Dr. K. Kunhikrishnan,
with kind regards from
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635.652:575.1.061.6

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 72-29 (1972)

INHERITANCE OF COLOURS IN *PHASEOLUS VULGARIS* L. III ON GENES FOR RED SEEDCOAT COLOUR AND A GENERAL SYNTHESIS

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(Received XI-VIII-1972)

CONTENTS

1. INTRODUCTION: 'YELLOW-BLACK' AND 'RED' COLOURS

In his article 'Inheritance of colour in *Phaseolus vulgaris* L. II. A critical review' (PRAKKEN, 1970) the present author discussed the genetics of the group of so-called *yellow-black seedcoat colours*, or somewhat more detailed, of the white-yellow-brown-violet-black colours. By comparing his own results over a long range of years (1930–1970) with those of other *Phaseolus* workers, in the first place Kooiman (1920, 1931) and Lamprecht (1932 and later), he came to the conclusion that, for this group, *the main results of all authors can be explained by the action of seven genes* or loci. The unfolding scheme presented at the end of this present article, opposite p. 82, shows their actions and interactions, and will first be explained and discussed.

The gene-symbols used are mostly those of Lamprecht, chosen by him, as far as possible, *on the basis of priority*. The phenotypic effects also are as described by Lamprecht, except for the genes *G* and *B* which, as explained by Prakken (1970), do *not* produce a brown hilumring. The phenotypic effects quite agree with those of the genes deduced by Kooiman (1920) from his cross, and to which he gave the *alphabetically chosen* symbols *A, B, C, D, E,* and F. In Kooiman's cross the gene *G* of Lamprecht was, according to Prakken (1940, 1970), homozygously present and therefore not found and named by him (that *G* continues the series *A-F* of Kooiman is quite accidental). This fact (i.e. the homozygosity *GG* in Kooiman's cross) was overlooked by most later investigators and this often caused difficulties and misinterpretations in attempts to obtain gene-homologization.

The seven genes (1–7), classified into three groups (*A*, *B*, *C*) in the usual way, and their phenotypic effects are described below (cf. also the scheme p. 82).

A. *Groundfactor* or *basic gene:*
   1. ***P*** (= Kooiman: *A*), the dominant 'groundfactor' or 'basic gene', left out in the scheme p. 82, is necessary for the plant to be able to produce seedcoat colour, all *pp* plants having white seedcoat (and also pure green seedlings and white flowers).

B. Three dominant *chromogenous factors* or *colour genes* (in the scheme: to the left), each producing, together i.e. complementary with the basic gene *P*, a distinct pale seedcoat colour:
   2. ***C*** (= Kooiman: *B*), the 'factor for ever-segregating mottling', *P.CC* (in the scheme: **II–1**) having a pale greenish yellow seedcoat, *P.Cc* (not represented in the scheme) being pale greenish yellow mottled upon white, i.e. 'dark pattern colour' *P.CC* upon 'background colour' *P.cc*, *P.cc* (scheme: **I–1**) of course being white. For the further alleles c^u, c^{ui} and c^{cr} cf. Prakken 1970, p. 4–5, and this article p. 5.
   3. ***D*** (symbol of Kooiman; = Lamprecht: *Ins* and *Can*), the 'hilumring factor', producing a brown hilumring but for the rest leaving the seedcoat almost colourless, whitish (= hilumring type, *P.D.*, scheme: **III–1** and the whole *row* **III**, i.e. in combination with the modifying genes practically unchanged).
   4. ***J*** (= Kooiman *C*; Prakken formerly: *Sh*), the 'shine factor', producing, as *D* does, a brown hilumring, but moreover giving the seedcoat a shiny pale yellowish or creamish pale buff colour (scheme: **V–1**) that shows an intense 'afterdarkening' in the course of months and years, as all genotypes with *J*; *J* is epistatic over the 'hilumring factor' *D*.

C. Three dominant *intensifying factors* or *modifying genes* (in the scheme: at the top) which together with the basic gene *P* alone do not produce any colour, but which, each in its specific way, have a *darkening influence* upon the pale seedcoat colour caused by basic gene *P* together with one or more of the three colour genes (*P.D.* however, the hilumring type of *row* **III**, is hardly or not influenced, cf. above):

5. ***G*** (in Kooiman's cross homozygously dominant), the 'yellowbrown factor', changing the greenish yellow colours of *column* **1** into the slightly less greenish or more yellowbrown colours of *column* **2**.
6. ***B*** (= Kooiman: *E*), the '(grey-)greenish brown factor', changing the greenish yellow colours of *column* **1** into the (grey-)greenish brown colours of *column* **3**; *G* and *B* together produce brown colours, *column* **4**.
7. *V* (= Kooiman: *F*), the 'violet factor', changing white flower (*P.vv*) or pale lilac flower ($P.V^{lae}$.) into violet flower (*P.V.*), also changing the pink anthocyanin of *P.vv* and $P.V^{lae}$. plants into violet, and at the same time producing bluish or violet to black colours in the seedcoat (*columns* **5–8**). It should be remarked here that the flowers of heterozygous plants $P.Vv^{lae}$ or *P.Vv* are of a clearly paler violet than those of homozygous *P.VV*-plants, and further that the difference between $P.V^{lae}$. and P.*vv* is in flower colour only.

The combined action of the three *colour genes C*, *D* and *J*, together with the basic gene *P*, results in the eight 'colour types' or 'colour groups' of *row* **I–VIII** below (and in the scheme p. 82):

<table>
<tr><td>I. <i>ccddjj</i> (kooiman: <i>bbddcc</i>):
white background colour</td><td rowspan="2">without brown hilumring</td><td rowspan="4"><i>mat and non-afterdarkening (jj).</i></td></tr>
<tr><td>II. <i>CCddjj</i> (Kooiman: <i>BBddcc</i>):
mat dark pattern colour group</td></tr>
<tr><td>III. <i>ccD.jj</i> (Kooiman: <i>bbD.cc</i>):
hilumring-type background colour</td><td rowspan="2">with a brown hilumring</td></tr>
<tr><td>IV. <i>CCD.jj</i> (Kooiman: <i>BBD.cc</i>):
mat dark pattern colour group</td></tr>
<tr><td colspan="2">V. <i>ccddJ.</i> (Kooiman: <i>bbddC.</i>):
shiny background colour group, always brown h. ring</td><td rowspan="4"><i>shiny and strongly afterdarkening, always brown hilumring (J.).</i></td></tr>
<tr><td colspan="2">VI. <i>CCddJ.</i>(Kooiman: <i>BBddC.</i>):
shiny dark pattern col. group, always brown h. ring</td></tr>
<tr><td colspan="2">VII. <i>ccD.J.</i> (Kooiman: <i>bbD.C.</i>):
as V, or slightly darker because of <i>D</i>.</td></tr>
<tr><td colspan="2">VIII. <i>CCD.J.</i>(Kooiman: <i>BBD.C.</i>):
as VI, or slightly darker because of <i>D</i>.</td></tr>
</table>

The three *modifying genes G, B.* and *V* have, as already mentioned, within each of the colour types, *row* **I–VIII** above, more or less the same, i.e. *their specific darkening effect*, and by their combined actions the colours of *columns* **1–8** below (and in the scheme) are produced, the colour name in *italics* representing the shiny dark pattern colours of *row* **VI** or **VIII**:

1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
ggbbvv	***G.bbvv***	***ggB.vv***	***G.B.vv***	***ggbbV.***	***G.bbV.***	***ggB.V.***	***G.B.V.***
	(K.: *GGeeff*)		(K.: *GGE.ff*)		(K.: *GGeeF.*)		(K.: *GGE.F.*)
pale greenish or creamish to *greenish yellow*	pale yellowish to *yellowbrown*	gray brown to *greenish brown*	pale soft brown to *dark brown*	gray violet to *dark violet*	brown gray to *dark brown violet*	dark greenish to *black*	(dark) mouse gray to *black*

By combining *rows* **I–VIII** and *columns* **1–8** the 64 genotypes of the scheme opposite p. 82 are obtained. In each compartment of it the name of the relevant colour is placed: uppermost in the compartment a more general name, mainly derived from the work of KOOIMAN and PRAKKEN, and below it the german name given by LAMPRECHT, together with, between brackets, his english name for it. It was LAMPRECHT who, by his accurate descriptions of especially the shiny ***J***-colours in the lower half of the scheme (with the help of various colour systems; and including the variability and the changes during ageing) made comparisons possible. Only among the mat colours in the upper-right quarter of the scheme (*jjV.*) the correspondence or homologization is less certain in a few cases, mainly caused by LAMPRECHT's wrongly ascribing of *hilumring-forming colour gene action* to the purely modifying genes *G* and *B* (cf. p. 2).

From the scheme the phenomena of dominant or recessive epistasis (= cryptomerie) can be read. In *row* **III**, the hilumring type background colour group ***ccD.jj***, the modifying genes *G*, *B* and *V* have no or hardly any influence, only *V* sometimes producing a slight glaucescent tinge, as it also can do in *row* **I**, *ccddjj*, therefore sometimes being indicated not as a 'modifying gene' but as a 'colour gene'. *Rows* **VII** and **VIII**, though ***D.J.***, hardly differ from *rows* **V** and **VI**, ***ddJ***: *J* is epistatic over *D-d*.- Also some other differences can be very slight, especially for *G-g*, see chapter III, cross 1, 5 and 6.

The genetic system for the *yellow-black colours* (PRAKKEN II, 1970) has been discussed here at some length, as the present author is convinced that the '*red*' *colours* accurately fit in with the same gene system, i.e. they form simple extensions to it.

The '*red*' or '*reddish*' *colours* are caused in two different ways, both often described in literature, but without ever having been satisfyingly connected, in a general way, with the whole of the 'yellow-black' system. These two ways are:

a. *Dominant red* is caused by the *colour gene R*, producing together with groundfactor *P* a pale lilac (red) colour without hilumring. There also exist red mottled (*M*), red striped (*S*) and otherwise red patterned types, very strongly linked with *R* or even allelic with it. LAMPRECHT at any case considers them as one allelic series, and he described (LAMPRECHT, 1947) seven alleles of it: R (= one-coloured red), R^{ma} (red *ma*rmoriert or mottled), R^{st} (= red *st*riped) ... to r (= non-red). This locus *R* in its turn is very strongly linked with the locus *C-c* for ever-segregating mottling. LAMPRECHT mentions a (small) number of crossing-over types, but other investigators (FEENSTRA, NAKAYAMA) did not find any recombination at all and they therefore considered all alleles as belonging to the locus *C*. In the course of the present study a few recombinational types were found (and further analysed), but these cases will not be treated now: *for ease of discussion* the very complicated situation will be looked at as the 'complex locus' *C*, with the alleles C-c-c^u...... C^r-C^m-C^{st}......, in a preliminary manner. In (a) following article(s) the present writer hopes to give a more detailed analysis of this 'complex locus', that not only influences seedcoat colour but also seedling-, flower-, plant- and fruit colour in various ways, as will appear in chapters III and IV.

b. *Recessive red* is caused by the alleles rk and rk^d of a *modifying gene*, the *Rk*-locus, named by SMITH, 1939. The symbol *Rk* has been derived from the name of the recessive red variety *R*ed *K*idney, *rk rk*.

Just as the 'alleles' of the 'complex locus' *C* have 'pleiotropic' influences upon the colour of other parts of the plant so has, as will appear in chapter IV, also Rk-rk-rk^d some pleiotropic action, viz. on colour of veins in the wings of the flowers.

The main points in the chapters III to V will be on the collaboration between the genes for 'yellow-black' and those for 'red' and upon the 'pleiotropic actions' of these genes for red, while also the action of a few new seedcoat genes will be described.

II. MATERIAL AND METHODS

The material analysed here consists of two groups of diallelic crosses between four varieties each, studied between 1934 and 1940. The results were not published before, except for a very short note (PRAKKEN, 1938) and except for the crosses between the three dark pattern types used (PRAKKEN, 1940, crosses 1, 4 and 5; see also PRAKKEN, 1970). From the many more crosses of that time they were chosen because of their being concerned with genes for *red seedcoat colours* and *the pleiotropic actions of them*. The description of parent varieties and their F_1's and the analysis of F_2 etc. will be made in chapter III (first group of four: crosses 1–6), chapter IV (second group of four: crosses 7–12) and chapter V (a few 'connecting crosses', 13–15). In this chapter II the mode of description or classification of the various colour characters and the difficulties connected with it will shortly be discussed.*

From the very beginning each seed planted and each plant grown from it received its own individual number, in such a way that mistakes were practically excluded: after emergence a stick with family and plant number was placed behind each tenth plant, sticks also being put at all open places (non-germinated seeds or dead plants), numbering and open places immediately being taken over upon the description lists, and all characters observed being noted in the relevant columns behind the numbering. Observed were colour of cotyledons and of hypocotyl, flower colour, colour of ripening fruit and ripe seed, and sometimes of still other parts, as basis of first leaf or stem colour. All observations were made by the author.

As most colours in these crosses are wellknown ones and described often, usually no detailed description will be given. None of the seven varieties ('Wagenaar' being used in both groups of four) possessed the 'violet factor' V, all being either V^{lae} or v. Seedling colour therefore was either pure green or with pink anthocyanin, flower colour white or pale lilac (and almost all colours between; never violet), colour of ripening fruit green, pink or intense violet-red (never violet), while seeds of non-red type belonged to *columns* **1–4** of the scheme and never to **5–8**. Further were all three non-patterned or one-coloured varieties used of 'dark pattern type', CC, therefore belonging, as all non-red selfcoloured offspring, to *rows* **II**, **IV**, **VI** or **VIII** of the scheme. The seedcoat colours with genes for red (C^m, C^{st} or $rk^d rk^d$) will generally be described in direct relation to their corresponding CC dark pattern colour.

Difficulties immediately began when trying to state the content of pink anthocyanin in cotyledons and hypocotyl. The quantity of this colour in each of them is, roughly estimated as the part of the surface covered with it, indicated as 'green' (0), 'pink 1', 'pink 2' etc. to 'pink 10'. Pink colour seldom comes higher then 6 or 7, while in V-plants the violet colour can reach 9 or even 10. At the lower end of the scale the purely green type is often clearly distinguishable, but not always; indications as 'green?' or 'p 0^+?' had to be intercalated between 'green' and 'pink 1'. The real situation often did not become clear before the analysis of F_3 was completed. By some special circumstances the difficulties can still be enlarged. Anthocyanin in the cotyledons always seems to be visible immediately after germination, while colour in the hypocotyl often not clearly develops before some days later. Because of the great number to be scored (about 8–10.000 yearly), and in spite of spreading the planting of seeds over a period of about two weeks, many were scored either too early, i.e. before antho-

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*To Mr. K. Knoop, attached to the Department of Genetics since 1930, the author owes much gratitude for his reliable many-sided help. During recent years much of the descriptive and analyzing work was made by Miss Tia bosma, in an intelligent and often independent way, for which I am much obliged. Gratitude is owed also to the former and the present chief-gardeners, Mr. J. Jansen and Mr. P. L. Visser, together with their co-workers, for taking care of the plants. Miss H. Boelema did the typing work in a very accurate way, for which I thank her much.

cyanin in the hypocotyl was developed, or too late, i.e. after the cotyledons had faded or had too much shrivelled. Scoring the germ plants twice could only be done in a few special cases. Not only *time* however, also *temperature* is of importance: with high temperature (in the field, or in letting e.g. the seeds producing F_1-plants germinate in the hot house) the development of seedling anthocyanin is less then with a lower one. For all these reasons a satisfying quantitative analysis was not possible, while the F_1-results (hot house) always have to be confronted with those of F_2-F_3.

Flower colour too, varying from purely white to pale lilac, gave many difficulties. Necessary for pale lilac flower as e.g. in 'Wagenaar' are at least three completely or incompletely dominant genes: the groundfactor *P.*, *T.* (*tt* gives seeds with a white part) and the factor $V^{lae}V^{lae}$. Heterozygosity for one or more of these genes, especially $V^{lae}v$, makes flower colour paler, so that in F_2-families after F_1-genotype $PpTtV^{lae}v$ (see cross no. 8) the whole range occurs: 'Wagenaar', 'slightly paler', 'much' and 'very much paler', 'almost white', 'white?' and 'white'. The problem is, however, much more complicated, for this intensity-gradation applies to *overall colour* only, while two special characteristics of part of the flower are left out of consideration, viz. *red tip of the standard* and *red veins in the wings*, see the schematical pictures of fig. 9, p. 65. Each of these two characters, as ultimately could be concluded, depends upon pleiotropic action of a gene for red seedcoat colour, viz. C^{st}. (red tip) and $rk^d rk^d$ (red veins).

As regards 'red tip standard' (or: red intensification) it was recorded as 'without' (- or 0), very small (1), small (2), medium (3), great (4; fig. 9, 12–15) or very great (5; covering about $\frac{1}{3}$–$\frac{1}{2}$ of the standard). But there had to be added 'all', 'most' or 'a few flowers'. And, the flowers being without red tip, 'all buds'. 'some buds', or 'a few young buds' could show it. In some of these latter cases or even in case of completely 'without', a new inspection after some sunny days could show most flowers and buds having a clear red tip. Also the place of flowers, hidden between the leaves or in full light at the top, was of importance. In many cases the offspring of plants had to be studied.

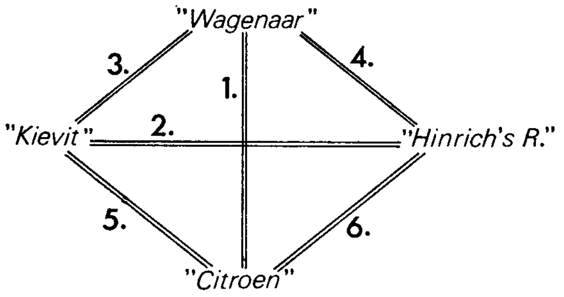
About the same applies to 'red veins wing', at least in the first years' F_1- and F_2-analysis. Beginning now at the other end, 'clear veins in the whole wing', gradation goes via 'faint' or 'very faint' in the whole wing; 'clear in lower half' and 'faint' or 'very faint'; 'trace in upper half?', to 'some bluish colourless veins in young buds' and 'quite without' in flowers and buds (= –). No simple classification possible, nowhere a clear separation. Because of these difficulties it was a very long way to the rather much simplified scheme of figure 9, which nevertheless, as far as my experience goes, correctly reflects the main relations between flower- and seedcoat colour.

Fruit colour appeared to be somewhat more simple: 'intense violet red', 'pink', 'very faint colour', with index 1–10 (depending upon the roughly valued mean colour-covered part of a few fruits being in the best judgeable stage, that of beginning ripening), and purely green (= –). Too young fruits are not yet fully coloured, in too ripe ones the colour has faded or quite disappeared.

The scoring of fruit colour was done together with the harvesting of a handful (or less) preferably ripe fruits. The paper bags for the fruits were, with the help of the lists, all numbered and family-wise bundled before the beginning of the harvest, because of the great differences in earliness. Before putting the harvested pods into the bags, fruit colour and some other characters (earliness, size) were noted on them. During autumn and winter, when the pods of each bag were shelled, fruit- and seedcoat colour could easily be compared and both characters (like the other ones) filled in upon the lists, so that all wished character-combinations later easily could be tabulated. The results of these numerous tabulations are discussed in the following chapters, III–V.

III. THE FIRST GROUP OF DIALLEL CROSSES BETWEEN FOUR VARIETIES; PLEIOTROPIC ACTIONS OF C-C^m-C^{st} (CROSSES 1–6).

flower: pale lilac
seedcoat: shiny pale greenish yellow dark pattern, CC



seedcoat:
shiny red mottled, C^mC^m
flower: pale lilac

seedcoat:
shiny red striped,
$C^{st}C^{st}$
flower: pale lilac

seedcoat: greenish yellow dark pattern
without brown hilumring, CC
flower: pale lilac

Figure 1. Scheme of the first diallelic cross between four varieties.

From the description of flower- and seedcoat colour above it already follows that segregations will be rather simple. All four varieties have totally coloured seed: $PPTT$. With respect to the 'complex locus' C both one-coloured (unpatterned) varieties are of dark pattern type, CC. The two other ones are resp. red mottled, C^mC^m, and red striped, $C^{st}C^{st}$. As regards the remaining two colour genes, 'Citroen', without brown hilumring, is $ddjj$, while the three other varieties all possess the 'shine factor', JJ, and 'Wagenaar' in addition, as will appear from its F_2 with 'Citroen', cryptomerically the 'hilumring factor', DD. As shiny pale greenish yellow (Wagenaar) and also shiny red mottled or striped (Kievit resp. Hinrich's Riesen) are the most recessive colours within the shiny and after-darkening group, their genotype for the three modifying genes is $ggbbV^{lae}V^{lae}$, while 'Citroen', as will appear, cryptomerically possesses the 'yellowbrown factor', GG. And as in none of the parents, nor in any F_2, recessive red colour appears, the four genotypes (in ***bold letters*** the genes for which segregation can occur) are as follows:

a. 'Wagenaar': $PPTTC\ C\ \boldsymbol{DDJJg\,g}\,bbV^{lae}V^{lae}RkRk$
b. 'Citroen': $PPTTC\ C\ \boldsymbol{d\ d\,j\,jGG}bbV^{lae}V^{lae}RkRk$
c. 'Kievit': $PPTTC^{m}C^{m}\ \boldsymbol{d\ dJJg\,g}\,bbV^{lae}V^{lae}RkRk$
d. 'Hinr.R.': $PPTTC^{st}C^{st}\ \boldsymbol{d\ dJJg\,g}\,bbV^{lae}V^{lae}RkRk$

Because of the strong (pleiotropic?) correlation between seedcoat-genotype at the *C* 'locus' and 'accompanying colours' of seedling, flower and fruit it may be valuable to present here the colours of the four varieties:

	cotyl.	*hypoc.*	*flower*	*tip standard*	*veins wing*	*fruit col.*	*seedcoat colour*
a. 'Wagenaar':	pink 4	pink 3	pale lilac	−red tip	−red v.	pink 2	shiny green. yell. d.p.
b. 'Citroen':	pink 2?	pink 3	pale lilac	−red tip	−red v.	pink 1	gr. yell. d.p.−hilumring
c. 'Kievit':	green	green	pale lilac	−red tip	−red v.	pink 2	shiny red mottled
d. 'Hinr.R.':	pink 3.5	± green	pale lilac	+slight r.t.	−red v.	violet red 6	shiny red striped

Cross 1: 'Wagenaar 'with 'Citroen'

Seedcoat colour inheritance in this cross has been discussed extensively before (PRAKKEN, 1940, cross 4, p. 351–364 and PRAKKEN, 1970a, p. 17–21), but because of its importance for the present diallel complex the results will shortly be repeated. As seen from the genotypes above the F_1 genotype was $PPTTCC$-$\boldsymbol{DdJjGg}bbV^{lae}V^{lae}RkRk$. The colours of parents and F_1 were:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit*	*seedcoat*	*scheme*
'Wag.':	pink 4	pink 3	pale lilac	−red tip	−red v.w.	pink 2	green yell. d.p.	**VIII-1**
'Citr.':	pink 2?	pink 3	pale lilac	−red tip	−red v.w.	pink 1	gr.yell. d.p.−h.r.	**II-2**
$F_1(CC)$:	pink 3	pink 1?	pale lilac	−red tip	−red v.w.	pink 1	yellowbrown	**VIII-2**

In discussing F_2, flower colour, tip standard and veins wing can be left out of discussion: they showed no segregation. The low hypocotyl value of F_1 may be the effect of hot house condition or too early observation, cf. F_2 below.

The shiny yellowbrown seedcoat of F_1 (scheme: **VIII–2**) immediately tells that 'Citroen' really possesses, cryptomerically, the 'yellowbrown factor' *G*. In the F_2-families (1508–1511'37 and 1646–1647'38), together 582 plants, 41 were without a brown hilumring, immediately suggesting that 'Wagenaar' possesses *both* colour genes that produce a brown hilumring, viz. the 'shine factor' *J* and, cryptomerically, the 'hilumring factor' *D*. F_1-genotype therefore is *(CC)DdJjGg*, and F_2 shows 1/16 *ddjj* (41, exp. 36.4).

Because of colour-gene genotype (*CC*) *DdJj*, four *rows* or colour-groups will be represented in F_2, viz. **II**, **IV**, **VI** and **VIII**, and because of the F_1-genotype $Gg(bbV^{lae}V^{lae})$ for the modifying genes, colour *columns* **1** and **2** only. See table 1, in which the actually found and the expected F_2-numbers are given. This F_2-analysis was completely confirmed by F_3 (PRAKKEN, 1940, 1970).

