pl. XXX 19" c (Cream Buff-Chamois); R.C. 325, 1—2 (Shamois). Or more orange: C.S. Pl. XV 16' b (Ochraceous Buff-Antimony Yellow); R.C. 324, 1—325,4. The blue violet tinge is C.S. Pl. L 69"" h and Pl. XLIV 61"" h (Slate Violet-Deep Slate Violet); R.C. the paler colours 201, 2—4 and 200,4 (Ageratum blue, Parma Violet), the darker colours 201,4, 205,4 and 202,4, but more greyish. Hilumring C.S. Pl. XV 17'—15' i—13' i (Yellow Ocher, Ochraceous Tawny, Tawny); R.C. 324, 3—4 (Hazel) and less bright than 322, 3—4 (Brownish terra cotta).

LAMPRECHT (1933, p. 258) says about this colour: „Die Bezeichnung dieser Farbe kann diskutiert werden. Ihre Ausbildung ist „nämlich in sehr hohem Grade von den Milieuverhältnissen abhängig. Ausserdem ist die Farbe auf der Testa in der Regel ungleichmässig verteilt. . . . Bei den in Schweden herrschenden Witterungsverhältnissen wird das Ageratumbrau gewöhnlich mehr oder weniger deutlich ausgebildet, in sehr warmen und trockenen Sommern, wie 1932, entsprach jedoch ein grösserer Teil der Proben Cinnamon Buff. Das Ageratumbrau ist in diesem Sommer kaum zur Ausbildung gekommen. In Gegenden mit wärmeren und trockneren Sommern mag die Bezeichnung Ageratumbrau daher vielleicht „weniger geeignet erscheinen“.

As said above (p. 195) the lack of bluish tinge in some plants or families of the Wagenaar × Fijne tros cross is caused genetically.

12. P J Sh  $\widehat{Cm} \widehat{Cm} G b V$ ; brown violet.

(cf. LAMPRECHT: Kastanienbraun, 1932a, p. 173).

R.C. between 314,4 (Maroon) and 193,4 (Dark Violet), but often darker, approaching 344,4 (Reddish black) and 345, 3—4 (Purple black). C.S. Pl. XIII 1' n—Pl. XXXIX 1"" m (Hay's Maroon, Warm Blackish Brown-Black); the browner colours Pl. II 8 n (Bay-Chestnut) but mostly violet tinged. Hilumring of the same colour as the seedcoat; just round the hilumring a paler, brownish ring (corona).

The violet colour in the seedcoat may be totally absent, especially in badly ripened or diseased seeds; then the colour is about R.C. 341, 3—4 or paler. In some cases it was difficult to distinguish the nos 6 (violet) and 12 (brown violet) clearly, especially in case of very dark colours. Discrimination between 12 (brown violet) and black (nos 18 and 24) was always possible, at least when the light was very good.

11. P J Sh  $\widehat{Cm} \widehat{Cm} G b V$ ; brown violet mottled, 12/10.

(cf. LAMPRECHT: Kastanienbraun/Ageratumblau).

The discrimination between 5 (violet mottled) and 11 (brown violet mottled) is mostly rather clear. The brown violet dark pattern colour is sometimes much faded.

13. P J Sh  $\widehat{cM} \widehat{cM} g B v$ ; gray brown.

(cf. LAMPRECHT: Havannabraun, 1932e, p. 57, 1933 p. 256).

Greyish brown colour, often with a very faint lilac or violet tinge. C.S. Pl. XL 17" a (Wood Brown-Avellaneous); the browner colours between the latter and Pl. XXIX 17" i (Tawny Olive); the seeds with faint violet tinge Pl. XLVI 15" a (Drab-colour). R.C. between 303, 1 (Snuff Brown) and 354, 1—2 (Otter brown), with a very faint violet tinge. Hilumring C.S. Pl. III 13 k (Amber Brown); R.C. 328, 3—4 and 321, 4 (Bistre, Dead leaf) and darker.

The „Havannabraun” colour of LAMPRECHT is somewhat brighter! The colours described here are distinctly darker and more greyish, less brownish and greenish.

15. P J Sh  $\widehat{Cm} \widehat{Cm} g B v$ ; greenish brown.

(cf. LAMPRECHT: Münzbronze, 1932a, p. 173).

C.S. Pl. III 17 m (Raw Umber) and lighter; the most greenish colour Pl. IV 19 m (Medal Bronze) and lighter; the most brown colour Pl. III 16 m and paler. R.C. the darkest colour 343, 3—4 (Chocolate), the greenest 298, 2—3 (Golden bronze green), the more brownish between 298, 2—3 and 303, 2—3 (Snuff Brown).

This greenish brown colour no. 15 is always markedly different from the brown colour no. 21 and also from the corresponding  $\widehat{cM} \widehat{cM}$  no. 13, which is more greyish. As to the comparison with LAMPRECHT's Münzbronze, my no. 15 is less greenish, more „chocolate”, especially the darkest colours.

14. P J Sh  $\widehat{Cm} \widehat{cM} g B v$ ; greenish brown mottled, 15/13.

(cf. LAMPRECHT: Münzbronze/Havannabraun).

Mottling always clear. Not easily confused with any other type.

16. P J Sh  $\widehat{cM} \widehat{cM} g B V$ ; gray brown tinged with slate blue.

(LAMPRECHT: till now not described).

Just as in the nos 4, 10 and 22, the extension of bluish tinge is extremely variable in seeds of one and the same plant. In some plants or families the bluish tinge is nearly (or totally) wanting. The colour without bluish tinge agrees exactly with the

corresponding gray brown v colour no. 13 (but the hilumring is less bright): C.S. Pl. XXIX 17" i (Tawny Olive), 15" i and k (Sayal Brown, Snuff Brown); R.C. 303,2 (Snuff Brown) and 307, 3—4 (Dark fawn). The darkest bluish tinge is C.S. Pl. XLVIII 43"" 1 (different Slate colours); in R.C. the exact colour is not to be found; between 231,3 (Indigo) and 348,2 (Bluish black). Paler colours (blended with the gray brown groundcolour) are R.C. 209, 3—4 (Smalt blue); C.S. between Pl. XLVIII 41"" i (Dark Medici Blue) and Pl. LII 35"" i (Castor Gray). The hilumring colour of the dark bluish tinged seeds is brown, covered with blue.

The black colour nos 17 and 18 will be described below together with 23 and 24.

19. P J Sh  $\widehat{Cm} \widehat{Cm} G B v$ ; (pale) brown.  
(cf. LAMPRECHT: Rhamninbraun, 1932e, p. 57).

This colour is rather variable. Brightest colour R.C. 297,2—4 (Brown pink); often more greyish, between R.C. 297,3—4 (Brown pink) and 303,2—4 (Snuff brown). In C.S. represented less exactly; the palest colours between Pl. XV 17' and 15' i (Yellow Ocher-Ochraceous Tawny); the darker colours between the above mentioned ones and Pl. XV 15' j. Hilumring R.C. 328,3 (Bistre)—308,3 (Fawn).

There are two colours which are sometimes difficult to distinguish from no. 19, viz. 21 and 13. No. 21 is the corresponding brown  $\widehat{Cm} \widehat{Cm}$  colour (cf. below) and is as a rule of a darker, deeper brown; the hilumring contrasts in number 19 much more strongly with the seed-coat than in number 21. Concerning the difficulties in discriminating between 19 (brown) and 13 (gray brown) I believe that the greyish tints in no. 19 are caused by the same very faint violet as sometimes appears in beans belonging to number 13.

As to the comparison with LAMPRECHT's Rhamninbraun, my no. 19 is generally somewhat more greyish, just as is the case with my no. 13 compared to LAMPRECHT's Havannabraun.

21. P J Sh  $\widehat{Cm} \widehat{Cm} G B v$ ; brown.  
(cf. LAMPRECHT: Mineralbraun, 1932a, p. 173).

C.S. rather exactly Pl. III 13 m, 15 k, 17 k (Argus Brown, Sudan Brown, Antique Brown).

R.C. 304,2—3 (Burnt Umber), but often somewhat less reddish, with transitions to 297,4 Hilumring very little contrasting with

the seedcoat; C.S. Pl. III 13 k and 15 k (Amber Brown, Sudan Brown); R.C. 308, 2—3 (Fawn) and 304, 2—4 (Burnt Umber).

For the difference between the brown colour no. 21 and the corresponding  $\widehat{cM} \widehat{cM}$  colour no. 19, cf. above.

The reddish Mineralbraun (R.C. 339) of LAMPRECHT does not occur in my materials; the other colours he refers to, are present.

20. P J Sh  $\widehat{cM} \widehat{cM}$  G B v; brown mottled, 21/19.  
(cf. LAMPRECHT: Mineralbraun/Rhamnibraun).

Mottling always easy to see.

22. P J Sh  $\widehat{cM} \widehat{cM}$  G B V; (pale) brown tinged with greyish indigo. (cf. LAMPRECHT: Graulich Indigo; 1933 p. 258).

This colour type again shows the same variability in the amount of bluish tinge as the numbers 4, 10 and 16; many mixed colours of brown and bluish occur. And, because the brown groundcolour is also rather variable (cf. no. 19), this no. is annoyingly multicoloured! See the backcross  $F_1 \times$  Fijne tros and reciprocal one (p. 196). Brown and greenish black seeds (at least near the hilum) sometimes occur in the same plant; in some plants or families the bluish tinge may be nearly (or totally) wanting.

The brown groundcolours are C.S. Pl. XV 17' i (Buckthorn Brown), 15' j—14' k (Ochraceous Tawny, Cinnamon Brown, Russet); sometimes more greyish, C. S. Pl. XXIX 16" i and 15" j. In R.C. 307, 4 (Dark fawn), 303, 2—3 (Snuff brown), 304, 2—3 (Burnt Umber). The darkest bluish tinge (close to the caruncula) is C. S. Pl. XLVIII 39''' k (Saccardo's Slate-Dark Greyish Blue Green), R.C. 232, 4 (Greyish Indigo). Sometimes more greenish: C.S. Pl. LI 23'''' j (Dark Olive Gray-Iron Gray). R.C. 351, 1 (Greenish black). Many paler brown-grey-green-bluish mixed colours occur! Hilum ring R.C. 322, 2—3 (Brownish terracotta), 308, 3 (Fawn) and darker, sometimes mixed with a bluish colour. It is not always possible to distinguish with absolute certainty between the nos 16 and 22. Generally speaking no. 16 is more gray-bluish, 22 rather brown-greenish blue.

LAMPRECHT (1933 p. 258) remarks about his colour „Graulich Indigo“: „Diese Testafarbe zeigt ähnlich wie Ageratumbrau eine „sehr ungleichmässige Verteilung und Ausbildung. Gleichwie bei „Ageratumbrau ist die Ausbildung von typisch Graulich Indigo sehr „von den Witterungsverhältnissen Abhängig.“

18. P J Sh  $\widehat{Cm}\widehat{Cm}$  g B V; black.

24. P J Sh  $\widehat{Cm}\widehat{Cm}$  G B V; black.

(Cf. LAMPRECHT: Schwarz; 1932a, p. 174).

R.C. 349,4 (Black, pure) with transitions to 348,4 (Bluish black), 350,3—4 (Ivory black) and 351,3—4 (Greenish black). C. S.Pl. LII n, LIII n and black. Hilumring black. It was not possible to make any sharp discrimination between the different black colours of the seedcoat.

LAMPRECHT (1932a, p. 174) describes a colour „(dunkel) Chromgrün”, which according to his experience always has the constitution PP CC JJ gg Bb Vv. In my material I also found this colour with possibly the same constitution, but not always markedly different from the remaining black colours (cf. p. 189 and p. 191). Of the self-coloured black-seeded plants out of backcross F<sub>1</sub> with Wagenaar one half is (P J Sh  $\widehat{Cm}\widehat{Cm}$ ) Gg Bb Vv, the other half is (P J Sh  $\widehat{Cm}\widehat{Cm}$ ) gg Bb Vv. All plants were black or very dark greenish black. Especially among the offspring of the latter (gg Bb Vv) some rather conspicuous greenish black seeds were found. This colour is C.S. Pl. XLII 37" n (Dusky Dull Green-Black) but much more shiny; R.C. between 236,4 (Chrome green) and 351,3 (Greenish black).

17. P J Sh  $\widehat{Cm}\widehat{cM}$  g B V; black mottled, 18/16.

(LAMPRECHT: till now not described).

23. P J Sh  $\widehat{Cm}\widehat{cM}$  G B V; black mottled, 24/22.

(cf. = LAMPRECHT: Schwarz/Graulich Indigo).

Though the background colour types of nos 17 and 23 can be discriminated, the mottled types must be taken together. The mottling is very conspicuous if the background colour is without any bluish tinge. In a few cases, when the tinge is extremely strong and dark the mottling is hardly to be discovered.

As to the sh colours (nos 25—48) I am not yet able to give as accurate a description of them as of the Sh colours (nos 1—24) because of their great variability.

25. P J sh  $\widehat{cM}\widehat{cM}$  g b v

31. P J sh  $\widehat{cM}\widehat{cM}$  G b v

37. P J sh  $\widehat{cM}\widehat{cM}$  g B v

43. P J sh  $\widehat{cM}\widehat{cM}$  G B v

} „Hilumring type”.

„Hilumring type” of pale rose flowering plants. Seedcoat very slightly coloured with a very pale greyish cream; in most cases a certain

„nervation” is to be seen. The hilumring types are with or without coloured „eye” around the hilumring. I am not quite sure of it as yet, but probably the colour of the eye is influenced by the factors G, B (and V) in an analogous manner as the corresponding totally coloured Sh numbers. — The pale cream colours are: C.S. paler than Pl. XXX 19" f (Cartridge Buff), sometimes with a touch of reddish; R.C. paler than: 66,1 (Pale Ecreu), 138,1 (Salmon flesh) and 135,1 (Pale pink). Hilumring: the paler colours C.S. Pl. III 15 i (Mars Yellow); R.C. 316,4 (Mars Yellow); the darker colours C.S. between Pl. II 11 k and Pl. III 13 k; R.C. 333, 3—4 (Indian Chestnut red), sometimes between this colour and 308,4 (Fawn).

About the same colour as the A b c D type of KOOIMAN and may be the pale buff or light ecru of the race Blue Pod Butter used by SHAW and NORTON.

27. P J sh  $\widehat{Cm} \widehat{Cm} g b v$ ; (dull) yellowish.

C.S. Pl. XVI 23' b (Citron Yellow) and 22' d—20' d (Barium, Straw and Naples Yellow). The same series in R.C.: 18, 1—2 (Sulphur Yellow), 30,3—4 (Cream Yellow), 29,3—4 (Naples Yellow).

This colour and the corresponding yellow Sh colour (Wagenaar type) could not always be nicely discriminated.

33. P J sh  $\widehat{Cm} \widehat{Cm} G b v$ .

About this colour (corresponding with the orange Sh colour no. 9) I have as yet no complete certainty. Probably it is yellowish and difficult to distinguish from the yellow no. 27.

39. P J sh  $\widehat{Cm} \widehat{Cm} g B v$ ; dull greenish brown.

About the same colour as the greenish brown Sh colour no. 15, but paler and less shiny (dull). R.C. between 298,1—2 (Golden bronze green) and 303,2 (Snuff brown). C.S. Pl. IV 191 (Orange Citrine-Medal Bronze) and (brownier) transitions to Pl. XV 16' k. (Cinnamon Brown-Dresden Brown).

45. P J sh  $\widehat{Cm} \widehat{Cm} G B v$ ; dull brown.

C.S. between Pl. III 13 m and 15 k (Argus Brown-Sudan Brown) or between Pl. XV 17' i and Pl. XXIX 15" i. R. C. 304,2 (Burnt Umber) with transitions to 303,2—3 (Snuff Brown).

26. P J sh $\widehat{Cm} \widehat{cM} g b v$	} mottled {	(dull) yellowish, 27/25.
32. P J sh $\widehat{Cm} \widehat{cM} G b v$		dull yellowish (?), 33/31.
38. P J sh $\widehat{Cm} \widehat{cM} g B v$		dull greenish brown, 39/37.
44. P J sh $\widehat{Cm} \widehat{cM} G B v$		dull brown, 45/43.



These mottled yellowish, yellowish(?), greenish brown and brown types by their dull dark pattern colour and especially by their nearly colourless background are greatly different from the corresponding Sh colours. The colour of no. 32 (yellowish?) is not yet known for a certainty.

- |  |   |                   |
|--|---|-------------------|
| 28. P J sh $\widehat{cM} \widehat{cM} g b V$ | } | „Hilumring type”. |
| 34. P J sh $\widehat{cM} \widehat{cM} G b V$ |   |                   |
| 40. P J sh $\widehat{cM} \widehat{cM} g B V$ |   |                   |
| 46. P J sh $\widehat{cM} \widehat{cM} G B V$ |   |                   |

„Hilumring type” of violet flowering plants. Seedcoat very slightly coloured, often showing a certain „nervation”. With or without coloured „eye” around the hilumring. The seedcoat colour is R.C. 6,1—2 (Purplish tinted white) and 9,2—3 (Fleshy white); the first of these colours is not accurately represented in C.S.; the second corresponds with Pl. XXX 21" f (Ivory Yellow). Sometimes near the caruncula and germ root a very small spot with a gray-greenish blue tinge: R.C. 206,1 (Succory blue); C.S. Pl. LII 35"" d (Dawn Gray). Hilumring: pale colour: C. S. Pl. XV 15' i (Ochraceous Tawny); R.C. 314,3 (Ru Ochre); darker colour: C.S. between Pl. III 13 k and Pl. XV 13' k; R.C. 308,3 (Fawn).

In most cases the difference between these V and the corresponding v hilumring types is very slight; but the hilumring colour of V plants is always less bright than that of v plants.

30. P J sh  $\widehat{Cm} \widehat{Cm} g b V$ ; dull violet.  
 36. P J sh  $\widehat{Cm} \widehat{Cm} G b V$ ; dull brown violet.  
 Often brown, nearly without violet.

I am not able to describe these colours 30 and 36 accurately, because of their great variability.

42. P J sh  $\widehat{Cm} \widehat{Cm} g B V$  and  
 48. P J sh  $\widehat{Cm} \widehat{Cm} G B V$ ; dull gray greenish black.  
 C.S. Pl. XLVI 21"" m and n (Olivaceous Black-Black) and 17"" n (Chaetura Black-Black). R.C. 351,2—4 (Greenish black) and 350, 1—2 (Ivory black).

- |  |   |         |   |                           |
|--|---|---------|---|---------------------------|
| 29. P J sh $\widehat{cM} \widehat{cM} g b V$ | } | mottled | } | dull violet, 30/28.       |
| 35. P J sh $\widehat{cM} \widehat{cM} G b V$ |   |         |   | dull brown violet, 36/34. |
| 41. P J sh $\widehat{cM} \widehat{cM} g B V$ |   |         |   | dull black, 42/40.        |
| 47. P J sh $\widehat{cM} \widehat{cM} G B V$ |   |         |   | dull black, 48/46.        |

The dull violet, dull brownviolet and dull black mottled types differ on account of their dull dark pattern colour and nearly colourless background greatly from the corresponding mottled violet and black Sh colours.

The difference between Sh shiny black mottled and sh dull black mottled with nearly colourless background may be seen in fig. 2.

#### § 6. *Relation between stem, flower and seedcoat colours*

In my cross a white seedcoat was always accompanied by white flower and green stem (hypocotyl and cotyledons); a coloured seedcoat always by coloured flower and stem.

The latter, however, is not always the case. On my reviewing the literature, the following statements may be made.

*a.* Coloured-seeded races may have coloured or white flowers.

White-seeded races nearly always have white flowers and a green stem. According to FRUWIRTH (1924 p. 179) „finden sich aber auch Formen, welche Rosa, Violet, Purpur als Blütenfarbe und Weiss als Samenfarbe zeigen”. In several descriptive works on bean varieties (VON MARTENSEN, DENAIFFE, TRACY, STEINMETZ) I found recorded only one white-seeded race with coloured flower (DENAIFFE p. 176: Haricot nain Prolifique; fleurs blanches, souvent plus ou moins teintées de rose; grains blancs). In the genetical literature I did not find any case mentioned.

*b.* Coloured-flowering races may have a stem (hypocotyl and cotyledons) with or without colour.

White-flowering races seem to have in all cases a green stem, at least green hypocotyl and cotyledons (MIYAKE c.s. 1930). According to FRUWIRTH (1924 p. 179) „ist weisse Blüte mit weissem Samen korrelativ verbunden, nach von TSCHERMAK auch mit Fehlen von violetten Flecken auf den Keimlappen”. Anthocyanin spots on the full grown pods of white-flowering plants may occur (TJEBBES and KOOIMAN V, 1921*b*; the author; cf. below).

About the appearance of colour in crossing colourless races, the following facts are known (in most cases a factorial analysis was not attained):

##### 1. S e e d c o a t.

White-seeded  $\times$  white-seeded,  $F_1$  coloured-seeded. The cross of

Davis Wax with Michigan White Wax (SHAW and NORTON, 1918 p. 65).

2. Flower (in coloured-seeded plants).

White-flowering  $\times$  white-flowering,  $F_1$  with coloured flower.

Mentioned by SHAW (1913 table 9); the parent plants did not have a totally coloured seedcoat, but an „eyed” one.

3. Stem (in coloured-flowering plants).

Green-stemmed  $\times$  green-stemmed,  $F_1$  with coloured stem. Some crosses mentioned by MIYAKE c.s. (1930); one parent with „striped” flower, the other with a totally coloured flower.

Stem and flower colour may either be paler or darker, either more reddish or more bluish. Up to now, however, only monofactorial segregations for stem and flower colour have been satisfactorily analysed.

SHAW published in 1913 „The inheritance of blossom colour in beans”, without giving a factorial analysis. The difficulties of classifying must have been rather great, as will be seen e.g. on close examination of his table 9, which contains many inconceivable results. The segregation into the flower colours „light pink” and „pink” was apparently monofactorial. Black-seeded beans seemed always to have a pink flower colour.

MIYAKE c.s. (1930) found monofactorial segregation for:

„pink” stem and flower (coloured dilutely) versus „red” stem and flower (coloured intensely).

TJEBBES and KOOIMAN (V, 1921*b*) reported a spontaneous hybrid of a light lilac-flowering race with red striped seedcoat and red striped pod. All the hybrid colours were darker and more bluish: flower violet, seedcoat bluish black striped, pod dark blue striped. The  $F_2$  segregated according to the ratio 4:3:9.

	pod colour	flower colour	seedcoat colour
4	{ 1 pale red } { 3 pale blue }	white	white
3	red	lilac	without blue
9	blue	{ 6 light violet } { 3 dark violet }	with blue

The segregation of my cross for the factors P and V shows the same relations in all respects:

	pod colour	flower colour	seedcoat colour
4	little spots (hypocotyl green!)	white	white
3	rose	pale rose or lilac	without blue
9	blue-violet	{ 6 violet-1 3 violet-2 or 3 }	{ with blue or violet }

The blue-factor Bl of TJEPPES and KOOIMAN and my factor V are possibly the same.

In many other investigations analogous relations between flower and seedcoat colours can be traced, though the required observations have hardly ever been made.

In this respect I want to refer to LAMPRECHT's investigations. The V-plants he used were the black wax varieties „Neger” (1932a, p. 178) and „Merveille du Marché” (p. 190). Their flower colour is R.C. 189, 1 (Bishops violet) but somewhat brighter. The v parent of his cross no. II has a yellow-brown (bistre) seedcoat (cf. my no. 9); the flower colour is R.C. 187,1 (Pale light lilac) but much paler. F<sub>1</sub> was violet flowering like one parent plant. LAMPRECHT does not mention the connection between flower and seedcoat colours in F<sub>2</sub>. Yet the above-mentioned facts were decisive for me (in connection with the seedcoat colours) to assume my factor V to be the same as LAMPRECHT's.

Many of LAMPRECHT's v-races (seedcoat Schamois, Bister, Münz-bronze, Mineralbraun) are white-flowering. White-flowering races with black or violet seedcoat have scarcely been described, unless they are partly coloured, „eyed-seeded”. The connection between flowercolour and „eyedness” of the seedcoat deserves closer investigation.

JOHANNSEN (1926 p. 443) crossed a white-flowering, yellow-seeded race with a violet-flowering, black-seeded one. F<sub>1</sub> violet-flowering, black-seeded. F<sub>2</sub>:

white-flowering (v)		violet-flowering (V)	
yellow-seeded	bronze-seeded	violet-seeded	black-seeded
39 (bv)	121 (Bv)	105 (bV)	293 (BV)

The influence on seedcoat colour of the factors B and V of LAMPRECHT and the author is the same as in this cross of JOHANNSEN.

To wind up with we may say that there is very little known with

certainly about the connection between stem, flower and seedcoat colours. Unifactorial segregation has been shown (or is at least probable) for the following flower-colours:

TJEBBES and KOOIMAN	lilac	violet
JOHANNSEN	white	violet
SHAW and NORTON	pale pink	pink
MIYAKE c.s.	pink	red
PRAKKEN	very pale rose (-lilac)	violet

In probably all these cases differences in flower- and seedcoat colours go together. With pale (or white) flower colour generally correspond yellow and brown seedcoat colours (and red?). With darker flower colour violet, brownviolet and black dark pattern colours (CC); the corresponding background colours (cc) are often variably tinged with violet or blue.

I may remind of the fact that in my P J Sh  $\widehat{cM}$   $\widehat{cM}$  V background colour types (nos 4, 10, 16 and 22) the violet tinge may be totally lacking. The corresponding V and v colours are nearly indistinguishable in that case.

### § 7. *Mottling*

In § 3 I ascribed the ever-segregating mottling to the influence of a dominant factor for mottling M, which locally suppresses the influence of the (complementary) colour factor C, while C and m are absolutely (or nearly absolutely) linked just as c and M.

This hypothesis of the linked factors C and M has consequences which I will deal with in giving a summary of the various views on the genetical base of mottling in beans.

As to their inheritance, two types of mottling in beans are known:

a. *True-breeding mottling* („konstante Marmorierung“) of many mottled races. Such a race crossed with a selfcoloured one gives a mottled  $F_1$  and  $F_2$  shows a segregation into 3 mottled and 1 selfcoloured (or, if one parent was white-seeded), into 4 white-seeded, 9 mottled and 3 selfcoloured. Part of the mottled  $F_2$  plants breeds true in  $F_3$ , the other part again segregates into 3 mottled:1 selfcoloured.

b. *Ever-segregating mottling* („Heterozygotmarmorierung“). In our crossing two selfcoloured plants a mottled  $F_1$  may appear. In  $F_2$  mottled and selfcoloured plants occur in the 1:1

ratio (if one parent was white-seeded, the  $F_2$  ratio is: 4 white-seeded, 6 mottled and 6 selfcoloured). None of the mottled  $F_2$  plants are true-breeding for mottling in  $F_3$  or later generations.

The phenotype of the two sorts of mottling is much the same and it seems doubtful to me, whether they can generally be distinguished one from the other.

According to TJEBBES and KOOIMAN (II, 1919) the pattern should be nearly the same; in the ever-segregating type, however, there should occur only one background and one dark pattern colour, whereas the dark pattern in true-breeding mottled plants which they investigated, consisted of two colours; in a „black” mottled bean e.g. of parts with very dark blue cells and parts with lighter blue ones.

KRISTOFFERSON (1924) writes: „As to the phenotype both are similar.”

And LAMPRECHT (1933 p. 260): „Es verdient hier besonders hervor-  
„gehoben zu werden, dass zwischen dem gewöhnlichen Typus von  
„konstanter Marmorierung, verursacht durch ein besonderes Mar-  
„moringen (M), und der durch die Konstellation C c beding-  
„ten Heterozygotmarmorierung kein sicherer Unterschied in Bezug  
„auf die Zeichnung der Marmorierung hat festgestellt werden kön-  
„nen”. In his latest article he says (1934 p. 179): „Sowohl die hetero-  
„wie die homozygotmarmorierten Samen zeigen in ihrer Zeichnung  
„eine recht beträchtliche Variation und scheinen auf Grund dieser  
„häufig nicht sicher voneinander unterschieden werden zu können. .  
„Für die heterozygotmarmorierten Samen ist von mir an einem  
„grossen Material nachgewiesen worden, dass die dunkleren Flecken  
„der Testa stets der durch einen Genotypus mit CC bedingten Testa-  
„farbe entsprechen, die des helleren Grundes einem im übrigen glei-  
„chen Genotypus mit cc. Hier ist die Farbenverteilung also in ihrer  
„Abhängigkeit von der genotypischen Konstitution vollkommen be-  
„kannt. Wie die Farbenverteilung bei den homozygotmarmorierten  
„Samen durch das Zusammenwirken von M mit den Farbgenen für  
„die Testafarbe beeinflusst wird, darüber scheint bisher nichts siche-  
„res bekannt zu sein. Aus oben Angeführtem geht klar hervor, dass  
„die Heterozygotmarmorierung nur zweifarbig auftreten kann. Die  
„homozygotmarmorierten Typen sind diesbezüglich kaum unter-  
„sucht. Soweit mir bekannt, kommen hauptsächlich dreifarbige  
„Kombinationen vor”.

In the earlier investigations (TSCHERMAK, EMERSON, SHULL a.o.) differences between the two types are not mentioned.

As to the genetical base of mottling in beans and the connection between true-breeding and ever-segregating mottling two contrary views exist:

a. The two types depend on different factors which are inherited independently (EMERSON'S first conception, KOOIMAN, LAMPRECHT).

b. The two types depend on the same factors (EMERSON-SPILLMAN, TSCHERMAK, SHAW and NORTON, the author).

As concerns the ever-segregating mottling, it is of importance to remark that the first investigators (TSCHERMAK, SHULL, EMERSON) did not observe that with every mottled type there go two self-coloured ones. Among mottled and selfcoloured beans in a cross they distinguished the same colours.

SHULL e.g. (1908) crossed:

„Long Yellow Six Weeks” (light pink flower, yellow seed as my Wagenaar race) with „White Flageolet” (white flower and seed). The  $F_1$  generation had pink flower and black mottled seed. In  $F_2$  he distinguished two main seedcoat colour types:

„brown” (= dark seal brown, dark greenish brown, dark yellow brown, light yellow) and

„black” (= black, weathered black, purple, violet; in some plants the colour is but partly black or violet and the other part is a brown colour „underlying” the black or violet).

The colours in  $F_2$  of this cross were probably the same as my Sh colours in the upper half of the scheme, table 31.

My factor B is probably SHULL'S „dark brown factor” D.

My factor V is his „anthocyanin producing factor” B.

On my factor G depends the unifactorial difference between SHULL'S races „Long Yellow Six Weeks” and „Ne Plus Ultra” (orange); this factor is not named by SHULL.

The figures in  $F_2$  were:

	„brown” (= my v)		„black” (= my V)		unclassified
	mottled	selfcoloured	mottled	selfcoloured	
white	160	39	59	154	159
Ratio:	16	6	6	18	18

Background colour cc and dark pattern colour CC were apparently taken together! „Brown” my columns I and III (v cc and v CC); „black” my columns IV and VI (V cc and V CC; probably all V cc colours, my column IV, were strongly tinged with violet; some plants showed a brown colour „underlying” the black or violet!)

SHULL rightly understood that these results were explainable on the assumption that all individuals heterozygous for a factor M have the mottled pattern, and that mm and MM are selfcoloured (those mm and MM types could not be distinguished in his opinion).

TSCHERMAK (1901, 1902, 1904, 1912) just as SHULL, distinguished among (ever-segregating) mottled beans and selfcoloured ones the same colours, viz. his main colour types

black	C B
violet	c B and
brown (with yellow)	C b and c b

His cross

„Weisse Wachsschwert” (white flower and seed) with

„Non plus Ultra” (pale violet flower, orange seedcoat) gave an

F<sub>1</sub> generation with dark violet flower and black mottled seed.

In F<sub>2</sub> TSCHERMAK could „leicht 20 verschiedene Farbenklassen konstatieren”. Apparently here too all my Sh colours occurred: segregation for my factors B (= C of TSCHERMAK), V (= B of TSCHERMAK) and probably for my factor G (G dominant or recessive does not alter the division into three main colour types black, violet and brown with yellow).

I discuss the cross Weisse Wachsschwert × Non plus Ultra, because TSCHERMAK gave (1902 Tab. II) of 98 F<sub>2</sub> individuals an accurate description as to their flower and seedcoat colours; later (1904 Tab. III) he gave of the same 98 individuals the division into the three main colour groups black, violet and brown.

In different F<sub>2</sub> families of this cross he found together:

white	mottled			selfcoloured			
99	163			167			(= 4:6:6)
	brown	violet	black	brown	violet	black	
	38	33	92	101	27	39	
ratio ±:	4	3	9	9	3	4	

So he found for the three colours „inversion of the ratio” among



mottled beans (4:3:9) and selfcoloured ones (9:3:4). TSCHERMAK suggested different possibilities as an explanation, but he finished (1912 p. 187) by saying: „Eine vollbefriedigende Erklärung der Umkehr des Spaltungsverhältnisses bleibt noch zu finden”.

By accurate comparison of his extensive description of flower and seedcoat colours of those 98  $F_2$  plants with their later division into black, violet and blue, I arrived at the apparent solution of this remarkable „inversion of the ratio”.

Among mottled seeds the normal 4:3:9 ratio is found, according to my factors B and V and possibly G (cf. the colours in the upper half of my scheme):

4  $\left\{ \begin{array}{l} 1 \text{ b v } \widehat{Cm} \widehat{cM} \\ 3 \text{ B v } \widehat{Cm} \widehat{cM} \end{array} \right\}$  „brown” mottled, with pale lilac flower.

(my nos 2, 8, 14 and 20).

3  $\text{ b V } \widehat{Cm} \widehat{cM}$ , violet mottled, with lilac or dark lilac flower.  
(my numbers 5 and 11).

9  $\text{ B V } \widehat{Cm} \widehat{cM}$ , black mottled, with lilac or dark lilac flower.  
(my numbers 17 and 23).

The „inversion” among the selfcoloured seeds is probably caused by the classification of the background colour types of black mottled seeds and violet mottled ones! Of these colours, my P J Sh  $\widehat{cM} \widehat{cM}$  V colours (nos 4, 10, 16 and 22), which are pale yellow, pale orange, gray brown and pale brown, variably tinged with violet or blue, TSCHERMAK may have classified:

a. Not a single one as „black”.

b. Those with strong violet or bluish tinge as „violet”.

c. Those without or with a faint tinge as „brown”.

Leaving out of consideration the groundfactor P, the ratio in the upper half of my scheme in table 31 (J and Sh dominant; segregation for the factor pair  $\widehat{Cm} \widehat{cM}$  and the factors G, B and V) is:

	v			V		
	$\widehat{cM}\widehat{cM}$	$\widehat{Cm}\widehat{cM}$	$\widehat{Cm}\widehat{Cm}$	$\widehat{cM}\widehat{cM}$	$\widehat{Cm}\widehat{cM}$	$\widehat{Cm}\widehat{Cm}$
g b	1	2	1	3	6	3
G b	3	6	3	9	18	9
g B	3	6	3	9	18	9
G B	9	18	9	27	54	27
	16	32	16	48!	96	48

Classified by  
Tschermak as:

selfcoloured „brown”.

mottled „brown”.

selfcoloured „brown”.

partly selfcoloured violet.  
partly selfcoloured brown.

24 mottled violet.

72 mottled black.

12 selfcoloured violet.

36 selfcoloured black.

Mottled: 32 brown, 24 violet, 72 black = 4:3:9.

Selfcoloured:

„brown” 16 + 16 + part of 48

violet 12 + remaining part of 48

black 36.

} The ratio 9:3:4 may result!

The flower colour of those 98 plants was (with 1 or 2 exceptions) in agreement with my view:

all selfcoloured and mottled black plants: lilac or dark lilac;

all selfcoloured and mottled violet plants: lilac or dark lilac;

all mottled brown plants: pale lilac;

selfcoloured brown plants: partly pale lilac, partly lilac or dark lilac.

EMERSON (1909a) was the first who tried to analyse the relation between true-breeding and ever-segregating mottling, after crossing a great number of white-seeded, mottled and selfcoloured varieties.

In his first hypothesis he assumed that both types of mottling depend upon different factors. The symbols he used were:

P = groundfactor for colour.

M = factor for true-breeding mottling;

MM and Mm mottled, mm selfcoloured.

X = factor for ever-segregating mottling;

xx and XX selfcoloured, Xx mottled.

(X of EMERSON = M of SHULL = B of KOOIMAN = C of LAMP-RECHT; EMERSON and SHULL, however, did not know the difference in colour between the homozygous types!).

The possible genotypes of the races are:

1. PP MM XX	mottled.	5. pp MM XX	} all white.
2. PP MM xx	mottled.	6. pp MM xx	
3. PP mm XX	selfcoloured.	7. pp mm XX	
4. PP mm xx	selfcoloured	8. pp mm xx	

According to these views, EMERSON expected the following ratios between white, mottled and selfcoloured beans:

Formulae mottled F <sub>1</sub>	F <sub>2</sub>		
	white	mottled	selfcoloured
1a. PP mm Xx	0	2	2
b. Pp mm Xx	4	6	6
2a. PP Mm XX (or xx)	0	3	1
b. Pp Mm XX (or xx)	4	9	3
3a. PP Mm Xx	0	14	2
b. Pp Mm Xx	16	42	6
4a. PP MM XX (or xx)		all mottled	
b. Pp MM XX (or xx)	1	3	0

EMERSON considered the possibility that M might cause mottling only in xx and not in XX plants; in this case the ratio in 3a and b (double heterozygous) would be:

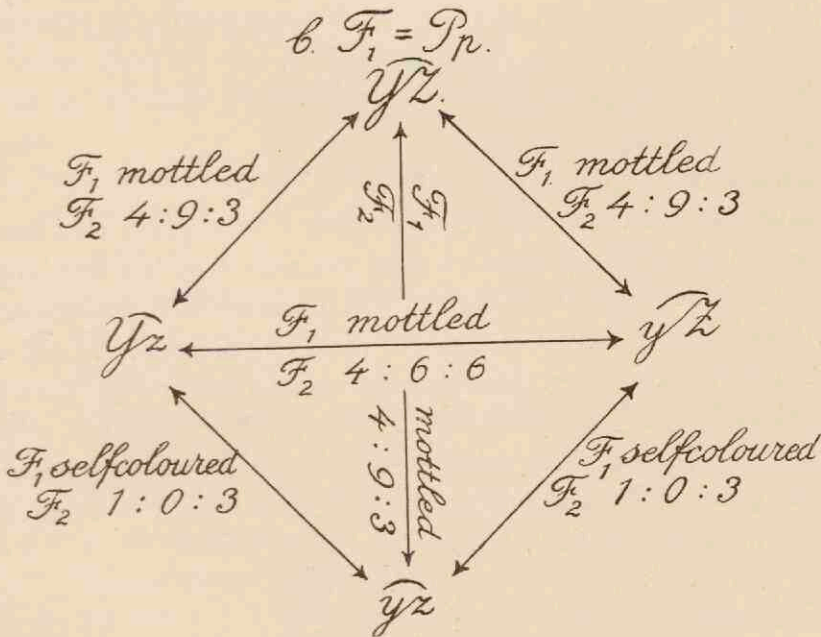
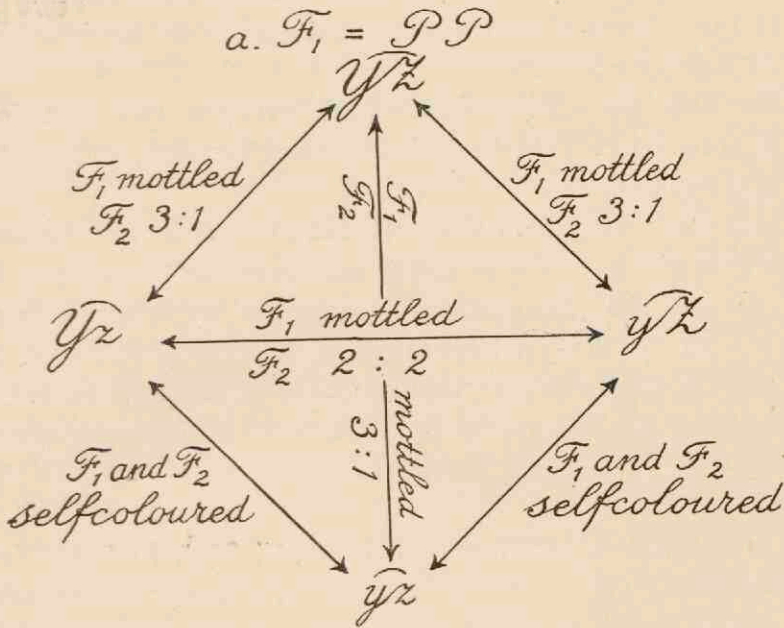
3a. PP Mm Xx	0	11	5
b. Pp Mm Xx	16	33	15

Analyzing the results of TSCHERMAK, SHULL and himself, EMERSON found no indication of ratios to be expected in case of double heterozygosity: Mm Xx.

EMERSON'S second hypothesis (1909b) about the connection between true-breeding and ever-segregating mottling was given on a suggestion of SPILLMAN. The two types of mottling would depend upon two factors, Y and Z, which factors are absolutely linked:

(PP) $\widehat{Y}Z \widehat{Y}Z$	true-breeding mottled race.
(PP) $\widehat{Y}z \widehat{Y}z$	} selfcoloured races.
(PP) $\widehat{y}Z \widehat{y}Z$	
(PP) $\widehat{y}z \widehat{y}z$	

In white-seeded races there may of course occur the same 4 types concerning Y and Z. The various possible crosses and their (white): mottled: selfcoloured  $F_2$  ratio are:



According to EMERSON all known facts could be explained by this  $\widehat{Yz-yZ}$  hypothesis as well as by his M X hypothesis of two independent factors.

For EMERSON the  $\widehat{Yz-yZ}$  hypothesis has two advantages:

1. The two types of mottling, phenotypically so much alike, depend on the same factors.
2. The ever-segregating mottled  $F_1$  between two selfcoloured races is more conceivable than with his monofactorial Xx hypothesis (or Mm of SHULL).

TSCHERMAK (1912) likewise attempted to consider the „konstante Marmorierung“ and „Heterozygotmarmorierung“ from the same point of view. His „Association-Dissociation“ hypothesis has some analogy with the  $\widehat{Yz-yZ}$  hypothesis of EMERSON-SPILLMAN. Both allow only of the ratio mottled: selfcoloured being 3:1 or 2:2. The hypothesis of the absolutely linked factors is, however, more in harmony with our general genetical conceptions.

The investigations of SHAW and NORTON (1918), KOOIMAN (1920) and LAMPRECHT (1931) gave an entirely new aspect to the matter! They stated that to every class of mottled seeds there does not belong one selfcoloured type with the same number, but always two types, each with half the number:

- 1 background colour type,
- 2 mottled beans,
- 1 dark-pattern colour type.

SHAW and NORTON and KOOIMAN tried to explain this fact in diametrically opposed ways. A third possible way has been chosen by the author. These three views I will discuss under *a*, *b* and *c*.

*a.* SHAW and NORTON (1918) persisted in using the  $\widehat{Yz-yZ}$  conception of EMERSON-SPILLMAN and assumed a „modifying“ factor M which is absolutely linked to the  $\widehat{Yz-yZ}$  factors. One of their coloured-seeded races (Blue Pod Butter) had a „pale buff“ seedcoat colour and produced a mottled  $F_1$  if crossed with their yellow, brown and black races.

Blue Pod Butter:	$\widehat{Yzm} \widehat{Yzm}$
Yellow, brown and black races:	$\widehat{yZM} \widehat{yZM}$
$F_1$ :	$\widehat{Yzm} \widehat{yZM}$ , mottled.

According to SHAW and NORTON the  $F_2$  of this mottled  $F_1$  always segregated into:

1 pale buff coloured:

2 mottled:

1 yellow, brown or black.

(These relations are apparently the same as in my sh sh colours!) SHAW and NORTON therefore concluded that a „modifying” factor M (linked with the Y-Z factor pair) must be dominant for the seedcoat to be able to show mottling or colour (other than the pale buff of Blue Pod Butter). True-breeding mottled races are  $Y\widehat{Z}M Y\widehat{Z}M$ . The only possible  $F_2$  ratios are 3:1 and 1:2:1 (analogous to EMERSON-SPILLMAN’s hypothesis).

b. KOOIMAN on the other hand (1920, 1931) abandoned the linked factor hypothesis and attributed the ever-segregating mottling to the heterozygous state of his (complementary) factor B.

LAMPRECHT (1932a) arrived at the same conclusion as KOOIMAN, but used the symbol C for the complementary factor involved.

True-breeding and ever-segregating mottling must now depend upon different factors and the expected ratios between mottled and selfcoloured seeds will be the same as in EMERSON’s first hypothesis.

According to KOOIMAN and LAMPRECHT mottled races (MM) may be (using LAMPRECHT’s symbol) cc or CC.

The possibilities in crossing a mottled race with a selfcoloured one are:

1. The mottled race is PP MM cc.

a. PP MM cc  $\times$  PP mm cc.

$F_1$  PP Mm cc.

$F_2$  segregates into 3 mottled: 1 selfcoloured.

b. PP MM cc  $\times$  PP mm CC.

$F_1$  PP Mm Cc.

$F_2$  segregates into 14 mottled: 2 selfcoloured.

2. The mottled race is PP MM CC.

a. PP MM CC  $\times$  PP mm CC.

$F_1$  PP Mm CC.

$F_2$  segregates into 3 mottled: 1 selfcoloured.

b. PP MM CC  $\times$  PP mm cc

$F_1$  PP Mm Cc.

$F_2$  segregates into 14 mottled: 2 selfcoloured.

So each mottled race, if crossed with a cc or with a CC self-coloured race must give an  $F_2$  ratio of 3:1 in the one and of 14:2 in the other case. Of these 14 mottled beans 12 should be MM or Mm; the remaining 2 mm Cc, i.e. beans of the ever-segregating type must appear!

To my knowledge, the proof that really a 14:2 ratio occurs has up to now not been given.