Looking at this F_2-table and at the scheme p. 82, it becomes clear that the intensity of phenotypic action of the modifying 'yellowbrown factor' *G* much depends on the genotype for *D–d* and *J–j*:
a. In ***(CC)ddjj***, mat dark pattern without hilumring, the influence of *G* is *hardly perceptible*: **II–1** → **II–2**.

b. In *(CC)D.jj*, mat dark pattern with brown hilumring, the influence of *G* is clear but rather small, *G* producing a yellowbrown *caruncula stripe*, at the same time slightly changing greenish yellow into (greenish) yellow or lemon colour: **IV–1** → **IV–2.**

c. In $(CC)^{dd}_{D.}J.$, shiny dark pattern with hilumring, *G* produces *its full conspicuous effect*, changing the shiny pale greenish yellow (shamois plus canary yellow) of 'Wagenaar'–type into yellowbrown: **VI–1** → **VI–2** and **VIII–1** → **VIII–2.**

TABLE 1. F_2-segregation in cross 1, 'Wagenaar' with 'Citroen'. Compare with the scheme p. 82, and exp. with PRAKKEN 1970, fig. 1, p. 19.

row **II**	: (CC)ddjj	*gg* = pale green. yellow without hilumring (column **1**) *G.* = pale (green.) yellow without hilumring (column **2**)	41 (exp. 36.4)
row **IV**	: (CC)D.jj	*gg* = pale green. yellow with brown h.r.. . . (column **1**)	30 (exp. 27.3)
		G. = pale (green.) yellow with h.r. and car.str. (column **2**)	85 (exp. 81.8)
row **VI** and **VIII**	: $(CC)^{dd}_{D.}J.\,gg$	= pale shiny green. yellow with hilumring (column **1**)	108 (exp. 109.1)
row **IV** and **VIII**	: $(CC)^{dd}_{D.}J.G.$	= shiny yellowbrown with hilumring . . (column **2**)	318 (exp. 327.4)
		total:	582

With a few words the anthocyanin colour in F_2-seedlings and fruits will be mentioned, giving as an example the values noted in fam. 1508'37:

	cotyledons						*hypocotyl*							*fruits*			
quantity pink	0	1	2	3	4	5	0	1	2	3	4	5	6	0	1	2	3
number of plants:	11?	30	25	14	18	1	8?	34	26	11	16	3	1	25?	37	7	1
mean value:	2.0 (other F_2-fam. 2–3)						2.0 (other F_2 fam. 2–3)							0.8			

Most plants gathered here under 0 were scored as 'green?', General experience in this cross, F_3 included, showed that *probably none of the* F_2*-seedlings was purely green*, i.e. all these *CC*-plants had some pink anthocyanin in cotyledons and (or) hypocotyl. As already mentioned all plants showed pale lilac flowers without red tip and without red veins wing.

Cross 2: Kievit with Hinrich's Riesen

Both parents in this cross have a shiny red patterned seedcoat with a brown hilumring (*JJ*), being shiny red mottled (C^mC^m) resp. shiny red striped ($C^{st}C^{st}$) upon a shiny and very pale buff background, about like **V–1** in the scheme. Their only genotypic difference precisely is C^m-C^{st}, the F_1-genotype being:

$$PPTTC^mC^{st}ddJJggbbV^{lae}V^{lae}RkRk$$

(for the constitution *dd* cf. crosses 5 and 6, with 'Citroen'). Therefore the present cross offers a simple opportunity for analyzing the pleiotropic actions of both alleles. The colours of both parents and F_1 are given below:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit*	*seedcoat*
'Kievit':	green	green	pale l.	—red tip	—red v.	pink 2	shiny red mottled
'Hinr.R.':	pink 3.5	± green	pale l.	+slight r.t.	—red v.	violet red 6	shiny red striped
$F_1(C^mC^{st})$:	green ?	± green	pale l.	+ very sl.r.t.	—red v.	violet red 5	shiny red mottled (slightly interm.)
	cf. F_2						

As the table above shows, the difference in 'accompanying colours' (*a.* cotyledons, *b.* hypocotyl, *c.* tip standard and *d.* fruit or pod colour) between 'Kievit' (C^mC^m) and 'Hinrich's Riesen' ($C^{st}C^{st}$) is rather extreme: low in C^mC^m and high in $C^{st}C^{st}$, especially the intense pod colour, violet red 6. The colours in F_1, C^mC^{st} (but one family of three plants), were intermediate or subdominant: *a* the 'green?' of cotyledons probable depended upon hot house influence, cf. F_2; *b* hypocotyl almost green; *c.* the red tip of standard still smaller than in 'Hinrich's Riesen' and *d.* fruit colour almost as intense as in 'Hinrich's Riesen', violet red 5; the dominance-relation for seedcoat pattern was *just the inverse*, F_1-seed being mottled almost as 'Kievit', but the pale buff spots somewhat greater, see fig.2.

In F_2 the homozygously striped seedcoat, $C^{st}C^{st}$, is immediately recognizable, while with some difficulty, and in very dubious cases with the help of F_3, the heterozygously mottled seeds (= plants, C^mC^{st}) can be distinguished, with the help of their slightly greater pale spots, from the homozygously mottled ones, C^mC^m, *cf.* again figure 2. For the three F_2-families the ultimate result, i.e. after studying F_3, cf. below, is given in table 2: a rather bad 1:2:1 ratio.

TABLE 2. F_2-segregation of the cross 'Kievit' with 'Hinr. Riesen'

	homoz. mottled (C^mC^m)	*heteroz. mottled* (C^mC^{st})	*striped* ($C^{st}C^{st}$)	*total*
fam. 1521'37:	11	31	28	70
fam. 1522'37:	16	29	15	60
fam. 1523'37:	18	31	21	70
	—	—	—	—
total:	45	91	64	200
expected:	50	100	50	

The table below shows the 'accompanying colours' of the three F_2-genotypes. The general agreement of the average values with those of parents and F_1 and the lack of clear recombinations shows, together with F_3 and with the following crosses, that they really are 'accompanying colours', i.e. that (preliminary) they can be considered as 'pleiotropic actions' of the C-alleles (the very few recombinations in some of the remaining crosses will be discussed in a following article, especially bearing on this 'complex locus' C). The average value's in C^mC^{st} all are between those of C^mC^m and $C^{st}C^{st}$:

seedcoat	*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*
C^mC^m(homoz.m.):	green	green	–red tip	pink 1.5(0–2)
$C^{st}C^{st}$(homoz.str.):	pink 3.3(1–5)	pink 0.6(0–2)	few: –r.t. most: +r.t.	violet red 5.6(4–7)
C^mC^{st} (heteroz.m.):	pink 1.8(0–4)	pink 0.2(0–1)	most: —r.t. few: +r.t.	violet red 4.8(3–6)

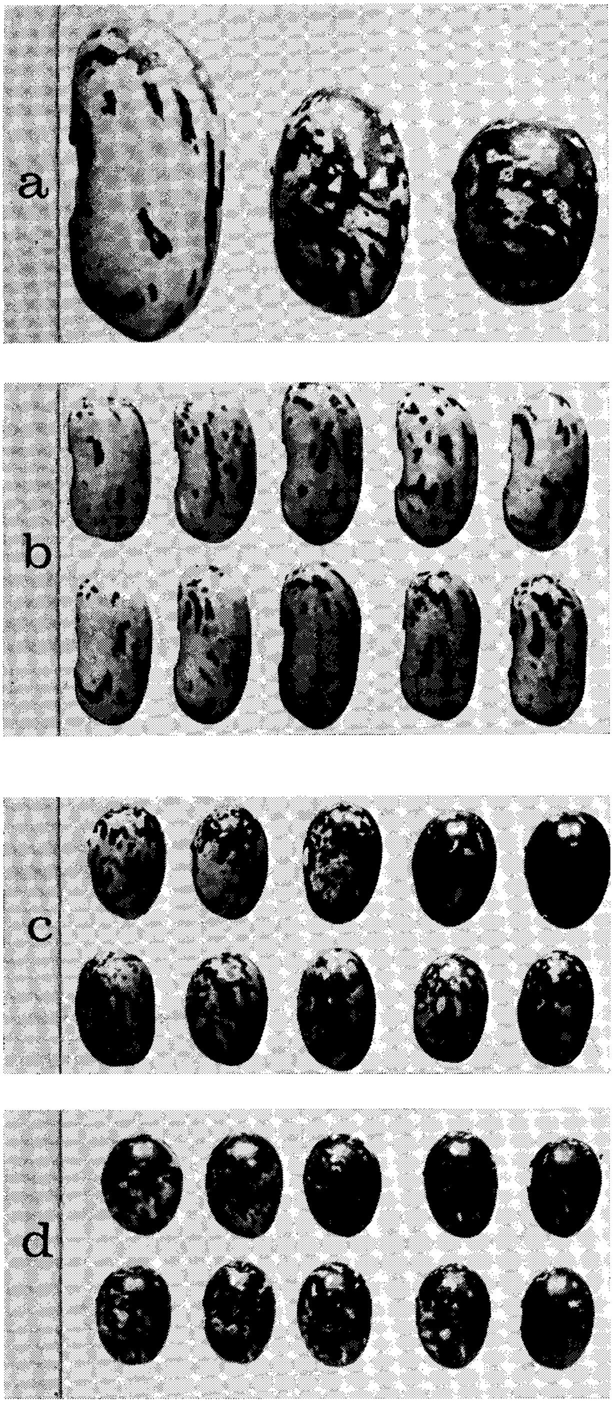


FIG. 2. Cross nr. 2, 'Kievit' with 'Hinrich's Riesen'.
a. One typical seed of 'Hinr. R.' ($C^{st}C^{st}$), F_1 ($C^{m}C^{st}$) and 'Kievit' ($C^{m}C^{m}$).
b. Five seeds from two plants of 'Hinrich's Riesen' ($C^{st}C^{st}$).
c. Five seeds from two plants of F_2-heterozygotes ($C^{m}C^{st}$).
d. Five seeds from two plants of 'Kievit' ($C^{m}C^{m}$).

The F_2-conclusion that *seedcoat type and 'accompanying colours' stay together*, was confirmed by the analysis of 23 F_3-families, 1837–1859'38:

a. Four F_3-families from clearly homozygously mottled F_2-plants gave typically mottled C^mC^m-plants only, all plants with totally green seedling, without any red tip standard and the fruits scored as pink 1–4, i.e. precisely the 'Kievit' characters, only fruit colour slightly more.

b. Four F_3-families from typically striped-seeded $C^{st}C^{st}$ F_2-plants gave striped-seeded $C^{st}C^{st}$ F_3-plants only, with accompanying characters as 'Hinrich's Riesen' or scored slightly lower:

number fam.	*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*
1837'38:	pink 3.0(1–4)	green or gr.?	—r.t. or +slight.	all ripe
1838'38:	pink 3.5(2–6)	green or gr.?	all +slight r.t.	violet red 5.0(4–6)
1839'38:	pink 2.4(2–3)	green or gr.?	—r.t. or + slight.	violet red 5.5(5–6)
1840'38:	pink 2.5(0–4)	green or gr.?	past out of flower	violet red 5.2(5–6)

c. Six F_3-families from easily recognizable heterozygously mottled C^mC^{st} F_2-plants all showed the expected 1:2:1 segregation. At that time (1938) it was possible to identify practically every C^mC^{st}-plant by their having, at least in the extreme seeds, greater shiny pale buff background spots. Together the six families gave:

$$18\ C^mC^m + 39\ C^mC^{st} + 22\ C^{st}C^{st}\ (\text{exp.: } 19.2 + 38.5 + 19.2).$$

Accompanying colours of all these F_3-plants were as to be expected, save for one, that because of spot size was classified as C^mC^m but that showed slightly pink in the cotyledons, a very slight red tip and fruit colour intense violet red 5. Offspring of it was bred and the F_4-family segregated and gave:

$$2\ C^mC^m + 10\ C^mC^{st} + 4\ C^{st}C^{st}\ (\text{exp.: } 4 + 8 + 4),$$

all showing seedling colour, tip standard and fruit colour quite as expected. This F_3-mother plant was about the only C^mC^{st}-plant that, in 1938 and later, with the help of spot size only, was misjudged as a homozygous C^mC^m-plant.

d. At last nine F_3-families, each of 15 plants, were bred from 'mottled' F_2-plants that (in 1937) could not, with the help of spot size only, with certainty be classified as C^mC^m or C^mC^{st}. Seven of these families, their seven F_2-mother plants having purely green seedlings, no red tip standard and green or slightly pink fruit, gave C^mC^m plants only, all with same accompanying colours. The remaining two F_3-families, however, segregated and together they gave:

$$4\ C^mC^m + 14\ C^mC^{st} + 4\ C^{st}C^{st}\ (\text{exp. } 5.5 + 11 + 5.5),$$

all F_3-plants of the three types with their 'normal' accompanying colours. The two F_2-mother plants concerned were precisely those with some 'suspecting' colours, both having the cotyledons scored as *pink*-2(hypocotyl as green and red tip not discovered), the fruit colour of one being violet red-5, the fruits of the other being ripe!

The final *conclusions* of cross 2, 'Kievit' with 'Hinrich's Riesen' therefore are:

1. Monofactorial segregation for C^m-C^{st} (LAMPRECHT: R^{ma}-R^{st})
2. Mottling is incompletely dominant over striping, the pale buff angular bacground spots of C^mC^{st} on the average and *especially in the more extreme seeds being greater and more drawn out* than those of C^mC^m (cf. fig. 2).
3. All 'accompanying colours' discussed (cotyledons, hypocotyl, tip standard and ripening fruit) show complete correlation with C^m-C^{st}, C^mC^{st} being more or less intermediate (to remark: red mottling of the seedcoat in C^mC^m is, as mentioned under 2, subdominant over the red striping in $C^{st}C^{st}$; *quite the reverse* with fruit colour: the intense violet red 6 of $C^{st}C^{st}$ is in C^mC^{st} subdominant over the slight pink of C^mC^m).

Cross 3: '*Wagenaar*' *with* '*Kievit*'.

As will be clear from foregoing discussion and descriptions, this cross between shiny pale greenish yellow dark pattern 'Wagenaar' (scheme: **VIII-1**) and shiny red mottled 'Kievit' is heterozygous for the 'complex locus' *C* only:

'Wagenaar': $PPTTC\ C\ \ DD\ JJggbbV^{lae}V^{lae}RkRk$
'Kievit': $PPTTC^mC^m(d\,d)JJggbbV^{lae}V^{lae}RkRk$

Therefore, as in cross 2, a very simple F_1-situation: heterozygous CC^m. The colour characters of both parents and of F_1 are tabulated below (those between square brackets need no further discussion):

	cotyl.	*hypoc.*	[*flower*	*tip stand*	*veins wing*]	*fruit*	*seedcoat*
'Wagenaar':	pink 4	pink 3	pale l.	—red t.	—red v.w.	pink 2	green.yell. d.p.
'Kievit':	green	green	pale l.	—red t.	—red v.w.	pink 2	red mottled
$F_1(CC^m)$:	pink 2	green (?)	pale l.	—red t.	—red v.w.	pink 1 à 2	double mottled

Reciprocal F_1-families were bred 1936–1938. As in some other cases there existed, sometimes very clear, *a difference in cotyledon colour between the reciprocal crosses*, in the sense that anthocyanine colour was less when the variety with green cotyledons was the mother, but data are *not quite consistent* and will not be discussed. Never any (other) difference between reciprocals was found. Germ plant colour of F_1 was intermediate, cf. with the three F_2-colour types below.

The seedcoat colour upon the F_1-plants is very important. In pattern and colours it shows the for CC^m-plants so well known 'double mottled' i.e. *three-coloured type*, to be described as follows:

1. '*main colour*', though much 'covered up' by red mottling, is the shiny pale greenish yellow dark pattern colour of the 'Wagenaar' parent;
2. '*red mottling*', as in the 'Kievit' parent, is over the greater part of this greenish yellow 'main colour', in at least *two intensities* (as really also in 'Kievit' itself), viz.
   a. an intense '*non diluted red*', not changed in tinge by the 'underlying' main colour, and
   b. a less intense '*diluted red*', with the underlying or intermingled (no anatomical analyses are alas available) greenish yellow colour translucing,

but nevertheless giving the impression of red; 'undiluted' and 'diluted red' together are somewhat less extensive than in homozygous C^mC^m;

3. '*pale buff background spots*' are present in the greenish yellow main colour (or in the red), rather inconspicuous and of about the same colour and size as in the red mottled 'Kievit' parent or as in ever-segregating Cc^u genotypes.

The three- (or four-) coloured pattern and the extension or overlapping of colours are difficult to describe accurately, and as a matter of fact the general appearance of seeds from one plant is *often very variable*.

In F_2, as to be expected, only the seedcoat types of parents and F_1 occur, in a ratio mostly not too much different from 1:2:1, see table 3.

TABLE 3. F_2-segregation of the cross 'Wagenaar' with 'Kievit' (d. p. = dark pattern).

	green.yellow d.p. (CC) (Wagenaar-type)	*double mottled* (CC^m) (F_1-type)	*red mottled* (C^mC^m) (Kievit-type)	*total*
fam. 1499'37:	48	55	40	143
fam. 1500'37:	40	60	34	134
fam. 1501'37:	27	62	22	111
fam. 1502'37:	22	49	28	99
fam. 1642'38:	10	21	7	38
total:	147 (exp. 131.2)	247 (exp. 262.5)	131 (exp. 131.2)	525

The 'accompanying colours' of the three F_2 seedcoat types again were, as in cross 2, about the same as in both parents and F_1, only the hypocotyl colour of CC being scored markedly lower than that of 'Wagenaar'. As the colour differences between the five F_2-families of table 3 were small, the mean colour values and width of variation are given for all families together:

seedcoat (all shiny)	*cotyledons*	*hypocotyl*	*fruit colour*
CC (pale green.yell. d.p.):	pink 3.4 (1–6)	pink 1.4 (0–4)	pink 1.5 (1–3)
C^mC^m (red mottled):	green (0)	green (0)	pink 1.9 (1–4)
CC_m (double mottled):	pink 1.5(0–5)	pink 0.3 (0–2)	pink 2.1 (1–5)

The F_2-segregation being clear and the 'accompanying colours' too, the number of F_2-plants taken to produce F_3 families was as low as 11 (families 1699–1709'38).

a. Three pale greenish yellow seeded CC F_2-plants gave together 24 F_3-plants, all with pale greenish yellow seedcoat, with cotyledons pink 3.9 (1–7), hypocotyl pink 3.2 (1–6; both seedling values, esp. hypocotyl, much higher then the average CC F_2-value), fruit colour not scored.

b. Three red mottled seeded C^mC^m F_2-plants also gave 24 F_3-plants with same seedcoat type and all with cotyledons and hypocotyl purely green, fruit colour about pink 2.

c. Five double mottled CC^m F_2-plants gave as expected segregating F_3-families, together:

	11 CC	28 CC^m	18 C^mC^m (exp. 14.2 + 28.5 + 14.2)
cotyledons:	pink 4.3 (1–7)	pink 2.1 (0–5)	pure green
hypocotyl:	pink 2.9 (0–4)	pink 1.5 (0–3)	pure green

fruit colour: mostly not scored

The final *conclusions* from the cross between 'Wagenaar' and 'Kievit' therefore are:

1. Segregation for the complex locus C only: C-C^m.
2. The heterozygote CC^m is 'double mottled', i.e. three- or better four-coloured: *a.* shiny greenish yellow dark pattern '*main colour*', *b.* this main colour is for the greater part covered by a '*red mottling*' in at least two intensities and *c.* in the main colour (or in the red) are '*pale buff background spots*' like those in ever-segregating Cc^u-types.
3. The accompanying colours, as far as different (cotyledons and hypocotyl), show complete correlation with the alleles C and C^m, CC having the most pink colour, C^mC^m being pure green and CC^m seedlings more or less intermediate.

Cross 4: 'Wagenaar' with Hinrich's Riesen'.

This cross, between shiny pale yellow dark pattern 'Wagenaar' (scheme: **VIII–1**) and shiny red striped 'Hinrich's Riesen', forms a very close parallel to cross 3, heterozygosity of F_1 again being at the complex locus C only, now CC^{st} instead of CC^m:

'Wagenaar': $PPTT\ C\ \ C\ \ \ DD\ JJggbbV^{lae}V^{lae}RkRk$
'Hinr. R.': $PPTT\ C^{st}C^{st}(d\ d)JJggbbV^{lae}V^{lae}RkRk$

The colour characters of parents and F_1 are tabulated below:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit col.*	*seedccat*
'Wagenaar':	pink 4	pink 3	pale l.	—red tip	—red v.	pink 2	green.yell.d.p.
'Hinr.R.':	pink 3.5	± green	pale l.	+ slight r.t.	—red v.	violet red 6	red striped
F_1 (CC^{st}):	pink 3 à 5	± green	pale l.	+ very sl.r.t.	—red v.	violet red 5	striped and mottled

From this table it appears that anthocyanin colour in the F_1-cotyledons is the same as in both parents; for F_1-hypocotyl cf. the values in F_2 CC^{st}-plants, table 5 below: intermediate. Flower and veins wing can be left out of consideration. The red tip of standard in F_1 is, as in cross 2 between 'Kievit' and 'Hinrich's R.', slighter than in the 'Hinrich's R.' parent, i.e. intermediate. Fruit colour, violet red 6 in the 'Hinrich's R.' parent is, again as in cross 2, subdominant: F_1 violet red 5.

The seedcoat of F_1 CC^{st}-plants is, as that of CC^m in cross 3, three- (or four-) coloured, but now not 'double mottled' but 'mottled and striped':

1. '*main colour*', the greenish yellow dark pattern colour of the 'Wagenaar' parent, now real main colour because the
2. '*red striping*' over it is but very partly 'covering' it. As with the red mottling of CC^m the red striping of CC^{st} also shows two 'intensities':
   a. intense '*non-diluted red*' and
   b. less intense '*diluted red*', together in extension slightly less than the stripes of $C^{st}C^{st}$-seed;
3. '*pale buff background spots*' are present in the greenish yellow 'main colour',

with quite the same size, number and form as in F_1 CC^m of cross 3, i.e. also here remembering of the ever-segregating mottling of Cc^u genotypes.

In F_2 of cross no 4, as in cross 3, a simple monofactorial segregation seemed to occur (safe for two deviating plants that not will be discussed in the present article), the three normal seedcoat types in colour and pattern being like 'Wagenaar', 'Hinrich's Riesen' and F_1, in the ratio: 1:2:1, see table 4.

TABLE 4. F_2-segregation of the cross 'Wagenaar' with 'Hinr. Riesen'. Two of the mottled-seeded plants were without red striping, see column 'deviating types'.

	green.yell. d.p. (Wag. type, *CC*)	*striped and mottled* (F_1-type, CC^{st})	*red striped* (Hinr.R. type, $C^{st}C^{st}$)	*'deviating types'*	*total* ('normals')
fam. 1503'37	18	38	20	(1)	76
fam. 1504'37	16	39	20	0	75
fam. 1505'37	30	45	11	0	86
fam. 1506'37	27	44	19	(1)	90
fam. 1507'37	16	29	14	0	59
fam. 1643'38	12	16	15	0	43
fam. 1644'38	4	16	10	0	30
fam. 1645'38	11	22	13	0	46
	—	—	—	—	—
total	134 (exp. 126.2)	249 (exp. 252.5)	122 (exp. 126.2)	(2)	505 (+ 2 dev.)

For one time the mean value and width of variation of the accompanying colours will, for F_2-families 1503–1507'37, be given completely, see table 5, from which table it becomes very clear that for the F_2 CC^{st}-groups the same intermediateness resp. subdominance exists as for F_1. In the F_2-families 1643–1645'38 this general trend was quite the same, with the peculiarity, however, that the pink-values were scored as rather lower, especially for the hypocotyl of the $C^{st}C^{st}$ genotype (this latter value, see table 5, was unusual high in F_2-1937, viz. averages from 0.1 tot 1.1, against the usual green or almost green). An explanation might be that up to 1937 the scale 1–5 was used and from 1938 scale 1–10, i.e. that all values of before 1938 had to be doubled. Other possibilities however, e.g. weather-influence or genetical differences, exist.

In this cross too, as in cross 3, the number of F_3-families was very small: 1710–1722'38. Offspring of the three normal F_2-types behaved as expected, for seedcoat colour and mostly for the accompanying colour characters too. Noteworthy was that in the three F_3-families from $C^{st}C^{st}$ F_2-plants the pink hypocotyl value again was slightly higher than usual, while the red tip was scored as very small, a few plants even as '-rep tip', but never a whole $C^{st}C^{st}$-family. In some of the crosses of the second group (chapter IV) genetic variability in size of red tip appeared very great.