Some crosses of SHAW and NORTON seem to prove the contrary! They crossed some mottled races with a cc race (Blue Pod Butter; their  $\widehat{Yz}m$ ) and with a yellow, brown or black CC race (their  $y\widehat{Z}M$  races). The results (derived from their table II) were:

Mottled parent	Selfcoloured parent	Mottled	Self-coloured	Total
Red Valentine	× Blue Pod Butter (cc) . . .	23	7	30
" "	× Giant Stringless (CC) . . .	55	14	69
Mohawk	× Blue Pod Butter (cc) . . .	15	4	19
"	× Giant Stringless (CC) . . .	25	4	29
Wardwell	× Blue Pod Butter (cc) . . .	45	12	57
"	× Golden Eyed Wax (CC) . .	21	12	33
Warwick	× Blue Pod Butter (cc) . . .	144	61	205
"	× Challenge Black Wax (CC)	34	13	47

It is impossible to find in each pair of these crosses the 7:1 ratio for the one and 3:1 for the other cross.

c. My own hypothesis closely approximates the  $\widehat{Yz} \widehat{yZ}$  hypothesis of EMERSON-SPILLMANN and has the same advantages and numerical results as concerns the possible ratio's mottled: self-coloured (cf. p. 223). In my opinion mottling (true-breeding and ever-segregating) is due to two factors which are absolutely (or nearly absolutely) linked:

the complementary factor C and

the factor for mottling M, which locally suppresses the action of the dominant complementary factor C.

$\widehat{C}\widehat{M} \widehat{C}\widehat{M}$  true breeding mottled race.

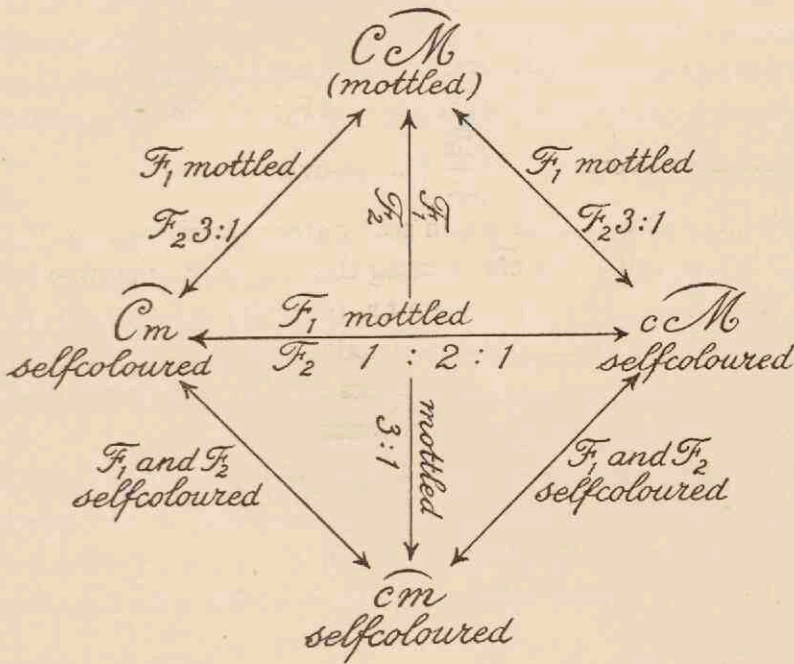
$\widehat{C}m \widehat{c}\widehat{M}$  ever segregating mottled type.

$\left. \begin{array}{l} \widehat{C}m \widehat{C}m \\ \widehat{c}\widehat{M} \widehat{c}\widehat{M} \\ \widehat{c}m \widehat{c}m \end{array} \right\} \text{selfcoloured races.}$

According to this hypothesis the dark pattern colour of mottled races is CC. I cannot judge whether this really always holds good in every case.

LAMPRECHT (VI; 1933 p. 313) says about the  $\widehat{Y}_z\widehat{y}Z$  hypothesis of EMERSON-SPILLMANN that all known facts about the two types of mottling can be explained with it. But „nur müsste dann die sehr „wenig wahrscheinliche Annahme gemacht werden, dass Y stets mit „C parallel geht und Z mit c oder umgekehrt. Dann erscheint diese „Theorie aber überflüssig und unnötig kompliziert.“ This objection does not obtain for my  $\widehat{Cm}\widehat{cM}$  hypothesis, though I must admit that a  $\widehat{cm}\widehat{cm}$  race up to now has not been found.

The possible crosses are:



MIYAKE c.s. (1931) mentioned some cases of crossing over which with the hypothesis of KOOIMAN and LAMPRECHT are not possible. The races involved were N7 with red flower and cream seedcoat and B2a with red flower and black seedcoat.  $F_1$  showed a black mottled seedcoat.  $F_2$  consisted of:

- 111 with dark-pattern colour: black, brown, purple.
- 273 mottled: black, brown and purple.
- 121 with background colour: cream.



In  $F_3$  they found that:

- a. 61 families of mottled  $F_2$  plants segregated into 322 dark pattern colour, 616 mottled, 269 cream.
- b. 30 families of dark pattern colour  $F_2$  plants gave only 577 dark pattern colour plants.
- c. 27 families of cream  $F_2$  plants gave only 609 cream.

These are the normal cases. They found, however, a few exceptions:

- d. 4 families of mottled  $F_2$  plants gave 32 mottled and 17 cream, but not a single of the dark pattern colour.
- e. 1 family of a dark pattern colour  $F_2$  plant segregated into 7 with the dark pattern colour and 4 cream.

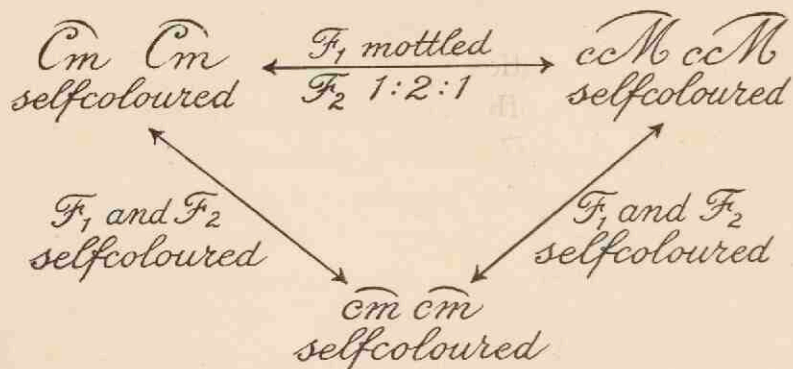
MIYAKE c.s. adopt the  $\widehat{Y}z \widehat{y}Z$  hypothesis of EMERSON-SPILLMAN and assume these factors for mottling to be „linked with a factor for cream”. I will discuss their results with the aid of my factors C and M.

The genetic constitution of the mottled  $F_1$  is  $\widehat{Cm}\widehat{cM}$ . Its gametes are:

$$\left. \begin{array}{l} \widehat{Cm} \\ \widehat{cM} \end{array} \right\} \text{non-cross-overs.} \quad \left. \begin{array}{l} \widehat{CM} \\ \widehat{cm} \end{array} \right\} \text{cross-overs.}$$

The 4 mottled  $F_2$  plants which segregated into mottled and cream may be considered as  $\widehat{CM}\widehat{cm}$ . Among their mottled offspring true breeding mottled plants ( $\widehat{CM}\widehat{CM}$ ) must occur. It is a pity that MIYAKE c.s. communicate nothing about an  $F_4$  generation of these plants. Now the possibility exists that the lack of dark pattern plants was merely a chance occurrence.

The  $F_2$  plant with dark pattern colour and segregating into 7 dark pattern colour and 4 cream will have been  $\widehat{cm}\widehat{Cm}$ . If my hypothesis is right, these cream  $F_3$  plants ( $\widehat{cm}\widehat{cm}$ ) cannot produce a mottled  $F_1$ , neither with a  $\widehat{cM}\widehat{cM}$ , nor with a  $\widehat{Cm}\widehat{Cm}$  race:



Here the test again fails, while the factorial analysis is not quite sufficient, so that no definite opinion can be expressed.

Striping and double mottling will be discussed in a later paper in view of the analysis of another cross. It seems to me possible that the inheritance of ever-segregating mottling, true-breeding mottling, striping and double mottling can be brought under the same point of view with the aid of a slight completion of the hypothesis given above.

## CHAPTER II

### CHARACTERS OF THE POD WALL

#### A. Strength of the string

##### § 1. *Previous investigations*

Difficulties in classification according to strength of string always played an important part in the investigations.

EMERSON (1904) reported on crosses between stringy and stringless podded varieties. The pods of  $F_1$  plants were sometimes intermediate between the parent races, while in other crosses they were very nearly stringless, so that the difference between them and the pods of the stringless parent was scarcely discernible. In the  $F_2$  generation of  $F_1$  hybrids in which stringlessness was dominant, only stringless and stringy forms occurred and no intermediate ones (65 stringless and 33 stringy). In the  $F_3$ -generation all stringy  $F_2$  plants bred true. Part of the stringless ones also bred true; the other part segregated into 139 stringless and 56 stringy.

Where the  $F_1$  was intermediate all three types occurred in the  $F_2$  (114 stringless, 80 intermediate, 78 stringy). As to strength of string the intermediates, however, varied more in the second than in the first generation. Part of the stringless and stringy  $F_2$  plants bred true. The remaining stringless and stringy plants and all intermediate ones segregated. From his table VIII we may derive as follows about the progeny of segregating  $F_2$  plants:

$F_2$ plants	$F_3$ families	
	stringless + intermediate	stringy
stringless . . . . .	51	19
intermediate . . . . .	63	38
stringy . . . . .	21	54

EMERSON therefore speaks of „reversal of dominance”.

WELLENSIEK (1922) crossed the stringy race Wagenaar with three different stringless races. In the  $F_1$  generation of the three crosses stringlessness appeared to be dominant, while in  $F_2$  a clear-cut monohybrid segregation occurred (41 : 18, 46 : 12 and 49 : 25; together 136 : 55). According to WELLENSIEK classification into stringless and stringy did not meet with difficulties.

JOOSTEN (1924) examined  $F_3$  and  $F_4$  generations of WELLENSIEK's material. He distinguished 4 degrees of stringiness. The clear monofactorial segregation into stringy and stringless seemed not to be confirmed.

JOOSTEN moreover tested a lot of so-called „stringless” races as to the degree of their stringlessness. For this purpose he worked out (according to length and strength of the string of boiled beans) a scale of „string numbers” ranging from 1—10. He pointed out the high variability of the character and the probable influence of external factors. On one and the same plant of some varieties pods with both weak or strong strings may occur. Really stringless races were not found.

At the same time he investigated the anatomical structure of the pod, especially of the sheath of the vascular bundle in the sutures. He distinguished two principal groups of sheath-types:

1. One type (type S) is characterised by the similarity of all the cells in the sheath; all are sclerenchymatic fibres, more or less impregnated with lignin.

2. The other type (HS) is characterized by a narrow group of wood cells, which may sometimes have sclerenchymatic fibres on the inside, found either alone or joined into larger or smaller groups. In varieties with type S not a single case of type HS occurred. In my investigation I have apparently to deal with the same two main types.

CURRENCE (1930) in crossing stringy and stringless races found in two crosses the  $F_1$  stringless, in an other one intermediate. He classified the  $F_2$  plants according to the area of sclerenchymatic fibres in the sheath: „stringless”, with an area of less than 0.005 square mm in each half of the sheath; „stringy”, with more than 0.005 square mm (this division lies between nos 3 and 4 of my fig. 4 p. 236). Furthermore,  $F_2$  plants yielding only progeny with an area of 0.005 square mm or more were considered as homozygous stringy;  $F_2$

plants yielding only progeny with less than 0,005 square mm as homozygous stringless; those plants of which the progeny included both groups were considered to be heterozygous. This method of classifying is rather arbitrary. According to  $F_2$  and  $F_3$  of his first cross ( $F_1$  stringless) he arrived at the following results:

27 „stringless” $F_2$ plants consisted of	{	9 homozygous stringless, 17 heterozygous and 1 homozygous stringy.
13 „stringy” $F_2$ plants consisted of	{	4 heterozygous 9 homozygous stringy.

The numbers of the three types (9 : 21 : 10) agree very well with the 1 : 2 : 1 ratio. For his second cross with stringless  $F_1$  CURRENCE arrived at the same result. The  $F_1$  of his third cross was distinctly stringy (intermediate). According to the  $F_3$  progeny he estimated that there were among 83  $F_2$  plants (classified as 19 stringless and 64 stringy): 8 homozygous stringless, 44 heterozygous and 30 homozygous stringy. These figures agree more or less with the ratio 1 : 8 : 7. In order to explain the data of his three crosses CURRENCE assumes one dominant factor S producing stringlessness and a second factor T, which, when present, inhibits the action of the first factor (i.e. only tt SS and tt Ss are stringless). The first two crosses would be of the type tt SS (stringless)  $\times$  tt ss (stringy),  $F_1$  stringless,  $F_2$  ratio 3 stringless: 1 stringy. The third cross would be tt SS (stringless)  $\times$  TT ss (stringy),  $F_1$  stringy,  $F_2$  ratio 3 stringless: 13 stringy; the stringless plants are tt SS and tt Ss. CURRENCE tried to explain EMERSON's results on the same lines.

The main objection to this hypothesis of CURRENCE is the arbitrary way of classifying into the two groups stringy and stringless, even in the third cross with intermediate  $F_1$ . The two types of sheaths, photographed by him, correspond exactly with the two main types of JOOSTEN and my-self (Cf. nos 2 and 8 of fig. 4).

### § 2. *The methods used*

The partly unclear, partly contradictory results of the investigations discussed above, showed the desirability of an accurate re-examination. The two main principles in investigating the inheritance of the string must be:

1. To examine the strength of string together with the microscopical anatomy.
2. To avoid an a priori division into only two or three types.

*Strength of the string.*

From each plant 3 nearly full-grown pods were taken. They were boiled (65 minutes) and afterwards stringed. After JOOSTEN's example I used a scale of „string numbers” ranging from 1 to 10 :

1. Without any string.
2. Length of string fragments less than 1 cm.
3. Length 1—2.5 cm.
4. Length 2.5—4 cm.
5. Length 4—5.5 cm.
6. *a.* Longer than 5.5 cm, but not continuous.  
*b.* Continuous, but very tender and weak string.
7. Continuous, rather weak string.
8. Continuous string, rather strong.
9. Continuous string, difficult to break; yet ravelling out when drawn between two finger nails.
10. Continuous string; hardly to be broken between the finger tops; not ravelling out between the nails.

Dorsal and ventral string numbers are calculated by averaging the numbers of three beans; the string number of each plant is the average of the six numbers.

In some cases the six numbers differ greatly, the probable error of the average therefore being high. But in most cases they do not diverge so much. Usually the ventral string number is somewhat lower than the corresponding dorsal one.

*The microscopical anatomy.*

Strength of string depends upon the cell types which compose the sheath of the vascular bundles in the dorsal and ventral sutures of the pod. At the beginning of my investigations I described the anatomy of the sheath in each plant (3 pods; 2 cross sections of each pod) as accurately as possible. The following points, which refer to all plants, soon became clear to me:

1. The sheath always takes up about the same area.
2. It consists of the same three cell types.

3. These cell types have always about the same relative position.

Only the percentages of each cell type are variable. Therefore the one thing I had to do was to ascertain (by estimating) the percentages of the area taken up by each of these three cell types. For this purpose I studied cross-sections of one nearly full-grown pod from each plant. After some experiments I chose the double-staining method with methyl-green and alum-carminé for the differentiation of the cell types (STRASBURGER, 1923 p. 231). Besides all investigations have been made with a polarization microscope.

1. The area (cf. fig. 3; plates I and II).

The sheath lies outside the dorsal and ventral vascular bundle.

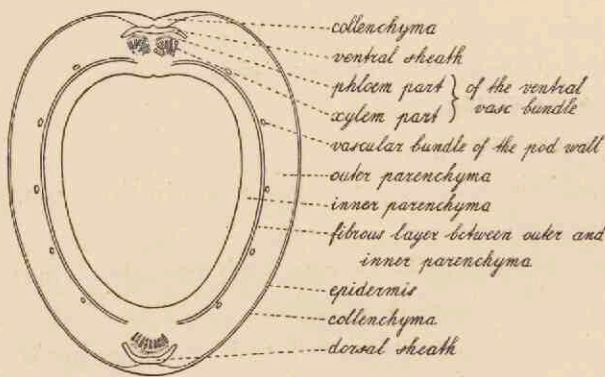


FIGURE 3. Cross-section of the pod.

The outer margin is formed by a crystal-layer (pl. II, nos 6 and 7). The inner margin is not so sharply marked. Yet outside the phloem portion of the vascular bundle we find as a rule some large parenchymatic cells (cf. plates I and II). They are considered

to form the inner margin of the sheath. Tearing off the string usually takes place along these cells. The number of cell-layers between the crystal-cells and those large parenchymatic cells varies for the dorsal sheath from 5 to 8, for the ventral one from 4 to 7. Outside the sheath collenchymatic cells are found (fig. 3; plates I and II); in other regions of the pod wall only the hypodermic layer is collenchymatic.

2. The cell types (cf. plates I and II).

a. Parenchymatic cells; non-lignified, with intercellular spaces; red-coloured by the alum-carminé.

b. Wood cells; cell wall only slightly thickened, strongly lignified. These cells are more or less isodiametrical (cf. pl. II nos 6 and 7). They are stained very dark by the methyl-green and do not show double refraction. Cf. the nearly black cell groups in plates I and II.

*c. Fibres*; cell wall strongly thickened. In longitudinal sections (pl. II no. 7) they show the typical characters of fibres: very much elongated, with narrow, oblique, simple pits. Stained with methyl-green their colour is a pale bluish green. They show a conspicuous double refraction.

3. The relative position (cf. fig. 4; plates I and II) and the percentages of the three cell types are best discussed in the description of the parent plants and  $F_1$ .

### § 3. Description of the parent plants and $F_1$

#### 1. Fijnetros.

The anatomical structure of the sheath is to be seen in fig. 4 nos 2 and 3 (sometimes between 3 and 4). Plate I no. 1 shows a micro-photograph of this type. The outer part of the sheath consists of wood cells (between 40 and 75%), the inner part of parenchymatic cells. The fibres very often form four more or less distinct cell groups. This anatomical structure of the sheath corresponds with JOOSTEN's type HS. In all Fijne tros plants I grew in the years 1930—1933 the percentage of fibres varied between 0 and 25, usually between 5 and 15. The strength of string in Fijne tros lies between 2—3 and 5—6.

1930 (35 plants). Highest percentage fibres 10 (1 plant); generally 5% or lower. Unboiled beans nearly stringless (boiled beans not examined). Two plants (6-29 and 6-34) were crossed with Wageenaar; their percentages of fibres were resp. 4 and 2 (average of 3 pods; 2 sections of each pod).

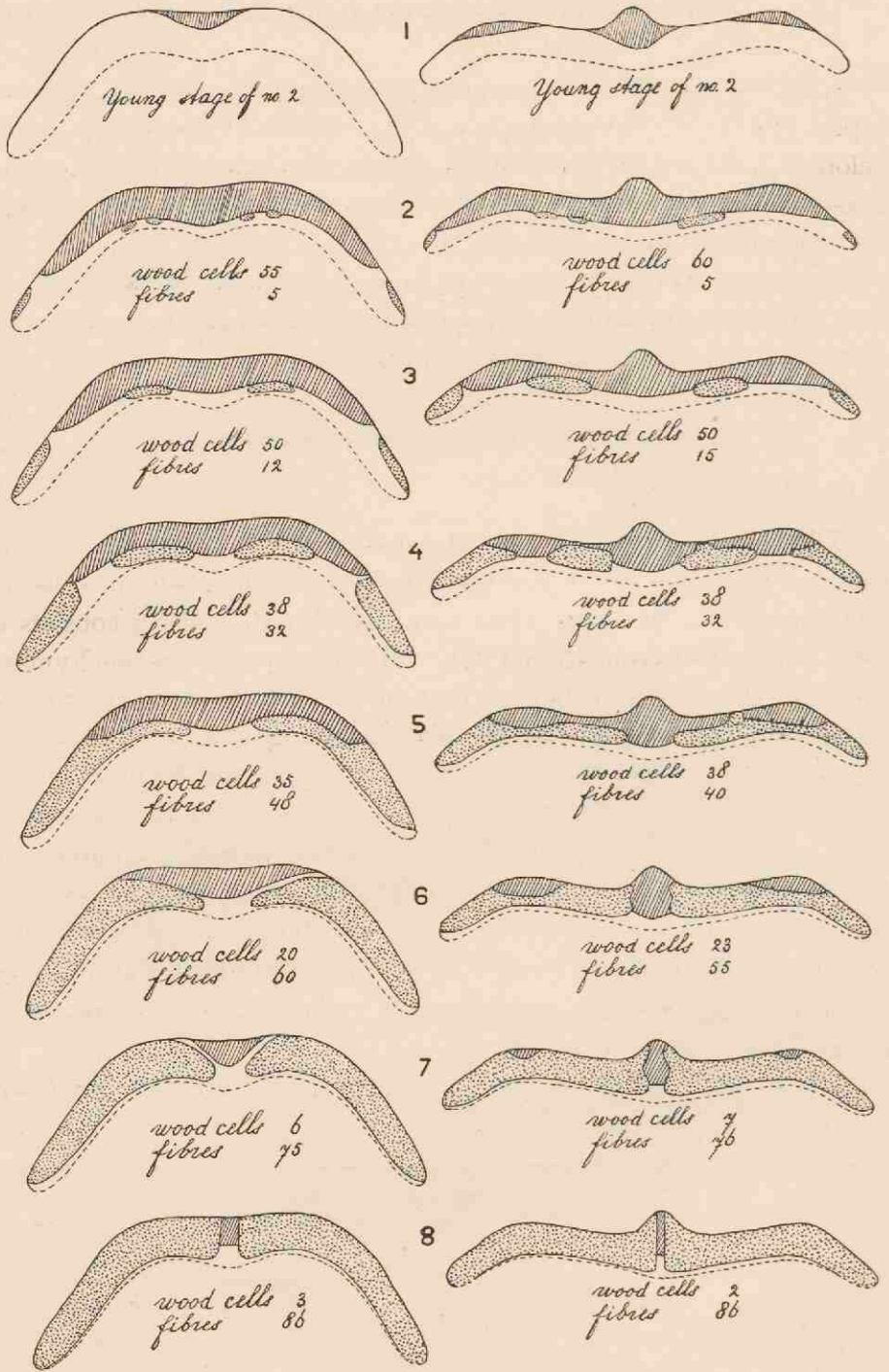
1931. Strength of string and percentages of fibres in familie 6—29 are given in the subjoined table.

		Strength of string					Total
		1—2	2—3	3—4	4—5	5—6	
Percentages of fibres	0—10				1		1
	10—20			5	6	4	15
	20—30				1	2	3
	30—40						
Total			5	8	6	19	



DORSAL SHEATH

VENTRAL SHEATH



parenchymatic cells
  wood cells
  fibres

FIGURE 4. Scheme of the various sheath types.

Fijne tros: nos 2 and 3, sometimes between 3 and 4.

Wagenaar: no. 8.

F<sub>1</sub>: nos 4, 5 and 6.

In F<sub>2</sub> all types 2—8 occur.

No. 1 is the young stage of no. 2, showing those parts of the wood cells which are first lignified.

In all plants the percentage of fibres was higher than in the mother plant 6-29 in 1930. External conditions may probably influence the percentage of fibres and the strength of string. I have tried to examine these influences by halving seedlings and cultivating the halves under different conditions of water supply. The results, however, were not quite decisive. — In family 6-34 there occurred 9 plants with strength 3-4 and 3 with 4-5; these plants have not been investigated anatomically.