The last two F_3-families came from the two plants with deviating seedcoat (and colour characters). Leaving them out of consideration the *conclusions* from the cross 'Wagenaar' with 'Hinrich's Riesen' are:

TABLE 5. Accompanying colours of the three genotypes CC, CC^{st} and $C^{st}C^{st}$ in the five F_2-families 1937 of the cross 'Wagenaar' with 'Hinr. Riesen'.

	nr. F_2-fam,	*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*
dark pattern like 'Wag.' (CC)	1503'37	pink 4.4 (2–6)	pink 2.9 (1–6)	all–red tip	pink 1.5 (0–2)
	1504'37	pink 4.5 (2–6)	pink 3.0 (1–5)	all–red tip	pink 1.5 (1–3)
	1505'37	pink 4.3 (2–6)	pink 2.6 (1–4)	all–red tip	pink 2.1 (1–4)
	1506'37	pink 3.8 (2–6)	pink 2.2 (0–5)	all–red tip	pink 1.3 (1–2)
	1507'37	pink 4.0 (1–6)	pink 2.0 (0–5)	all–red tip	pink 1.0 (1 or ripe)
str. and mottl. like F_1 (CC^{st})	1503'37	pink 3.8 (1–6)	pink 2.0 (1–4)	most–, few trace r.t.	vi. red 5.1 (4–6)
	1504'37	pink 3.9 (2–6)	pink 2.8 (1–6)	most–, few trace r.t.	vi. red 4.9 (4–6)
	1505'37	pink 3.7 (1–6)	pink 1.8 (0–5)	most–, few trace r.t.	vi. red 5.0 (4–6)
	1506'37	pink 3.2 (0?–6)	pink 1.4 (0–4)	most–, few trace r.t.	vi. red 4.9 (4–6)
	1507'37	pink 2.8 (1–4)	pink 1.4 (0–4)	most–, few trace r.t.	vi. red 5.0 (5, one 6)
red striped like 'Hinr.R' ($C^{st}C^{st}$)	1503'37	pink 3.3 (1–5)	pink 0.6 (0–2)	few–, most slight r.t.	vi. red 5.6 (5–6)
	1504'37	pink 2.3 (1–4)	pink 1.1 (0–2)	few–, most slight r.t.	vi. red 5.5 (5–6)
	1505'37	pink 2.4 (1–4)	pink 0.6 (0–2)	few–, most slight r.t.	vi. red 5.4 (5–6)
	1506'37	pink 2.0 (0–5)	pink 0.4 (0–2)	few–, most slight r.t.	vi. red 5.5 (5–6)
	1507'37	pink 2.1 (0–4)	pink 0.1 (0–1)	few–, most slight r.t.	vi. red 5.8 (5–6)

1. Segregation for the 'complex locus' C only: C-C^{st}.
2. The heterozygote CC^{st} is 'striped and mottled', i.e. three- or better four-coloured: *a.* shiny greenish yellow dark pattern colour as 'Wagenaar', here, more than in CC^m of cross 3, the real *'main colour'*, *b. 'red striping'* in at least two intensities over it, and *c.* in the main colour *'pale buff background spots'* as in CC^m or Cc^u.
3. The accompanying colours, as far as different (here mainly tip standard and fruit colour), show complete correlation with the alleles C and C^{st}, CC having no red tip standard and a slightly pale pink fruit, $C^{st}C^{st}$ (mostly) showing a slight red tip and intense 'violet red 6' fruit, CC^{st} being intermediate resp. subdominant: (often) very slight red tip and intense 'violet red 5' fruit. Seedlings of both homozygous types show pink, the hypocotyl of $C^{st}C^{st}$ very little.

Cross 5: 'Citroen' with 'Kievit'.

Compared with cross 3, 'Wagenaar' with 'Kievit', the 'Wagenaar' parent, $CCDDJJgg$, is replaced by 'Citroen', pale greenish yellow without brown hilumring and, cryptomerially, with the yellowbrown factor G: $CCddjjGG$ (scheme: II–2):

'Citroen': $PPTTC\ C\ \ dd\ \ jjGGbbV^{lae}V^{lae}RkRk$
'Kievit': $PPTTC^mC^m(dd)JJgg\ bbV^{lae}V^{lae}RkRk$
$F_1(CC^m)$: $PPTTC\ \ C^m\ \ dd\ \ Jj\ Gg\ bbV^{lae}V^{lae}RkRk$

In the colour table for parents and F_1 the pale lilac flower colour, lacking red intensification tip standard and lacking red veins wing are here (not in the observations) from the beginning left out (h.r. = hilumring):

	cotyledons	*hypocotyl*	*fruit colour*	*seedcoat colour*
'Citroen':	pink 2?	pink 3?	pink about 1	pale green.yell. dark p., –h.r.
'Kievit':	green	green	pink about 1	shiny red mottled, +h.r.
F_1 (CC^m):	green (?)	green (?)	pink 1 à 2	shiny double mottled, +h.r.
	cf. with CC^m in F_2			

Seedling colour of 'Citroen' is not precisely known, that of F_1 probably shows hot-house influence.

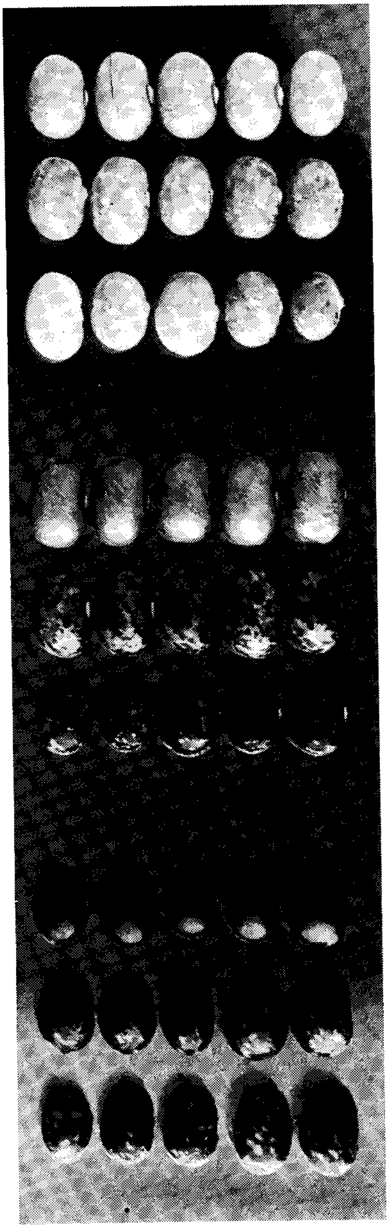
The 'double mottled' seedcoat colour of F_1 at once reveals, like the yellowbrown F_1-colour in cross 1, that in 'Citroen' the 'yellowbrown factor' G is cryptomerically present, for its three (or four) colours are:

1. its *'main colour'* is shiny yellowbrown (as dark pattern colour **VI–2** or **VIII–2** in the scheme), and not the greenish yellow 'Wagenaar' colour (**VI–1** or **VIII–1**) as in cross 3;

2. *'orangered mottling'* is over the greater part of it, as usual in two 'densities'
   a. *non-diluted,* really giving the impression of (orange)red,
   b. *diluted,* i.e. with the underlying on probably better the intermingled 'main colour' translucing and therefore giving more the impression of yellowbrown,

3. *'pale buff background spots'*, precisely as in crosses 3 and 4, are in the main colour (or in the orange red mottling), i.e. these spots are unchanged by the

FIG. 3. Cross 5, 'Citroen with 'Kievit', F_2.
Centre: the nine F_2-phenotypes, each represented by five seeds from one plant.
To the left: the F_2-numbers found and expected.
To the right: seedcoat description and genotype(s); parents and F_2 indicated with **bold letter**. Further explanation see text.



99 (exp. $^1/_4$ 93,5)	29 (exp. 23.4)	*a.* pale greenish yellow dark pattern, without hilumring (**II–1**, *CC dd jj gg*, and **II–2**, *CC dd jj G.* = **'Citroen'**).
	42 (exp. 46.8)	*b.* double mottled, without hilumring (*CC^m* etc., 'main colour': pale greenish yellow, as above).
	28 (exp. 23.4)	*c.* pale lilac red mottled upon white, without hilumring (*C^mC^m dd jj gg* and *C^mC^m dd jj G.*).
69 (exp. $^3/_{16}$ 70.1)	12 (exp. 17.5)	*a.* shiny green.yellow dark pattern, with hilumring (**VI–1**, *CC dd J. gg*, slightly afterdarkened).
	38 (exp. 35.1)	*b.* shiny double mottled, with hilumring (*CC^m* etc., 'main colour': shiny green. yellow).
	19 (exp. 17.5)	*c.* shiny red mottled, with hilumring (*C^mC^m dd J. gg* = **'Kievit'**).
206 (exp. $^9/_{16}$ = 210.4)	61 (exp. 52.6)	*a.* shiny yellowbrown dark pattern, with hilumring (**VI–2**, *CC dd J. G.*).
	97 (exp. 105.2)	*b.* shiny double mottled, with hilumring (*CC^m dd J. G.*, 'main colour'; yellowbrown = **F_1**).
	48 (exp. 52.6)	*c.* shiny orange red mottled, with hilumring (*C^mC^m dd J. G.*).

total: 374 plants.

'yellow-brown factor' *G*, just as in the ever-segregating type Cc^u (*u* comes from *u*nchangeable).

Pattern, colours, the kind of dilution etc. are better recognizable then in cross 3 (*gg*), but as variable, and will not be discussed in detail; compare the F_2-types in fig. 3.

Four F_2-families were bred, 1524–1526'37 and 1655'38, each family showing the same *nine* seedcoat colour types, caused by the segregation for C-C^m, *J-j* (shine factor) and *G-g* (yellowbrown factor). No segregation for the 'hilumring factor pair' *D-d* occurred, which means that 'Kievit', like 'Citroen', was *dd*. The four families, 374 plants, are treated together, see fig. 3, were each row contains five seeds from one plant.

The nine types are in *three groups of three*. The upper row in each group is the *CC*-dark pattern type, the middle one the corresponding double mottled CC^m-type, the lower one the homozygously mottled C^mC^m.

The upper group of three rows (99 plants; exp. $\frac{1}{4}$ = 93.5) contains the mat types without a brown hilumring, *ddjj* (showing that 'Kievit' has the genotype *dd*); the group contains both *gg* and *G.*, indistinguishable however, for in these mat *jj*-types the 'yellowbrown factor' *G* has but a hardly perceptible influence, cf. p. 9–10.

The middle and lower group together represent the shiny (*dd*) *J.*-types, in which the 'yellowbrown factor' *G* exerts its full influence: middle group, (*dd*)*J.gg*, 69 plants (exp. 3/16 = 70.1) and lower group, (*dd*)*J.G.*, 206 plants (exp. 9/16 = 210.4). The numbers do not suggest any clear linkage between C-C^m, *J-j* and *G-g*.

Analysis of the accompanying colours in F_2 (and F_3) showed that these are *not at all influenced by J or G but exclusively depend upon* C-C^m. For the three F_2-families of 1937 the values (mean and variation) were:

seedcoat type	*cotyledons*	*hypocotyl*	*fruit colour*	*number of plants*	
CC (dark pattern):	pink 4.1 (1–7)	pink 4.6 (2–8)	few scored, all green or pink 1 and 2	77	total 276
C^mC^m (mottled):	green	green		130	
CC^m (double mottl.):	pink 1.7 (0–6)	pink 2.2 (2–5)		69	

This means, as in cross 3: most pink seedling colour in *CC*, intermediate in CC^m, C^mC^m completely green. The pink-values are unexpectedly high, so the values given for 'Citroen' (p. 19) are probably too low.

F_3 consisted of 49 families, 1860–1908'38, and as a whole it completely confirmed the F_2-analysis and the 'pleiotropic actions' as described above. F_3-families after shiny F_2-plants, fig. 3 middle group *ddJ.gg* and lower group *ddJ.G.*, gave no difficulties at all and will be left out here. Only F_2-plants belonging to the upper group, $ddjj\,\genfrac{}{}{0pt}{}{gg}{G}$ and their F_3-offspring, will shortly be discussed.

In this group without brown hilumring the influence of *G-g* is, as already mentioned, hardly or not at all visible. The hilumring-like dark ring in the pale greenish yellow *CC*-type of the upper row in figure 3 (scheme: **II–1** and **II–2**) is not a 'real hilumring' but a blue-green 'corona', just outside it. A corona is not always present but, in spite of much care, I never have been able to clearly trace its genetics. The C^mC^m-seeds of the third row are not really red mottled, but *pale lilac mottled on white background.* The three-coloured CC^m-type of the row between has pale greenish yellow 'main colour', with 'lilac mottling' over it and 'white background mottling' in it, the pale greenish yellow and the white often hard to distinguish.

Extension and intensity of the lilac mottling in both genotypes, $(ddjj)C^mC^m$ and $(ddjj)CC^m$, is extremely variable, both within and between plants. From eight homozygously pale lilac mottled C^mC^m F_2-plants, *with a decreasing visibility of the lilac mottling* (from 'all seeds mottled' to 'all seeds practically white'), F_3-families were bred, 1860–1867'38. Result: F_3-families varying from 'all plants with clearly mottled seeds', family 1860, to 'all plants practically white seeded', fam. 1867 (viz. 8 with 'pure white seeds' and 2 with 'white seeds, except for faint tiny dots or stripes in a few a them'). This means a clear correlation, i.e. genetic influence, but in spite of much scrutinizing, no gene(s) responsible for it could be sharply pointed out. In the shiny *J.*-types the variability of the red usually is less conspicuous.

The *conclusions* from cross number 5, 'Citroen' with 'Kievit' are:

1. The action on seedcoat pattern and colour of C-C^m and also the 'pleiotropic action' on the accompanying colours are quite the same as in cross number 3, 'Wagenaar' with 'Kievit' (C^mC^m: pure green seedlings).
2. Moreover the actions and interactions of 'shine factor' J and 'yellowbrown factor' G are analysed and found to fit in completely with the scheme p. 82.

Cross 6: 'Citroen' with 'Hinrich's Riesen'.

Just as cross 5 corresponds to 3, so corresponds cross 6 to cross 4. The only difference between 5 and 6 therefore is in the complex locus C: F_1 not CC^m, but CC^{st}:

'Citroen': $PPTTC\ \boldsymbol{C}\ \ dd\ \ \boldsymbol{jj}\ \boldsymbol{GG}bbV^{lae}V^{lae}RkRk$
'Hinr.R.': $PPTT\boldsymbol{C^{st}C^{st}}(dd)\boldsymbol{JJ}\ \boldsymbol{gg}\ bbV^{lae}V^{lae}RkRk$
$F_1(CC^{st})$: $PPTTC\ \ \boldsymbol{C^{st}}\ dd\ \ \boldsymbol{Jj}\ \boldsymbol{Gg}bbV^{lae}V^{lae}RkRk$

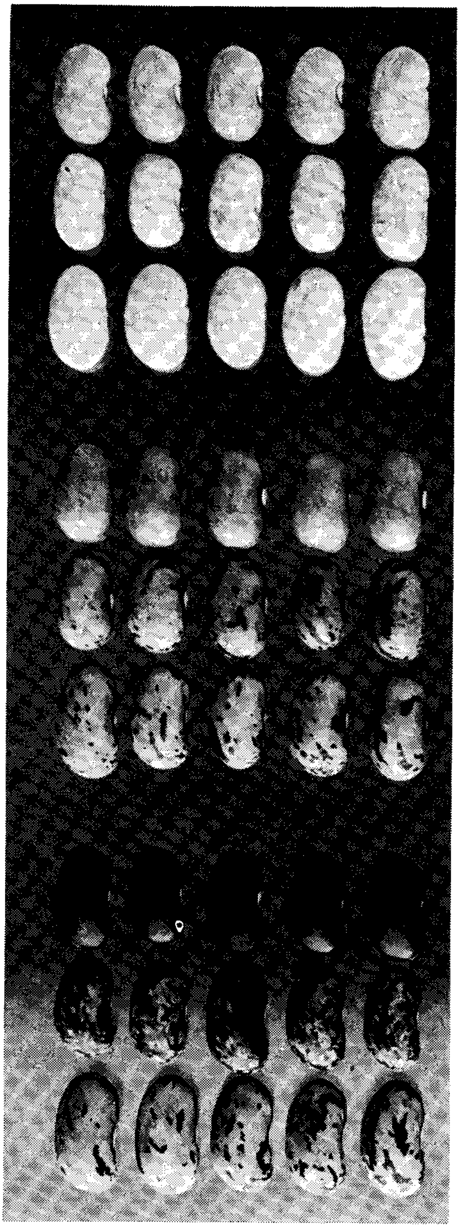
But two F_1-plants were bred ('lilac flower' and 'without red veins' are left out from description):

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*	*seedcoat colour*
'Citroen':	pink 2?	pink 3 ?	— red tip	pink 1	green. yell. d.p. −h.r.
'Hinr.R.':	pink 3 à 4	± green	+ slight r.t.	violet red 6	red striped +h.r.
$F_1(CC^{st})$:	pink 4	pink 2	+ very slight r.t.	violet red 5	str. and mottl. + h.r.

The threecoloured seeds of the F_1-plants have, as in cross 5, yellowbrown (Gg) as '*main colour.*' This colour is very conspicuous because the '*orangered striping*' is much less extensive then the 'orangered mottling' in cross 5; also the '*pale buff background spots*' in the yellowbrown main colour are very clear: they are not influenced by 'yellowbrown factor' G, cf. row 2 from below in fig. 4. Fruit colour again is subdominant violet red 5, red tip intermediate, seedling with pink.

In 1937 F_2-families 1527 and 1528 were bred, together 148 harvested plants. As shown by fig. 4, the F_2-segregation was exactly parallel with that in cross 5,

Fig. 4. Cross 6, 'Citroen' with 'Hinrich's Riesen', F_2
Centre: the nine F_2-phenotypes, each represented by five seeds from one plant.
To the left: the F_2-numbers found and expected.
To the right: seedcoat description and genotype(s), the parents and F_1 indicated with **bold letter**. Further explanation see text.



39 (exp: $^1/_4$ = 37.0)	13 (exp. 9.25)	*a.* pale greenish yellow dark pattern, without hilumring (**II–1**, *CC dd jj gg*, and **II–2**, *CC dd jj G.* = **'Citroen'**).
	15 (exp. 18.50)	*b.* striped plus mottled, without h.r. (CC^{st} etc., 'main colour': pale greenish yellow).
	11 (exp. 9.25)	*c.* pale lilac (red) striped, without hilumring ($C^{st}C^{st}$ *dd jj gg* and $C^{st}C^{st}$ *dd jj G.*).
28 (exp.: $^3/_{16}$ = 27.7)	8 (exp. 6.9)	*a.* shiny greenish yellow dark pattern, with hilumring (**VI–1**, *CC dd J. gg*, slightly afterdarkened).
	12 (exp. 13.9)	*b.* shiny striped plus mottled, with hilumring (CC^{st} etc., 'main colour': shiny greenish yellow).
	8 (exp. 6.9)	*c.* shiny red striped, with hilumring ($C^{st}C^{st}$ *dd J. gg* = **'Hinr. Riesen'**).
81 (exp.: $^9/_{16}$ = 83.3)	20 (exp. 20.8)	*a.* shiny yellowbrown dark pattern, with hilumring (**VI–2**, *CC dd J. G.*).
	42 (exp. 41.7)	*b.* shiny striped plus mottled, with hilumring (CC^{st} *dd J. G.*, 'main colour.': yellowbrown = $\mathbf{F_1}$).
	19 (exp. 20.8)	*c.* shiny orangered striped, with hilumring ($C^{st}C^{st}$ *dd J. G.*).

total: 148 plants

the *nine* types after F_1 CC^{st} *(dd)* ***JjGg*** each being represented by five seeds from one plant. It is clear that 'Hinrich's Riesen', as 'Kievit', is recessive *dd*.

Figure 4 needs little commend: the lower group of three types is *J.G.* (9/16), the middle group *J.gg* (3/16) and the upper one $jj\genfrac{}{}{0pt}{}{gg}{G.}$ (¼). As in cross 5 the F_2-numbers in cross 6 also suggest independent segregation, at least no case of clear linkage.

One F_2-plant showed a deviating seedcoat colour: yellowbrown 'main colour' with orangered 'striping' but *without* the pale buff 'background mottling' as in normal CC^{st}. Therefore in a sense complementary to the two deviating individuals in cross 4, 'Wagenaar' with 'Hinrich's Riesen', that possessed the pale buff 'background mottling' in the 'main colour' but *lacked* the 'red mottling' of normal CC^{m}. As mentioned there (p. 17), discussion of accompanying colours, offspring and further crosses will be made in (a) following article(s), together with other results and a thorough literature-discussion on the 'complex locus' *C*.

Looking now at the accompanying colours in the normal F_2-plants, their correlation with *CC*, $C^{st}C^{st}$ and CC^{st} is again very clear: all mean values of CC^{st} are between those of the parent types. No totally green seedlings occur, while hypocotyl colour of $C^{st}C^{st}$, as in the other cases, is low. The tip of standard in $C^{st}C^{st}$ is slight, it is still slighter in CC^{st}, and completely lacking in all *CC*-plants. Violet red fruit of $C^{st}C^{st}$ is subdominant over the weak pink of *CC*. See table below:

seedcoat type	*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*	*number*
CC (dark pattern):	pink 3.8 (1–6)	pink 4.9 (2–6)	— red tip	pink 1.7 (1–4)	41
$C^{st}C^{st}$ (striped):	pink 2.4 (1–4)	pink 0.9 (0–4)	+ mostly slight r.t.	viol. red 4.8 (4–6)	38
CC^{st} (str. and m.):	pink 3.4 (1–6)	pink 4.0 (2–6)	± few slight r.t.	viol.red 4.1 (4–5)	69

F_3 of the present cross consisted of 35 families, 1909–1944'38, after all nine F_2-phaenotypes. It confirmed the F_2-results, not only for seedcoat colour segregation but for the 'pleiotropic' accompanying colours too. As in cross five, only the offspring of hilumringless $C^{st}C^{st}ddjj$ and $CC^{st}ddjj$-plants will be discussed.

Four 'lilac striped' homozygous $C^{st}C^{st}ddjj$-plants were used, the F_3-families being numbered 1909–1912, *according to decreasing visibility of the lilac striping* in the F_2-mother plants, from 'faint striping in most seeds' to 'trace of striping in few of the seeds'. The demonstration of genetic difference between F_2-plants was less clear than in the case of cross number 5, 'Citroen' with 'Kievit' (cf. fam. 1860–1867'38, p.22), for in most plants of the four F_3-families practically all seeds were described as pure white, only a few seeds showing a very faint lilac striping. Nevertheless the accompanying colours were quite as to be expected: almost all plants slight to clear red tip of standard, and all plants, if not completely ripe, with intense violet red fruit colour, the mean in the four families being 6.0, 6.1, 6.2 and 6.8.

Four three-coloured $CC^{st}ddjj$ F_2-plants gave a quite analogous F_3-result: accompanying colours as to be expected, but hardly any trace of lilac striping in the seedcoat of $C^{st}C^{st}$ or CC^{st}-plants.

Conclusions from cross 6, 'Citroen' with 'Hinrich's Riesen':

1. The action of C-C^{st} on seedcoat pattern and colour and also the 'pleiotropic

action' on the accompanying colours are quite the same as in cross number 4, 'Wagenaar' with 'Hinrich's Riesen': $C^{st}C^{st}$ almost always slight red tip standard and always intense violet red 6 fruit colour.

2. The actions and interactions of 'shine factor' J and 'yellowbrown factor' G are as in cross number 5, 'Citroen' with 'Kievit', i.e. fitting in with the scheme p. 82.

IV. THE SECOND GROUP OF DIALLEL CROSSES BETWEEN FOUR VARIETIES; PLEIOTROPIC ACTIONS OF P-p, T-t, C-C^{st}, $(V\text{-})V^{lae}$-v, Rk-Rk^{d} (CROSSES 7–12).

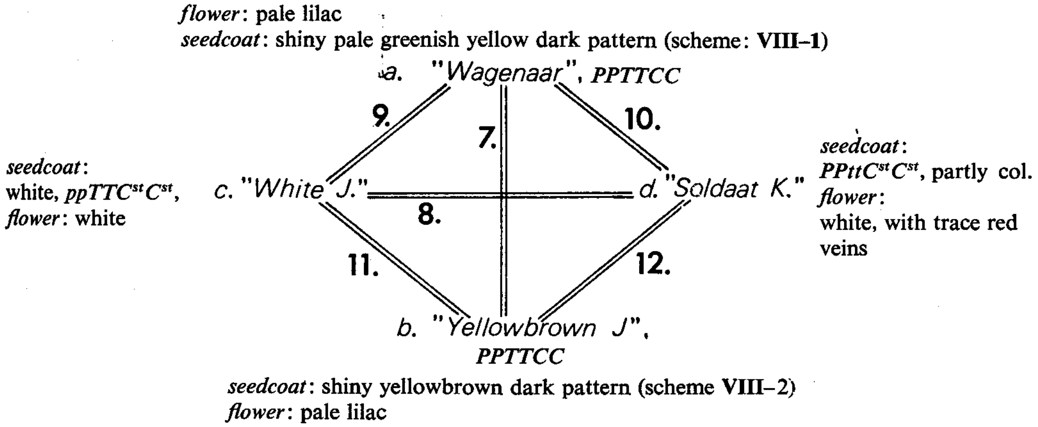


Figure 5. Schema of the second diallelic cross between four varieties.

Of these four varieties 'Wagenaar' is the one already known from the foregoing chapter III. Its seedcoat is shiny pale greenish yellow to canary, scheme **VIII–1**, genotype: $PPTTCCDDJJggbbV^{lae}V^{lae}RkRk$.

As to the origin of the three other types little can be told. 'Yellowbrown J', differing from 'Wagenaar' only by possessing the 'yellowbrown factor' G (scheme: **VIII–2**) and 'White J', recessive for the 'ground factor', pp, are forms with which the chief gardener JANSEN during the years 1930–1934 made some crossing- and selection-experiments and which he kindly put at my disposal. 'Soldaat K.' I received thanks to Mr. KNOOP from his home district Betuwe, between Rhine and Waal. Its seeds have a partly white seedcoat, while the coloured part, round the hilumregion, principally contains six 'colour centres', in this variety more or less fused into the one typical 'soldier' figure, but in other cases represented by six (or less) separate dots of extremely variable expression, within and between plants (cf. fig. 6 p. 29 and fig. 7 p. 31). The coloured part in variety 'Soldaat K.' shows *a red background colour*, slightly lighter than 'garnet brown' in RIDGWAY, Color Standards, Plate I, 3k. The colour at all probability depends upon the allel for dark recessive red, $rk^{d}rk^{d}$, SMITH and BECKER MADSEN, 1948; upon it are the fine beginning parts of striping, not red stripes however, slightly darker than the background red, but very dark grey violet stripes, because of the 'grey-greenish brown factor', BB, and of the 'recessive red factor', $rk^d rk^d$. It may be mentioned that, precisely as 'Soldaat K', also 'White J.' has (cryptomerically) the genes $C^{st}C^{st}$ and $ggBB$, but instead of $rk^d rk^d$ it is like the remaining two varieties $RkRk$. All four varieties have the 'shine factor', JJ, while three of them are $V^{lae}V^{lae}$ (pale lilac flower) and only 'White J' vv (white flower, also produced by pp and tt). The complete genotypes can now be given and be confronted with the F_1-, F_2- and F_3-results:

a. 'Wagenaar': $PPTT\ C\ \ C\ DD\ JJ\,gg\ bbV^{lae}V^{lae}Rk\ Rk$
b. 'Yellowbr.J.': $PPTT\ C\ \ C\ DD\ JJGG\,bbV^{lae}V^{lae}Rk\ Rk$
c. 'White J.': $pp\,TT\ C^{st}C^{st}\ ,\ .\ JJ\,gg\,BB\,v\ \ \ v\ \ \ Rk\ Rk$
d. 'Soldaat K': $PP\,tt\ \ C^{st}C^{st}\ .\ .\ JJ\,gg\,BBV^{lae}V^{lae}rk^d\ rk^d$

The homozygous presence of 'shine factor' J in all four varieties means that only shiny, afterdarkening colours will occur, it therefore being impossible to judge, within this group of crosses, about the presence or not of the 'hilumring factor' D.

As remarked in chapter I there exist correlations between seedcoat colour and the colour of other plant parts (here called: accompanying colours), depending upon 'pleiotropic actions', in this group of crosses by the loci P, T, the multiple allelic 'complex locus' C and the at least triple allelic loci V and Rk. Below the four seedcoat colours are tabulated together with their accompanying colours and this table should be compared with the four genotypes above:

	cotyl.	*hypoc.*	*flower*	*tip stand*	*veins wing*	*fruit colour*	*seedcoat colour*
a. 'Wagenaar':	pink 4	pink 3	pale lilac	— red t.	— red v.	pink 2	pale greenish yell.d.p.
b. 'Yellowbr.J.':	pink (2?)	pink 3	pale lilac	— red t.	— red v.	pink 2 à 3	yellowbrown d.p.
c. 'White J.':	green	green	white	— red t.	— red v.	green (or sl. pale col.)	white
d. 'Soldaat K.':	green	green	white	— red t.	+ trace r.v.	usually green	partly col., striped on recessive red

Figure 9, p. 65 shows the relations between flower- and seedcoat colour, as deduced from parents and F_1-F_3 or F_4 of this group of crosses.

Cross 7: 'Wagenaar' with 'Yellowbrown J.'

This is a very simple cross, the parents (scheme: **VIII–1** resp. **VIII–2**) differing for the 'yellowbrown factor' G only, F_1 being yellowbrown, Gg. F_2-analysis was already made in PRAKKEN I, 1940, cross 1 p. 344: families 1491–1492'37 and 1640'38, together 257 harvested plants, viz. 192 yellowbrown ($G.$) and 65 gg (exp. $\frac{1}{4} = 64.3$) as the shiny pale greenish yellow to canary 'Wagenaar' parent. As regards seedling colour all F_1 and F_2 plants possessed pink anthocyanin in the cotyledons, the extension varying from 1 to 6. Most hypocotyls also showed pink colour, but rather many were scored as 'green' or 'green?': possibly observation was too early. At any case not a single totally green seedling occurred. As to be expected, all F_2-plants had pale lilac flower ($V^{lae}V^{lae}$), none showed red tip standard (CC) and none red veins wing ($RkRk$), while the fruits showed but little pink colour (CC). Cf. fig. 9, cross 7, flower type nr. 7.

Cross 8: *'White J.' with 'Soldaat K.'*

The genotypes of parents and F_1 are (D-d unknown):

'White J.': $\boldsymbol{ppTTC^{st}C^{st}\,..JJggBB\,v\quad v\quad RkRk}$
'Soldaat K.': $\boldsymbol{PP\,tt\;C^{st}C^{st}\,..JJggBBV^{lae}V^{lae}rk^{d}rk^{d}}$
F_1 ($C^{st}C^{st}$): $\boldsymbol{PpTt\;C^{st}C^{st}\,..JJggBBV^{lae}v\quad Rkrk^{d}}$

The colours of parents and F_1 were scored as:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit col.*	*seedcoat col.*
'White J.':	green	green	white	— red tip	— red veins	almost green	white
'Sold. K.':	green	green	white	— red tip	+ trace r.v.	green	partly col.
F_1 being:	green(?)	green	very pale l.	+ clear r.t.	— red veins	violet red 6–7	totally col.
	cf. *P.T.* in F^2						

Both parents, *pp*(*TT*) and *PPtt*, have green cotyledons and green hypocotyl, white flower, no red tip standard and practically green fruit (in 'White J.' there is some very pale anthocyanin). Their flowers are represented in fig. 9. by resp. 1 (pure white) and 2 (small bits of red veins in lower half of the wings). The coloured part of the seedcoat in 'Soldaat K'. shows the begin-parts of a dark violet striping ($C^{st}C^{st}$), upon a shiny recessive red background ($rk^{d}rk^{d}$).

The F_1-plants have totally coloured seed (*PpTt*; 'White J.' therefore is *TT*) of the typically striped type, cf. e.g. fig. 2 (both parents therefore $C^{st}C^{st}$); its background is not recessive red but shiny very pale buff ($Rkrk^{d}$; 'White J.' therefore *RkRk*), and the stripes upon it are greyish violet (*ggBB*, see next crosses). The intense F_1-pod colour, violet red 6–7, fits in with the genotype $C^{st}C^{st}$, and so does the clear red tip of standard; the wings are without red veins. The extremely pale lilac overall colour of the F_1-flower depends, as F_2 will show, in the first place upon heterozygosity $V^{lae}v$ (that it is 'Soldaat K.' that possesses V^{lae} will not become clear before the next crosses, 9 and 10), but to a lesser degree also upon heterozygosity *PpTt*. The F_1-flower colour of cross 8 therefore lies between flower 14 and 15 in fig. 9, but very near 14. The 'green(?)' or 'green' scored for the *PpTt* F_1-seedlings at last is unreliable (hot house? time of observation?) and has to be compared with the seedling colour of *P.T.* F_2-plants, see below.

In this way the cryptomeric genes of especially the 'White J' parent could almost completely be deduced from the F_1-phenotype. The probable F_1-genotype, $\boldsymbol{PpTtC^{st}C^{st}..JJggBBV^{lae}vRkrk^{d}}$, will now be compared with the F_2- and F_3-segregations.

F_2-families were first studied in 1935, fam. 688–699, but classification, especially of flower colour, appeared quite impossible because of the almost continuous variation in overall colour (from pure white to pale lilac as 'Wagenaar'), the variation in size of red tip and the variation in type of red veins (if present). Seedcoat colour was less difficult to judge, sharp classification was possible, and therefore 74 F_3-families were bred, 1097–1170'36, representing all F_2 seedcoat types. These F_3-families were analysed for all characters and compared with the F_2-parents. The experience so gained summer 1936 and winter 1936–'37 made clear many details of classifications and correlations, to be used in the F_2-analysis of 1937.

TABLE 6. F_2 of cross 8 (1936 and 1937), 'White J.' with 'Soldaat K.' Among *P.T.* (totally coloured seeds) 'fl.wh.' means *vv* and 'fl.col.' means V^{lae}. Among *P.tt* (= partly coloured seeds) '+cl' resp. '−cl' is 'circumlineated' (*clcl*) resp. 'non-circumlineated' (*Cl.*), see fig. 7.

Year and number fam.	*pp* white seeds	*P.tt* partly col. seeds				*P.T.* totally col. seeds				total number F_2-plants
		$rk^d rk^d$ rec.red		*Rk.* non-rec.red		$rk^d rk^d$ rec. ed		*Rk.* non-rec.red		
		+cl *clcl*	—cl *Cl.*	+cl *clcl*	—cl *Cl.*	fl.wh. *vv*	fl.col. V^{lae}.	fl.wh. *vv*	fl.col. V^{lae}.	
1936:										
fam. 1031–1036	306	5	44	18	127	48	108	123	323	1102
		49		145		156		446		
1937:										
fam. 1483	18	1	1	1	7	0	10	7	27	72
fam. 1484	15	1	4	3	11	0	11	5	21	71
fam. 1485	14	0	1	1	6	3	9	12	22	68
fam. 1486	15	0	4	1	5	3	5	9	29	71
total 1937	62	2	10	6	29	6	35	33	99	282
		12		35		41		132		
total '36 + '37	368	7	54	24	156	54	143	156	422	1384
		61		180		197		578		
		241				775				
expected	346	64.9		194.6		194.6		583.9		1384
		259.5				778.5				

The F_2-results of 1936 and '37 are given in table 6, separately, as a few of the 1936-families gave very highly deviating numbers, especially for overall flower colour in the group with totally coloured seed (P.T.vv, white flower, against P.T.V^{lae}., from almost white to pale lilac as 'Wagenaar'), probably mainly caused by at that time not-yet-overcome classification difficulties.

In both years the segregation for *PpTt* agreed rather well with the expected 4*pp*: 3*P.tt*: 9*P.T.*, for both years together 368*pp* (exp. 346), 61 + 180 = 241 *P.tt* (exp. 259.5) and 197 + 578 = 775 *P.T.* (exp. 778.5): probably independent segregation.

The white-seeded plants (*pp*) are not further subdivided. Both the (*P.*)*tt* partly coloured ones (see figure 6) and the (*P.*)*T.* totally coloured ones are first subdivided into recessive reds ($rk^d rk^d$; dark grey-violet striped on red background, like 'Soldaat K.') and non-recessive reds (*Rk.*; grey-violet striped on pale buff background, like F_1), the four types, $ttrk^d rk^d$, *ttRk.*, $T.rk^d rk^d$ and *T.Rk.*, in both years and also together clearly showing the proportion 1:3:3:9, i.e. independent segregation between *T-t* and Rk-rk^d, cf. the lower lines of table 6 (numbers: 61 + 180 + 197 + 578).

The second subdivision in the group *P.T.*, with totally coloured seeds, is into 54 + 156 = 210 *P.T.vv*, white flower, 143 + 422 = 565 *P.T.*V^{lae}., coloured flower in all intensities from almost white, $PpTtV^{lae}v$, to pale lilac as 'Wagenaar', $PPTTV^{lae}V^{lae}$; the paler making influence of heterozygosity $V^{lae}v$ is much more important than that of *Tt* and *Pp*. It may be repeated that *V^{lae}–v influences overall flower colour only*, not the red tip or the red veins. Both these characters are even more clearly visible in the white *vv*-flowers than in the V^{lae}.–ones. Segregation between the four gene pairs *P-p*, *T-t*, Rk-rk^d and V^{lae}-*v* seems to be independent.

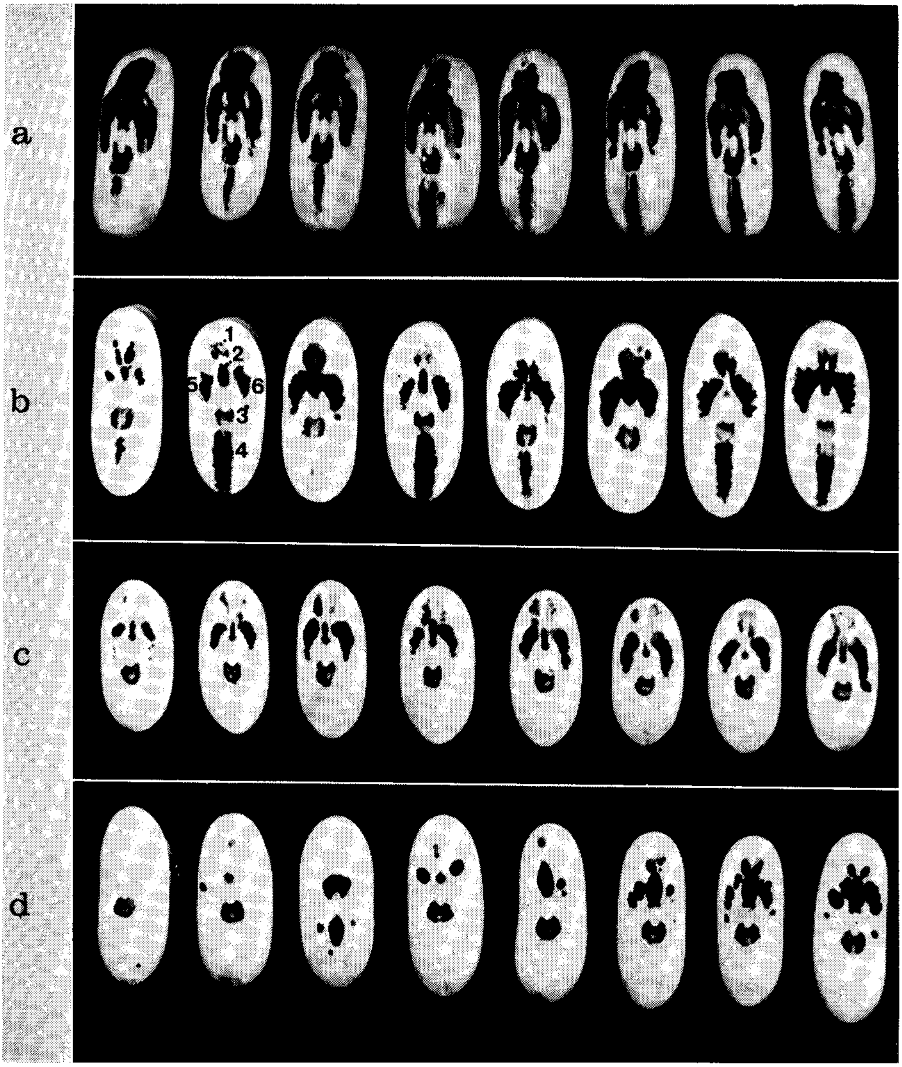


FIG. 6. The 'soldier type' (LAMPRECHT, 1934, fig. 18 p. 201: '*virgarcus*') and related types of partly coloured seedcoat. It has 6 (or less) colour centres, 1–6, cf. row *b*, no. 2 from left. Further genetic analysis is, because of the great non-genetic variability (within and between plants, between years etc.) very difficult. Each row of eight seeds comes from one plant. The median centres (1–4) often are subdivided into two. – See also figure 8.
a: Seeds of a typical F_2-specimen like variety 'Soldaat K.'
b, *c*, and *d*: further specimen from F_2-families.

All *P.tt* partly coloured plants have a white flower that is not influenced by V^{lae}-v. Yet this group in table 6 also shows a second subdivision, indicated as '+cl' and '—cl' and only observable in partly coloured seeds (cf. fig. 7). It will be discussed a little further on.

First the observations on the 'accompanying colours' in the *pp*, *P.tt* and *P.T.* groups will be discussed. In a condensed manner they are given in the table below:

genotype	*cotyl.*	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit colour*
a. *pp* (368):	green	green	white	— red tip	— red v.	green or very pale pink 1–3
b. *P.tt* (241):	green	green	white	— red tip	$rk^d rk^d$: + trace r.v. *Rk.*: — red v.	mostly pure green, cf. below
c. *P.T.* (775):	pink 0–5 (mean ± 3)	most green few pink 1–2	pale 1. to white	all clear + red tip	$rk^d rk^d$: + red v. *Rk.*: — red v.	violet red 6–8

A few remarks on this table may be made.

a. The pure green *pp* F_2-seedlings, later white flowering 'without red tip standard' and 'without red veins wing' follow the normal picture. The fruit colour of these *pp*-plants mostly looks like green, but narrow inspection often showed a very pale pink anthocyanin colour. TJEBBES and KOOIMAN (1921) even could in a homozygously striped F_2-family, segregating for *P*-*p* and V-V^{lae}, distinguish between pale red or pale pink, in $ppV^{lae}V^{lae}$, and pale blueviolet fruit colour, in *ppV.*; as mentioned on p. 6 the 'violet-factor' *V* is not present in the varieties used here.

b. The *P.tt* plants, with partly coloured seed, also have, like *pp*, always pure green cotyledons and hypocotyl and white flower without red tip; they usually have green fruits, that however, under special conditions as fruit lying on the moist ground, can show some clear anthocyanin development. An important observation was that all 61 *P. tt*-plants that possessed the recessive red seed-coat colour, $rk^d rk^d$, showed, precisely as the 'Soldaat K.' parent, *a 'trace of red veins' in the lower half of the wings* (cf. fig. 9, cross 8, flower type 2). In none of the 180 *P.ttRk.* plants was this 'trace of red veins' found.

c. The *P.T.* F_2-plants at last (all $C^{st}C^{st}$) almost all clearly showed pink cotyledons, the hypocotyl usually being green or almost so, which agrees with the situation in the crosses of chapter III: $C^{st}C^{st}$-plants rather high anthocyanin content in the cotyledons but very little in the hypocotyl. And, also as in chapter III, but more intense, the flower of the $P.T.C^{st}C^{st}$-plants in cross 8 showed a clear red tip and the fruit a heavy violet-red 6–8. As regards 'red veins wing' the 197 recessive red plants, $P.T.(C^{st}C^{st})rk^d rk^d$ all showed red veins over the whole wings, while the 578 $P.T.(C^{st}C^{st})Rk.$-plants were scored as without red veins: pleiotropic action of *Rk*-rk^d apparently, as in the remaining crosses with 'Soldaat K.', cf. crosses 10 and 12 below. In *P.T.*- and almost as well in *P.tt*-plants the distinction between '+ veins' and '— veins' was completely sharp.

The second type of subdivision in the *P.tt*-plants is, as already mentioned,

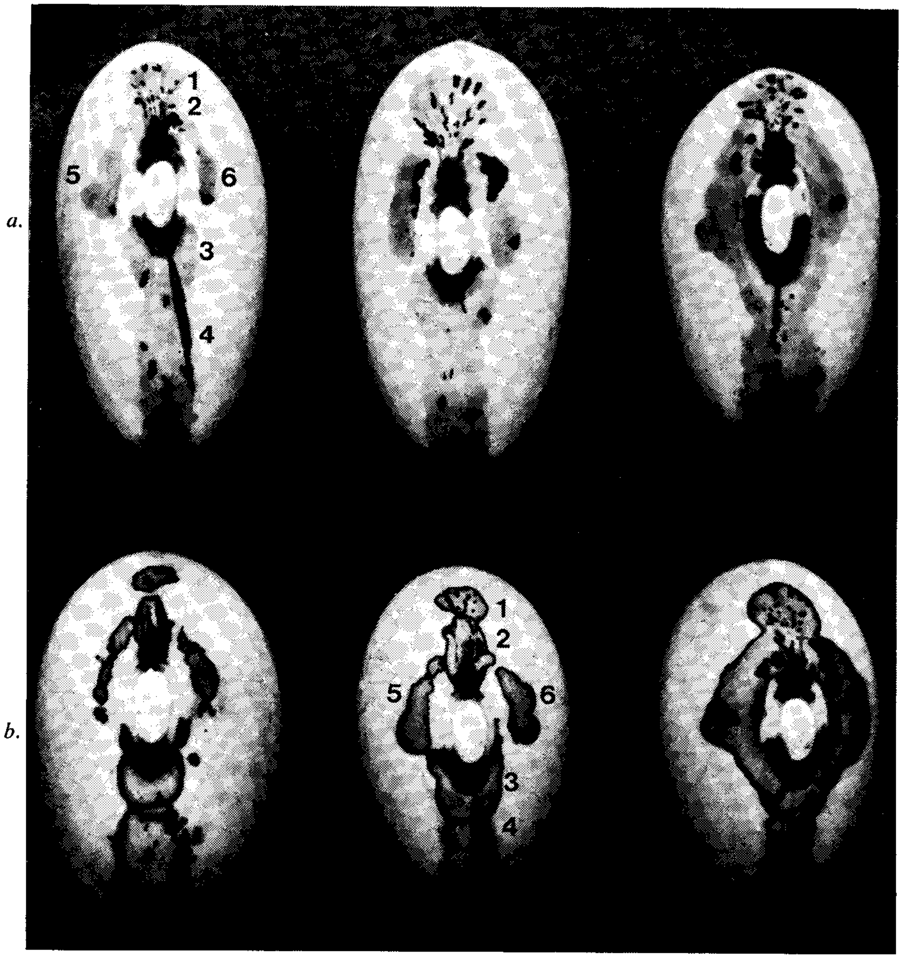


FIG. 7. Cross 8, 'White J.' with 'Soldaat K.'. Three seeds from two partly coloured (*P.tt*) F_2-plants. Both plants homozygously striped ($C^{st}C^{st}$), with shiny greyish violet stripes ($JJggBBV^{lae}V^{lae}$) upon pale buff background (*Rk.*).

a. 'Normal soldier type', the six colour centres (1–6) more or less united.

b. 'Circumlineated soldier' (*clcl*; from *c*ircum*l*ineatus); each of the colour centres and even the smallest dots bordered by a sharp precipitation-like line. In this type the 'fusing'. of centres is, from left to right, clear to follow.

shown in fig. 7, were the three upper seeds (from one plant) represent an original partly coloured type (as Soldaat K.) and the three lower ones (also from one plant) a very typical new type, indicated as 'circumlineatus', '+cl', the original type being non-circumlineated, '–cl.' In the '+cl' type the coloured part (or the separate units of it, even the finest colour dot) is sharply demarcated from the white part of the seedcoat by a narrow line (of a clear orange in *Rk.*-seeds and of a much darker colour in $rk^d rk^d$-ones), giving the impression of some sort of *precipitation* on the border between the coloured and uncoloured parts.

Among the *241 P. tt*-plants the numbers of both types (cf. table 6) are:

	among $rk^d rk^d$		*among Rk.*		*together*	
	'+cl'	'—cl'	'+cl'	'—cl'	'+cl'	'—cl'
1936:	5	44	18	127	23	171
1937:	2	10	6	29	8	39
'36 + '37:	7	54	24	156	31	210
					241	

The new type seems recessive, but its number is clearly less than one fourth: 31/241 = 0.1286, the shortage being about the same among $rk^d rk^d$ and *Rk*. The shortage might e.g. depend upon *weakness* of the monofactorial recessive *clcl*-type or upon *linkage* of *Cl-cl* with *T-t* or with *P-p*, the 'lacking' number of *clcl*-plants being either among the totally coloured *P.T.*-group (plus *ppT.*) or among the white-seeded *pp*-group: 'Soldaat K', being *(PP)ttClCl* (repulsion phase) or 'White J.' being *pp(TT)clcl* (linkage phase).