1932. The three families belonged to the progeny of family 6-29 1931. Their string numbers and percentages of fibres are given in the subjoined tables. Family 173 (string number mother plant 3.6; percentage of fibres 10):

		Strength of string					Total
		1-2	2-3	3-4	4-5	5-6	
Percentages of fibres	0-10				4	1	5
	10-20			2	2	2	6
	20-30				1		1
	30-40						
Total				2	7	3	12

Family 178 (string number mother plant 4.4; percentage of fibres 6):

		Strength of string					Total
		1-2	2-3	3-4	4-5	5-6	
Percentages of fibres	0-10			2	3		5
	10-20				5		5
	20-30				1		1
	30-40						
Total				2	9		11

Family 179 (string number mother plant 5.4; percentage of fibres 25):

		Strength of string					Total
		1—2	2—3	3—4	4—5	5—6	
Percentages of fibres	0—10			1	0	2	3
	10—20			1	0	5	6
	20—30				2		2
	30—40						
Total			2	2	7	11	

The mother plant of family 179 had the strongest string and highest percentage of fibres among the members of family 6—29 in 1931. It appears from the tables that in 1932 family 179 had the highest strength of string, though not a single plant reached the string number 6. Slight genetical differences seem probable.

1933. Cf. table 32. Between these families no conspicuous differences are found. Remarkable is one plant with strength 6.8 in family 327.

## 2. Wagenaar.

The anatomy of the sheath is shown in fig. 4 no. 8 and pl. II no. 5. Nearly the whole sheath consists of fibres. These fibres are separated into two parts by a small group of wood cells and parenchymatic cells in the middle. This group of cells nearly always has the same shape as in fig. 4 and pl. II. In the dorsal sheath the wood cells may be totally lacking in a few cases; the fibres then form one continuous group. In the ventral sheath the group of wood cells and parenchymatic ones is extremely narrow and is formed, without any exception, by the two epidermal cell layers. The Wagenaar sheath corresponds with JOOSTEN's type S (cf. p. 231).

Both anatomical structure and strength of string show hardly any variability in the Wagenaar race. The string number is nearly always 10, never lower than 9.

## 3. F<sub>1</sub> generation.

Its anatomy corresponds with fig. 4 nos 4, 5 or 6; pl. I no. 2 or between 2 and 3. The percentage of fibres varies (one pod of each

plant has been investigated) between 20 and 65. Fig. 4 and plate I show clearly that the relative position of the cell types is exactly the same as in the Fijne tros race. The groups of fibres, however, are greater and often form (fig. 4 nos 5 and 6) one continuous group in each half of the sheath. In the ventral sheath the wood cells often lie in three groups, separated by fibres.

The three  $F_1$  plants in 1931 showed (5 pods stringed and 5 anatomically investigated) the following figures:

	String number			% fibres	% wood cells
	dorsal	ventral	average		
55-2 . . . . .	7.6	7.0	7.3	50	30
55-4 . . . . .	7.5	7.8	7.7	50	26
55-6 . . . . .	7.6	6.6	7.1	56	24

The remaining  $F_1$  plants (1932 and 1933) are shown in table 33. The strength of string always lies between 6 and 8. The probable error of these string numbers is very small. The pods of some plants with strength 6—7 received the qualification „rather young” (based upon the very young seeds in the examined pods).

The variability in the percentage of fibres in these  $F_1$  plants is very high. Partly this will be due to the fact that but one pod of each plant has been examined. In the  $F_2$  generation no differences between the progenies of  $F_1$  plants with 20 and with 50% fibres have been found (cf. next § and table 37).

#### § 4. Analysis of the $F_2$

In the correlation tables 34, 35 and 36 the three  $F_2$  families of 1932 (55-2, 55-4 and 55-6) are shown, arranged according to strength of string and percentage of fibres. The correlation between these two characters is rather strong and it might have been even stronger, if the anatomy of more than one bean could have been investigated. In a sheath without or nearly without fibres the percentage of wood cells probably slightly influences the strength of string.

In some cases of very bad agreement between string number and percentage of fibres I find the probable cause in my notes, viz. that

only one very bad pod was available for the string investigation. Another remarkable cause of discrepancies between the two characters was the following. In  $F_2$  some plants have pods with strong ventral curvature. When I gathered these pods it might happen that the ventral string broke in one or more places without my noticing it. The same breaking may occur in the boiled strongly curved beans. This breaking of the string in curved beans I have not sufficiently realized in the beginning of the  $F_2$  investigation. After becoming aware of it, I reexamined the records, and found indeed that in some cases of strong discrepancies (high percentage of fibres, low string number) in curved beans the ventral string number was extremely low; sometimes the unusual high strength of the short ventral string fragments was mentioned. A third cause of inaccuracy lies in the difficulty of always using the same standard for the strength of string. In spite of these and possibly other causes of inaccuracy the  $F_2$  and  $F_3$  results lead to very definite conclusions.

The undermost rows of the three tables 34, 35 and 36 show that a division into three groups, *Fijne tros*,  $F_1$  and Wagenaar (according to strength of string) is impossible. Nor can we discern a definite Wagenaar type from a not-Wagenaar type, though the number of plants with strength 8—9 is not very high.

With regard the anatomy of the sheath all types of fig. 4 or plates I and II occur. From this continuous series it becomes entirely clear that the relative position of the three cell types is always the same. In this respect I wish to mention a remarkable analogy. Figure 4 no. 1 shows those parts of the wood cells of no. 2 which are lignified first; these parts are exactly the same as the narrow groups of wood cells in the sheath types nos. 6 and 7.

Though the anatomical structures showed a continuous series, the pure stringy type (i.e. the Wagenaar-type) always could be nicely discriminated. Its characteristics are (cf. fig. 4 no. 8; pl. II no. 5): sheath entirely consisting of fibres, except for the narrow rectangular part in the middle, which in the ventral sheath is strictly limited to the continuation of the two epidermal cell layers.

This pure stringy (Wagenaar) type is to be found in the correlation tables 34, 35 and 36 under the group with 80% fibres or more. It will be seen that nearly all  $F_2$  Wagenaar-types have the string num-

ber 9—10 and likewise that nearly all  $F_2$  plants with string number 9—10 are of the pure stringy Wagenaar type.

All  $F_2$  families investigated are found in table 37 (in table 36 only part of fam. 55-6 is recorded). Each family shows a clear cut monofactorial segregation (1 : 3) into a pure stringy type (Wagenaar) and a not pure stringy one. All families together give:

	not pure stringy	pure stringy (Wagenaar)	total
Observed . . . . .	1088	350	1438
Expected 3 : 1 . . .	1078.5	359.5	
D/m . . . . .	0.58		

In table 37 there is a difference between the three  $F_2$  families of 1932 and those of 1933. In the first three families many not pure stringy plants occur with string number 8—9 and even a few with 9—10; their average strength is 6.30. In the families of 1933 on the other hand, the pure stringy (Wagenaar) type is by its strength of string markedly different from the remaining not pure stringy plants. Not any of the latter has a string number 9—10 and only a few 8—9; their average strength is 5.76.

I am not certain what this difference between the  $F_2$  families of 1932 and 1933 means. Some  $F_1$  mother plants of the latter families indeed had a somewhat lower string number and a lower percentage of fibres than the three  $F_1$  plants in 1931. It must, however, be remarked that of each  $F_1$  plant in 1932 only one pod was investigated anatomically (in 1931 five) and that the  $F_2$  families 393—400 (1933) in table 37 do not show differences between the progeny of  $F_1$  plants with a high and that of  $F_1$  plants with a low percentage of fibres. Moreover strength of string and percentages of fibres in the Wagenaar and Fijne tros parent plants (and their progeny; compare the table on p. 235 with the first table on p. 237) of the two groups of  $F_2$  families were the same. Possibly the differences between the  $F_2$  families of 1932 and those of 1933 may be (partly) due to weather influences or to differences in classification caused by the subjective method of determining the strength of string.

§ 5. *F<sub>3</sub> generation and backcrosses*

As might be expected all pure stringy  $F_2$  plants (Wagenaar type) breed true in the  $F_3$  (table 38). The strength of string is nearly always 9—10. Many hundreds of these  $F_3$  plants have been investigated anatomically; their sheath always shows the characteristics of the pure stringy Wagenaar type.

In tables 39 and 40 the  $F_3$  progeny of not pure stringy  $F_2$  plants is found. The families in the two tables have been arranged according to increasing strength of string in the  $F_2$  mother plants. Those in table 39 segregate the pure stringy (Wagenaar) type, while those in table 40 do not.

As to the segregating families in table 39 the numbers of the two types always fit in very well with the 3 : 1 ratio. In all these families together there occur:

	not pure stringy	pure stringy	total
Observed . . . . .	475	163	638
Expected 3 : 1 . . . . .	478.50	159.50	
D/m . . . . .	0.32		

The  $F_2$  mother plants, however, vary in their strength of string between 3.5 (with 10% fibres) and 9.4 (with 82% fibres). The ratio of the pure stringy type (controlled in its anatomical structure) is exactly the same in all families. We find for instance:

	not pure stringy	pure stringy
in the first 12 families . . . . .	163	59 (expected 55.50)
in the last 12 families . . . . .	216	71 (expected 71.75)

As to the not pure stringy type there are, however, striking differences between the families! If the  $F_2$  mother plant has a low string number and percentage of fibres, the two types may be easily discerned in the  $F_3$  family; not pure stringy types with a higher string

number than 6—7 or 7—8 do not occur. In families of  $F_2$  plants with high string number and percentage of fibres the two types on the contrary can not be discriminated by strength of string at all: many plants with string numbers 8—9 and 9—10 are not of the pure stringy Wagenaar type. Discrimination, however, is always possible by means of anatomical investigation.

Table 40 shows the  $F_3$  families which do not segregate the pure stringy type (progeny of 55-2 kept apart from 55-4; in table 39 the two progenies have been arranged in one series). Possibly some families might have segregated the pure stringy type, if a greater number of  $F_3$  plants could have been examined. Here as well as in the segregating families, there is a correlation between strength of string in the  $F_2$  mother plants and in their  $F_3$  progeny, though there is some regression. A comparison of table 40 with table 32 (Fijne tros families in 1933) shows that no  $F_3$  families with lower string numbers than those of table 32 occur among the families of table 40.

In table 41 the  $F_2$  mother plants of all  $F_3$  families are represented; they are arranged according to strength of string, percentage of fibres and their  $F_3$  progeny (non-segregating, segregating and pure stringy). 29 families segregate the pure stringy type, 24 families do not. This serious divergence from the expected 2 : 1 ratio may be partly due to the very low number of plants which has been investigated in some of the non-segregating families.

From these  $F_1$ ,  $F_2$  and  $F_3$  results we may conclude that one main factor is responsible for the differences between the sheath types of Wagenaar and Fijne tros. The  $F_1$  is intermediate, though approaching the Fijne tros parent. In  $F_2$  only one fourth, the homozygous pure stringy plants (Wagenaar type) may be discerned from the remaining not pure stringy ones; the pure stringy type therefore might be indicated as „recessive”.

The stringiness of the not pure stringy types (homozygous and heterozygous) is influenced by other factors. For me it is impossible to say with certainty something about their number and character. Especially the heterozygous type seems to be greatly influenced by these factors. As a result some families with a nearly „stringless” mother plant (e.g. string number 4) segregate into „stringless” and „pure stringy” without (or nearly without) „intermediate” forms with string numbers 6, 7, 8 or 9 (cf. table 43, families 496, 507, 503).



The backcrosses of  $F_1$  with the two parent types confirmed the monofactorial scheme of the inheritance of stringiness. In the backcross with Fijne tros not a single pure stringy plant has been found. The string numbers in this backcross were:

1—2	2—3	3—4	4—5	5—6	6—7	7—8	8—9	9—10	total.
0	4	16	32	22	32	42	3	0	151

In the backcross with Wagenaar (table 42) there occurred:

	not pure stringy	pure stringy (Wagenaar)	total
Observed . . . . .	163	139	302
Expected 1 : 1 . . . . .	151	151	
D/m . . . . .	1.38		

The not pure stringy backcross plants of 1933 had lower string numbers than those of 1932 (cf. table 42). Exactly the same difference as had been found between the  $F_2$  families of those years (cf. p. 241). I am not certain about the cause of it. It may be due to genetical differences in the Wagenaar race. Possibly, however, the differences are caused by weather influences or by the subjective method of determining the strength of string. All not pure stringy backcross plants are heterozygous for the main factor and therefore in all their progenies the pure stringy type must appear. These progenies are given in table 43. No. 492 (12 individuals) is the only family which does not segregate the expected pure stringy type.

As concerns the symbolizing of the main factor for stringiness CURRENCE used the symbol S for the monofactorial difference between stringy and stringless types. The symbol S, however, is generally used (TSCHERMAK, TJEPPES and KOOIMAN) for the striped character of the seedcoat. I, therefore, will use the abbreviation St to symbolize the monofactorial main difference between the two races.

Fijne tros (nearly stringless) St St.

Wagenaar (pure stringy) st st.

## B. Toughness of the pod wall

§ 1. *Previous investigations*

When the pod wall is characterized, two main types are generally distinguished:

1. Tough, parchmented or fibrous.
2. Tender, non-parchmented or fibreless.

EMERSON (1904, p. 54) found a „strong tendency toward dominance of tenderness, the pods of first generation hybrids being „almost as tender as the tender podded parent”. In the second generation (different crosses combined) he found 22 tender-podded plants, 38 intermediates and 17 tough-podded ones.

TJEBBES and KOOIMAN (VII, 1922) on the other hand observed in  $F_1$  dominance of the parchmented type. In  $F_2$  they found segregation into 174 parchmented and 38 non-parchmented; 130 segregating  $F_3$  families segregated into 1572 and 512. They therefore suggest a monofactorial segregation.

TSCHERMAK (1901 and 1902) mentioned dominance of „gewölbt” over „eingezogen”. He found (1922 p. 40) in the cross „Tausend für Eine”  $\times$  „Anker” among 94  $F_2$  plants „16 mit Schnür-oder Perlhülsen, 78 mit glattgewölbten Hülsen (vermutlich 3 : 13), was auf bifaktorielle Grundlage hinweist”.

CURRENCE (1930) reported on  $F_1$ ,  $F_2$  and  $F_3$  of crosses between fibrous and fibreless pods, of which the  $F_1$  was always fibrous. The difficulties of properly classifying the  $F_2$  plants appeared to be very great. Of 23  $F_2$  plants e.g., which had been classified as fibrous, there appeared to be according to their  $F_3$  progeny: 7 homozygous fibreless, 11 heterozygous and 5 homozygous fibrous (Cf. his table VI).

LAMPRECHT (1932b, p. 306ff.) distinguished the two main types „einfach gewölbt” and „ingeschnürt”. He obtained entirely new results, which may be shortly reviewed. Cross XVII: Both parents and  $F_1$  „einfach gewölbt” (one of the parents less typical).  $F_2$  segregated into 563 „einfach gewölbt” and 34 „ingeschnürt” ( $= 1/16$ ). Among the first group typical and less typical forms occur in the ratio 1 : 2. „Dies lässt die Annahme wahrscheinlich erscheinen, dass „teils die beiden für die Ausbildung der einfach gewölbten Hülse „verantwortlichen Faktoren je für sich eine weniger typisch ge-

„wölbte Hülse bedingen und dass dies teils auch für die in diesen „beiden Faktoren heterozygoten Typen der Fall ist; bei dieser „Annahme haben wir mit folgendem theoretischen Verhältnis zu „rechnen: 5 typisch einfach gewölbt: 10 weniger typisch gewölbt: „1 eingeschnürt.... Damit soll nicht behauptet werden, dass es „sich so verhalten muss. Die weniger typisch gewölbten Hülsen „könnten auch durch den Effekt anderer in den in Rede stehenden „Biotypen vorkommenden Faktoren bedingt werden“. Cross XVIII: Again both parents and  $F_1$  „einfach gewölbt“. In  $F_2$  segregation of  $1/64$  „eingeschnürt“ (1635 and 30). Cross XII: Between an „einfach gewölbt“ and an „eingeschnürt“ race;  $F_1$  „einfach gewölbt“. In  $F_2$  the ratio of the two types is 9 : 7 (348 and 311).

The results of these three (and other) crosses LAMPRECHT explains by the adoption of the four factors Fa, Fb, Fc and Fd. „Fa ist ein „Faktor, dessen Anwesenheit erforderlich ist, wenn es überhaupt „zur Ausbildung einer einfach gewölbten reifen Hülsenwand kommen soll. Er wirkt demnach als Grundfaktor. Fb, Fc und Fd sind „drei Faktoren, die je für sich allein, aber nur bei Anwesenheit von „Fa zur Ausbildung einer einfach gewölbten, reifen Hülse führen“.

Further on I shall have to revert to his view about the anatomical base of the pod wall character.

The cross *Fijne tros* × *Wagenaar* is of a type up to now not described as far as I know.

## § 2. *Description of the parent plants and $F_1$*

Figures 5 and 6 show the full grown and the dry pods of *Wagenaar*,  $F_1$  and *Fijne tros*; on fig. 7 halves of dry pods are to be seen.

*Fijne tros* is a race with non-parchmented, tender pod wall, which in the ripe pods is greatly constricted between the seeds and then has a much shrivelled surface. A membrane (parchment layer) is never found in boiled beans.

The *Wagenaar* race has a „semi-parchmented“ pod wall, which in the ripe pod is only slightly constricted and shrivelled in a rather variable degree. *Wagenaar* can be threshed. (*Fijne tros* cannot). In boiled beans a thin, weak membrane can be shown by scraping off the outer, soft layers.

The  $F_1$  pod wall is strongly parchmented, neither constricted nor shrivelled. The dry pods sometimes dehisce of their own accord

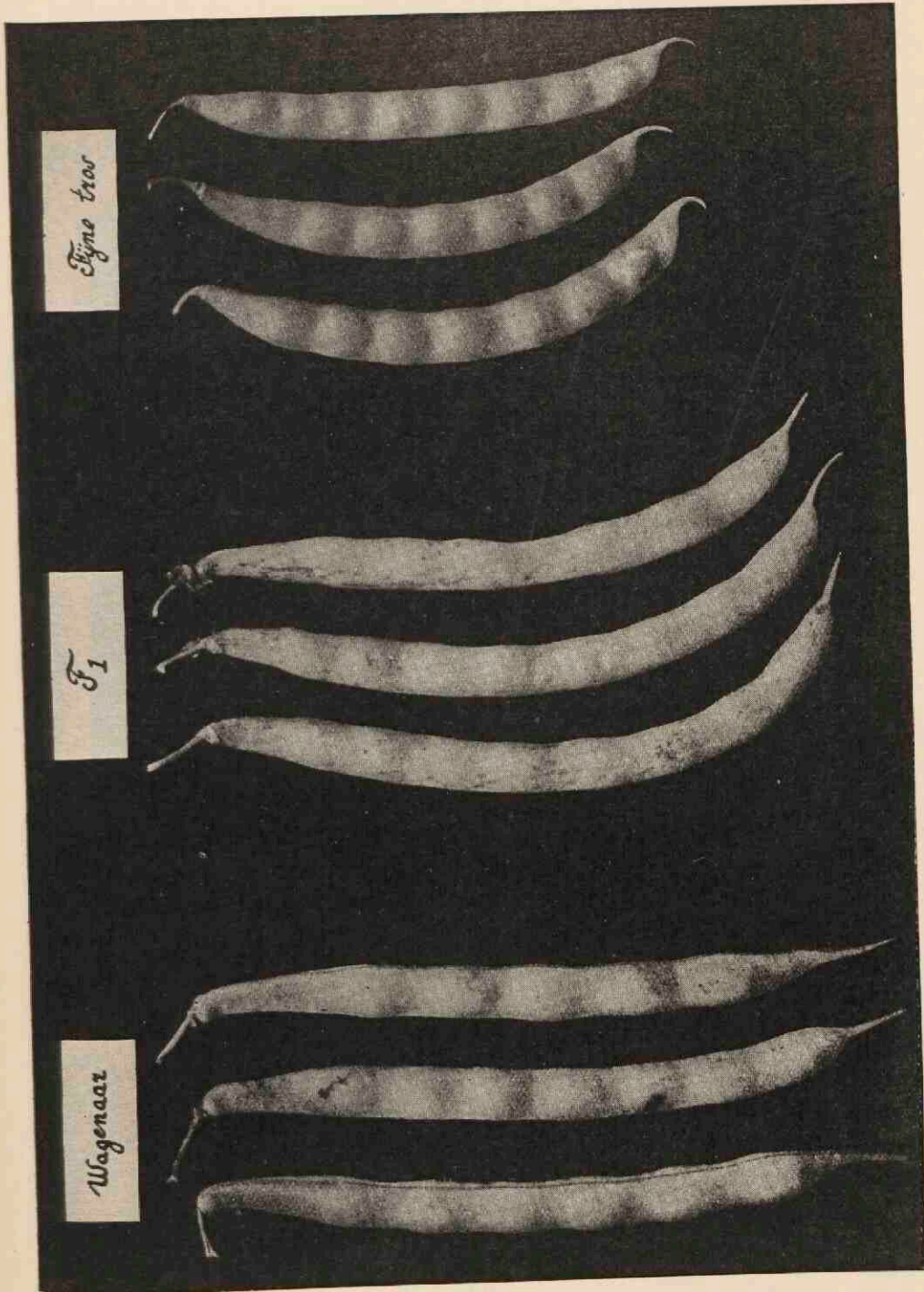


FIGURE 5. Full grown pods.



FIGURE 6. Dry pods.

and roll up spirally. In boiled beans the membrane is extremely thick and tough.

As regards the anatomy (cf. fig. 3, p. 234) the pod wall of each of the three types consists of an outer parenchyma (with the vascular bundles) and an inner parenchyma. In the Wagenaar race

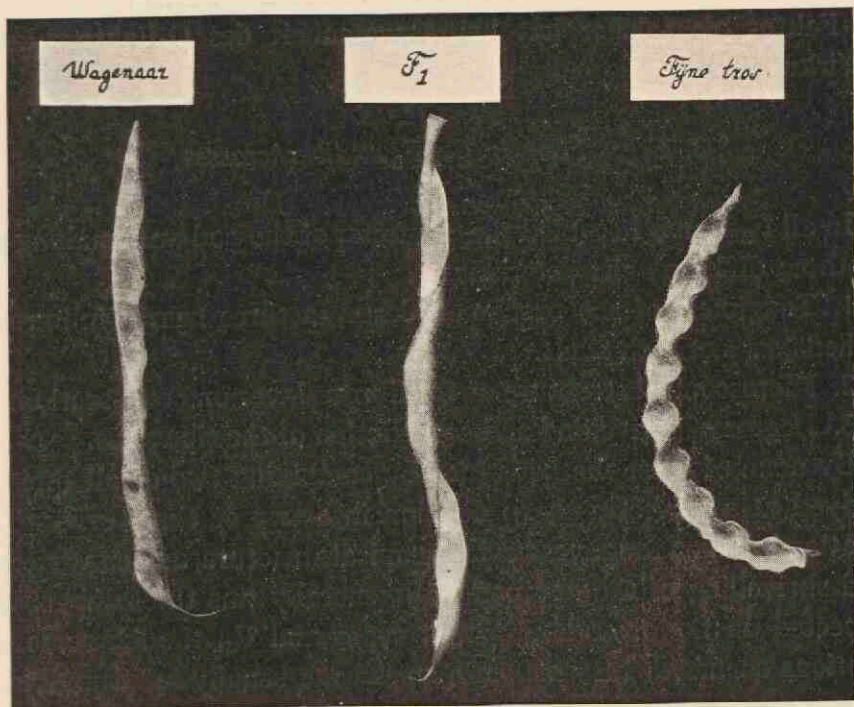


FIGURE 7. Halves of dry pods.

outer and inner parenchyma are separated by a layer of fibrous cells, which run obliquely across the pod wall. Only the cells in the outer part of the layer are somewhat thickened and lignified. This lignified part is rather variable; sometimes true fibres are not found at all, in other cases the greater part of the layer is lignified.