Here the earlier mentioned (p. 27) 74 completely analysed F_3-families of 1936 became of value. The families segregating for *Cl-cl* (and not for *P-p* or *T-t*) clearly showed monofactorial recessiveness of the 'circumlineated' type and no weakness at all of *clcl* (= '+cl'), cf. below.

Among *P.* the numbers 241 *tt* and 775 *T.* are close to 1:3 (exp. 254 and 762), so no linkage between *P-p* and *T-t* is detected. The share of *clcl* among the *P.tt* plants being 0.1286, and assuming a really independent segregation between *P-p* and *T-t*, the shortage of *clcl* should be caused by linkage, in the repulsion-phase, between *T-t* and *Cl-cl*, the share of recombinant gametes, *TCl* and *tcl*, being about $\sqrt{0{,}1286} = 0{,}359 = 35.9\%$.

For a control on this result the 74 F_3 families mentioned above, 1097–1170'36, again are of use. Among the 74 F_2-mother plants used were:

a. 11 *partly coloured, 'circumlineated'* (*P.ttclcl*), from which 4 appeared to be *PP* and 7 *Pp*, all *P.* offspring being *ttclcl.*

b. 19 *partly coloured, 'non-circumlineated'* (*P.ttCl.*), and from these appeared to be:

2 (exp. 2.1) *PP(tt)ClCl* (together 35 *PP(tt)ClCl* F_3-plants)
4 (exp. 4.2) *PP(tt)Cl cl* (segregating in 14 *clcl* + *43* Cl.)
6 (exp. 4.2) *Pp(tt)ClCl* (segregating in 19 *pp* + 78 *P.ClCl*)
7 (exp. 8.4) *Pp(tt)ClCl* (segr. into 32 *pp* + 20 *P.(tt)clcl* + 66 *P.(tt)Cl.*

Nothing that points to linkage between the loci *P* and *Cl.*

c. 14 *totally coloured, without segregating in* F_3 *any partly coloured seed,* therefore being *P.TT* (5 *PPTT* and 9 *PpTT*). This group of F_3-families can of course not give information on linkage between the loci *T* and *Cl.*

d. 30 at last were *totally coloured and did segregate plants with partly coloured seedcoat,* the F_2-parents therefore being $P.Tt \begin{cases} clcl, \text{ or} \\ Clcl, \text{ or} \\ ClCl. \end{cases}$

It is this group *d.* of F_2-plants and F_3-families that can and must show the effect of linkage between *T-t* and *Cl-cl*. As *P-p* and *T-t* are independent the constitution *PP* or *Pp* of the F_2-mother plants does not matter (11 appeared *PP* and 19 *Pp*, very near the expected 1:2 ratio, a new corroboration of independency between *P-p* and *T-t*). A handicap is of course the small number of F_3-plants per family, mostly about 20. Below the analysis of this group follows.

Assuming $\frac{1}{3}$ of the gametes produced by F_1 being recombinant ones (near to 35.9%, see above), the constitution of the $\frac{1}{2}$ or 18/36 F_2-*Tt*-plants (among *PP* and *Pp*) theoretically should be as follows:

$^{18}/_{36}$ *Tt* and from these
- $^{4}/_{18}$ *clcl* → (segregating (*tt*)*clcl* only)............................group **a.**
- $^{10}/_{18}$ *Clcl*
  - $^{2}/_{18}$ $\frac{TCl}{tcl}$ → (giving 4 (*tt*)*clcl* against 5 (*tt*)*Cl.*)...............group **b.**
  - $^{8}/_{18}$ $\frac{Tcl}{tCl}$ → (giving 1 (*tt*)*clcl* against 8 (*tt*)*Cl.*)...............group **c.**
- $^{4}/_{18}$ *ClCl* → (giving (*tt*)*ClCl* only) ....group **d.**

The 30 F_3-families from *P.Tt* F_2-plants could be grouped as follows:

Group **a**, *Ttclcl*: 4 families (exp. 6.7), together 80 F_3-plants.

Group **b** + **c**, *TtClcl*: 6 families (much less then expected, because of the low number of plants per F_3 family; especially most F_2-plants of group **c** will escape observation, as the ratio *clcl:Cl.* is but 1 to 8. The actual numbers in these 6 families are given in table 7.

TABLE 7. F_3-segregation in families from F_2-plants of cross 8 that belonged to group **b.** $(P.\frac{TCl}{t\,cl})$or group c. $(P.\frac{Tcl}{t\,Cl})$.

number F_3-fam	F_3-offspring				total number
	white pp	*partly col., circ. P.ttclcl*	*partly col., non-circ., P.ttCl.*	*totally col. P.T.*	
1162	5	1	1	3	10
1137	0	1	2	16	19
1127	4	1	2	13	20
1129	5	1	2	12	20
1148	5	1	2	15	23
1169	0	1	6	11	18

Sharp distinction between the groups **b**. and **c**. is of course impossible. Family 1169 in all probability shows the original repulsion phase (group **c**), while certainly part of the five 1 + 1 or 1 + 2 (*clcl* + *Cl.*) families belong to group **b**, (*P.*) $\frac{TCl}{tcl}$, linkage and crossing over (probably about 40%) thus being proved.

Group **d**, consists of 20 families in which the partly coloured *tt*-plants all are *non-circumlineated*, but because of the small number of *tt*-plants (1 × 1, 3 × 2, 5 × 3, 4 × 4, 4 × 5, 1 × 6, 1 × 10 and 1 × 11) certainly many of these 20 F_2-plants really belong to group **c** or **b**.

Summarizing, the present cross 8, 'White J.' with 'Soldaat K.', has affirmed and refined the observations of many earlier investigators on the *pleiotropic actions* of *P-p* and *T-t*; the *pleiotropic action* of $C^{st}C^{st}$ (red tip standard and intense violet red fruit) is in agreement with the results gained in the crosses of chapter III; the present cross further shows that V^{lae}-*v* influences flower colour only (while the allel *V*, violet factor, has *pleiotropic action* upon seedling-, plant-, flower-, fruit- and seedcoat colour); and, for the first time, it shows the *pleiotropic action* of Rk-rk^d: *Rk. without* and rk^drk^d(recessive red seedcoat) *with* red veins in wings of the flower, in white-flowered $ttrk^drk^d$ plants, with partly coloured seedcoat, always visible as 'trace of red veins' in the lower half of the wings. At last the cross proved that *Cl-cl* (symbol from *circumlineated*, as the *tt*-plants, with partly coloured seeds, in case of *clcl* have the coloured part(s) surrounded by a sharp demarcation-line) is linked, in the repulsion fase, with *T-t* and independently inherited from *P-p*, 'Soldaat K.' being *(PP)ttClCl* (non-circumlineated) and 'White J' being *(pp) TTclcl*. The various correlations between flower- and seedcoat colour are vizualised, though much schematized, in figure 9, cross 8.

Cross 9: *'Wagenaar' with 'White J.'*

From foregoing crosses the genotypes of both parents are in the main known. In cross 8, 'White J' with 'Soldaat K', it could however not be decided which of the parents was $V^{lae}V^{lae}$ and which one *vv* and not before the present cross it becomes clear that it was 'White J.' that contributed *v*. And it is in the present (and the next) cross that the action of the gene pair *B-b* can be followed, both in the *'yellow-black'* *C*-group and in the *'red'* C^{st}-group. Genotypes of parents and F_1 are:

'Wagenaar': $\boldsymbol{PP}TTC\ \ C\ \ (DD)JJgg\,\boldsymbol{bb}V^{lae}V^{lae}RkRk(\,.\,.\,)$
'White J.': $\boldsymbol{pp}\,TTC^{st}C^{st}\,(\,.\,.\,)JJgg\boldsymbol{BB}\,v\ \ \ v\ \ \ RkRk(clcl)$
F_1 being: $\boldsymbol{Pp}\,TTC\ \ C^{st}\,(\,.\,.\,)JJgg\boldsymbol{Bb}V^{lae}\,v\ \ \ RkRk(.cl)$

The colours of parents and F_1 were:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit*	*seedcoat*
'Wagenaar':	pink 4	pink 3	pale lilac	— red tip	— red v.	pink 2	green. yelld.p.
'White J.':	green	green	white	— red tip	— red v.	almost green	white
$F_1(CC^{st})$:	pink 2.5	pink 0.5?	very pale l.	+ trace r.t.	— red v.	viol. red 5–6	str. and mottl.

But few F_1-plants were bred, 1936 and 1937. Their colour characters have to be compared with those of the CC^{st} F_2-colour group, cf. below. The very pale lilac of the F_1-flower depends on the double heterozygosity $PpV^{lae}v$ ('White J.' therefore being *vv*). The 'trace red tip' of F_1 (not always visible), the 'violet red fruit 5–6' and the threecoloured 'striped and mottled' seedcoat depend on the heterozygosity CC^{st}. The 'main colour' of F_1's threecoloured seedcoat was not pale greenish yellow (= schamois) as in the 'Wagenaar' parent (scheme: **VI–1** or **VIII–1**) but *grey-greenish brown* (münzbronze, buffy citrine; scheme **VI–3** or **VIII–3**). From numerous analyses of various investigators this difference is known to be caused by the '(grey-)greenish brown factor' *B*, apparently present in the 'White J.' parent and also in 'Soldaat K.', cf. cross 8. This F_1 'main colour' greenish brown therefore makes it probable, and it will be confirmed by the F_2-segregation below, that the '(grey)greenish brown factor' B of the *C-c* (c^u ... etc.) yellow-black system, in the red striped ($C^{st}C^{st}$) or in the red mottled (C^mC^m) types changes the 'red' into 'greyish violet'. The striping over the greenish brown 'main colour' of the seed produced by F_1 really was a greyish violet. The background mottling in it was of the same shiny pale buff as in $C^{st}C^{st}$ resp. C^mC^m, i.e. not influenced by (*G*), *B* (or *V*).

After this analysis of parents and F_1, the F_2-segregation, for **$PpCC^{st}BbV^{lae}v$**, hardly needs any further explanation (see table 8.). Among the coloured-seeded (*P.*) F_2-plants the dark pattern type is represented by *CCB.* (grey-greenish brown) and *CCbb* (the re-appearing greenish yellow, as 'Wagenaar') and, parallel with it, the homozygously striped type by $C^{st}C^{st}B.$ (greyish violet) and $C^{st}C^{st}bb$ (red). The heterozygotes, CC^{st}, are *threecoloured*, see the table.

TABLE 8. F_2-seedcoat colour in cross 9, 'Wagenaar' with 'White J.'

Family number	*pp* = white seed coat	*P.* = totally coloured seedcoat						total number F_2 plants
		CC = dark pattern		CC^{st} = striped and mottl.		$C^{st}C^{st}$ = striped seed		
		bb = gr.y. $vv+V^{lae}$.	*B.* = gr.br. $vv+V^{lae}$	*bb* = gr.y. $vv+V^{lae}$	*B.* = gr.br. $vv+V^{lae}$	*bb* = red $vv+V^{lae}$	*B* = gr.viol. $vv+V^{lae}$	
1493'37	32	2+1	7+10	1+6	10+34	2+3	5+16	129
1494'37	21	0+1	5+1	0+3	5+4	2+3	3+12	60
1495'37	7	0+0	1+6	2+1	5+12	0+2	2+6	44
1641'38	34	0+1	3+17	4+13	9+23	1+5	3+14	127
total	94	2+3	16+34	7+23	29+73	5+13	13+48	360
		5!?	50	30	102	18	61	
		CC = dark pattern colours:		CC^{st} = threecoloured:		$C^{st}C^{st}$ = striped on pale buff background		
		pale gr. yellow dark p.	greenish brown dark p.	*main colour'*: as *CC* (to the left) *'striping'*: as $C^{st}C^{st}$ (to the right) *'background mottling'*: pale buff		red striped	greyish violet striped	

The monofactorial segregations were:

1. White, *pp*, against coloured: 94 *pp* (exp. 90.0) and 266 *P*.
Among the 266 *P.*:
2. Dark pattern, *CC*, heterozygous, and striped, $C^{st}C^{st}$: 55 (exp. 66.5), 132 (exp. 133.0) and 79.
3. Without green. brown factor, *bb*, against *B.*: 53 *bb* (exp. 66.5) and 213 *B.*
4. White flower, *vv*, against pale lilac, V^{lae}.: 72 *vv* (exp. 66.5) and 194 V^{lae}.
The bifactorial ones were:
1, 2, 3. *P-p* probably independent from *C-*C^{st}, *B-b* and V^{lae}-*v*, cf. 2, 3 and 4 above.
And among the 266 *P.*-plants:

Expected:	16.6	+ 49.7	+ 49.7	+ 149.1
4.C-B:	5 *CCbb*	+ 50 *CCB.*	+ 48 $C^{st}.bb$	+ 163 $C^{st}.B.$
or:	18 $C^{st}C^{st}bb$	+ 61 $C^{st}C^{st}B.$	+ 35 *C.bb*	+ 152 *C.B.*
5. C-V^{lae}:	18 $C^{st}C^{st}vv$	+ 61 $C^{st}C^{st}V^{lae}.$	+ 54 *C.vv*	+ 133 $C.\ V^{lae}.$
or:	18 *CCvv*	+ 37 $CCV^{lae}.$	+ 54 $C^{st}.vv$	+ 157 $C^{st}.V^{lae}.$
6. B-V^{lae}:	14 *bbvv*	+ 39 $bbV^{lae}.$	+ 58 *B.vv*	+ 155 $B.V^{lae}.$

For the very low number of 5 *CCbb* (a parental combination) no explanation can be given (D/m = 3.7). Conclusion is that among 1–6 above no case of clear linkage occurs.

With respect to the '*accompanying colours*' in this cross, there is influence of *P-p* and *C-*C^{st}, V^{lae}*-v* influencing flower colour only and *B-b* seedcoat colour only. The effects are quite as to be expected from all foregoing crosses and they are tabulated below (for the 233 plants of fam. 1493–1495'37 only) and are to be compared with parents and F_1:

genotype	*cotyledons*	*hypocotyl*	*flower*	*tip standard*	*fruit colour*
white (*pp*, 60):	green	green	white	— red tip	green or very pale anth. 1–4
dark p. (*P.CC*, 27):	pink 3.0(1–5)	pink 2.3(1–5)	15 *vv* 19 $V^{lae}.$	— red tip	pink 2.2 (1–5)
striped ($P.C^{st}C^{st}$, 56)	pink 2.3 (2–5)	pink 0.4 (0–4)	14 *vv* 42 $V^{lae}.$	+ mostly clear	viol.red 6.4 (4–7)
three-col. ($P.CC^{st}$, 83)	pink 3.5(1–6)	pink 2.3(0–5)	23 *vv* 60 $V^{lae}.$	+ very small	viol. red 5.6 (4–6)

A few remarks on this 'accompanying colour' table for F_2 may be made. This cross was the only one in which germ plant colour of CC^{st} in F_2 was not clearly intermediate, but as high as in homozygous *CC*-plants. The homozygous $C^{st}C^{st}$-plants, however, followed the general experience and showed a very low mean anthocyanin colour in the hypocotyl, 0.4. In $C^{st}C^{st}$-plants the red tip standard was usually clear but rather small, while in CC^{st}-plants it was, if observed at all, usually very small. In this connection it was striking that among the 'white flowered' $CC^{st}vv$ plants only one individual was scored as '— red tip', but among $CC^{st}V^{lae}.$ many more: *vv*, far from making the red tip smaller or paler makes it, on the contrary, *more easy to score* (quite the same applied to visibility of 'red veins wing', as will appear in crosses 10 and 12). – An observation always made in this connection was the following. From many F_2 CC^{st}-plants scored as '— red tip', in this or in other crosses an F_3 family was bred for control, and always many or at least a few F_3-plants '+ red tip' appeared, while these '+ red tip' usually just were the homozygous $C^{st}C^{st}$-plants. Ultimate conclusion therefore: $C^{st}C^{st}$ always has a red tip, bigger or smaller, depending upon both, genetic as well as environmental causes, see chapter II.

In family 1641'38, after an F_1 sister-plant to the mother of family 1493'37, values for germ plant colour were much lower, while mean fruit colour values were quite the same. The material, however, is not sufficient to make clear the cause from it: (mainly) genetically, (mainly) environmentally or both.

One last remark. Striping in the threecoloured-seeded CC^{st} F_2-plants, especially in $CC^{st}B.$ with greenish brown as 'main colour', varied much in intensity or in contrast with the main colour, i.e. in visibility. F_3-segregation, nevertheless usually appeared the normal one: $\frac{1}{4}$ dark pattern, CC + $\frac{1}{2}$ threecoloured, CC^{st} + $\frac{1}{4}$ (more or less pale) striped, $C^{st}C^{st}$. In one F_2-plant, however, striping was not at all present, nor did it appear in its F_3-family of 16 plants. This case will be discussed, together with the other rare cases of separation between striping and mottling (p. 17 and p. 24) in a following special article on the 'complex locus' *C*.

Summarizing the results of cross 9, 'Wagenaar' with 'White J.', it can be said that the *pleiotropic actions* of *P-p* and C-C^{st} as found in preceding crosses are confirmed (see also fig. 9, cross 9), that the 'grey-greenish brown factor' *B* in the yellow-black *C-c* group changes (pale) greenish yellow or canary into (grey-) greenish brown and that *the same gene B* changes red striped $C^{st}C^{st}$-seeds (resp. C^mC^m ones) into greyish violet striped (resp. mottled) ones. V^{lae}-v influences, as in other crosses (8 and 11), flower colour only.

Cross 10: *'Wagenaar with' 'Soldaat K.'*

As in cross 9 the genotypes of both parents are in the main known. Just as cross 9, 'Wagenaar' with 'White J., showed that 'White J.' possessed *vv*, so in the present cross it will be confirmed that 'Soldaat K.' is $V^{lae}V^{lae}$. Like in cross 9 the action of *B-b* can be compared in yellow-black *C* and in *dominant red* striped R^{st}, but here moreover in *Rk*. (non-recessive red) and rk^drk^d (*recessive red*):

'Wagenaar': $PPTT\,C\;\;C\;\;(DD)JJgg\mathbf{b\,b}V^{lae}V^{lae}\mathbf{Rk\;\;Rk}(\,.\;.\,)$
'Soldaat K.': $PP\mathbf{t\,t}\;C^{st}C^{st}(\,.\;.\;.\,)JJgg\mathbf{BB}V^{lae}V^{lae}\mathbf{r\,k^d\;\;rk^d}(ClCl)$
F_1 being: $PPTt\;C\;\;C^{st}(D\,.\,)JJgg\mathbf{Bb}V^{lae}V^{lae}\mathbf{Rk\;\;rk^d}(Cl.)$

The colours were:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit*	*seedcoat*
'Wagenaar':	pink 4	pink 3	pale l.	— red t.	— red v.	pink 2	green. yell. d.p.
'Sold.K.':	green	green	white	— red t.	+ trace r.v.	green	striped on red
$F_1(CC^{st})$:	pink 2	green(?)	pale l.	— red t.(?)	— red v.	viol.red 5	striped and mottl. (=three-coloured)
	cf. CC^{st} in F_2						

Heterozygosity for F_1 (three plants: fam. 1034'36) was as to be seen above $\mathbf{TtCC^{st}BbRkrk^d}$. Its colour characters, esp. those with (?), should be compared, as in the preceding cases, with those of the CC^{st} F_2-group below (p. 38). The pale lilac flower colour of F_1 confirms that 'Soldaat K.', cryptomerically, has the gene V^{lae}. The lack of red veins depends upon the gene *Rk* from 'Wagenaar' and the 'violet red 5' fruit colour upon C^{st} from 'Soldaat K.'. The three-coloured seedcoat is, as to be expected, accurately the same as in cross 9 ($CC^{st}ggBb$), the 'main colour' being greenish brown, the 'striping' over it greyish violet and the 'background mottling' in it very pale buff. See further the F_2-analysis.

From each F_1-plant a rather small F_2-family could be bred, families 1496–1498'37, together 194 harvested plants. The F_2-segregation is shown in table 9: in the upper part, *a.*, the partly coloured *tt* and in the lower part, *b.*, the T.-plants with totally coloured seed; both, *a.* and *b.*, divided into the three groups *CC*, CC^{st} and $C^{st}C^{st}$, each group being subdivided, according to *B-b* and Rk-rk^d, into four sub-groups, see table.

TABLE 9. Seedcoat colour in F_2 of cross 10, 'Wagenaar' with 'Soldaat J'. In the lower part of the table the colours and the connections between them are explained.

	CC = dark pattern colours				CC^{st} = striped and mottled				$c^{st}c^{st}$ = striped seedc. colours				total
	bb		*B.*		*bb*		*B.*		*bb*		*B.*		
	$rk^d rk^d$	*Rk.*	$rk^d rk^d$	*Rk.*	$rk^d rk^d$	*Rk.*	$rk^d rk^d$	*Rk.*	$rk^d rk^d$	*Rk.*	$rk^d rk^d$	*Rk.*	
a. partly coloured seedcoat (tt):													
1496'37	0	0	1	1	0	2	1	6	0	0	1	3	15
1497'37	0	1	2	4	0	4	1	4	0	2	0	6	24
1498'37	0	0	0	4	0	0	4	3	0	1	0	5	17
total *tt*	0	1	3	9	0	6	6	13	0	3	1	14	56 *tt*
	13				25				18				
b. totally coloured seecoat (T.):													
1496'37	0	2	2	2	0	3	5	12	0	1	3	5	35
1497'37	0	2	5	4	2	7	7	15	0	3	3	5	53
1498'37	0	4	1	5	0	5	9	11	1	3	2	9	50
total *T.*	0	8	8	11	2	15	21	38	1	7	8	19	138 *T.*
	27				76				35				
total *tt+T.*	0	9	11	20	2	21	27	51	1	10	9	33	194 *tt+T.*
	40				101				53				
	dark pattern colours *(CC)*				striped and mottled (CC^{st}) (= 'threecoloured')				striped seedcoat col. $(C^{st}C^{st})$				
	reddish colour (over pale green.yellow)	pale greenish yellow (canary) (= **'Wagenaar'**)	dark greenish brown with reddish haze over it	(grey-) greenish brown	1. *'main colour'*: as CC (to the left) 2. *'striping'*: ± as $C^{st}C^{st}$ (to the right) 3. *'background mottling'*: reddish (with $rk^d rk^d$) pale buff (with *Rk.*)				dark red striped on *red* background	red striped on *pale buff* background	blackish greyish violet stripes on *red* backgr. (= **'Sold. K.'**)	greyish-violet stripes on *pale buff* background	

In the *CC(JJ) shiny dark pattern group* the *Rk.* non-recessive red colours are of course (as in cross 9) (grey-)greenish brown, *B.* (scheme: **VI–3** or **VIII–3**), and pale greenish yellow, *bb* (scheme: **VI–1** or **VIII–1**). The latter colour, *CCbbRk.*, is by $rk^d rk^d$ changed into *a real reddish colour* (with pale greenish yellow under it), while the greenish brown, *CCB.Rk.*, by $rk^d rk^d$ is not so much changed, $CCB.rk^d rk^d$ showing a reddish haze over the (darker) grey-greenish brown. In the $C^{st}C^{st}$ *(JJ) shiny striped group* the *Rk.* non-recessive reds have either greyish violet stripes as F_1, *B.*, or clear red stripes already known from chapter III, *bb*, both colours upon a pale buff background. By $rk^d rk^d$ the pale buff background of both, *B.* and *bb*, is changed into the typical recessive red background (as in the 'Soldaat K.' parent), while the red stripes of *bb* become slightly darker and the greyish violet stripes of *B.* much darker, like the blackish grey-violet stripes of 'Soldaat K.' that really has the genotype $C^{st}C^{st}(JJ)gg\text{-}BBrk^d rk^d$. In the striped and mottled $CC^{st}(JJ)$ group at last three colours are combined: dark pattern 'main colour', the correspondent 'striping' over it, and the 'background mottling' in it: pale buff when *Rk.* and red when $rk^d rk^d$. In the lower part of table 9 the colours and the connections between them are once more explained.

According to table 9 the monofactorial segregations were:

1. Partly coloured, *tt*, against *T.*: 56 (exp. 48.5) and 138.
2. Dark pattern, *CC*, heterozygous, and striped, $C^{st}C^{st}$: 40 (exp. 48.5), 101 (exp. 97) and 53.
3. Without 'greenish brown factor', *bb*, against *B.*: 43 (exp. 48.5) and 151.
4. Recessive red, $rk^{d}rk^{d}$, against *Rk.*: 50 (exp. 48.5) and 144.