In the Fijne tros race a fibrous layer does not occur. Yet the separation between inner and outer parenchyma is usually clear, on account of some differences in cell width and shape, the occurrence of crystal-cells and sometimes of a few scattered fibres.

In all  $F_1$  plants the fibrous layer is as thick as (or even somewhat thicker than) in the Wagenaar race; it is totally lignified. The cell walls, however, are never very much thickened.

So the three types Fijne tros, Wagenaar and  $F_1$  seemed to be quite different. In the second generation therefore the bifactorial ratio 4 : 3 : 9 might be expected, analogous to results obtained with *Pisum sativum* (WELLENSIEK, RASMUSSEN) and *Vicia Faba* (SIRKS 1932, p. 319: „der Faktor Q verursacht eine lederartige Hülsestruktur, welche vom S-Faktor verstärkt werden kann; der „S-Faktor als solcher hat bei Abwesenheit des Q-Faktors keine „Wirkung““).

### § 3. Segregation in $F_2$ , $F_3$ and backcrosses

In all  $F_2$  plants I studied the character of the pod wall, making use of three different characteristics:

1. Toughness of the parchment-layer in three nearly full grown boiled beans of each plant.
2. Microscopical structure of the fibrous layer on cross-section.
3. Degree of shrivelling and constriction of the ripe pods.

By none of these methods (nor by combining two or all three) I arrived at a perfectly sharp division into two or three types. The relation between toughness, microscopical structure, and constriction and shrivelling of the dry pod wall generally was the same as was expected on the ground of parent types and  $F_1$ , though some exceptions occurred. Intermediate types were usually intermediate in all respects.

The only fairly marked division was into *n o n-p a r c h m e n t e d* (Fijne tros type) and *p a r c h m e n t e d* (in all degrees). In some intermediates between Fijne tros and Wagenaar the anatomical structure was decisive for discriminating the non-parchmented type: total lack of the fibrous layer; some scattered fibres or groups of fibres may occur. In a very few cases the existence of a layer was doubtful and could not be ascertained with certainty from cross-sections.

In the  $F_2$ -families the number of this purely non-parchmented type was always about  $\frac{1}{4}$  (highest D/m value 0.88). All families together (table 44) gave:

	non-parchmented	parchmented	total
Observed . . . . .	310	958	1268
Expected 1 : 3. . . . .	317	951	
D/m . . . . .	0.45		

Among the 302 backcross plants  $F_1 \times$  Wagenaar and the reciprocal cross not a single non-parchmented plant occurred. Discrimination between Wagenaar and  $F_1$  type was not possible.

The backcross plants Fijne tros  $\times F_1$  could easily be divided into 87 non-parchmented (3 less typical) and 56 parchmented (most of them of the  $F_1$  type; 6 more or less Wagenaar type). The deviation of the expected monofactorial backcross numbers 71.5 : 71.5 is very great,  $D/m = 2.58$ . This backcrossing, however, was chiefly done with a view to seedcoat colour of coloured flowering plants; as the castration of the Fijne tros mother plant was performed less accurately than in other crosses, there may be among the white flowering, non-parchmented plants some pure Fijne tros individuals. The figures in the backcross are:

	white-flowering		violet-flowering	
	non-parchmented	parchmented	non-parchmented	parchmented
Observed . . . . .	46	27	41	29
Expected 1 : 1 : 1 : 1 . . . . .	35.75	35.75	35.75	35.75
D/m . . . . .	2.01	1.71	1.06	1.32

In the  $F_3$  generation all non-parchmented  $F_2$  plants bred true; fibres may occur, but only in scattered groups between outer and inner parenchyma, never forming a more or less continuous layer.

Of parchmented  $F_2$  plants 38  $F_3$  families segregated into both types; 25 families did not segregate the non-parchmented Fijne tros type (expected according to the 2 : 1 ratio 42 and 21). The segregating families are to be found in table 45. The agreement with the unifactorial ratio is quite satisfactory:



	non-parchmented	parchmented	doubtful	total
Observed . . . . .	170	539	7	716
Expected 1 : 3. . . . .	179	537		

(The 7 doubtful plants have not been investigated anatomically).

F<sub>2</sub> plants of the strongly parchmented F<sub>1</sub>-type sometimes segregated (except for non-parchmented plants) into strongly and semi-parchmented, in other cases the latter type was not found or only in a few plants. Semi-parchmented F<sub>2</sub> plants generally gave none or only few of the strongly parchmented type. It was, however, on the very ground of the F<sub>3</sub> segregations impossible to conclude to a bifactorial segregation.

Figure 8 shows a plant of the non-parchmented „Perfect” race, of which one branch bears three pods of the parchmented type. It may be of some importance with a view to the inheritance of this pod character to examine the offspring of this plant. WOYCICKI (1930) mentioned a probable case of mutation from non-parchmented into parchmented in the variety „Japonaise”.

Now I will revert to LAMPRECHT's investigations. He writes (1932*b*, p. 309): „Die Steifigkeit der Bauch- und Rückennaht beruht auf „einer Einlagerung von Sklerenchymzellenbändern, was u.a. von „JOOSTEN (1927) untersucht worden ist. Die Steifigkeit der übrigen „Hülse wird durch Einlagerung einer Kollenchymzellenschicht unter „der Epidermis verursacht”. And (p. 314): „Mit ziemlicher Wahrscheinlichkeit kann angenommen werden, dass diese Faktoren (i.e. „Fb, Fc and Fd) für einen Verholzungsprozess der unter der Epidermis gelegenen Kollenchymzellenschicht verantwortlich zu machen „sind”.

If LAMPRECHT's supposition about the collenchymatic layer as the anatomical base of his types „einfach gewölbt” and „ingeschnürt” is confirmed by further anatomical investigations, there would be two quite different types of toughness of the pod wall.

About the connection between his pod wall characters „einfach gewölbt” and „ingeschnürt” and stringiness LAMPRECHT writes

(1932*b*, p 308): „Ein weiteres Charakteristikum (der eingeschnürten „Hülsen) gegenüber der ersten Gruppe ist ferner, dass hier auch „Rücken- und Bauchnaht der Hülsen beim Reifen in hohem Grade „nachgeben und eingezogen werden. In der ersten Gruppe gewahrt „man auch bei den weniger typisch einfach gewölbten Hülsen stets



FIGURE 8. Somatic variation in the tender-podded „Perfect” race.

„eine gewisse Steifigkeit der Rücken- und Bauchnaht. Unter den „Typen mit eingeschnürten Hülsen scheinen demnach keine solchen „mit stärkerer Fädigkeit vorzukommen”. And about the possible influence of the „groundfactor” Fa (p. 314): „Es verbleibt zu unter- „suchen ob es bei Anwesenheit von Fa bzw. fa allein zur Ausbildung „nur eines unbedeutenden Sklerenchymstreifens längs der Rücken-

„naht (und vielleicht auch längs der Bauchnaht), der sogenannten „Fädigkeit der Bohnenhülsen, kommt oder nicht, und inwiefern „sich Fa hierin von fa unterscheiden lässt“.

In the cross Fijne tros with Wagenaar toughness of the pod wall and stringiness are quite independent of each other, both characters depending on a different main factor. Only one  $F_2$  family (55-4 1932) has so far been investigated with a view to linkage relations. In this family the four possible types occurred in the expected 1 : 3 : 3 : 9 ratio of independent inheritance.

	non-parchmented		parchmented		total
	pure stringy	not pure stringy	pure stringy	not pure stringy	
Observed . . . .	25	96	96	271	488
Expected					
1 : 3 : 3 : 9 .	30.5	91.5	91.5	274,5	

As it is not possible to decide about the homology of the main factor for toughness of the pod wall in the cross Fijne tros  $\times$  Wagenaar with one of the factors of LAMPRECHT, I will use the symbol To for this factor.

Wagenaar (semi-parchmented) To To.

Fijne tros (non-parchmented) to to.

## SUMMARY

1. Seedcoat colour is produced by the „groundfactor” P (fundamental gene of LAMPRECHT, ferment factor of KOOIMAN) together with at least one „complementary factor” (colour genes of LAMPRECHT; chromogenous factors of KOOIMAN). „Modifying factors” (intensifying factors of Kooiman) only influence the colours produced in case of cooperation between groundfactor and complementary factors. White-seeded plants generally have white flowers and green stems.

2. Segregation for stem and flower colour in the cross Fijne tros with Wagenaar depends upon the „groundfactor” P and the „violet factor” V. Fijne tros (pp VV) has a green stem, white flowers and white seedcoat. Wagenaar (PP vv) a rose stem, very pale rose flowers and yellowish seedcoat. F<sub>1</sub> (Pp Vv) has a dark blue violet stem and violet flowers; its seedcoat is „black mottled” (dark pattern colour black; background colour brown, variably tinged with greyish indigo). F<sub>2</sub> segregates according to the 4 : 3 : 9 ratio into the three stem and flower colour types. As regards the violet flower colour Vv plants are of a somewhat paler violet than the VV ones. In F<sub>2</sub> there is a shortage of the rose type, together with an excess of the violet one. This shortage (and excess) are even more strongly marked in F<sub>3</sub> families which segregate for the two factors P and V, and could as yet not be explained.

3. The mottled seedcoat in the cross is of the ever-segregating type. It is supposed to depend upon the factor M for mottling, which locally suppresses the influence of the dominant (complementary) factor C; these two factors are absolutely (or nearly absolutely) linked. Fijne tros  $\widehat{cM} \widehat{cM}$ , Wagenaar  $\widehat{Cm} \widehat{Cm}$ , F<sub>1</sub>  $\widehat{Cm} \widehat{cM}$ , i.e. mottled. Each mottled plant segregates into:

- 1 background colour type  $\widehat{cM} \widehat{cM}$ ,
- 2 mottled-seeded plants ( $\widehat{Cm} \widehat{cM}$ ) and
- 1 dark pattern colour type ( $\widehat{Cm} \widehat{Cm}$ ).

4. Segregation for seed coat colour. As the segregation into coloured-seeded (-flowering) and white-seeded (-flowering) is unifactorial, both parent races must have at least one complementary factor in common. It is therefore not possible for me to judge about the complementary or modifying character of the factors involved in the segregation. All Sh colours correspond with the J colours of LAMPRECHT. I therefore use the factor symbols C, G, B and V in agreement with LAMPRECHT (according to the latter, all these factors are complementary ones). If LAMPRECHT's complementary factor J is supposed to be homozygously dominant in Fijne tros and Wagenaar, the (modifying) factor Sh I must suppose to be homozygously dominant in LAMPRECHT's colours.

All PJSh plants have a shiny seed coat. The various PJShC colours (shiny dark pattern colours) depend upon the influence of the „orange factor" G, the „gray greenish brown factor" B and the „violet factor" V.

yellowish (Wagenaar)	PJShCgbv (no. 3)	} v = pale rose flower and rose stem.
orange (=yellow brown)	PJShCGbv (no. 9)	
greenish brown	PJShCgBv (no. 15)	
brown	PJShCGBv (no. 21)	
violet	PJShCgbV (no. 6)	} V = violet flower violet stem.
brown violet	PJShCGbV (no. 12)	
black	PJShCgBV (no. 18)	
„	PJShCGBV (no. 24)	

The PJSh c v colours (shiny background colours in pale rose flowering plants) do not much differ from the corresponding yellowish, orange, greenish brown and brown PJSh C v dark pattern colours; they are as a rule somewhat paler (with the greenish brown PJSh C g B v colour, however, a more gray brown c colour corresponds).

The PJSh c V colours (shiny backgroundcolours in violet flowering plants) usually differ greatly from the corresponding violet, brown violet and black PJSh C V dark pattern colours. They are but partly tinged with violet or blue. These tinges are extremely variable in beans of the same plant; in some plants they are totally lacking. The non-tinged beans (or parts of beans) much resemble the pale yellow, pale orange, gray brown and (pale) brown PJSh c v background colours in pale rose flowering plants; their hilumring colour, however,

is less bright. The 8 PJSh c shiny background colours may be indicated as follows:

pale yellowish	PJSh cgbv (no. 1)	} v = rose stem.
pale orange	PJSh cGbv (no. 7)	
gray brown	PJSh cGBv (no. 13)	
(pale) brown	PJSh cGBv (no. 19)	
pale yellowish tinged with plumbago violet	PJSh cgbV (no. 4)	} V = violet stem.
pale orange tinged with ageratum blue	PJSh cGbV (no. 10)	
gray brown tinged with slate blue	PJSh cGBV (no. 16)	
(pale) brown tinged with greyish indigo	PJSh cGBV (no. 22)	

The „shine” factor Sh influences the C dark pattern colours and the c background colours in quite a different manner.

All PJsh C dark pattern colours are somewhat paler and especially less shiny than the corresponding PJSh C shiny dark pattern colours.

All PJsh c background colours have a yellow brown hilumring, but for the rest their seedcoat is nearly colourless: hilumring type. The factors G, B and V influence hardly or not at all this P J sh c hilumring type; in violet V plants the hilumring is somewhat less bright than in rose v plants.

5. The strength of string. Strength of string mainly depends upon the percentage of fibres in the sheath of the vascular bundles in dorsal and ventral sutures. The following points refer to all plants:

a. The ventral sheath consists of 4—7, the dorsal of 5—8 cell layers.

b. In each sheath there occur parenchymatic cells, wood cells and fibres.

c. These three cell types always have the same relative position (cf. fig. 4).

Of each plant the „string number” (1—10) of boiled pods and the anatomical structure of the sheath were determined. Wagenaar (fig. 4 no. 8) is a pure stringy type, string number always 9—10. Its sheath consists entirely of fibres, except for a narrow part in the middle. Fijne tros (fig. 4 nos 2 and 3) is so-called stringless. Its string number varies between 2—3 and 5—6, mostly it is 3—5. Slight genetical differences probably occur. The sheath mainly consists of wood cells (40%—75%); the fibres usually form four small groups. Their per-

centage varies between 0 and 25; as a rule it lies between 5 and 15. The  $F_1$  (fig. 4, nos 4, 5 and 6) is intermediate, though approaching the Fijne tros type. Strength of string 6.5—7.5. The percentage of fibres (one pod per plant investigated) varies between 20 and 65. In  $F_2$  (and  $F_3$ ) the pure stringy Wagenaar type (st st) reappears in a clearly unifactorial way; it invariably breeds true. The percentage of fibres and the strength of string in homozygous and heterozygous St plants are influenced by other factors. According to their  $F_3$  generation St St  $F_2$ -plants vary between string numbers 2—3 (nearly without fibres) and 7—8 (with  $\pm 50\%$  fibres); St st plants between string numbers 3—4 (with  $\pm 10\%$  fibres) and 9—10 (with  $\pm 85\%$  fibres).

$F_3$  families with lower string numbers than in the Fijne tros race have not been found. In a sheath without or nearly without fibres the percentage of wood cells may slightly influence the strength of string.

6. Toughness of the pod wall. A tough or parchmented pod wall is due to a fibrous layer between inner and outer parenchyma. In the Fijne tros race the fibrous layer is totally lacking; the dry pod is conspicuously constricted and shrivelled. The Wagenaar race has a rather weak fibrous layer; only part of its cells are lignified. In  $F_1$  the fibrous layer is extremely thick and hard; all its cells are lignified. The dry pod is not constricted or shrivelled at all. In  $F_2$  a 4 : 3 : 9 ratio might be expected. The segregation into non-parchmented (to to) versus parchmented (To To) is unifactorial. Distinguishing the parchmented pods into two or more types, however, seems to be impossible. Hence we are unable to judge, whether we have to deal with one or possibly with more additional factors by which the influence of the To factor is intensified.

7. Leaving out all not quite certain factors the formulae for stem, flower and seedcoat colours, mottling, strength of string and toughness of the pod wall are:

Fijne tros pp JJ ShSh (or Shsh)  $\widehat{cM}$   $\widehat{cM}$  GG BB VV StSt toto;

Wagenaar PP JJ ShSh  $\widehat{Cm}$   $\widehat{Cm}$  gg bb vv stst ToTo.

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TABLES 1—45

TABLE 1. Segregation for stem and flower colours in  $F_2$ ; each young plant in flowerpot twice examined; only those plants with green cotyledons and hypocotyl have been examined as to flower colour.

No. Fam. and year	Green plants white flower	Rose plants				Violet plants all recognized at the first examination	Total	Expected ratio		
		1st. exam. (cotyledon)	2nd exam. (hypoc.)	3d exam. (flower)	Total			green	rose	violet
								4	3	9
52-1, '33	<b>65</b>	24	<sup>1)</sup> 9	1	<b>34</b>	<b>126</b>	225	56,25	42,19	126,56
52-2, '33	<b>77</b>	31	4	0	<b>35</b>	<b>148</b>	260	65,00	48,75	146,25
52-3, '33	<b>27</b>	10	1	0	<b>11</b>	<b>69</b>	107	26,75	20,06	60,19
52-4, '33	<b>33</b>	11	5	0	<b>16</b>	<b>77</b>	126	31,50	23,63	70,87
52-5, '33	<b>38</b>	14	6	0	<b>20</b>	<b>79</b>	137	34,25	25,69	77,06
52-10, '33	<b>93</b>	70	8	0	<b>78</b>	<b>194</b>	365	91,25	68,44	205,31
52-13, '33	<b>10</b>	9	1	0	<b>10</b>	<b>23</b>	43	10,75	8,06	24,19
52-15, '33	<b>39</b>	18	2	0	<b>20</b>	<b>69</b>	128	32,00	24,00	72,00
52-18, '33	<b>29</b>	16	2	0	<b>18</b>	<b>59</b>	106	26,50	19,87	59,63
52-19, '33	<b>21</b>	13	7	0	<b>20</b>	<b>62</b>	103	25,75	19,31	57,94
Total	<b>432</b>	216	45	1	<b>262</b>	<b>906</b>	1600	400,00	300,00	900,00
Expected 4:3:9	<b>400</b>				<b>300</b>	<b>900</b>				
D/m	1.85				2.43	0.30				

<sup>1)</sup> Many of the plants in this column were „suspect” at the first examination.

TABLE 2. F<sub>2</sub> segregation for stem and flower colours. The 33 plants under the heading of „Green stem, died young”, have been divided between white flowering and pale rose flowering plants, as in about  $\frac{1}{3}$  of the latter the hypocotyl and cotyledon colour had not been observed.

No. Fam. and year	Green stem white fl.	Green stem (died young)	Rose stem and (or) pale rose fl.	Violet stem and flower				Total	Expected ratio		
				violet-1 fl.	violet-2 or 3 fl.	fl. colour not noted or only as violet	total num- ber violet		green	rose	violet
									4	3	9
55-2,'32	<b>65</b>	6	<b>30</b>	90	37	18	<b>145</b>	246	61,50	46,13	138,37
55-4,'32	<b>110</b>	9	<b>84</b>	206	102	26	<b>334</b>	537	134,25	100,69	302,06
55-6,'32	<b>122</b>	13	<b>106</b>	167	80	50	<b>297</b>	538	134,50	100,87	302,63
393,'33	<b>9</b>	0	<b>7</b>	13	8	4	<b>25</b>	41	10,25	7,69	23,06
394,'33	<b>5</b>	1	<b>5</b>	15	12	1	<b>28</b>	39	9,75	7,31	21,94
395,'33	<b>7</b>	0	<b>5</b>	8	9	2	<b>19</b>	31	7,75	5,81	17,44
395,'33	<b>7</b>	1	<b>5</b>	17	7	3	<b>27</b>	40	10,00	7,50	22,50
397,'33	<b>7</b>	1	<b>8</b>	10	11	3	<b>24</b>	40	10,00	7,50	22,50
398,'33	<b>8</b>	1	<b>7</b>	15	4	5	<b>24</b>	40	10,00	7,50	22,50
399,'33	<b>11</b>	1	<b>3</b>	15	8	2	<b>25</b>	40	10,00	7,50	22,50
400,'33	<b>7</b>	0	<b>11</b>	11	5	6	<b>22</b>	40	10,00	7,50	22,50
Total	<b>358</b>	33	<b>271</b>	567	283	120	<b>970</b>	1632	408,00	306,00	918,00
	<b>26</b>	$\frac{1}{3}$	<b>7</b>								
	<b>384</b>		<b>278</b>				<b>970</b>				
Ex- pected											
4:3:9	<b>408</b>		<b>306</b>				<b>918</b>				
D/m	1.37		1.78				2.59				

TABLE 3. True-breeding  $F_2$  families of PP VV and PP vv  $F_2$  plants.

No. Fam.	Flower colour	White fl.	Pale rose fl.	Violet
	$F_2$ plant	green stem	rose stem	-2 or 3 fl. violet stem
455	violet 2?	0	0	22
457	" 2	0	0	19
416	" 2	0	0	41
469	" 2	0	0	10
477	" 2	0	0	14
481	" 2	0	0	9
432	pale rose	0	32	0
443	" "	0	32	0
515	" "	0	32	0
518	" "	0	16	0
401	" "	0	36	0
402	" "	0	18	0
423	" "	0	28	0
479	" "	0	16	0
480	" "	0	16	0

TABLE 4.  $F_3$  families of Pp vv plants.


No. Fam.	Flower colour $F_2$ plant	White fl. green stem	Green stem (died young)	Pale rose fl. rose stem	Total	Expected ratio	
						green 1	rose 3
429	pale rose	9	6	24	39	9.75	29.25
436	" "	7	0	16	23	5.75	17.25
437	" "	7	0	17	24	6.00	18.00
442	" "	2	0	22	24	6.00	18.00
448	" "	7	0	21	28	7.00	21.00
450	" "	4	0	12	16	4.00	12.00
451	" "	5	1	34	40	10.00	30.00
403	" "	13	1	25	39	9.75	29.25
404	" "	9	0	30	39	9.75	29.25
420	" "	6	0	18	24	6.00	18.00
466	" "	1	0	7	8	2.00	6.00
Total		70	8	226	304		
		5		3			
		75		229	304		
Expected 1:3 D/m		76		228			
		0.13					

TABLE 5. F<sub>3</sub> families of Pp VV plants.

No. Fam.	Flower colour F <sub>2</sub> plant	White fl. green stem	Violet fl. violet stem	Total	Expected ratio	
					1	3
430	violet 2	9	31	40	10.00	30.00
431	" 2	5	19	24	6.00	18.00
444	" 1-2	10	14	24	6.00	18.00
445	" 1-2	6	26	32	8.00	24.00
452	" 1	6	17	23	5.75	17.25
461	" 1-2	5	28	33	8.25	24.75
407	" 2	5	15	20	5.00	15.00
409	" 2	7	16	23	5.75	17.25
424	" 2	11	21	32	8.00	24.00
Total		64	187	251		
Expected 1:3		62.75	188.25			
D/m		0.18				

TABLE 6. F<sub>3</sub> families of PP Vv plants.