Bifactorial segregations were as follows:

Expected:	12.1	+ 36.4	+ 36.4	+ 109.1
1. *T-C*:	18 $ttC^{st}C^{st}$	+ 38 *ttC.*	+ 35 $T.C^{st}C^{st}$	+ 103 *T.C.*
or:	13 *ttCC*	+ 43 ttC^{st}.	+ 27 *T.CC*	+ 111 $T.C^{st}$.
2. *T-B* :	10 *ttbb*	+ 46 *ttB.*	+ 33 *T.bb*	+ 105 *T.B.*
3. *T-Rk* :	10 $ttrk^{d}rk^{d}$	+ 46 *ttRk.*	+ 40 $T.rk^{d}rk^{d}$	+ 98 *T.Rk.*
4. *C-B* :	9 *CCbb*	+ 31 *CCB.*	+ 34 $C^{st}.bb$	+ 120 $C^{st}.B.$
or:	11 $C^{st}C^{st}bb$	+ 42 $C^{st}C^{st}B.$	+ 32 *C.bb*	+ 109 *C.B.*
5. *C-Rk* :	10 $C^{st}C^{st}rk^{d}rk^{d}$	+ 43 $C^{st}C^{st}Rk.$	+ 40 $C.rk^{d}rk^{d}$	+ 101 *C.Rk.*
or:	11 $CCrk^{d}rk^{d}$	+ 29 *CCRk.*	+ 39 $C^{st}.rk^{d}rk^{d}$	+ 115 $C^{st}.Rk.$
6. *B–Rk* :	3 $bbrk^{d}rk^{d}$	+ 40 *bbRk.*	+ 47 $B.rk^{d}rk^{d}$	+ 104 *B.Rk.*

Clearest indication for linkage is in 6, *B-Rk*, the recombinant value being calculated as 26.4 ± 6.6 or, among the totally coloured ones only, as 27.5 ± 7.8. It must be remarked that 194 is a low number and the number of 3 double recessives very low. The same linkage will be met and discussed in cross 12, p. 48.

Accompanying colours of F_2 will shortly be discussed. As to be expected the plants with partly coloured seed, *tt*, showed green cotyledons and hypocotyl and 'white' flower without red tip standard, the *Rk.*-plants also without red veins wing, but the recessive reds, $rk^{d}rk^{d}$, all with trace of red veins, as the 'Soldaat K.' parent or slightly more or less. The fruits of the *tt*-plants practically always were green, cf. however p 30. For plants with totally coloured seed, *T.*, the accompanying colours are tabulated below:

genotype	*cotyledons*	*hypocotyl*	*flower*	*tip stand.*	*veins wing*	*fruit colour*
dark pattern (*CC*):	3.9 (1–6)	1.6 (0–5)	pale l.	all —tip	*Rk.*: —red veins $rk^{d}rk^{d}$: +red v.	pink 1.4 (0–3)
striped ($C^{st}C^{st}$):	2.9 (0?–5)	0.1 (0–2)	pale l.	—tip?, sl.t. to clear t.	*Rk.*: —red veins $rk^{d}rk^{d}$: +red v.	violet red 5.9 (5–8)
threecol. (CC^{st}):	3.0 (0?–5)	0.9 (0–4)	pale l.	—tip to slight tip	*Rk.*: —red veins $rk^{d}rk^{d}$: +red v.	viol. red 5.1 (3–6)

Conclusion has to be that all T. F_2-plants have some pink anthocyanin in the germ plant, especially in the cotyledons, the striped seeded ones however, as in the other cases, none or very little in the hypocotyl. All flowers pale lilac, red tip always lacking in *CC*, lacking to slight in CC^{st} and slight to clear in $C^{st}C^{st}$ (in the few $C^{st}C^{st}$ plants scored as '—red tip', it probably has been overlooked by the allover pale lilac flower colour, $V^{lae}V^{lae}$, as always shown by F_3-families). Fruit colour for the three types is as usual, the heterozygotes CC^{st} but slightly below $C^{st}C^{st}$-colour. Red veins wing are lacking in *Rk.* and always present in $rk^{d}rk^{d}$, recessive red seeded plants.

As regards the partly-colouredness, the F_2 segregated for one more gene pair. Of the 56 *tt*-plants, with partly coloured seeds, only 14, exactly $\frac{1}{4}$, showed the typical 'soldier' figure of the parent race, six (or less) colour centres, often as separate units, being visible (cf. fig. 6 or 7). In the remaining 42 *tt* plants the coloured part was greater, the white part being restricted, in extreme cases to a very small area, dorsal-terminally localized in the radicula half of the seed. F_2 (and F_3) showed that the difference depends upon *one main gene pair* with an intermediate, variable heterozygote (plus, probably, a gene pair with a much smaller action). The main gene pair is, preliminarily, indicated as *Restr-restr*, from ***restrictus***, the 'soldier type' with its six colour centra being *restr restr*. The heterozygous genotype, *tt Restr restr*, shows a variable expression that can come very near the 'soldier type', but that can always be distinguished from it by the presence of two more colour centra, 7 and 8, cf. fig. 8. The comprehensive literature on partly-coloured *Phaseolus* seed, mainly from LAMRPECHT and SCHREIBER, will not be analysed now and the symbol *Restr-restr* is but used preliminarily.

F_3 was represented bij only 13 families, 2240–22521938. It confirmed seed-coat colour analysis and also the experience regarding the accompanying colours. The CC^{st} F_2-parents of fam. 2246 and 2247 showed less violet red in the fruit than normal: 3 or 3–4 instead of (4,) 5, 6. The F_3 heterozygotes showed the same low values, the homozygotes $C^{st}C^{st}$ slightly more, 'violet red 4–5'. In no other cases the fruit colour of $C^{st}C^{st}$-plants or families was as low as this.

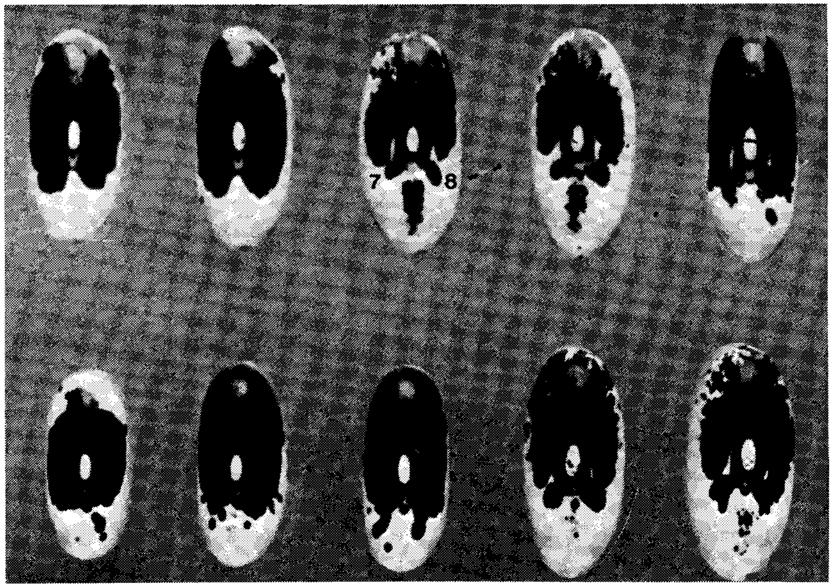


FIG 8. Seeds of two plants with the genotype *P.tt Restr restr*. The type can be distinguished from *P. tt restr restr* (soldier-type) by the presence of *two more colour centra*, 7 and 8, see middle seed in upper row. Cf. figs. 6 and 7.

Summarizing the results of cross 10, 'Wagenaar' with 'Soldaat K.' it can be stated that the pleiotropic actions of T-t and C-C^{st} as found in preceding crosses are confirmed. Also the pleiotropic action of Rk-rk^{d} as described in cross 8, 'White J' with 'Soldaat K', is confirmed: $P.\,\frac{T.}{tt}\,Rk.$ is *without red veins wing* and $P.\,\frac{T.}{tt}\,rk^{d}rk^{d}$ always *with red veins*; in totally coloured $T.$ over the whole wing and in the partly white-seeded tt-plants a trace of red veins in the lower half of it. The 12 colour types depending on the segregation for C-C^{st}, B-b and Rk-rk^{d} are described. The main gene pair that influences the extension of the coloured (or white) part of the seedcoat received (preliminary) the symbol *Restr-restr*, *restr restr* having 6 (or less) colour centres and *Restr restr* two more, centres 7 and 8, see fig. 8; the white part of *Restr Restr* can be very small.

Cross 11: *'Yellowbrown J.' with 'White J.'*

From this cross some small F_2-families and an extensive F_3, fam. 706–775'35, were bred from crosses made by chief-gardener JANSEN. Much experience was gained, but no complete understanding was reached. Later this F_3-material and F_4-families derived from it will be returned to.

In 1936 three F_1-plants after own crosses were bred. Genotypes of the parents and F_1 are:

'Yellowbr. J.': $\boldsymbol{PPTT\;C\;\;C}\;(DD)\boldsymbol{JJGG\;bbV^{lae}v^{lae}}RkRk(\,.\;.\quad.\quad.\,)$
'White J.': $\boldsymbol{pp\,TT\;C^{st}C^{st}}(\,.\;.\,)\boldsymbol{JJ\;gg\;\;BBv\quad v}\;\;RkRk(clcl\;restr\;restr)$
'F_1 being: $\boldsymbol{Pp\,TT\;C\;\;C^{st}}(D\,.\,)\boldsymbol{JJ\;Gg\;\;BbV^{lae}v}\;\;RkRk(cl\,.\;restr\quad.\,)$

Because of homozygous JJ the hilumring gene pair D-d can not be discussed and because of homozygous TT the action of Cl-cl and *Restr-restr*, visible in tt plants, cannot be seen. Segregation in F_2 must be visible for $\boldsymbol{PpCC^{st}GgBbV^{lae}v}$.

Colour characters of parents and F_1 were:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	[*veins wing*]	*fruit*	*seedcoat*
'Yellowbr.J.':	pink (2?)	pink 3	pale l.	— red tip	— red v.	pink 2–3	yell.br. d.p.
'White J.':	green	green	white	— red tip	— red v.	pale pink 1–2	white
F_1 (CC^{st}):	green(?)	green	very p.l.	+ trace r.t.	— red v.	violet red 6	str. and mottl.
	cf. CC^{st} in F_2						(three-coloured)

These colours need hardly any commend as they are explained by the genotype. Of much interest is the 'main colour' of the threecoloured seed of F_1, genotype $GgBb$, i.e. dominant for 'yellowbrown factor' and for '(grey-)greenish brown factor': it really is dark brown, as the CC G.B. dark pattern colour **VI–4** or **VIII–4** in the scheme, the 'striping' over it is very dark (blackish)brown, the 'background mottling' is again pale buff (= not influenced by G and B).

From the three own F_1-plants three F_2-families were bred and, supported by the extensive experience already gained, completely analysed, see table 10, in which segregation for V^{lae}-v that influences flower colour only, has been left out.

With heterozygosity *GgBb* there are, in each of the three main F_2-groups, *CC*, CC^{st} and $C^{st}C^{st}$, four colours to be expected.

a. In the dark pattern type, *CC* it are:

P.JJCCggbb = scheme **VI–1** or **VIII–1** = pale greenish yellow (canary)
P.JJCCG.bb = scheme **VI–2** or **VIII–2** = yellowbrown
P.JJCCggB. = scheme **VI–3** or **VIII–3** = (grey-)greenish brown
P.JJCCG.B. = scheme **VI–4** or **VIII–4** = dark brown

b. In the corresponding striped types, $C^{st}C^{st}$, it are (see table 10):

$P.JJC^{st}C^{st}ggbb$	: red striped,	on pale buff
$P.JJC^{st}C^{st}G.bb$	: orange red stiped,	on pale buff
$P.JJC^{st}C^{st}ggB.$	: greyish violet striped,	on pale buff
$P.JJC^{st}C^{st}G.B.$	: dark (blackish) brown striped,	on pale buff

c. In the four threecoloured CC^{st}-types the colours in each of the four are:
'*main colour*' as the corresponding colour in CC,
'*striping*' over it as the corresponding colour in $C^{st}C^{st}$,
'*mottling*' in it always pale buff, as the background in $C^{st}C^{st}$.
These relations are once more explained in the lower part of table 10.

TABLE 10. Seedcoat colour in F_2 of cross 11, 'Yellowbr.J.' with 'White J.'

	white seedcoat pp	totally coloured seedcoat (P.)												total
		dark p. colour (*CC*)				str. and mottl. (CC^{st})				striped seedcoat ($C^{st}C^{st}$)				
		ggbb	*G.bb*	*ggB.*	*G.B.*	*ggbb*	*G.bb*	*ggB.*	*G.B.*	*ggbb*	*G.bb*	*ggB.*	*G.B.*	
1037'36	36	2	7	4	18	4	9	19	32	2	7	7	25	172
1038'36	40	0	9	3	23	2	11	14	58	2	7	11	20	200
1482'37	16	1	3	0	6	0	5	4	13	1	5	4	6	64
total	92	3	19	7	47	6	25	37	103	5	19	22	51	436
		76				171				97				
		CC = dark pattern				CC^{st} = three-coloured				$C^{st}C^{st}$ = striped				
		greenish yellow (**VI-1** or **VIII-1**)	yellow brown (**VI-2** or **VIII-2**)	grey-greenish brown (**VI-3** or **VIII-3**)	(dark)brown (**VI-4** or **VIII-4**)	'*main colour*': as *CC* (to the left) '*striping*': ± as $C^{st}C^{st}$ (to the right) '*backgr. mottling*': all pale buff (Rk.)				red striped	orangered striped	greyish-viol. striped	dark (blackish) brown striped	
										background: all pale buff (Rk.)				

The monofactorial segregations, cf. table 10, were:

1. white, *pp*, against coloured, *P.*: 92 (exp. 109) and 344.
   Among the 344 coloured seeded plants:
2. dark pattern, *CC*, heterozygous, CC^{st}, and striped, $C^{st}C^{st}$: 76 (exp. 86) 171 (exp. 172) and 97.
3. without, *gg*, against *with* 'yellowbrown factor', *G.*: 77 (exp. 86) and 267.
4. without, *bb*, against *with* 'grey-greenish brown factor', *B.*: 80 (exp. 86) and 264.

5. white flower, *vv*, against pale lilac, V^{lae}. (not in table): 87 (exp. 86) and 257.

The numbers for bifactorial segregations (and possible linkages) were:

1–4. No clear linkage of *P-p* with one of the other gene pairs existed, see the monofactorial segregations 2–5 above.

Bifactorial segregations for the 344 *P.*-plants were:

Expected:	21.5	64.5	64.5	193.5
5. *C-G* :	27 $C^{st}C^{st}gg$	70 $C^{st}C^{st}G$.	53 $C.\ gg$	194 $C.\ G$.
or:	10 $CCgg$	66 CCG.	70 $C^{st}.\ gg$	198 $C^{st}.\ G$.
6. *C-B* :	22 $CCbb$	54 CCB.	55 $C^{st}.\ bb$	213 $C^{st}.\ B$.
or:	24 $C^{st}C^{st}bb$	73 $C^{st}C^{st}B$.	53$C.\ bb$	194 $C.\ B$.
7. $C\text{-}V^{lae}$:	23 $C^{st}C^{st}vv$	74 $C^{st}C^{st}V^{lae}$.	55 $C.\ vv$	192 $C.\ V^{lae}$.
or:	12 $CCvv$	64 CCV^{lae}.	66 $C^{st}.\ vv$	202 $C^{st}.\ V^{lae}$.
8. *G-B*:	14 $ggbb$	66 ggB.	63 $G.\ bb$	201 $G.\ B$.

9. and 10., the relations of *G-g* and *B-b* to V^{lae}-v, have not been worked out (independence *G-B-V* often proved).
General conclusion after checking: no case of clear linkage.

The 'accompanying colours' will be discussed in a few remarks, as the normal tabulation was less easy.

All *pp*-plants gave the normal picture: quite green seedlings, purely white flower, fruit some pale anthocyanin, seed white.

The seedling colour of the *P.(TT)* plants was variable, though two points seemed clear: none of them probably was quite without anthocyanin and secondly, as in all other cases, the hypocotyl of the homozygous $C^{st}C^{st}$ plants was usually green. Also for the further C-C^{st} characteristics the situation was quite normal:

CC , all without red tip, fruit about pink 3 (1–5),
$C^{st}C^{st}$, all with red tip, fruit violet red, slightly over 7
CC^{st} , 171 plants, were very instructive. Like normal their violet red fruit colour was slightly less than with $C^{st}C^{st}$, viz. about 6(5–7), but especially the relation of 'red tip' to V^{lae}-v is important. Among the 128 $CC^{st}V^{lae}$.-plants many were scored as '— red tip' or 'trace red tip?', while among the 43 $CC^{st}vv$ but two were scored as '— red tip': experience with F_3 and F_4 has learned that on white *vv*-colour the smallest red tip is more easy noticed then on (very) pale lilac overall colour, V^{lae}.. In F_3 from both above mentioned $CC^{st}vv$-plants without red tip, fam. 1555 and 1556'37, the red tip was for that matter clearly visible.

F_3- and F_4-families were bred in 1935 (fam 706–775, see p. 41), 1936 (fam. 1196–1224) and 1937 (1555–1566), as preparation for an accurate F_2-analysis, for control of diagnosis, or for checking of 'deviations'. Here only a few remarks will be made. Generally it can be stated that hardly any real deviations from the often mentioned pleiotropic relations occurred, see however below.

An important group deviating plants were F_2 '$P.CC^{st}$'-ones in which the *striping was not at all detected* (gave F_3-fam. 1196–1200) or *was but hardly visible* (gave F_3-fam. 1201–1204). These F_2-mother plants were all scored as '— red tip' or 'very small red tip', but their fruits showed the normal 'violet red 5–7' colour. Eight of these nine F_3-families segregated normally into $\frac{1}{4}$ *CC* (— red tip, fruit slightly pink, seedcoat dark pattern), $\frac{1}{2}$ CC^{st} (without or with very small red tip, fruit normal 'violet red 5–7', stripes on the three-coloured seedcoat usually faint but almost always visible) and $\frac{1}{4}$ $C^{st}C^{st}$ (small red tip, fruit 'violet red 6–8', stripes on seedcoat somewhat pale). From these and other careful studies during 1935–1938 I received the impression that there exists, in addition to C-C^{st}, (at least) *one more gene pair* that regulates size of the red tip standard and also contrast or visibility of seedcoat- striping in CC^{st}- and $C^{st}C^{st}$-plants, but due to the high weather-caused variability, the situation could not completely be cleared up. In the nineth family, no.1200, the striping had really completely disappeared, but this family will be analysed (as other 'crossing-over' individuals, see p. 17, 24 and 37) in a special article on the 'complex locus *C*'.

One group of F_2-plants and F_3-families remained rather puzzling. F_3-families 1214–1218'1936 came from *CC* dark pattern seeded F_2-plants the flower of which had been described as white (*vv*) but 'with or probably with a trace of red tip standard in some flowers or buds', though *P.CC*(*vv*) generally shows no red tip. All five families (accidentally?) segregated for *P-p* and the whiteseeded *pp*-offspring was always scored as having 'green seedlings' and 'pure white flower', while at least part of the *P.CC* (*vv*) plants, with some pink in the seedlings, again were scored as 'white' and 'with a *trace* of red tip', though usually 'on the verge of visibility'. The writer has no explanation, though fruit colour too seemed slightly higher than normal in *P.CC*-plants.

The next four families, 1219–1222'36, really came from *P.CC* dark pattern seeded plants with somewhat more and slightly more intense pink fruit colour than normal for such plants. Their offspring too showed a slightly higher extension (average: 4.2, 3.8, 3.6 and 4.0) and intensity of the pink than usual, but both extension and intensity remained below the violet red of CC^{st} or $C^{st}C^{st}$ while no 'red tip standard' was observed.

The general conclusion from cross 11, 'Yellowbrown J.' with 'White J.', F_1 $PpCC^{st}GgBbV^{lae}v$, is that the pleiotropic actions of *P-p* and C-C^{st}, save for a few doubtful cases (*P.CC* plants with possibly a *trace* red tip), are confirmed. Important is that F_1 had the genotype $(PpJJ)CC^{st}$***G.B.*** and that therefore the colour series *ggbb*, *G.bb*, *ggB.* and *G.B.* could be studied and compared as:

CC, dark pattern types (scheme **VI**– or **VIII-1, -2, -3, -4**),
$C^{st}C^{st}$, *striped types* and
CC^{st}, *threecoloured types,*
} cf. page 42 and table 10

No clear cases of linkage were found. – See also fig. 9, cross 11.

Cross 12: '*Yellowbrown J.*' *with* '*Soldaat K.*'

This appeared to be *the cross with far the most difficulties and complications*! The genotype of parents and F_1, as far as known up to now (save for *Restr Restr*, *ClCl* and *Def Def* of 'Yellowbrown J.' or *defdef* from soldaat K.', that will be learned from the present cross) is:

'Yell.br.J.': *PPTT C C ..JJGGbb*$V^{lae}V^{lae}$ ***Rk Rk*** (***Restr Restr*** *ClCl* ***Def Def***)
'Soldaat K.': *PP **tt*** $C^{st}C^{st}$*..JJ* ***ggBB***$V^{lae}V^{lae}$***rk***^{d} ***rk***^{d} (***restr restr*** *ClCl* ***def def***)
F_1 being: *PPTt C* C^{st}*..JJ**GgBb***$V^{lae}V^{lae}$***Rk rk***^{d} (***Restr restr*** *ClCl* ***Def def***)

During 1936, '37 and '38 small F_1 families were bred, all together 14 plants. The colour characters of parents and F_1 were:

	cotyl.	*hypoc.*	*flower*	*tip stand*	*veins wing*	*fruit col.*	*seedcoat col.*
'Yell.br.J.':	pink 2(?)	pink 3	pale l.	— red tip	— red veins	pink 2 à 3	yell.br. d.p.
'Sold.K.':	green	green	white	— red tip	+ trace r.v.	green	partly col.
F_1 (CC^{st}):	pink 1(?)	green(?)	pale l.	+ trace r.t.	— red veins	viol.red 5–6	totally col.
	cf. CC^{st} in F_2						

For seedling colour see, as in the other crosses, the corresponding F_2-group. The remaining accompanying colours follow from the F_1 genotype. The totally coloured seedcoat is of course threecoloured: CC^{st}. Thanks to the genotype (*JJ*) ***GgBb*** its three colours are, as in cross 11:

'main colour': dark brown (as *CC*-colour **VI–4** or **VIII–4** in the scheme),
'stripes over it': very dark blackish brown (variable colour),
'mottling in it': the normal pale buff (= not influenced by G or B).

Five F_2 families were bred: 1487–1490'37 and 1639'38. Together they gave 532 completely (or almost so) described F_2-plants, cf. table 11. As in cross 10, 'Wagenaar' with 'Soldaat K.', $\frac{1}{4}$ of F_2 was partly coloured *tt* (upper part *a.* of the table) and $\frac{3}{4}$ totally coloured *T.* (lower part *b.* of the table). Segregation in cross 10 and cross 12 is the same, except for the fact that cross 12 moreover segregates for the 'yellowbrown factor' pair *G-g*, the heterozygous part of the F_1-genotype being ***TtCC***st***GgBbRkrk***^{d} (and ***Restr rest*** for colour-extension in the partly-coloured seeded *tt*-plants of F_2). The three main colour groups in F_2 therefore will be *CC*, CC^{st} and $C^{st}C^{st}$ (both in *tt* and *T.*), each group subdivided, in case of complete dominance, into 8 types: for *G-g*, *B-b* and *Rk-rk*^{d}. Leaving dominant red (C^{st}.) and recessive red ($rk^{d}rk^{d}$) first out of consideration, i.e. restricting us to the shiny dark pattern colours (*JJ*)*CCRk.*, represented in rows **VI** and (or) **VIII** of the scheme p. 82, the four F_2-colours depending upon segregation for *GgBb* were easily recognized.:

1. (*CCJJ*) ***ggbb*** (*Rk.*): pale greenish yellow (canary), scheme: **VI–1** or **VIII–1**,
2. (*CCJJ*) ***G.bb*** (*Rk.*): yellowbrown, scheme: **VI–2** or **VIII–2**,
3. (*CCJJ*) ***ggB.*** (*Rk.*): (grey-)greenish brown, scheme: **VI–3** or **VIII–3**,
4. (*CCJJ*) ***G.B.*** (*Rk.*): dark brown, scheme: **VI–4** or **VIII–4**: this dark brown is the 'main colour' in the seed of F_1.

The corresponding colours of the F_2 $C^{st}C^{st}$-shiny striped types appeared to be, according to F_2, F_3 and F_4 experience:

1a. ($C^{st}C^{st}$*JJ*) ***ggbb*** (*Rk.*):	red striped	upon pale buff backgr.
2a. ($C^{st}C^{st}$*JJ*) ***G.bb*** (*Rk.*):	orangered striped	upon pale buff backgr.
3a. ($C^{st}C^{st}$*JJ*) ***ggB.*** (*Rk.*):	greyish violet striped	upon pale buff backgr.
4a. ($C^{st}C^{st}$*JJ*) ***G.B.*** (*Rk.*):	dark (blackish) (very variable) brown striped	upon pale buff backgr.

The pale buff background is not influenced by G-g, B-b or V-v.

The four corresponding threecoloured heterozygotes $CC^{st}Rk.$ always showed:
as 'main colour' the colours *1*, *2*, *3*, or *4* above,
as 'striping' over it the colours *1a*, *2a*, *3a*, resp. *4a*, and
as 'background mottling' for all four the *pale buff* background of $C^{st}C^{st}Rk.$

In describing the 12 $Rk.$-colours above, viz. the CC-dark pattern group, the $C^{st}C^{st}$-striped group and the threecoloured CC^{st}-group, all three groups segregating for G-g and B-b, we started from the shiny dark pattern group $CCJJ$, for four main reasons:

a. The group of the 8 shiny dark pattern colours (scheme p. 82, row **VI, 1–8** and/or **VIII, 1–8**) is the most accurately analysed and described colour group, and also the group in which older (KOOIMAN, 1920, LAMPRECHT, 1932, PRAKKEN, 1934) and younger authors (FEENSTRA, 1960, NAKAYAMA, since 1957) repeatedly came to the same genetical scheme, viz. segregation for G-g, B-b and V-v (or V^{lae}).

b. An accurate description of all colours, variability included, with the help of some of the more generally used four or five colour systems would become very long and still be very unsatisfying and confusing.

c. Also the use of coloured pictures (or fotographs) is unsatisfying, as the likeness hardly ever is complete and often very poor.

d. The precise aim of the present article is to bring the '*yellow-black colours*' and the '*dominant red*' and '*recessive red*' colours *into the same genetical scheme, and to describe all gene actions as far as possible in general terms.*

In describing now the 12 'recessive red' $rk^{d}rk^{d}$-colours occurring in cross no. 12, one-for-one corresponding to the 12 $Rk.$-colours described above, quite the same method will be followed, i.e. the starting again will be from the four shiny dark pattern colours $(CCJJ)^{gg\ bb}_{G.\ B.}\,(Rk.)$ described above under *1.*, *2.*, *3.* and *4.*, in each of them replacing $Rk.$ by $rk^{d}rk^{d}$:

1b. $(CCJJ)$ ***ggbb*** $(rk^{d}rk^{d})$: really reddish (= red over pale greenish yellow)
2b. $(CCJJ)$ ***G.bb*** $(rk^{d}rk^{d})$: slightly orange reddish (= red over yellowbrown)
3b. $(CCJJ)$ ***ggB.*** $(rk^{d}rk^{d})$: dark grey-greenish brown with slight reddish haze over it.
4b. $(CCJJ)$ ***G.B.*** $(rk^{d}rk^{d})$: (very) dark brown with slight reddish haze over it.

In the same way, compared with the four $(C^{st}C^{st}JJ)$ $Rk.$ striped types above (*1a*, *2a*, *3a*, and *4a*,), the corresponding $rk^{d}rk^{d}$ striped types are:

1c. $(C^{st}C^{st}JJ)$ ***ggbb*** $(rk^{d}rk^{d})$: dark red striped upon reddish background
2c. $(C^{st}C^{st}JJ)$ ***G.bb*** $(rk^{d}rk^{d})$: dark orange red striped upon reddish background
3c. $(C^{st}C^{st}JJ)$ ***ggB.*** $(rk^{d}rk^{d})$: (very) dark greyish viol. striped upon reddish background
4c. $(C^{st}C^{st}JJ)$ ***G.B.*** $(rk^{d}rk^{d})$: very dark (blackish) variablebrown striped upon reddish background

The background is hardly or not influenced by G-g, B-b, (or V-v).

The four corresponding threecoloured heterozygotes $(CC^{st})rk^drk^d$ always showed:

as 'main colour' the colours *1b.*, *2b.*, *3b.* or *4b.*,
as 'striping' over it the colours *1c.*, *2c.*, *3c.* resp. *4c.*,
as 'background mottling' in it for all four the *reddish* background colour of $C^{st}C^{st}rk^drk^d$.

This whole explanation means that F_2 of the present cross (the *tt*- and the *T.*-types) should be subdivided into 12 rk^drk^d + 12 *Rk.* colours, i.e. should show 24 columns. In table 11 however but 12 columns are present: segregation for *G-g* has been left out, and therefore the structure of the table is precisely the same as of table 9, for F_2 of cross 10, 'Wagenaar' with 'Soldaat K.', which cross does not segregate for *G-g*.

The reason for this simplification is an unfortunate complication, viz. segregation of a type that I found mentioned casually only once in the *Phaseolus-*

TABLE 11. Seedcoat colour in F_2 of cross 12, 'Yellowbrown J'. with 'Soldaat K.'. The F_1-genotype, as far as heterozygous, was $TtCC^{st}GgBbRkrk^dRestr\ restr\ Def\ def$, but in the table the segregation for *G-g*, *Def-def* and *Restr-restr* has been left out, cf. text.

	dark pattern col. (*CC*)				striped and mottled (CC^{st})				striped seedcoat ($C^{st}C^{st}$)				total
	bb		*B.*		*bb*		*B.*		*bb*		*B.*		
	rk^drk^d	*Rk.*	rk^drk^d	*Rk.*	rk^drk^d	*Rk.*	rk^drk^d	*Rk.*	rk^drk^d	*Rk.*	rk^drk^d	*Rk.*	
a. Partly coloured seedcoat (tt):													
1487'37	0	1	1	1	3	3	7	9	0	1	1	4	31
1488'37	0	1	0	4	0	3	0	10	0	2	3	3	26
1489'37	0	1	1	4	0	2	4	8	0	0	2	4	26
1490'37	0	1	3	4	1	2	3	4	0	2	0	8	28
1639'38	0	1	3	4	0	2	6	6	0	2	2	6	32
total *tt*	0	5	8	17	4	12	20	37	0	7	8	25	143
	30				73				40				
b. Totally coloured seedcoat (T.):													
1487'37	3	4	7	10	3	9	8	23	1	3	4	11	86
1488'37	0	1	6	6	3	9	8	18	0	5	4	12	72
1489'37	2	4	5	10	3	8	10	17	1	4	4	5	73
1490'37	1	6	4	8	2	8	9	21	0	4	2	6	71
1639'38	1	4	2	16	2	6	8	16	0	8	4	19	86
total *T.*	7	19	24	50	13	40	43	95	2	24	18	53	388
	100				191				97				
total *tt* + *T.*	7	24	32	67	17	52	63	132	2	31	26	78	531
	130				264				137				

CC = dark pattern:

grey-greenish brown *and* dark brown (*ggB.* and *G.B.*)
dark greenish brown *and* darker brown with reddish haze (rk^drk^d) over it (*ggB.* and *G.B.*)
pale greenish yellow *and* yellowbr. (*ggbb* and *G.bb*)
reddish colour (rk^drk^d; over pale gr.yell. *and* over yellowbrown (*ggbb* and *G.bb*)

CC^{st} = threecoloured

'main colour':
as *CC* (to the left)
'striping':
as $C^{st}C^{st}$ (to the right)
'background mottling':
red (with rk^drk^d) or
pale buff (*with Rk.*)

$c^{st}C^{st}$ = striped:

greyish violet *and* dark brown str., both on *pale buff* (Rk.) backgr.
dark greyish v. *and* very darkbr. str., both on *red* (rk^drk^d) backgr.
red *and* orangered striped, both on *pale buff* (*Rk.*) backgr.
(dark) red *and* (dark) or. red str., both on *red* (rk^drk^d) backgr.

literature (KAJANUS 1914). It depends upon a gene pair that in F_3 of this cross partly and many years later completely has been analysed by the present author, and that by him is given the symbol *Def-def*, derived from *defectus*: the action of the 'yellowbrown factor' *G.* is *counteracted by def def*, in such a way that in the shiny dark pattern colour *(CCJ.) G. defdef the yellowbrown is but partly developed*, mainly at the ventral side, an irregular shaped dorsal part of variable size not being yellowbrown but showing the pale greenish yellow of *(CCJ.) gg*. In shiny yellowbrown *G.* colour it hardly produces any difficulty, but in *(CCJ.) G.B.*, shiny dark brown, *def def* has the analogous suppressing action upon *G.*, less clearly deliminated however and changing the dark brown more or less towards greenish brown. And as *rkrk*, by darkening and by causing a reddish haze, changes the greenish brown (ggB.Rk) in the direction of dark brown, it is clear that, also in the threecoloured types (but less in the striped $C^{st}C^{st}$-ones), classification for *G-g* becomes difficult and had to be left out from table 11, so that each of the 12 columns contains *gg* + *G.* colours. Distinction between *bb* and *B.* is not at all deminished.

The main monofactorial segregations are:

1. Partly coloured, *tt*, against *T.*: 144 (exp. 133) and 388.
2. Dark pattern (*CC*), heterozygous, and striped ($C^{st}C^{st}$): 130 (exp. 132.7), 264 (exp. 265.6) and 137.
3. Without greenish brown factor, *bb*, against *B.*: 133 (exp. 132.7 and 398).
4. Recessive red, rk^drk^d, against *Rk.*: 147 (exp. 132.7) and 384

In segregations 2, 3 and 4, just above, one *tt*-plant with completely white seed could of course not be included. All segregations were also studied two by two for linkage relations. As in cross 10 (table 9 and p 39) so was in cross 12 but one case of clear linkage found, the same one as in cross 10, viz. between the '(grey)-greenish brown locus', *B-b*, and the 'locus for recessive red', $Rk\text{-}rk^d$, in the repulsion phase.

As this linkage will appear of much importance (see chapter VII) the complete facts are given below:

	$bbrk^drk^d$	$bbRk.$	$B.rk^drk^d$	$B.Rk.$	total	% recombinant gametes
cross 10:	3	40	47	104	194	26.4±6.6
cross 12:	26	107	121	277	531	41.8±3.5
together:	29	147	168	381	725	38.8±3.1

The difference (15.4) between 26.4 and 41.8 is rather high, but because of the low number in cross 10 the D/M of the difference is but 15.4:7.5 = 2.1, and therefore it seems allowed to take both families together.

Tabulation of the accompanying colours in this cross is somewhat difficult, but F_2 and a very extensive F_3 showed that principally there are hardly any differences with the preceding crosses, at least not with respect to *T-t* and $C\text{-}C^{st}$ (*G-g* and *B-b* never influence them), only $Rk\text{-}rk^d$ needing some discussion, partly with the help of the 125 F_3 and F_4 families: 1945–2028 and 2199–2226'38 and 2683–2695'39.

In F_2 of cross 12 it already became clear that there was some complication

The colour characters were:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit*	*seedcoat*
'Hinr.R.':	pink 3.5	± green	pale l.	+ slight r.t.	— red v.	viol.red 6	red striped
'White J.':	green	green	white	— red t.	— red v.	almost green	white
$F_1(C^{st}C^{st})$:	green(?)	green(?)	very p.l.	+ slight r.t.	— red v.	viol.red 6	greyish viol.str.
	cf. however F_2						

The very pale lilac F_1-flower agrees with $V^{lae}v$, and that the striping is not red but greyish-violet depends upon *B* from 'White J.'.

The F_2 families, 1517–1518'37 and 1651–1652'38 gave, as expected, a simple segregation for seedcoat colour, see table 12, with rather to many whites, *pp*:

TABLE 12. F_2-segregation cross 14, 'Hinrich's Riesen' with 'White J.'

family number	White seeded *pp*	red striped $P.C^{st}C^{st}JJbb$ $(vv+V^{lae}.)$	greyish-viol. str. $P.C^{st}C^{st}JJB.$ $(vv+V^{lae}.)$	total
1517'37	22	12 (2+10)	40 (9 + 31)	74
1518'37	17	3 (1+2)	30 (5+25)	50
1651'38	22	9 (2+7)	31 (8+23)	62
1652'38	28	14 (4+10)	36 (13+23)	78
total	89	38 (9+29)	137 (35+102)	264
exp. 4:3:9	66	49.5	148.5	

Among the 175 *P.*-plants segregation was:

bbvv	$bbV^{lae}.$	*B.vv*	$B.V^{lae}$	*total*
9 (exp. 10.9)	29 (exp. 32.8)	35 (exp. 32.8)	102 (exp. 98.5)	175

These numbers agree well with independent segregation for *B-b* and V^{lae}-*v*, 1:3:3:9.

The 'accompanying colours' in F_2 generally agreed with expectation, though seedling colour was low:

	cotyl.	*hypoc.*	*flower*	*tip stand.*	*veins wing*	*fruit colour*
$pp(C^{st}C^{st})$:	green	green	white	— red tip	— red v.	very pale pink 0–3
$P.C^{st}C^{st}$:	pink 1.2 (0–4)	pink 0.3 (0–2)	white to pale 1.	+ slight r.t. (a few – tip)	— red v.	violet red 6.8 (5–8)

A few *P.* seedlings were scored as 'green' 'green' for hypocotyl and cotyledons. but even these were not totally green as the *pp*-plants: they always showed some pink anthocyanin colour at the base of the first-leaf lamina, never found in *pp*-plants. Red tip standard varied from '-tip' via 'trace?' and 'trace' to 'slight red tip', while F_3-families of this cross were not bred. Fruit colour was quite as to be expected.

Cross 15: *'Hinrich's Riesen' with 'Soldaat K.'*

The genotypes of parents (those of 'Hinrich's Riesen' placed between brackets will become known by the present cross) and F_1 are:

'Hinr. R.': $PPTTC^{st}C^{st}ddJJgg\,\mathbf{b}\,\mathbf{b}\,V^{lae}V^{lae}\mathbf{RkRk}$ (*restr restr ClCl* . .   ).
'Sold.K.': $PP\mathbf{t}\,\mathbf{t}\,C^{st}C^{st}\,..\,JJgg\mathbf{BB}\,V^{lae}V^{lae}\mathbf{rk^{d}rk^{d}}$ (*restr restr ClCl def def*).
F_1 being: $PP\mathbf{T}\,\mathbf{t}\,C^{st}C^{st}d\,.\,JJgg\mathbf{B}\,\mathbf{b}\,V^{lae}V^{lae}\mathbf{Rkrk^{d}}$ (*restr restr ClCl def* .).

Two F_1-families were bred, 1306c'37 (4 pl.) and 1590'38 (5pl.). F_1-plant 1306c–2 gave F_2-family 1658'38 and 1306c–1 gave F_2-family 2488'39, from which latter family fruit- and seedcoat colour are not known. These details are mentioned because of some unexpected or contradicting results, see below.

Colours of parents and F_1 (fam. 1306c'37) were:

	cotyl.	*hypoc.*	*flower*	*tip stand*	*veins wing*	*fruit*	*seedcoat*
'Hinr.R.':	pink 3.5	green	pale l.	+ slight r.t.	— red v.	violet-red 6	red striped
'Sold.K.':	green	green	white	— red t.	+ trace r.v.	green	partly col.
$F_1(C^{st}C^{st})$:	pink 1.8	green	pale l.	+ slight r.t.	— red v.	violet-red 6	greyish viol.str.
	cf. $T.\,C^{st}C^{st}$ in F_2						

The F_1-colours above are those of family 1306c'37 and the pink 1.8 cotyledon colour comes from the pink values 1, 2, 2 and 2 for resp. plant 1, 2, 3 and 4. The green hypocotyl colour is as to be expected in $C^{st}C^{st}$ F_1-plants and also the remaining colours are in agreement with the F_1 genotype. As regards seedcoat colour, the red stripes of 'Hinr. R.' are changed into greyish-violet by *B* of 'Soldaat K.', while the recessive red background of 'Soldaat K.' is changed into pale buff by *Rk* from 'Hinr. R.'.

Only one F_2-family, 1658'38, was completely analyzed. Its seedcoat colours were:

	$bbrk^{d}rk^{d}$	$bbRk.$	$B.\,rk^{d}rk^{d}$	$B.Rk.$	*total*
a. partly col. (*tt*):	1	2	3	13	19
b. totally col. (*T.*):	2	17	12	33	64
total (*tt* + *T.*):	3	19	15	46	83

These F_2-numbers are too small for making a dependable linkage analysis, but at least in the *T.*-group and also in the total numbers there is some indication of linkage between *B-b* and $Rk\text{-}rk^{d}$, the same as in crosses 10 and 12: weak linkage in the repulsion phase. The no less than 13 *ttB.Rk.*-individuals (see above) are rather disturbing in this connection, but as all *tt*-plants were of the *restr restr* type (with 6 or less colour centres, in some cases extremely small) a few mis-classifications might be possible. When it is further noticed that among the 19 *tt*-plants no 'circumlineated' *clcl* types occurred, the genotype of 'Hinrich's Riesen' placed between brackets, *restr restr ClCl*, is explained. As both parents lack the 'yellowbrown factor' *G*, it is impossible to decide between *Def Def* or *def def*, the latter being the genotype of 'Soldaat K.' (cf. cross 12, p. 48).

The unexpected or contradicting results mentioned before were in some of the accompanying colours in F_1 and F_2. Mother plant of F_2-family 1658'38 above was F_1-plant 1306c–2 1937. Its cotyledon colour was scored as pink 2, its hypocotyl, as is normal in $C^{st}C^{st}$, as green. Among the 64 totally coloured (T.) F_2-plants most hypocotyls were green (= pink o) and a few pink 1, average value pink 0.1, quite as to be expected. Unexpected, however, was the very low pink colour of the cotyledons: 3 = ?, 42 = green, 17 = pink 1 and 2 = pink 2, average value as low as pink 0.4 (F_1 mother plant: pink 2). F_2-family 2488'39 however, the F_1-mother plant of which but showed cotyledon colour pink 1, gave much higher F_2-values. Seedcoat colour of this family is not available, but flower-colour was 22 white = *tt* and 57 pale lilac (*T.*). In these 57 *T.*-plants the hypocotyl-colour values were: 1 = ?, 38 = green (= pink 0), 12 pink 1, 5 = pink 2 and 1 = pink 3, average pink 0.4; the cotyledon-values were: 1 = ?, 1 = green, 4 = 1, 17 = 2, 26 = 3, 7 = 4 and 1 = 5, average pink value 2.7. – This contrast between the two sister F_2-families, 1658'38 and 2488'39, has probably to be looked at as the most extreme case of influence by time (of scoring) or of temperature (during seedling development). The case has not been investigated further, as during the winter 1939–40 I left the country. When returning during the winter 1945–'46 the whole seed material 1934–1939 had died by moisture and low temperature in a severely damaged institute.

The second point, not quite unexpected, referred to the red veins, more or less clearly visible in $rk^d rk^d$, invisible in *RkRk* and usually in $Rkrk^d$ too. During 1935–'37 it happened in a small number of cases that an F_2-*T.Rk.*-plant (totally coloured, non-recessive red seedcoat) had been scored as having, either over the whole wings or especially in the upper part of it, a very fine doubtful red veining, indicated as '+ ? red veins?' or later as '+ red veins, but in reality–'. Seeds from a few of such F_2-plants were used for a control F_3-family. These control families always gave $\frac{1}{4}$ $rk^d rk^d$ plants (recessive red seeds) with *very clear red veins*, while part of the *Rk.* plants again showed the same type of *extremely fine doubtful red veins*. Conclusion: in case of '*very clear* red veins wing' in the $rk^d rk^d$ plants, the $Rkrk^d$-plants can show the phenomenon described above, i.e. *Rk* being incompletely dominant or, the same, rk^d incompletely recessive.

Now the situation in F_1-family 1306c'37 that gave F_2-family 1658'38 and 2488'39 (from the latter family no seedcoat colour known): all four plants of 1306c'37 were scored as '– red veins'. Of F_2-family 1658'38 all 2 + 12 = 14 $T.rk^d rk^d$ plants showed '+ *very clear* red veins', while the 17 + 33 = 50 *T.Rk.*-plants ultimately all were classified '–red veins', more than half of them, however, of the type '+ r.v., but in reality –', certainly the $Rkrk^d$ heterozygotes.

With F_1-family 1590'38 the circle became closed: its five plants all were scored as '+ very fine r.v. in wings of open flowers or in upper half of wings fullgrown buds, but in reality – red veins'. Family 1590'38 is the only F_1 $Rkrk^d$family in which this observation was made. This may depend upon the year after year *more accurate scrutinizing*, but also upon the fact that this F_1 really was the *most homozygous one for genes intensifying the red veins*, or possibly upon both causes together. F_2 from F_1-1590'38 has alas not been studied.

VI. DISCUSSION OF AND CONCLUSIONS FROM THE PRESENT CROSSES

A. *Introduction*

The material analysed consists of two groups of diallelic crosses (chapter III and IV) plus three 'connecting crosses' (chapter V). The 'names' of the parent varieties, their pheno- and genotypes and the crossing schemes are given at the beginning of chapter III (crosses 1–6) and chapter IV (crosses 7–12; the connecting crosses of chapter V are numbered 13–15. At the end of each cross 1–12 the main conclusions are mentioned.

First aim of the analysis was to find out the relation between the socalled 'yellow-black group' of seedcoat colours (scheme p. 82) and the group of 'red or reddish' ones. Except for seedcoat colour, the author also scored various other colour characters over the whole lifetime, for each individual plant: colour of cotyledons and hypocotyl, flowers (including presence and size or intensity of 'red tip standard' and 'red veins wing') and of the ripening fruits. By these methods (see chapter II) and by an intensive comparison with the results of other investigators (with all generally used colour-systems at hand, see end of the references) it was possible to come to general conclusions on the inheritance of seedcoat colour, including the interrelations between 'yellow-black' and 'red' colours and the pleiotropic actions of the seedcoat colour genes, apparently fitting in with practically all other studies.

Below the main genes concerned and the 'names' we use for them are given, grouped into four catagories, and the genes that have pleiotropic actions written in ***bold*** letters:

a. Two genes necessary for total seedcoat colour:

- ***P***, basic gene or *groundfactor*, all *pp*-plants being whiteseeded.
- ***T***, gene for *totally coloured seedcoat*, *tt*-plants having 'partly-coloured partly-white' seedcoat.

b. Three dominant colour genes, giving together with groundfactor *P* a very pale colour:

- *C*, the 'complex locus' (or: strongly linked loci) *for ever-segregating mottling* of the yellow-black group (C = dark pattern allele, c = background allele, c^u = allele for unchangeable background: Cc and Cc^u are mottled) and *for dominant red* colours (C^r = one-coloured red, C^m = red mottled and C^{st} = red striped; LAMPRECHT: resp. R, R^{ma} and R^{st}). The real structure of this 'complex locus' will be discussed in (a) following article(s).
- *D*, the '*hilumring factor*', producing a brown hilumring but further leaving the seedcoat whitisch or not changing its colour; *P.D.* is not influenced by *G*, *B* and *V*.
- *J*, *J*, the '*shine factor*', also producing a brown hilumring, making the seedcoat shiny creamish pale buff; all J.-colours are shiny and much after-darkening.

c. Three *dominant* modifying (= darkening) genes:

- *G*, the '*yellowbrown factor*'.
- *B*, the '*(grey-)greenish brown factor*'.
- *V*, the '*violet factor*', alleles V, V^{lae} and v (V sometimes produces, with *P* only, a slight pale glaucescent tinge).

d. One *recessive* modifying (= darkening) gene:

Rk, the '*locus for recessive red colour*': $rkrk$ and rk^drk^d.

Starting from this Introduction, A, the further discussions will be made under the headings:

B. Seedcoat colour analysis of the crosses (p. 55–60).
C. Pleiotropic actions of seedcoat-colour genes (p. 60–66).
D. Some further results (new genes and linkages) (p. 66–68).
E. A complete synthesis of seedcoat colour inheritance (p. 68–78).

B. *Seedcoat colour analysis of the crosses*

The first group of crosses, chapter III, crosses 1–6.

The four parental genotypes were concluded to be:

'Wagenaar':	$(PPTT)\mathbf{C\ C\ DDJJgg}\ (bbV^{lae}V^{lae}RkRk)$,
'Citroen':	$(PPTT)\mathbf{C\ C\ dd\ jjGG}\ (bbV^{lae}V^{lae}RkRk)$,
'Kievit':	$(PPTT)\mathbf{C^mC^m dd\ JJgg}\ (bbV^{lae}V^{lae}RkRk)$,
'Hinr. R.':	$(PPTT)\mathbf{C^{st}C^{st} dd\ JJgg}\ (bbV^{lae}V^{lae}RkRk)$,

i.e. only the three loci of the (complementary) *colour genes* were involved (but because of CC, C^mC^m and $C^{st}C^{st}$ no recessive whiteseeded P.-plants segregated) *and* the locus of the *modifying gene* 'yellowbrown factor' G.