No. Fam.	Flower colour F <sub>2</sub> plant	Pale rose fl. rose stem	Violet fl. violet stem	Total	Expected 1 : 3	
					1	3
427	violet 1	6	37	43	10.75	32.25
441	" 1	10	23	33	8.25	24.75
447	" 1	15	29	44	11.00	33.00
449	" 1	5	20	25	6.25	18.75
460	" 1	6	14	20	5.00	15.00
529	" 2-1	8	14	22	5.50	16.50
405	" 1	5	19	24	6.00	18.00
408	" 1	2	7	9	2.25	6.75
410	" 1	11	29	40	10.00	30.00
414	" 1	10	30	40	10.00	30.00
425	" 1-2	5	29	34	8.50	25.50
467	" 1	5	13	18	4.50	13.50
Total		88	264	352		
Expected 1:3		88	264			
D/m		0.00				

TABLE 7. F<sub>3</sub> families of Pp Vv plants.

No. Fam.	Flower colour F <sub>2</sub> plant	White fl. green stem	Green stem (died young)	Pale rose fl. rose stem	Violet fl. violet stem	Total	Expected ratio		
							4	3	9
F <sub>2</sub> family 55-2									
406	violet 1	9	0	2	13	24	6.00	4.50	13.50
411	" 1	7	1	3	14	25	6.25	4.69	14.06
412	" 1	10	2	4	16	32	8.00	6.00	18.00
413	" 1	13	2	10	15	40	10.00	7.50	22.50
415	" 1	12	0	6	20	38	9.50	7.12	21.38
417	" 1	11	0	2	23	36	9.00	6.75	20.25
418	" 1	12	1	4	26	43	10.75	8.06	24.19
419	" 1	5	1	5	14	25	6.25	4.69	14.06
421	" 1	1	3	4	16	24	6.00	4.50	13.50
422	" 1?	1	2	1	12	16	4.00	3.00	9.00
468	" 1	3	0	1	14	18	4.50	3.37	10.13
470	" 1	6	0	3	8	17	4.25	3.19	9.56
471	" 1	1	0	1	7	9	2.25	1.69	5.06
472	" 1	8	0	8	21	37	9.25	6.94	20.81
476	" 1	3	1	1	7	12	3.00	2.25	6.75
478	" 2 or 1	11	0	2	12	25	6.25	4.69	14.06
F <sub>2</sub> family 55-4									
426	violet 1	4	0	8	20	32	8.00	6.00	18.00
428	" 1	8	0	1	23	32	8.00	6.00	18.00
433	" 1	9	2	5	24	40	10.00	7.50	22.50
434	" 1	9	0	5	18	32	8.00	6.00	18.00
435	" 1	6	1	2	23	32	8.00	6.00	18.00
438	" 1	10	0	7	23	40	10.00	7.50	22.50
439	" 1-2	8	0	4	28	40	10.00	7.50	22.50
440	" 1	5	2	7	26	40	10.00	7.50	22.50
446	" 1	5	2	0	17	24	6.00	4.50	13.50
453	" 1	5	0	7	20	32	8.00	6.00	18.00
454	" 1	13	7	4	24	48	12.00	9.00	27.00
456	" 1	11	1	7	34	53	13.25	9.94	29.81
458	" 1	11	0	5	34	50	12.50	9.38	28.12
459	" 1	5	0	2	28	35	8.75	6.56	19.69
462	" 1	2	0	4	14	20	5.00	3.75	11.25
463	" 1	4	1	3	17	25	6.25	4.69	14.06
516	" 1	6	1	7	36	50	12.50	9.38	28.12
517	" 1	7	0	3	15	25	6.25	4.69	14.06
522	" 1	2	0	3	7	12	3.00	2.25	6.75
523	" 1	2	1	2	7	12	3.00	2.25	6.75
524	" 1	3	0	1	16	20	5.00	3.75	11.25
525	" 1	10	1	3	18	32	8.00	6.00	18.00
526	" 1	5	3	4	14	26	6.50	4.87	14.63
527	" 1	2	1	4	13	20	5.00	3.75	11.25
528	" 1	4	1	2	14	21	5.25	3.94	11.81
Total		269	37	157	751	1214			
		28	← ^ →	9					
		297		166	751				
Expected		303.50		227.62	682.88				
4:3:9									
D/m		0.43		4.53	3.94				



TABLE 8. First and second sowings of  $F_3$  families; first sowing showed a great shortage of rose plants.

No. Fam.	First sowing (1933)					Second sowing (spring 1934)			
	White fl. green stem	Green stem (died young)	Pale rose fl. rose stem	Violet fl. violet stem	Total	Green stem	Rose stem	Violet stem	Total
428	8	0	1	23	32	12	14	41	67
446	5	2	0	17	24	11	9	28	48
459	5	0	2	28	35	11	3	26	40
435	6	1	2	23	32	6	6	28	40
458	11	0	5	34	50	12	4	24	40
Total	35	3	10 5.78%	125	173	52	36 15.32%	147	235

TABLE 9. First and second sowings of  $F_3$  families; first sowing contained the expected  $\frac{3}{16}$  rose plants or more.

No. Fam.	First sowing (1933)					Second sowing (spring '34)			
	White fl. Green stem	Green stem (died young)	Pale rose fl. rose stem	Violet fl. violet stem	Total	Green stem	Rose stem	Violet stem	Total
426	4	0	8	20	32	13	14	45	72
438	10	0	7	23	40	9	7	32	48
440	5	2	7	26	40	13	4	23	40
453	5	0	7	20	32	14	8	32	54
Total	24	2	29 20.14%	89	144	49	33 15.42%	132	214



TABLE 11. Selfcoloured yellowish (no. 3) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .		White	Pale rose
Seedcoat colour . . . . .		White	Yellowish
Colour number . . . . .		49	3
Genotype	No. Fam.		
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb vv	493	3	13
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb vv	500	0	15
Total number coloured . . . . .			28

TABLE 12. Selfcoloured orange (no. 9) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .		White	Pale rose		Total numbers coloured
Seedcoat colour . . . . .		White	Yellowish	Orange	
Colour number . . . . .		49	3	9	
Genotype	No. Fam.				
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg bb vv	494	2	1	13	14
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg bb vv	502	6	0	2	2
Total numbers coloured . . . . .			1	15	16
Expected ratio 1:3 . . . . .			4.00	12.00	
D/m . . . . .			1.73		

TABLE 13. Selfcoloured greenish brown (no. 15) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .		White	Pale rose		Total number coloured
Seedcoat colour . . . . .		White	Yellowish	Green. brown	
Colour number . . . . .		49	3	15	
Genotype	No. Fam.				
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg Bb vv	465 <sup>a</sup>	0	6	14	
Expected ratio 1:3 . . . . .			5.00	15.00	20
D/m . . . . .			0.50		

TABLE 14. Selfcoloured brown (no. 21) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour. . . . .		White	Pale rose				Total numbers coloured
Seedcoat colour . . . . .		White	Yell.	Orange	Green. brown	Brown	
Colour number . . . . .		49	3	9	15	21	
Genotype	No. Fam.						
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	483	0		1	5	6	12
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	484	1		6	3	4	13
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	485	6	1	4	1	5	11
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	491	3			3	2	5
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	492	0		1	1	10	12
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	495	11	1	6	4	10	21
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	505	0		6	5	17	28
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb vv	506	7	2	1	2	12	17
Total numbers coloured . . . . .			4	25	24	66	119
Expected ratio 1:3:3:9 . . . . .			7.44	22.31	22.31	66.94	
D/m. . . . .			1.30	0.64	0.40	0.17	

TABLE 15. Selfcoloured violet (no. 6) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour. . . . .		White	Pale rose	Violet-1,2	Total numbers coloured
Seedcoat colour . . . . .		White	Yellow	Violet	
Colour number . . . . .		49	3	6	
Genotype	No. Fam.				
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb Vv	487	2	5	12	17
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb Vv	488	0	7	16	23
PP JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb Vv	489	0	1	9	10
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ gg bb Vv	465b	6	3	7	10
Total numbers coloured . . . . .			16	44	60
Expected ratio 1:3 . . . . .			15	45	
D/m. . . . .			0.30		

TABLE 16. Selfcoloured brown violet (no. 12) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour. . . . .	White	Pale rose		Violet-1,2		Total numbers coloured	
Seedcoat colour . . . . .	White	Yell.	Orange	Violet	Brown violet		
Colour number . . . . .	49	3	9	6	12		
Genotype	No. Fam.						
PP JJ Sh Sh $\widehat{C}_m \widehat{C}_m$ Gg bb Vv	465c	0		1	1	13	15
Pp JJ Sh Sh $\widehat{C}_m \widehat{C}_m$ Gg bb Vv	490	5	1	0	3	7	11
Total numbers coloured . . .			1	1	4	20	26
Expected ratio 1:3:3:9 . . . .			1.63	4.87	4.87	14.63	
D/m. . . . .			0.51	1.90	0.44	2.12	

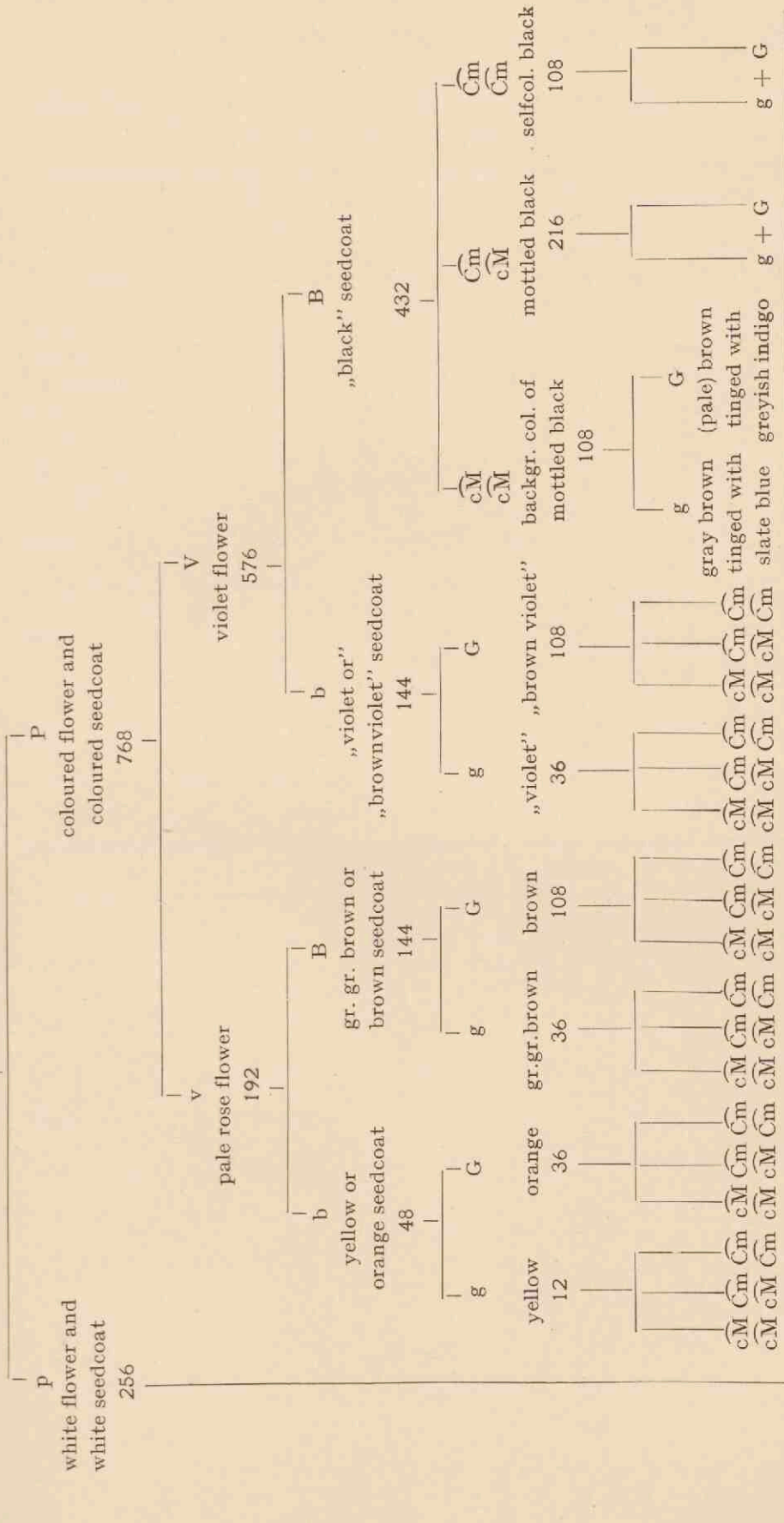
TABLE 17. Selfcoloured black (no. 18) of backcross  $F_1 \times$  Wagenaar, selfed

Flower colour. . . . .	White	Pale rose		Violet-1,2		Total numbers coloured	
Seedcoat colour . . . . .	White	Yell.	Gr. brown	Violet	Black		
Colour number . . . . .	49	3	15	6	18		
Genotype	No. Fam.						
Pp JJ Sh Sh $\widehat{C}_m \widehat{C}_m$ gg Bb Vv	498	2		1	1	2	4
Pp JJ Sh Sh $\widehat{C}_m \widehat{C}_m$ gg Bb Vv	513	10	2	6	9	15	32
Pp JJ Sh Sh $\widehat{C}_m \widehat{C}_m$ gg Bb Vv	514	4	1	3	6	8	18
Total numbers coloured . . .			3	10	16	25	54
Expected ratio 1:3:3:9 . . . .			3.37	10.13	10.13	30.37	
D/m. . . . .			0.21	0.05	2.05	1.47	

TABLE 18. Selfcoloured black (no. 24) of backcross  
 $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .	White	Pale rose				Violet-1, 2		Total number coloured
Seedcoat colour . . . . .	White	Yell.	Orange	Gr. brown	Brown	Violet	Black	
Colour number . . . . .	49	3	9	15	21	6+12	18+24	
Genotype	No. Fam.							
Pp JJ Sh Sh $\widehat{Cm} \widehat{Cm}$ Gg Bb Vv	512	1			3	4	12	20
Expected ratio 1:3:3:9:12:36. .		0.31	0.94	0.94	2.81	3.75	11.25	





Colour no.	49	1	2	3	7	8	9	9	13	14	15	19	20	21	21	4	5	6	10	11	12	16	22	17	+ 23	18	+ 24
Number of seeds	256	3	6	3	9	18	9	9	18	9	18	27	54	27	9	18	9	9	27	54	27	27	81	216	81	108	

SCHEME OF THE EXPECTED RATIO IN F<sub>2</sub> FAMILIES WHICH SEGREGATE FOR THE FACTORS P—p,  $\widehat{Cm}$ — $\widehat{cM}$ , G—g, B—b AND V—v. ALL PLANTS ARE JJ Sh Sh. COLOUR TYPES ARRANGED IN THE SAME WAY AS IN TABLE 19.





TABLE 20.  $F_2$  segregation for the  $\widehat{Cm-cM}$  factors and for the factors G, B and V (derived from table 19).

	Mott- led $\widehat{Cm}$ $\widehat{cM}$	Selfcoloured			Total numbers coloured	Expected 1:3:3:9: 3:9:36	D/m
		$\widehat{cM}$ $\widehat{cM}$	$\widehat{Cm}$ $\widehat{cM}$	$\widehat{Cm}$ $\widehat{Cm}$			
Yellowish . . . . .	not classified				14	14,72	0.19
Orange . . . . .	21	13	12	25	46	44,16	0.29
Gr. gr. brown . . . . .	21	11	13	24	45	44,16	0.13
Brown . . . . .	60	40	30	70	130	132,47	0.23
„Violet” . . . . .	31	11	9	20	51	44,16	1,06
„Brownviolet” . . . . .	65	31	28	59	124	132,47	0.80
„Black” . . . . .	265	148	119	267	532	529,88	0.14
Total . . . . .	463	254	211	465	942	942,02	
Expected ratio 2:1:1	464	232	232				
D/m . . . . .	0.07	1.67	1.59				

TABLE 21. Unifactorial ratios in  $F_2$  for the factors G, B and V (derived from table 19).

	g	G	Total	b	B	Total	v	V	Total
	14	46	60	14	45	59	14	51	65
	45	130	175	46	130	176	46	124	170
	51	124	175	51	532	707	45	532	707
	40	108	148	124			130		
Total . . . . .	150	408	558	235	707	942	235	707	942
Expected 1:3 . . . . .	139.50	418.50		235.50	706.50		235.50	706.50	
D/m . . . . .	1.02			0.04			0.04		

TABLE 22. Segregation for seedcoat colour in 54 F<sub>2</sub> families (F<sub>1</sub> plant 55-4).

No. Fam.	Probable constitution F <sub>2</sub> plant	Col. number	Wp	Pale yell.			Orange brown			Gr. gr. brown			Brown		"Violet"		"Brown-violet"		"Black"		Total		
				1	2	3	7	8	9	13	14	15	19	20	21	4	5	6	10	11		12	16
443	PP JJ Sh Sh cM cM GG bb vv	8	49	6	4	21	4	21	7	19	20	21	4	5	6	10	11	12	16	22	17	18	32
432	PP JJ Sh Sh cM cM Gg bb vv	8		3	4		7	12	7														32
450	Pp JJ Sh Sh cM cM Gg bb vv	9		3	4		7	12	9														16
515	PP JJ Sh Sh cM cM gg Bb vv	14		11	2?		6	5	6														21
451	Pp JJ Sh Sh cM cM gg Bb vv	14		16	3		2	12	6														35
442	Pp JJ Sh Sh cM cM gg BB vv	15					4		22														24
518	PP JJ Sh Sh cM cM Gg BB vv	19					4			11													15
437	Pp JJ Sh Sh cM cM Gg BB vv	19					4			12													23
429	Pp JJ Sh Sh cM cM GG Bb vv	20					1	1	2	3	7	3											26
448	Pp JJ Sh Sh cM cM GG BB vv	20								6	8	5											26
436	Pp JJ Sh Sh cM cM GG BB vv	21								(or 7)	(or 4)	16											23
526	Pp JJ Sh Sh cM cM gg bb Vv	5		13?	0?										5	6							19
531	Pp JJ Sh Sh cM cM gg bb Vv	5		13?	2										3	9	4						38
426	Pp JJ Sh Sh cM cM gg bb Vv	6			8												20						32
455	PP JJ Sh Sh cM cM gg bb VV	6														14							14
444	Pp JJ Sh Sh cM cM GG bb VV	10																10					19
441	PP JJ Sh Sh cM cM Gg bb Vv	10					6											14					29
449	PP JJ Sh Sh cM cM Gg bb Vv	10					5											6					13
522	Pp JJ Sh Sh cM cM Gg bb Vv	10					3											5					12
523	Pp JJ Sh Sh cM cM GG?bb Vv	10					1											4					7
458	Pp JJ Sh Sh cM cM Gg bb Vv	11					1	1	1									6	14				45
†439	Pp JJ Sh Sh cM cM Gg?bb Vv	11					1	1	2									8	12				38
430	Pp JJ Sh Sh cM cM GG bb VV	11																7	11				28
531 <sup>a</sup>	Pp JJ Sh Sh cM cM GG bb Vv	12							3									3					7
463	Pp JJ Sh Sh cM cM Gg bb Vv	12					2		1									4					22
528	Pp JJ Sh Sh cM cM Gg bb Vv	12							2									(or 5)					20
434	Pp JJ Sh Sh cM cM GG bb Vv	12																					32
527	Pp JJ Sh Sh cM cM GG bb Vv	12																					18
452	Pp JJ Sh Sh cM cM gg Bb VV	16																					17
428	Pp JJ Sh Sh cM cM gg Bb Vv	16																					32
524	Pp JJ Sh Sh cM cM gg Bb Vv	16																					19
§446	Pp JJ Sh Sh cM cM gg BB Vv	16																					19
440	Pp JJ Sh Sh cM cM gg Bb Vv	17																					35
457	PP JJ Sh Sh cM cM gg Bb Vv	17																					39
529	PP JJ Sh Sh cM cM gg Bb Vv	17																					17
460	PP JJ Sh Sh cM cM Gg Bb Vv	22																					12
525	Pp JJ Sh Sh cM cM Gg Bb Vv	22																					25
459	Pp JJ Sh Sh cM cM GG Bb Vv	22																					30
462	Pp JJ Sh Sh cM cM Gg BB Vv	22																					19
453	Pp JJ Sh Sh cM cM Gg BB Vv	22																					32
465 <sup>f</sup>	Pp JJ Sh Sh cM cM Gg Bb VV	22																					11
445	Pp JJ Sh Sh cM cM Gg Bb VV	22																					24
457	PP JJ Sh Sh cM cM Gg BB VV	22																					16
456	Pp JJ Sh Sh cM cM GG Bb Vv	23																					46
454	Pp JJ Sh Sh cM cM Gg Bb Vv	23																					28
516	Pp JJ Sh Sh cM cM Gg Bb Vv	23																					49
438	Pp JJ Sh Sh cM cM Gg BB Vv	23																					38
530	Pp JJ Sh Sh cM cM Gg BB Vv	23																					18
517	Pp JJ Sh Sh cM cM Gg BB Vv	23																					31
427	PP JJ Sh Sh cM cM GG BB Vv	23																					24
433	Pp JJ Sh Sh cM cM Gg Bb Vv	24																					37
435	Pp JJ Sh Sh cM cM Gg Bb Vv	24																					29
431	Pp JJ Sh Sh cM cM GG Bb VV	24																					18
461	Pp JJ Sh Sh cM cM Gg Bb VV	24																					28

Of these 54 F<sub>2</sub> plants were:  
 PP 12 (exp. 18)  
 Pp 42 (exp. 36)  
 GG 16 (exp. 13,3)  
 Gg 24 (exp. 26,7)  
 gg 14  
 BB 13 (exp. 11,3)  
 Bb 21 (exp. 22,7)  
 bb 20

† 439 was probably Gg; the brown violet seeds, however, were difficult to distinguish from the violet ones.  
 \*) (Variable!)  
 § 446 was Vv; the family contained many violet-1 flowers; in a later sowing a normal number of pale rose flowers appeared; cf. table 8.

TABLE 22. Segregation for seedcoat colour in 54 F<sub>2</sub> families (F<sub>1</sub> plant 55-4).

No. Fam.	Probable constitution F <sub>2</sub> plant	Col. number	Wp	Pale yell.			Orange			Gr. gr. brown			Brown		„Violet”		„Brown-violet”		„Black”		Total	
				1	2	3	7	8	9	13	14	15	19	20	21	4	5	6	10	11		12
443	PP JJ Sh Sh cM cM GG bb vv	8		4	2	1	4	2	1	7												32
432	PP JJ Sh Sh cM cM Gg bb vv	8		6			7	12	7													32
450	Pp JJ Sh Sh cM cM Gg bb vv	9	4	3					9													16
515	PP JJ Sh Sh cM cM gg Bb vv	14		1	1	2				6	5	6										21
451	Pp JJ Sh Sh cM cM gg Bb vv	14	5	1	6	3				2	12	6										35
442	Pp JJ Sh Sh cM cM gg BB vv	15	2							4		22										24
518	PP JJ Sh Sh cM cM Gg BB vv	19								4												15
437	Pp JJ Sh Sh cM cM Gg BB vv	19	7							4												23
429	Pp JJ Sh Sh cM cM GG Bb vv	20	9				1	1	2													26
448	Pp JJ Sh Sh cM cM GG BB vv	20	7																			26
436	Pp JJ Sh Sh cM cM GG BB vv	21	7																			23
526	Pp JJ Sh Sh cM cM gg bb Vv	5	4	1	3	0																19
531	Pp JJ Sh Sh cM cM gg bb Vv	5	16	1	3	2																38
426	Pp JJ Sh Sh cM cM gg bb Vv	6	4			8																32
455	PP JJ Sh Sh cM cM gg bb VV	6																				14
444	Pp JJ Sh Sh cM cM GG bb VV	10	9																			19
441	PP JJ Sh Sh cM cM Gg bb Vv	10					6															29
449	PP JJ Sh Sh cM cM Gg bb Vv	10					5															13
522	Pp JJ Sh Sh cM cM Gg bb Vv	10	2	1			3															12
523	Pp JJ Sh Sh cM cM GG?bb Vv	10	2				1															7
458	PP JJ Sh Sh cM cM Gg bb Vv	11	11				1	1	1													45
†439	PP JJ Sh Sh cM cM Gg?bb Vv	11	8				1	1	2													38
430	Pp JJ Sh Sh cM cM GG bb VV	11	5																			28
531a	Pp JJ Sh Sh cM cM GG bb Vv	12	1																			7
463	Pp JJ Sh Sh cM cM Gg bb Vv	12	4			2																22
528	Pp JJ Sh Sh cM cM Gg bb Vv	12	4																			20

No. Fam.	Probable constitution F <sub>2</sub> plant	Col. number	Wp	Pale yell.			Orange			Gr. gr. brown			Brown		„Violet”		„Brown-violet”		„Black”		Total	
				1	2	3	7	8	9	13	14	15	19	20	21	4	5	6	10	11		12
434	Pp JJ Sh Sh cM cM GG bb Vv	12	9																			32
527	Pp JJ Sh Sh cM cM GG bb Vv	12	2																			18
452	Pp JJ Sh Sh cM cM gg Bb VV	16	5																			17
428	Pp JJ Sh Sh cM cM gg Bb Vv	16	8																			32
524	Pp JJ Sh Sh cM cM gg BB Vv	16	3																			19
§446	Pp JJ Sh Sh cM cM gg BB Vv	16	5																			19
440	Pp JJ Sh Sh cM cM gg Bb Vv	17	5																			35
457	PP JJ Sh Sh cM cM gg Bb Vv	17																				39
529	PP JJ Sh Sh cM cM gg Bb Vv	17																				17
460	PP JJ Sh Sh cM cM Gg Bb Vv	22																				12
525	Pp JJ Sh Sh cM cM Gg Bb Vv	22	10																			25
459	Pp JJ Sh Sh cM cM GG Bb Vv	22	5																			30
462	Pp JJ Sh Sh cM cM Gg BB Vv	22	2																			19
453	Pp JJ Sh Sh cM cM Gg BB Vv	22	5																			32
465f	Pp JJ Sh Sh cM cM Gg Bb VV	22	3																			11
445	Pp JJ Sh Sh cM cM Gg Bb VV	22	5																			24
457	PP JJ Sh Sh cM cM Gg BB VV	22																				16
456	Pp JJ Sh Sh cM cM GG Bb Vv	23	11																			46
454	Pp JJ Sh Sh cM cM Gg Bb Vv	23	12																			28
516	Pp JJ Sh Sh cM cM Gg Bb Vv	23	6																			49
438	Pp JJ Sh Sh cM cM Gg BB Vv	23	10																			38
530	Pp JJ Sh Sh cM cM Gg BB Vv	23	4																			18
517	Pp JJ Sh Sh cM cM Gg BB Vv	23	10																			31
427	PP JJ Sh Sh cM cM GG BB Vv	23																				24
433	Pp JJ Sh Sh cM cM Gg Bb Vv	24	9																			17
435	Pp JJ Sh Sh cM cM Gg Bb Vv	24	6																			37
431	Pp JJ Sh Sh cM cM GG Bb VV	24	2																			29
461	Pp JJ Sh Sh cM cM Gg Bb VV	24	5																			18

Of these 54 F<sub>2</sub> plants were:  
 PP 12 (exp. 18)  
 Pp 42 (exp. 36)  
 GG 16 (exp. 13,3)  
 Gg 24 (exp. 26,7)  
 gg 14  
 BB 13 (exp. 11,3)  
 Bb 21 (exp. 22,7)  
 bb 20

† 439 was probably Gg; the brown violet seeds, however, were difficult to distinguish from the violet ones.

\*) (Variable!)

§ 446 was Vv; the family contained many violet-1 flowers; in a later sowing a normal number of pale rose flowers appeared; cf. table 8.

TABLE 23. Mottled yellowish (no. 2) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .	White	Pale rose			Total number coloured	
Seedcoat colour . . . . .	White	Yellowish				
Colour number . . . . .	49	1	2	3		
Genotype . . . . .	No. Fam.					
PP JJ Sh Sh $\widehat{Cm} \widehat{cM} gg bb vv$	449	0	6?	16	5	27
„	465 <i>d</i>	0	8?	14	6	28
Total numbers coloured . . .			14?	30	11	55
Expected ratio 1:2:1. . . . .			13.75	27.50	13.75	

TABLE 24. Mottled orange (no. 8) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .	White	Pale rose						Total number coloured	
Seedcoat colour . . . . .	White	Yellowish			Orange				
Colour number . . . . .	49	1	2	3	7	8	9		
Genotype . . . . .	No. Fam.								
PP JJ Sh Sh $\widehat{Cm} \widehat{cM} Gg bb vv$ . .	501	0	2	5	3	4	9	5	28
Expected ratio 1:2:1:3:6:3 . . . . .			1.75	3.50	1.75	5.25	10.50	5.25	
$\widehat{cM} \widehat{cM} + \widehat{Cm} \widehat{cM}$ + $\widehat{Cm} \widehat{Cm}$ . . . . .			10 (exp. 7)			18 (exp. 21)			

TABLE 25. Mottled greenish brown (no. 14) of backcross  
F<sub>1</sub> × Wagenaar, selfed.

Flower colour . . . . .	White	Pale rose							Total numbers coloured
Seedcoat colour . . . . .	White	Yellowish			Greenish brown				
Colour number . . . . .	49	1	2	3	13	14	15		
Genotype . . . . .	No. Fam.								
Pp JJ Sh Sh $\widehat{Cm}$ cM gg Bb vv	486	5	1	2	2	1	2	4	12
PP        "        "	507	0		2	1	7	8	2	20
Pp        "        "	465e	3		1		1			2
Total numbers coloured . . . . .			1	5	3	9	10	6	34
Expected ratio 1:2:1:3:6:3 . . . . .			2.12	4.25	2.12	6.38	12.75	6.38	
$\widehat{cM}\widehat{cM} + \widehat{Cm}\widehat{cM} + \widehat{Cm}\widehat{Cm}$ . . . . .			9 (exp. 8.50)			25(exp.25.50)			



TABLE 27. Mottled violet (no. 5) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . . . .	White		Pale rose		Violet-1, 2.		Total numbers coloured		
	White		Yellowish		„ Violet”				
	49		1	2	3	4		5	6
Seedcoat colour . . . . .									
Colour number . . . . .									
Genotype . . . . .	No. Fam.								
Pp JJ Sh $\widehat{Cm} \widehat{cm}$ gg bb Vv . . .	9		1	1	1?	10	7	2	22
Pp . . . . .	9		1?	1?	2	4	6	5	19
Pp . . . . .	3		1	1	1	2	9	3	16
Total numbers coloured . . . . .			2?	3?	4?	16	22	10	57
Expected ratio 1:2:1:3:6:3 . . . . .			3.56	7.13	3.56	10.69	21.37	10.69	
$\widehat{Cm} \widehat{cm} + \widehat{Cm} \widehat{cm} + \widehat{Cm} \widehat{cm}$ . . . . .			9(exp.14.25)		48 (exp. 42.75)				



TABLE 28. Mottled brownviolet (no. 11) of backcross  $F_1 \times$  Wagenaar, selfed.

Flower colour . . .	Pale rose			Violet-1, 2.			Total numbers coloured
	White	Yellowish	Orange	„Violet“	„Brownviolet“		
Seedcoat colour . .	White						
Colour number . .	49	1 2 3 7 8 9	4 5 6 10 11 12				
Genotype . . .	No. Fam.						
Pp JJ Sh Sh							
$\widehat{Cm} c\widehat{M} Gg bb$							
Vv . . . . .	496	1	2 1	1 1	3	9	
Pp	509	12	2 4 3	4 6 1	4 10	37	
PP	510	0	2 7 1	2 6 2?	2 7	39	
PP	511	0	4 3	4	3 8	27	
Total numbers		2 2 ? 4 17 8	6 17 4 9 28 15			112	
Expected ratio							
1:2:1:3:6:3:		1.75 3.50 1.75 5.25 10.50 5.25	5.25 10.50 5.25 15.75 31.50 15.75				
3:6:3:9:18:9							
$\widehat{Cm} c\widehat{M} + \widehat{Cm}$							
$\widehat{Cm} + \widehat{Cm} c\widehat{M}$		4(exp.7.00)	29(exp.21.00)	27(exp.21.00)	52(exp.63.00)		



TABLE 30. Segregation for the factor Sh in  $F_3$  families of Sh sh  $F_2$  plants ( $F_2$  family 55-2). Because of some difficulties in classifying I have refrained from tabulating the various colours.

No. Fam.	The probable constitution of the $F_2$ plant was	Colour no. $F_2$ plant	White	sh	Sh	Total numbers coloured
404	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ Gg Bb vv	20	9	10	20	30
403	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ gg Bb vv	14	13	12	10	22
423	PP JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ GG Bb vv	20	0	6	22	28
420	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{Cm}$ Gg? bb vv	9	6	1	15	16
468	Pp JJ Sh sh $\widehat{cM}$ $\widehat{cM}$ GG Bb Vv	22	3	4	9	13
467	PP JJ Sh sh $\widehat{cM}$ $\widehat{cM}$ gg bb Vv	4	0	4	11	15
413	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ GG bb Vv	11	13	5	15	20
412	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ gg bb Vv	5	10	8	11	19
415	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ GG bb Vv	11	11	7	18	25
414	PP JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ gg bb Vv	5	0	10	17	27
421	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{Cm}$ Gg bb Vv	12	1	3	14	17
422	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{Cm}$ gg bb Vv	6	2	1	7	8
425	PP JJ Sh sh $\widehat{Cm}$ $\widehat{Cm}$ gg Bb Vv	18	0	6	23	29
424	Pp JJ Sh sh $\widehat{Cm}$ $\widehat{cM}$ Gg BB VV	23	10	6	11	17
477	PP JJ Sh sh $\widehat{Cm}$ $\widehat{Cm}$ G ?BB VV	18 or 24	0	6	8	14
Total numbers coloured . . . . .				89	211	300
Expected ratio 1:3 . . . . .				75	225	





TABLE 32. Strength of string in „Fijne tros” 1933.

No. Fam. 1933	Motherplant 1932				String numbers 1933						total	average strength in the family
	String number			% fibres	1-2	2-3	3-4	4-5	5-6	6-7		
	dor- sal	ven- tral	aver- age									
323	5.7	4.2	4.9	9	2	9	5				16	3.69
324	5.2	4.0	4.8	15			12	3	2		17	3.91
325	4.7	4.0	4.4	4	2	11	6				19	3.71
326	5.2	4.3	4.7	10	1	7	7	2			17	4.09
327	4.2	3.6	3.9	4	2	8	6		1		17	3.91
328	3.6	3.4	3.5	5	2	5	9	3			19	4.18
Total					9	52	36	7	1		105	

TABLE 33. Strength of string and percentages of fibres in the  $F_1$  plants of 1932 and 1933 (three pods stringed; one anatomically investigated).

	Strength of string										Total
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10		
0-10											
10-20											
20-30						1	4				5
30-40						4	4				8
40-50						5	9				14
50-60						3	12				15
60-70						2	4				6
70-80											
> 80											
Wagenaar- type											
Total						15	33				48

TABLE 34.  $F_2$ -family 55-2 1932; classified according to strength of string and percentages of fibres.

	Strength of string										Total
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10		
0-10			6	19	5						30
10-20				5	8	2					15
20-30				4	8	6	1				19
30-40					4	5	5				14
40-50					3	3	3				9
50-60						6	12	6			24
60-70						3	16	8	1		28
70-80							4	9	1		14
> 80							1	3	1		5
Wagenaar-type				1		1	1	2	58		63
Total			6	29	28	26	43	28	61		221

TABLE 35.  $F_2$ -family 55-4 1932; classified according to strength of string and percentages of fibres.

	Strength of string										Total
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10		
0-10		8	41	38	8	4					99
10-20			6	17	14	8	2	1			48
20-30			1	8	12	7	6				34
30-40				2	6	16	4				28
40-50				1	9	13	10				33
50-60					2	10	19	4			35
60-70					1	6	21	12			40
70-80						2	11	18			31
> 80							1	15	6		22
Wagenaar-type					1	1	1	2	116		121
Total	0	8	48	66	53	67	75	52	122		491





TABLE 38. F<sub>3</sub> families of pure stringy (Wagenaar type) F<sub>2</sub> plants. A few plants have an „abnormal” sheath: part of the fibres are without thickening layers and of an irregular appearance on cross-section.

No. Fam.	F <sub>2</sub> mother plants			type	Strength of string in the F <sub>3</sub> plants										Total number	Remarks
	Strength of string				1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10			
	dorsal	ventral	average													
F <sub>2</sub> plants of family 55-4																
428	10.0	10.0	10.0	pure stringy										32	32	All pure stringy.
429	10.0	10.0	10.0	„										23	23	„ „ „
430	9.8	10.0	9.9	„, but abnormal										2	21	23 „ „ „, but many abnormal
F <sub>2</sub> plants of family 55-2																
431	10.0	9.8	9.9	pure stringy										18	18	All pure stringy
432	10.0	10.0	10.0	„										27	27	„ „ „
434	10.0	10.0	10.0	„										28	28	„ „ „
438	10.0	10.0	10.0	„										3	32	35 „ „ „
439	9.4	8.8	9.1	„										25	25	„ „ „
441	10.0	9.0	9.5	„										15	15	„ „ „
444	9.8	10.0	9.9	„										18	18	„ „ „
445	9.5	9.8	9.6	„										23	23	„ „ „
523	10.0	10.0	10.0	„										7	7	„ „ „
524	9.8	9.6	9.7	„										19	19	„ „ „
526	10.0	10.0	10.0	„										16	16	„ „ „
402	10.0	10.0	10.0	pure stringy										1	1	16 18 „ „ „; the plant with strength 7-8 is abnormal.
F <sub>2</sub> plants of family 55-2																
410	10.0	10.0	10.0	„										25	25	All pure stringy
415	10.0	10.0	10.0	„										25	25	„ „ „
419	9.4	8.6	9.0	„										21	21	„ „ „
423	10.0	10.0	10.0	„										16	16	„ „ „
466	9.3	0.9	9.2	„										3	3	„ „ „
468	10.0	10.0	10.0	„										2	2	„ „ „
470	10.0	9.3	9.7	„										17	17	„ „ „
476	10.0	10.0	10.0	„										11	11	„ „ „
478	10.0	10.0	10.0	„										18	18	„ „ „
481	9.5	10.0	9.8	„										5	5	„ „ „

TABLE 39. F<sub>3</sub> families which segregate the pure stringy (Wagenaar) type. The families are arranged according to increasing strength of string in the F<sub>2</sub> mother plants.

No. Fam.	F <sub>2</sub> mother plants				Strength of string in the F <sub>3</sub> plants										Total numbers			Expected pure stringy	D/m							
	Strength of string				not pure stringy (not Wagenaar type)										pure stringy (Wagenaar)											
	dorsal	ventral	average	% fibres	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	8-9	9-10	not pure stringy	pure stringy (Wagenaar)			total						
																					not pure stringy	pure stringy (Wagenaar)	total			
520	3.7	3.3	3.5	10															3	10	3	13	3.25	0.16		
421	5.4	3.2	4.3	17?		1	1	2	4	3									5	11	5	16	4.00	0.58		
450	5.4	3.2	4.3	28			1	2											5	4	5	9	2.25	2.13		
454	5.2	5.0	5.1	20			1	3	3	4	2								1	13	2	15	3.75	1.05		
451	6.6	4.6	5.6	33				9	4	5	1									6	19	6	25	6.25	0.12	
403	6.8	4.8	5.8	16			2	3	1	1	5									9	13	9	22	5.50	1.72	
427	6.8	5.6	6.2	40				5		5	7									8	22	8	30	7.50	0.21	
518	6.5	6.0	6.3	30			1			1	2	1		4						3	9	3	12	3.00	0.00	
448	7.0	6.8	6.9	50			1	3	2		4									3	10	3	13	3.25	0.16	
469	7.0	6.7	6.9	65						1		2	1	1						1	5	1	6	1.50	0.47	
516	7.0	7.0	7.0	40				4	4	3	4	5	5	1						9	26	9	35	8.75	0.10	
440	7.0	7.2	7.1	70			1	4	5	1	6	4								1	4	21	5	26	6.50	0.68
443	7.3	7.0	7.1	78				4	2	3	5	9	2							4	25	4	29	7.25	1.39	
472	7.4	7.0	7.2	43				2		1	2	6	10	7						9	28	9	37	9.25	0.09	
409	7.5	7.0	7.3	50				1	3	1	1	3	2							3	11	3	14	3.50	0.31	
404	7.2	7.6	7.4	65			2	3	5		1	4		1						8	16	8	24	6.00	0.94	
459	7.4	7.6	7.5	55				2	4		9		1							9	16	9	25	6.25	1.27	
477	8.0	8.0	8.0	50					1		2	1	3	3						5	31	5	36	9.00	1.54	
433	8.0	8.0	8.0	58					2	4	7	10	7	1						1	4	11	5	16	4.00	0.58
515	8.3	7.7	8.0	60				2	3		4	2								4	11	5	16	4.00	0.58	
405	8.4	8.2	8.3	70						2	3	3	3	4						4	15	4	19	4.75	0.40	
418	8.7	8.0	8.3	80				1	1	3	2	5	7							10	19	10	29	7.25	1.18	
471	8.2	8.6	8.4	60					1		1	1	1							2	4	2	6	1.50	0.47	
446	8.4	8.4	8.4	85				2	2	1	1	2	3	3						4	14	4	18	4.50	0.27	
457	8.4	9.0	8.7	70						1	2	1	2	3						6	9	6	15	3.75	1.35	
436	8.8	8.6	8.7	80				2	1	1	3	1	6	2						3	16	3	19	4.75	0.93	
447	9.0	8.7	8.8	74			5	6	4	2	6	4	3							6	30	6	36	9.00	1.15	
456	9.0	9.2	9.1	83					1	3	6	10	5	2						10	27	10	37	9.25	0.28	
458	9.5	9.3	9.4	82				1	1	6	6	8	6	2						12	30	12	42	10.50	0.53	
Total																										
Expected ratio 3 : 1																										
D/m																										

TABLE 38. F<sub>3</sub> families of pure stringy (Wagenaar type) F<sub>2</sub> plants. A few plants have an „abnormal” sheath: part of the fibres are without thickening layers and of an irregular appearance on cross-section.

No. Fam.	F <sub>2</sub> mother plants			type	Strength of string in the F <sub>3</sub> plants										Total number	Remarks		
	Strength of string				1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10					
	dorsal	ventral	average															
F <sub>2</sub> plants of family 55-4																		
428	10.0	10.0	10.0	pure stringy										32	32	All pure stringy.		
429	10.0	10.0	10.0	"										23	23	" " "		
430	9.8	10.0	9.9	" , but abnormal										2	21	23	" " " , but many abnormal	
F <sub>2</sub> plants of family 55-2																		
431	10.0	9.8	9.9	pure stringy										18	18	All pure stringy		
432	10.0	10.0	10.0	"										27	27	" " "		
434	10.0	10.0	10.0	"										28	28	" " "		
438	10.0	10.0	10.0	"										3	32	35	" " "	
439	9.4	8.8	9.1	"										25	25	" " "		
441	10.0	9.0	9.5	"										15	15	" " "		
444	9.8	10.0	9.9	"										18	18	" " "		
445	9.5	9.8	9.6	"										23	23	" " "		
523	10.0	10.0	10.0	"										7	7	" " "		
524	9.8	9.6	9.7	"										19	19	" " "		
526	10.0	10.0	10.0	"										16	16	" " "		
402	10.0	10.0	10.0	pure stringy										1	1	16	18	" " " ; the plant with strength 7-8 is abnormal.
F <sub>2</sub> plants of family 55-2																		
410	10.0	10.0	10.0	"										25	25	25	All pure stringy	
415	10.0	10.0	10.0	"										25	25	" " "		
419	9.4	8.6	9.0	"										21	21	" " "		
423	10.0	10.0	10.0	"										16	16	" " "		
466	9.3	0.9	9.2	"										3	3	" " "		
468	10.0	10.0	10.0	"										2	2	" " "		
470	10.0	9.3	9.7	"										17	17	" " "		
476	10.0	10.0	10.0	"										11	11	" " "		
478	10.0	10.0	10.0	"										18	18	" " "		
481	9.5	10.0	9.8	"										5	5	" " "		

TABLE 39. F<sub>3</sub> families which segregate the pure stringy (Wagenaar) type. The families are arranged according to increasing strength of string in the F<sub>2</sub> mother plants.

No. Fam.	F <sub>2</sub> mother plants				Strength of string in the F <sub>3</sub> plants										Total numbers			Expected pure stringy	D/m						
	Strength of string			% fibres	not pure stringy (not Wagenaar type)										pure stringy (Wagenaar)										
	dorsal	ventral	average		1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	8-9	9-10	not pure stringy	pure stringy (Wagenaar)			total					
																					not pure stringy	pure stringy (Wagenaar)	total		
520	3.7	3.3	3.5	10															3	<b>10</b>	<b>3</b>	13	3.25	0.16	
421	5.4	3.2	4.3	17?		1													5	<b>11</b>	<b>5</b>	16	4.00	0.58	
450	5.4	3.2	4.3	28			1												5	<b>4</b>	<b>5</b>	9	2.25	2.13	
454	5.2	5.0	5.1	20				1											1	<b>13</b>	<b>2</b>	15	3.75	1.05	
451	6.6	4.6	5.6	33					9										6	<b>19</b>	<b>6</b>	25	6.25	0.12	
403	6.8	4.8	5.8	16						2									9	<b>13</b>	<b>9</b>	22	5.50	1.72	
427	6.8	5.6	6.2	40														8	<b>22</b>	<b>8</b>	30	7.50	0.21		
518	6.5	6.0	6.3	30															3	<b>9</b>	<b>3</b>	12	3.00	0.00	
448	7.0	6.8	6.9	50															1	<b>5</b>	<b>1</b>	6	1.50	0.47	
469	7.0	6.7	6.9	65															3	<b>10</b>	<b>3</b>	13	3.25	0.16	
516	7.0	7.0	7.0	40															9	<b>26</b>	<b>9</b>	35	8.75	0.10	
440	7.0	7.2	7.1	70															1	<b>4</b>	<b>5</b>	26	6.50	0.68	
443	7.3	7.0	7.1	78															4	<b>25</b>	<b>4</b>	29	7.25	1.39	
472	7.4	7.0	7.2	43															9	<b>28</b>	<b>9</b>	37	9.25	0.09	
409	7.5	7.0	7.3	50															3	<b>11</b>	<b>3</b>	14	3.50	0.31	
404	7.2	7.6	7.4	65															2	<b>3</b>	<b>5</b>	24	6.00	0.94	
459	7.4	7.6	7.5	55															8	<b>16</b>	<b>8</b>	25	6.25	1.27	
477	8.0	8.0	8.0	50															9	<b>16</b>	<b>9</b>	25	6.25	1.27	
433	8.0	8.0	8.0	58															1	<b>4</b>	<b>10</b>	4	3.50	0.31	
515	8.3	7.7	8.0	60															4	<b>10</b>	<b>4</b>	14	3.50	0.31	
405	8.4	8.2	8.3	70															5	<b>31</b>	<b>5</b>	36	9.00	1.54	
418	8.7	8.0	8.3	80															1	<b>4</b>	<b>11</b>	5	4.00	0.58	
471	8.2	8.6	8.4	60															4	<b>15</b>	<b>4</b>	19	4.75	0.40	
446	8.4	8.4	8.4	85															10	<b>19</b>	<b>10</b>	29	7.25	1.18	
457	8.4	9.0	8.7	70															2	<b>4</b>	<b>2</b>	6	1.50	0.47	
436	8.8	8.6	8.7	80															4	<b>14</b>	<b>4</b>	18	4.50	0.27	
447	9.0	8.7	8.8	74															6	<b>9</b>	<b>6</b>	15	3.75	1.35	
456	9.0	9.2	9.1	83															3	<b>16</b>	<b>3</b>	19	4.75	0.93	
458	9.5	9.3	9.4	82															6	<b>30</b>	<b>6</b>	36	9.00	1.15	
Total																				12	<b>30</b>	<b>12</b>	42	10.50	0.53
Expected ratio 3 : 1																				475	<b>163</b>		638	159.50	
D/m																				0.32					

TABLE 40.  $F_3$  families which do not segregate the pure stringy (Wagenaar) type. The families are arranged according to increasing strength of string in the  $F_2$  mother plants.

No. Fam.	$F_2$ mother-plants				Strength of string in the $F_3$ plants (not a single pure stringy type)										Total number	Average strength in the family
	Strength of string			% fibres	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10			
	dorsal	ventral	average													
$F_2$ plants of family 55-4																
519	2.7	2.0	2.3	1			2	1						3	3.83	
522	3.4	2.4	2.9	4	1		4		4	1		1		10	4.50	
527	3.5	2.8	3.1	7	3		4	5	1					14	4.14	
521	3.7	3.3	3.5	4			1	1	4					6	5.00	
426	4.2	3.0	3.6	4	4		10	13	4					31	3.98	
530	3.8	3.6	3.7	2	1		3	6	7	1				18	4.66	
461	4.0	3.4	3.7	4	8		8	10	1	2				29	3.84	
460	5.0	3.0	4.0	2			1	2	2	2				7	5.21	
442	6.3	4.0	5.1	26			8	11	3					22	4.27	
525	6.0	4.5	5.3	15				1	2	4	2	1		10	6.50	
462	5.4	5.4	5.4	6			1	7	9	2				19	5.13	
449	6.6	4.2	5.4	49			2	2	2	2	2			10	5.50	
437	7.0	5.7	6.3	50	1		7	9	3	3				23	4.50	
517	6.8	6.0	6.4	23			5	4	4	2	1			16	4.88	
435	6.5	7.3	6.9	55			8	5	6	1	6			26	5.19	
$F_2$ plants of family 55-2.																
480	4.7	2.7	3.7	2			6	4	2	1				13	4.35	
473	5.0	3.0	4.0	4				1	2					3	5.17	
407	6.3	4.8	5.5	26			2	4	7	3				16	5.13	
467	6.0	5.3	5.6	27	1		3	3	4	4				15	4.97	
416	6.0	5.8	5.9	26				8	11	6	1	1		27	5.27	
406	6.2	5.8	6.0	12				2	1	7	7	1		18	6.72	
424	6.5	6.5	6.5	22						3	10	4	1	18	7.67	
479	6.0	7.0	6.5	33				6	7	1				14	5.14	
401	7.6	7.6	7.6	50				1	10	19	4	2		36	6.39	



TABLE 42. Strength of string in backcross F<sub>1</sub> with Wagenaar.

Back-crossed in the year	Grown in the year	Strength of string in the backcross plants										Total numbers				
		not pure stringy										pure stringy		not pure stringy	pure stringy (Wagenaar)	total
		1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	< 9	9-10				
1931	1932			5	16	19	29	18	17	1	6	82	<b>105</b>	<b>88</b>	193	
1932	1933			10	12	16	15	4	1		4	47	<b>58</b>	<b>51</b>	109	
Total				15	28	35	44	22	18	1	10	129	<b>163</b>	<b>139</b>	302	
Expected ratio 1 : 1												151	151			
D/m												1.38				

TABLE 43. Progeny of not pure stringy (not Wagenaar type) backcross plants of F<sub>1</sub> with Wagenaar after selfing. All families (except 492) segregate the pure stringy (Wagenaar) type.

No. Fam.	Backcross-plants				Strength of string in the progeny of backcross plants										Total numbers			Expected pure stringy		
	Strength of string			% fibres	not pure stringy (not Wagenaar type)										pure stringy (Wagenaar)		total			
	dorsal	ventral	average												not pure stringy	pure stringy (Wagenaar)				
					1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	8-9			9-10			
Of F <sub>1</sub> -plant 55-4.																				
498	3.6	3.0	3.3	5			1							3	1	<b>4</b>	<b>1</b>	5	1.25	
496	4.8	3.8	4.3	5		1	1	1	3	1					1	<b>7</b>	<b>1</b>	8	2.00	
486	4.8	3.8	4.3	5		2	2	1	3	4	1			1	3	<b>13</b>	<b>4</b>	17	4.25	
488	4.5	5.0	4.8	10?			1	3	4	2	7	5			3	<b>22</b>	<b>3</b>	25	6.25	
497	5.8	5.0	5.4	10				1	4	2					1	<b>7</b>	<b>1</b>	8	2.00	
482	5.7	5.3	5.5	10			1	3	3	2	3				4	<b>12</b>	<b>4</b>	16	4.00	
494	5.8	5.3	5.5	45			1		5		1	1			4	<b>8</b>	<b>4</b>	12	3.00	
492	6.6	5.0	5.8	34				2	2	3	3	2			0	<b>12</b>	<b>0</b>	12	3.00	
485	6.3	5.7	6.0	30				2	3	4	3				5	<b>12</b>	<b>5</b>	17	4.25	
483	7.3	7.3	7.3	40				1	1	2	2	2	2		1	<b>10</b>	<b>1</b>	11	2.75	
Of F <sub>1</sub> -plant 55-6.																				
507	5.5	4.0	4.8	4		1	5	5	3	1					5	<b>15</b>	<b>5</b>	20	5.00	
503	5.8	3.8	4.8	6			4	8	8	1					1	5	<b>21</b>	<b>6</b>	27	6.75
505	6.3	4.7	5.5	32?		1	1	9	3	2	2				3	<b>18</b>	<b>3</b>	21	5.25	
504	7.0	5.8	6.4	40			4	4	3	5				1	6	<b>16</b>	<b>7</b>	23	5.75	
512	6.5	6.0	6.3	15		1	1	5	3	4	4	2			7	<b>20</b>	<b>7</b>	27	6.75	
506	7.5	5.3	6.4	?			2	4	2	4	3				6	<b>15</b>	<b>6</b>	21	5.25	
514	7.0	7.0	7.0	40				5	2	4	3	1			6	<b>15</b>	<b>6</b>	21	5.25	
511	7.4	7.0	7.2	52		1		3	4	6	3	3			5	<b>20</b>	<b>5</b>	25	6.25	
510	8.5	7.0	7.8	60		2	5	2	6	9	1				11	<b>25</b>	<b>11</b>	36	9.00	
Total												272	80	352	88.00					
Expected ratio 3 : 1												264.00	88.00							
D/m												0.98								

TABLE 44.  $F_2$  segregation for the pod wall characters: non-parchmented versus parchmented in all degrees. All plants have been examined anatomically.

No. Fam.	Non-parchm.	Parchmented	Total	Exp. ratio 1 : 3		D/m
55-2 '32	51	170	221	55.25	165.75	0.66
55-4 '32	121	367	488	122.00	366.00	0.10
55-6 '32	66	215	281	70.25	210.75	0.58
393 '33	10	24	34	8.50	25.50	0.60
394 '33	10	27	37	9.25	27.75	0.28
395 '33	9	20	29	7.25	21.75	0.75
396 '33	8	28	36	9.00	27.00	0.38
397 '33	10	26	36	9.00	27.00	0.38
398 '33	7	27	34	8.50	25.50	0.60
399 '33	7	30	37	9.25	27.75	0.85
400 '33	11	24	35	8.75	26.25	0.88
Total	310	958	1268	317.00	951.00	
D/m				0.45		

TABLE 45. Segregating  $F_3$  families of  $F_2$  plants with parchmented pod.

No. Fam.	Non-parchm.	Parchmented	Doubtful	Total	Expected ratio 1 : 3	
403	1	21		22	5.50	16.50
406	3	19		22	5.50	16.50
407	5	11		16	4.00	12.00
409	5	12		17	4.25	12.75
410	9	28		37	9.25	27.75
415	10	14	2	26	6.50	19.50
419	5	16		21	5.25	15.75
423	4	12		16	4.00	12.00
424	6?	12?	?	18	4.50	13.50
470	3	14		17	4.25	12.75
472	11	26		37	9.25	27.75
473	1	1		2	0.50	1.50
476	2	7	1	10	2.50	7.50
479	5	8		13	3.25	9.75
480	3	8	2	13	3.25	9.75
426	4	27		31	7.75	23.25
428	5	27		32	8.00	24.00
430	2	21		23	5.75	17.25
434	7	21		28	7.00	21.00
437	8	15		23	5.75	17.25
438	5	30		35	8.75	26.25
439	8	17		25	6.25	18.75
440	5	21		26	6.50	19.50
445	6	17		23	5.75	17.25
446	2	16		18	4.50	13.50
448	6	7		13	3.25	9.75
449	4	4	2	10	2.50	7.50
457	3	12		15	3.75	11.25
515	5	11		16	4.00	12.00
517	4	12		16	4.00	12.00
520	3	10		13	3.25	9.75
521	2	4		6	1.50	4.50
522	3	7		10	2.50	7.50
523	2	5		7	1.75	5.25
524	5	14		19	4.75	14.25
525	1	9		10	2.50	7.50
526	3	13		16	4.00	12.00
527	4	10		14	3.50	10.50
Total	170	539	7	716	179.00	537.00

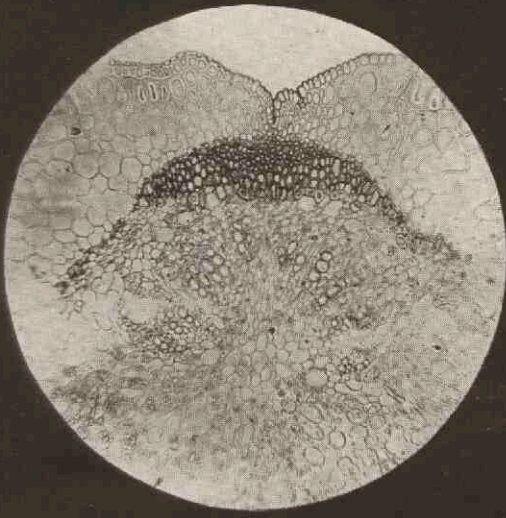




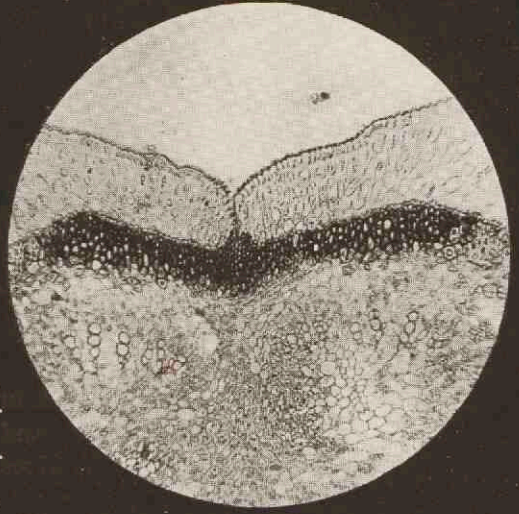
## PLATE I

Various sheath types ( $\pm 60 \times$ )

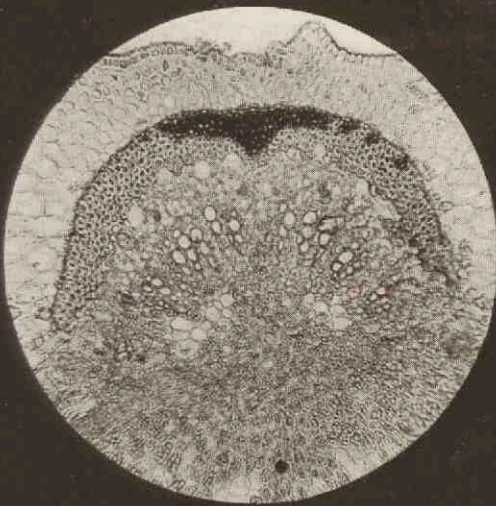
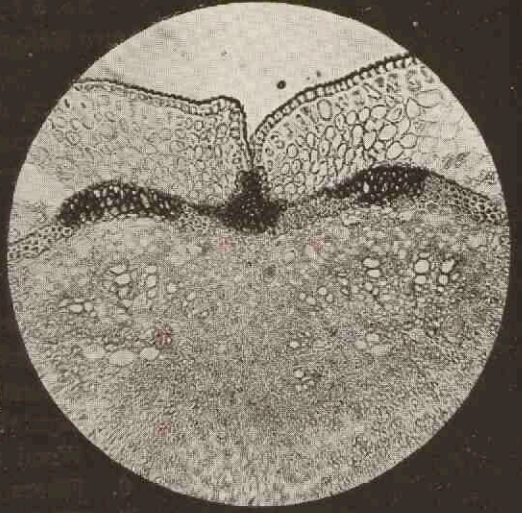
No. 1		
(Fijne tros)		
Dorsal		Ventral
4.3	string number	5.0
50	% wood cells	75
5	% fibres	10
No. 2		
Dorsal		Ventral
6.8	string number	6.5
35	% wood cells	40
35—40	% fibres	35
No. 3		
Dorsal		Ventral
9.0	string number	9.0
15—20	% wood cells	5
65—70	% fibres	80



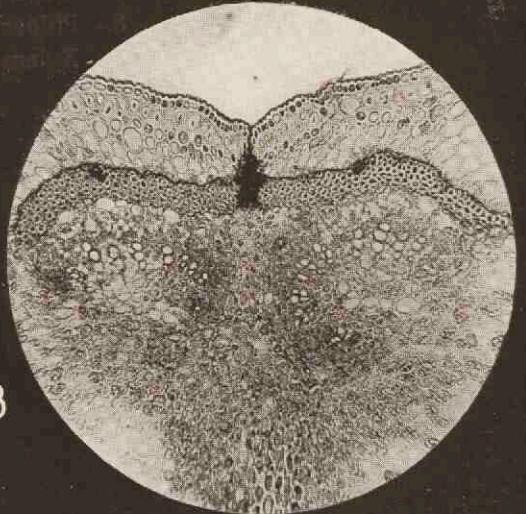
1



2



3



Various sheath types.

## PLATE II.

### Various sheath types

#### No. 4 ( $\pm 60 \times$ )

Dorsal		Ventral
9.0	string number	9.0
10	$\frac{0}{0}$ wood cells	4
80	$\frac{0}{0}$ fibres	85

#### No. 5 ( $\pm 60 \times$ ).

(pure stringy Wagenaar).

Dorsal		Ventral
10.0	string number	10.0
4	$\frac{0}{0}$ wood cells	3
85—90	$\frac{0}{0}$ fibres	90

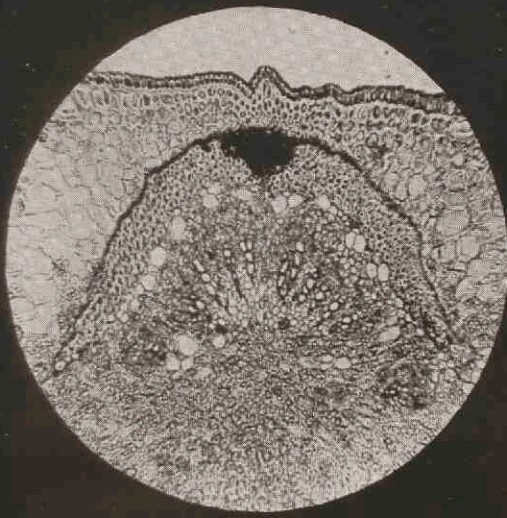
#### No. 6

Transversal section ( $\pm 160 \times$ )

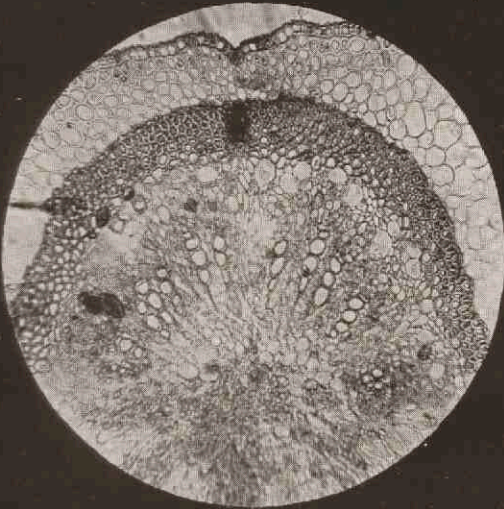
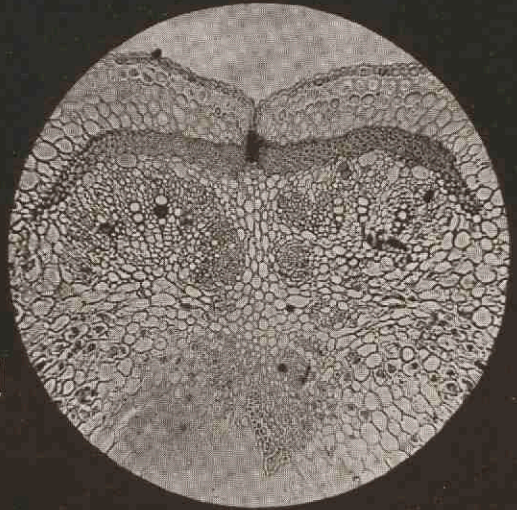
#### No. 7

Radial section ( $\pm 140 \times$ )

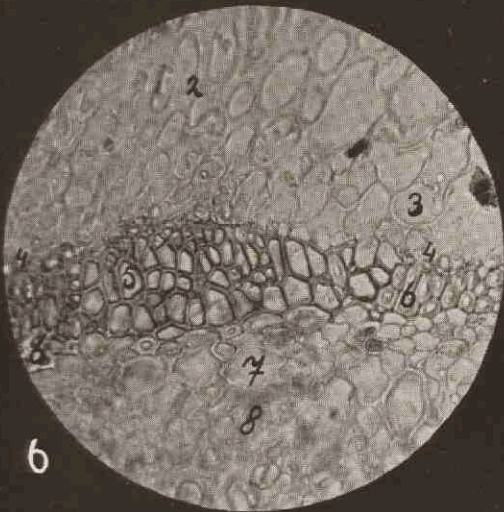
1. Epidermis.
2. Collenchyma.
3. Parenchyma.
4. Crystal-layer.
5. Wood cells and
6. Fibres of the sheath.
7. Wide parenchymatic cells.
8. Phloem part.
9. Xylem part of the vascular bundle.



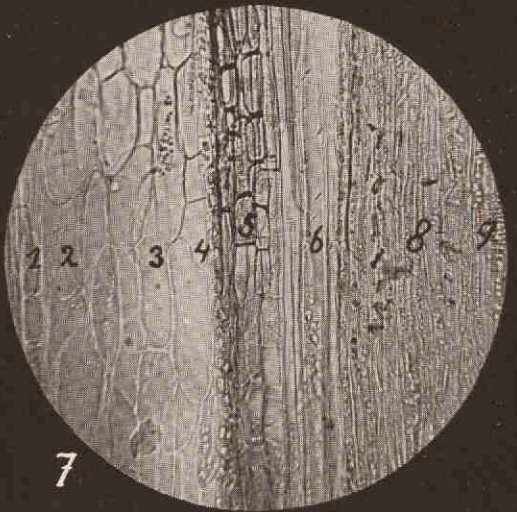
4



5



6



7

Various sheath types.



## STELLINGEN

### I

Physische en chemische invloeden wijzigen de percentages van „rand” en „midden” copulatie in *Ustilago promycelia*. Het is door de proeven van Hüttig evenwel niet bewezen, dat deze wijzigingen uitsluitend of voornamelijk berusten op verschuiving in de percentages van prae- en postreductie.

W. HÜTTIG, *Zeitschrift f. Botanik*, 1930 en 1933.

### II

De omschrijving die GOLDSCHMIDT geeft van het begrip „epistasie” is niet juist.

R. GOLDSCHMIDT, *Einführung in die Vererbungs-wissenschaft*, 1928.

### III

Konstante en altijd splitsende marmering, streping en dubbele marmering van de zaadhuid van *Phaseolus vulgaris* berusten waarschijnlijk op twee bijna absoluut gekoppelde reeksen van multiple allelomorphen.

### IV

Noch het bestaan van kort-periodische schommelingen in de  $\text{CO}_2$  assimilatie, noch het regelmatig pulseeren van huidmondjes als mogelijke oorzaak ervan, zijn als afdoend bewezen te beschouwen.

MAXIMOW, *Ber. d. D. Bot. Ges.* 46, 1928.

### V

De lage temperatuur, die wintergranen gedurende eenigen tijd noodig hebben om tot normale ontwikkeling te komen, kan door een periode van korte daglengte bij hogere temperatuur vervangen worden.

MAXIMOW, *Jahrb. wiss. Bot.* Bd 64, 1925, p. 702



## VI

Voor de veronderstelling van RAY NELSON, dat de verdeling van aangetaste en niet aangetaste zaden van mozaiek-zieke boonenplanten zou berusten op bouw of verloop van de vaatbundels, bestaan weinig aanwijzingen.

RAY NELSON, *Agric. Exp. Stat.*, Michigan,  
*Techn. Bull.* 118, 1932.

## VII

Ook voor *Cryptomeria* geldt de spruit-theorie zooals die voor de vruchtschub der *Abietinae* door ALEXANDER BRAUN, VELENOVSKÝ e.a. geformuleerd is.

## VIII

De term „hoogveen” behoort slechts in engere, physiognomische beteekenis gebruikt te worden.

## IX

De verschijnselen van steriliteit, fertiliteit en bastaardsplitsing kunnen niet gebruikt worden voor omschrijving van het soortbegrip.

## X

Het feit, dat bij mensch en rund in ongeveer 20% der gevallen het foramen ovale gedurende het heele leven open blijft, heeft, mits de Ductus Botalli gesloten is, voor den bloedsomloop geen verdere beteekenis.

## XI

De door SMITH WOODWARD als *Eoanthropus dawsoni* beschreven skeletresten zijn niet alle afkomstig van dezelfde species.