Cross 1, 'Wagenaar', shiny pale greenish yellow, with 'Citroen', pale (greenish) yellow without brown hilumring, has extensively been discussed in PRAKKEN I (1940) and PRAKKEN II (1970). It was this cross that made clear that the 'yellowbrown factor' G has no hilumring-producing action: from the fact that the F_1-plants showed a shiny yellowbrown seedcoat (scheme: **VI–2** or **VIII–2**) it followed that the 'yellowbrown factor' G was, cryptomerically, present in the hilumringless 'Citroen' parent (scheme- **II–2**), while the bifactorial F_2 segregation for hilumring, viz. 1/16 without it, made clear that 'Wagenaar' possessed *both* dominant hilumring producing colour genes, 'hilumring factor' D and 'shine factor' J ($CCDDJJggbbV^{lae}V^{lae}$, scheme: **VIII–1**). – The total F_2-segregation (table 1, p. 10) quite agreed with these considerations:

$1/16\ (CC)ddjj\left\{\begin{matrix} gg \\ G. \end{matrix}\right\} =$ (mat) pale greenish yellow without hilumring, scheme: **II–1** and **II–2**

$3/16\ (CC)D.jj\left\{\begin{matrix} gg \\ G. \end{matrix}\right\} =$ (mat) pale greenish yellow with a brown hilumring, scheme: **IV–1** and **IV–2**, the latter with car. str.

$$12/16\ (CC)\ {dd \atop D.}\ J.\left\{\begin{array}{ll} 3/16\ gg = & \text{shiny pale greenish yellow,} \\ & \text{scheme: } \mathbf{VI\text{–}1} \text{ and } \mathbf{VIII\text{–}1} \\ 9/16\ G. = & \text{shiny yellowbrown,} \\ & \text{scheme: } \mathbf{VI\text{–}2} \text{ and } \mathbf{VIII\text{–}2}. \end{array}\right.$$

From this it becomes clear that:
in $(CC)\ ddjj$ the yellowbrown factor G is *almost without influence*,
in $(CC)\ D.jj$ its *influence is very small* (*caruncula stripe*), while only
in $(CC)\ {dd \atop D.}\ J.$ it has the *very great influence* from which the name comes;
and further that:

in the shiny *J.*-types the 'hilumring factor' *D* is practically without influence.

As will appear in crosses 2, 5 and 6, the same statements hold good for the dominant red colours: (C^rC^r), C^mC^m and $C^{st}C^{st}$, resp. the heterozygotes (CC^r), CC^m, CC^{st} and C^mC^{st}.

Cross 2, between shiny red mottled 'Kievit' and shiny red striped 'Hinrich's Riesen', both with shiny pale buff background, gave F_1-plants that produced shiny red upon pale buff mottled seeds, but the pale buff background spots in the C^mC^{st}-seeds were on the mean *slightly greater* than in C^mC^m and especially *much more variable in size*: mottled appeared to be sub-dominant over striped. All their other genes being the same, the F_2 (table 2 p. 11 and fig. 2) showed monofactorial segregation into C^mC^m, C^mC^{st} and $C^{st}C^{st}$, corroborated by F_3, also the pleiotropic actions of C^m and C^{st}, cf. under chapter C of this discussion.

Crosses 3 and 4, between 'Wagenaar' (shiny pale greenish yellow, *CC*, scheme: **VIII–1**) on the one side, and on the other side shiny red mottled 'Kievit', C^mC^m, resp. shiny red striped 'Hinrich's Riesen, $C^{st}C^{st}$, gave very simple results, as had to be expected for two reasons. Firstly, C-C^m-C^{st} almost behaved as multiple alleles: but two deviating plants were found (table 4). Secondly both, shiny greenish yellow and shiny red mottled or red striped, are known to be the most recessive colour type in their series of shiny colours: *ggbbvv* (or $V^{lae}V^{lae}$).

For both crosses the seeds of F_1-plants, CC^m and CC^{st} resp., were *threecoloured,* showing a combination of the parental colours:

1. '*main colour*', esp. in CC^{st} and less pronounced (i.e. more covered by red) in CC^m, was the shiny pale greenish dark pattern colour of the 'Wagenaar' parent;
2. '*red mottling*' (cross 3) resp. '*red striping*' (cross 4) partly covered or locally replaced this 'main colour', the extension of the red being slightly less than in C^mC^m resp. $C^{st}C^{st}$.
3. '*pale buff background spots*' were present in the greenish yellow main colour, of a type and size strongly reminding of the spots in heterozygously mottled *Cc* or Cc^u plants in the yellow-black group.

F_2-segregation for seedcoat colour was monofactorial:

cross 3 (table 3, p. 15):
$^1/_4$ *CC*, shiny pale greenish yellow (**VIII–1** and ev. **VI–1**).
$^2/_4$ CC^m, threecoloured, i.e. double mottled.
$^1/_4$ C^mC^m, shiny red mottled upon pale buff.

cross 4 (table 4, p. 17; two deviating plants):
$^1/_4$ CC, shiny pale greenish yellow (**VIII–1** and ev. **VI–1**).
$^2/_4$ CC^{st}, threecoloured, i.e. mottled and striped.
$^1/_4$ $C^{st}C^{st}$, shiny red striped upon pale buff.

Crosses 5 and *6*, between 'Citroen' (scheme: **II–2**) on the one side, and on the other side shiny red mottled 'Kievit' resp. red striped 'Hinrich's Riesen' are quite in accordance with the results of crosses 1–4.
The genotypes are:

$$\text{‘Citroen’:}\quad (PPTT)\ C\ C\quad \boldsymbol{dd\,j\,jGG}(bbV^{lae}V^{lae}RkRk)$$

$$\left.\begin{array}{l}\text{‘Kievit’ resp.}\\ \text{‘Hinr.R.’}\end{array}\right\}(PPTT)\left\{\begin{array}{l}C^mC^m\\ C^{st}C^{st}\end{array}\right\}\boldsymbol{dd\,JJ\,gg}\ (bbV^{lae}V^{lae}RkRk)$$

$$\text{‘F}_1\text{ therefore:}\ (PPTT)\left\{\begin{array}{l}CC^m\\ CC^{st}\end{array}\right\}\boldsymbol{dd\,JjGg}\ (bbV^{lae}V^{lae}RkRk)$$

F_2-segregation (see fig. 3 and 4, p. 20 and 23) was, except for CC^m against CC^{st}, exactly the same for both crosses. The $^1/_4$ without brown hilumring showed that both, 'Kievit' and 'Hinrich's Riesen', *lacked the hilumring factor D*: segregation was for $\left.\begin{array}{l}CC^m\\ CC^{st}\end{array}\right\}(dd)\ JjGg$ only, resulting in the three groups of three rows each in fig. 3 and 4, every row coming from one plant. The upper group of three in both figures is $ddjj\left\{\begin{array}{l}gg\\ G.\end{array}\right.$, *G-g* being practically without influence, the middle group is *ddJ. gg* (shiny), while the lowest group is *ddJ. G.* (shiny). Within each group of three applies:

a. = dark pattern type, *CC*,
b. = threecoloured type, CC^m resp. CC^{st},
c. = homozygously mottled resp. striped type, C^mC^m resp. $C^{st}C^{st}$.

In the upper group, *ddjj*, the background colour in *b* and *c* is *pure white*, in the middle and lowest group, *(dd)JJ*, it is *shiny pale buff* (while in *D.jj*, if it had been present, it would have been *whitish*). See further the numbers (left) and the colour description (right) in figs. 3 and 4.

The second group of crosses, chapter IV, crosses 7–12.

The four parental varieties of this group showed a much greater genotypic diversity than those of the first group, as eight of the nine loci appeared to be involved.

'Wagenaar': $PPTTC\ \ C\quad DD\ JJ\,g\,g\,b\,b\,V^{lae}V^{lae}RkRk$
'Yellowbr. J.': $PPTTC\ \ C\ \ (DD)JJGGb\,b\,V^{lae}V^{lae}RkRk$
'White J.': $ppTTC^{st}C^{st}\ \ .\ .\ JJ\,g\,gBB\ v\quad v\quad RkRk$
'Soldaat K.': $PPtt\ \ C^{st}C^{st}\ \ .\ .\ JJ\,g\,gBB\,V^{lae}V^{lae}rk^drk^d$

Only the locus *J* was homozygously dominant in the four parent varieties, because the three coloured-seeded parent varieties, and all F_1, F_2, etc. colours, *CC*, CC^{st} and $C^{st}C^{st}$, are of the *shiny and afterdarkening type*, *JJ*. The *CC*-dark pattern colours therefore belong to *row* **VI** (or **VIII**) of the scheme p. 82. For the present purpose, analysis of seedcoat colour, the segregation *P-p* can be left out of consideration, and also *T-t*, as *tt*-colours (partly white seedcoat) go quite parallel with the *T.*-ones. *D-d* cannot be judged because of homozygosity *JJ*, and V^{lae}-*v* at last influences flower colour only (pale pink versus white). Essential for the discussion here are therefore only: $C\text{-}C^{st}$, *G-g*, *B-b* and $Rk\text{-}rk^{d}$. As 'Soldaat K.' is the only parent variety with *recessive red colour*, the crosses 7, 9 and 11, between 'Wagenaar', 'Yellowbrown J.' and 'White J.', will first be discussed (see scheme of crossings, p. 25): all *RkRk*, and segregating only for $C\text{-}C^{st}$, *G-g* and *B-b*. This means that of the shiny dark pattern colours, *CCJJ*, only the colours **VI**–(or **VIII**)–**1**, **2**, **3** and **4** appear (cf. scheme p. 82), in the first three crosses (7 ,9 and 11) combined with *dominant red* (*RkRk*), in the latter three (8, 10 and 12) with *dominant* (*Rk.*) and with *recessive red* ($rk^{d}rk^{d}$).

Cross 7, 'Wagenaar' (scheme: **VIII–1**) with 'Yellowbrown J.' (scheme: **VIII–2**), gave the expected shiny yellowbrown F_1, *Gg*, and a monofactorial F_2-segregation, into 65 shiny pale greenish yellow (*gg*; scheme: **VIII–1**) and 192 shiny yellowbrown (*G.*; scheme: **VIII–2**).

Cross 9, 'Wagenaar' with 'White J.' gave F_1-plants with *threecoloured seed*, striped and mottled, the 'main colour' being (see scheme p. 82) like shiny dark pattern colour **VI–3**: grey-greenish brown, Lamprecht's 'münzbronze' or 'buffy brown'. The F_1-genotype must be: $(PpTT)CC^{st}(D.JJgg)\mathbf{Bb}(V^{lae}vRkRk)$. F_2 (see table 8, p. 35) gave $^1/_4$ *pp*, no partly-coloured seeded *tt*, $^3/_{16}$ *P.vv*, i.e. white flowered plants with coloured seed, and no $rk^{d}rk^{d}$-recessive red seeded plants; from this the genotype of 'White J.' could be concluded really to be $ppTT\text{-}C^{st}C^{st}.\ .(JJ)ggBBvvRkRk$. From table 8 it is further to be seen that the 266 *P.*-plants segregated into $^1/_4$ *CC* (55 dark pattern types), $^2/_4$ CC^{st} (132 threecoloured, i.e. striped and mottled) and $^1/_4C^{st}C^{st}$ (79 striped), all of shiny *JJ*-type, and each of the three groups subdivided for the 'grey greenish brown factor' *B*. For *CC*-dark pattern this means: *ggbb* (like the pale greenish yellow 'Wagenaar' parent, scheme: **VI–1** or **VIII–1**; number unexpectedly low) and *ggB.* (grey-greenish brown, as the 'main colour' of F_1; scheme: **VI–3** or **VIII–3**). For $C^{st}C^{st}$, homozygously striped, it appeared to be: *ggbb*, *shiny red striped* upon shiny pale buff background, and gg*B.*, shiny *greyish-violet striped*, also on pale buff background. The corresponding threecoloured heterozygotes CC^{st} at last showed the combination of *CC*- and $C^{st}C^{st}$-colours:

	$(JJ)CC^{st}ggbb$	$(JJ)CC^{st}ggB.$	
'main colour':	pale greenish yellow (**VI–1**)	grey-greenish brown (**VI–3**)	like F_1-type
'stripes':	red	greyish violet	
'backgr.mottling':	pale buff	pale buff	

Cross 11, 'Yellowbrown J.' with 'White J.'. Yellowbrown J.' differs from 'Wagenaar' in cross 9 only in that it possesses the 'yellowbrown factor' *G*. In the seed of the F_1-plants, in both cases CC^{st}, this is expressed by the fact that its 'main colour' is dark brown, viz. *GgBb*, like dark pattern colour *(JJ)G.B.*, scheme: **VI–4** (LAMPRECHT: 'mineralbraun' or mineral brown). For F_2 (see table 10 p. 42) this means that in each of the three types *CC*, CC^{st} and $C^{st}C^{st}$, four colours occur, viz. *ggbb*, *G.bb*, *ggB.* and *G.B.*, in the ratio 1:3:3:9. Table

10 shows that this rather precisely is the case, see the numbers behind 'total' in the table. Below these 'total' numbers of the table the colour 'names' or better rough indications of the colours, all *RkRk*, are given:

CC (*dark pattern*):

1. *ggbb* : pale greenish yellow or 'Wagenaar' type (scheme: **VI–1**).
2. *G. bb*: yellowbrown, like 'Yellowbr.J.' (scheme: **VI–2**).
3. *ggB.* : grey-greenish brown (scheme: **VI–3**).
4. *G. B.*: dark brown, the 'main colour' of F_1 (scheme: **VI–4**).

$C^{st}C^{st}$ (*striped*, all on pale buff background):

1. *ggbb* : red striped on pale buff backgr.
2. *G. bb*: orange red striped on pale buff backgr.
3. *ggB.* : greyish-violet striped on pale buff backgr.
4. *G. B.*: dark (to blackish) brown str., rather variable on pale buff backgr.

CC^{st} (*threecoloured*, i.e. striped and mottled):

1.
2. 'main colour', like *CC*-dark pattern colours 1–4,
3. 'stripes' over it, like the stripes in $C^{st}C^{st}$, 1–4,
4. 'mottling' in it always pale buff, like the backgr. colour in $C^{st}C^{st}$

Now the crosses in which moreover is segregation for Rk-rk^d: 8, 10 and 12.

Cross 8, 'White J.' with 'Soldaat K.', see fig. 5 p. 25, makes the connection between crosses 7, 9 and 11 treated above (all *RkRk*) and crosses (7), 10 and 12. Both the latter crosses have, like cross 8 itself, the recessive red 'Soldaat K.', rk^drk^d, as one of the parents. This latter variety has a partly coloured seedcoat, *PPtt* (see figs. 6 and 7). The coloured part shows *very dark greyish violet stripes on a red(dish) background* (rk^drk^d). The seeds of the F_1 (totally coloured: *PpTt*) were *greyish-violet striped on a pale buff background* ($Rkrk^d$), precisely as the $C^{st}C^{st}(JJ)gg\,B.\,(RkRk)$ type described just before, this F_1 however being heterozygous, $Rkrk^d$. In the F_2 (table 6, p. 28) these two colour types were the only ones that occurred, among the totally coloured *T.*-plants and also among the partly coloured *tt*-plants, in the expected ratio, see the lower lines of the table. The genotypes for both parents could be concluded and the only difference of importance for seedcoat colour really is Rk-rk^d:

'White J.': $ppTTC^{st}C^{st}..JJggBBVv\ v$ **RkRk** (for *restr restr* cl cl }
'Soldaat K.': $PPtt\ C^{st}C^{st}..JJggBBV^{lae}V^{lae}$**$rk^drk^d$** (for *restr restr ClCl* } see D.).

Crosses 10 and 12. The fact just mentioned, i.e. that the only genetic difference in seedcoat colour genes between 'White J.' and 'Soldaat K.' that really matters is *RkRk* against rk^drk^d, has an important consequence. It means that the F_2-segregations for seedcoat colour in crosses 10 and 12 will be the same as in crosses 9 resp. 11, but in 10 and 12 *moreover for* Rk-rk^d, cf. fig. 5. p. 25:

10. 'Wagenaar' with 'Soldaat K.',

$F_1 = PPTtCC^{st}..JJgg\,\mathbf{Bb}V^{lae}V^{lae}\mathbf{Rkrk^d}$;

12. 'Yellowbrown J.' with 'Soldaat K.',

$F_1 = PPTtCC^{st}..JJGgBbV^{lae}V^{lae}\boldsymbol{Rk}rk^{d}$.

This again means that, at least in the F_2 of cross 12 that segregates for *G-g* and *B-b*, the four genotypes

ggbb, *G.bb*, *ggB.* and *G.B.*

occur within the following forms:

a. $(JJ)CC\ \ Rk.$, four *shiny dark pattern colours* of the yellow-black group (scheme: **VI–1, –2, –3** and **–4**)

b. $(JJ)C^{st}C^{st}Rk.$, four *shiny homozygously striped colours*, i.e. with two alleles for dominant red.

c. $(JJ)CC^{st}\ \ Rk.$, four *shiny threecoloured types*, with one allel for dominant red (C^{st}).

d. $(JJ)CC\ \ rk^{d}rk^{d}$, four *shiny recessive reds*, corresponding with a.

e. $(JJ)C^{st}C^{st}rk^{d}rk^{d}$, four *shiny recessive reds*, corresponding with b.

f. $(JJ)CC^{st}\ \ rk^{d}rk^{d}$, four *shiny recessive reds*, corresponding with c.

Altogether 6 × 4 = 24 types, showing the integration between *yellow-black* colours, *dominant red* and *recessive red.* The segregations and colour-descriptions are to be found in table 9, p. 38 and table 11, p. 47. They will, however, not be discussed here, but they will be used in the last part of this discussion, *a complete synthesis of seedcoat colour inheritance* (p. 68–79).

C. *Pleiotropic actions of seedcoat colour genes*

In the enumeration of the main seedcoat colour genes on p. 54 those loci that appeared to have *pleiotropic colour actions* upon other plant parts are written with a bold letter:

P, ***T***, ***C***, ***V*** and ***Rk***;

those that did not have such a detectable pleiotropic action are written with normal letter: the colour genes *D* (hilumring factor) and *J* (shine factor) and the modifying genes *G* (yellowbrown factor) and *B* (greenish brown factor). Of the five loci with pleiotropic action it is only the 'complex locus' *C* that segregates (C-C^{m}-C^{st}) in the first group of crosses, chapter III, while in the second group, chapter IV, all five loci show segregation.

P, *the basic gene or groundfactor*

A long series of investigators has observed that whiteseeded *pp*-plants always have pure green seedling and white flowers. Stems and fruits also look green, at least superficially, but a more close inspection shows that some pale anthocyanin colour usually does occur. In the present study the only *pp*-variety, 'White J.' had its fruit colour described as 'almost green'. The fruit colour of its F_1 families (crosses 8, 9, and 11, see fig. 5, p. 25), genotype *PpT.*, in all three cases was the colour as to be expected on the ground of the further genotype, esp. the loci ***C*** and ***V***, cf. below. In F_2 most *pp*-plants showed in their ripening fruit a (very) pale pink 1–3 or 1–4, while in some plants they were scored as pure green, especially in cross 8, the F_1 of which was *PpTt*, see under ***T*** below. In the present material the allel *V* was lacking, only V^{lae} and *v* being present, and therefore only pale pink and no pale violet anthocyanin colour occurred in (stems and) fruit walls of *pp*-plants. As far as known to me Tjebbes and Kooiman (V, 1921) were the only investigators that observed the $V\text{-}V^{lae}$ action in whiteseeded *pp*-plants. Their F_1-plants were homozygously $C^{st}C^{st}$, while segregation among others was for *P-p* and $V\text{-}V^{lae}$. Among the *P.* F_2-plants this resulted in $^1/_4$ $V^{lae}V^{lae}$ with intense (violet-)red fruits (cf. under *C* below) and $^3/_4$ V. plants with black-violet fruit colour. Parallel with this $V\text{-}V^{lae}$ segregation among the *P.*-plants a segregation among the whiteseeded *pp*-plants was observed (and corroborated by F_3-observations): $^1/_4 ppV^{lae}V^{lae}$ with pale pink to pale red fruit colour and $^3/_4$ *ppV.*, with pale violet fruit colour, both types of *pp* being easy distinguishable (Tjebbes and Kooiman did not use $V\text{-}V^{lae}$ but *Bl-bl*, see under chapter E, p. 70).

T, the factor for totally coloured seedcoat.

For *T.–tt* my observations for the greater part agree with those of other investigators: *tt*-plants have, also when the white part of the seedcoat is extremely small or even in (almost) all seeds invisible, pure green cotyledons and hypocotyl, white flowers and usually green (i.e. anthocyaninless) ripening fruits. In the present study the only variety with partly coloured seedcoat, *tt*, was the recessive red 'Soldaat K.', rk^drk^d. In connection with this rk^drk^d genotype, the flower was *not completely white*, but showed in the lower half of the wings fine fragments of '*red veins*', cf. fig. 9, flower 2. Also most *tt* rk^drk^d F_2-plants showed the same character (not, however, $pprk^drk^d$-plants). See further under the gene ***Rk*** below. Precisely the same type of flower, probably also from *tt* rk^drk^d-plants, is pictured in Miyake, Imai and Tabuchi (1930, Pl. I, 6), as far as known to me the only place were 'red veins wing' are observed. – Rests to state that the green fruit colour of *tt*-plants usually is a real green (as contrasted with the pale anthocyanin mostly present in the 'green' fruits of *pp*-plants, see above under ***P***), save for the fact that under special circumstances, viz. when ripening fruits are lying on the wed ground, a clear anthocyanim colour of normal intensity can locally have been developed.

C, the 'complex locus' for ever-segregating and constant mottling etc.

Under this symbol *C* are dealt with the alleles of the 'locus for eversegregating mottling' within the yellow-black group of colours, $C\text{-}c\text{-}c^u\ldots$, and (preliminarily) also those of the alleles for 'dominant red' C^r, C^m, $C^{st}\ldots$. The alleles occurring in the present crosses are *C* (dark pattern allel), C^m (allel for red mottling) and C^{st} (allel for red striping) and mainly these three will be discussed. It may be remembered that not only the three homozygous seedcoat colour types can sharply be distinguished, *CC*, C^mC^m and $C^{st}C^{st}$, but also the three heterozygous ones CC^m, CC^{st} and C^mC^{st} from the homozygous ones. (The very few gametes and plants that resulted from recombination within the 'complex locus' will, as mentioned before, not be discussed in the present article.)

At the beginning of chapters III and IV the genotype of the four parent varieties and all their colour characters are to be found, at the beginning of each cross those of the two parents and F_1, while in each cross, after the F_2 seedcoat colour analysis, the 'accompanying colours' are discussed. In connection with the *C*-locus are of importance the colour of: cotyledons, hypocotyl, tip of standard and ripening fruit. The conclusions to be drawn from chapter III for *C*, C^m and C^{st} are quite parallel with those for *C* and C^{st} in chapter IV, save may be for some differences in extent or intensity of the colours, differences that I was unable to analyse genetically. It is only in chapter IV that moreover the complicating segregations for *P-p* and *T-t* (and Rk-rk^d) occur, see ***P*** and ***T*** above.

Looking at the F_2 and the F_3 from all crosses it became clear that, in *P.T.*-plants, the homozygous genotypes *CC*, C^mC^m and $C^{st}C^{st}$ always showed pleiotropic actions as follows (in V^{lae}. or *vv*-genotypes; *V* was not present and therefore no violet occurred):

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
C C (dark pattern):	pink	pink	— red tip	slightly pink
C^mC^m (red mottled):	green	green	— red tip	slightly pink
$C^{st}C^{st}$ (red striped):	pink	almost green	+ red tip	intense violet-red

('— red tip' and '+ red tip' is 'without' and 'with red tip standard')

A few supplementary remarks on this table may be made. As shown by the tables and the discussions in crosses 2, 3 and 5, with red mottled 'Kievit' as one of the parents (cf. fig. 1, p. 8) the 'green' colour of (*P.T.*) C^mC^m-seedlings is *pure green*, without any visible trace of anthocyanin, and so it was in all other C^mC^m-varieties and their offspring I have seen (at least when $C^mC^mV^{lae}$. or C^mC^mvv, for when dominant 'violet factor' *V.* was present a *trace of violet* anthocyanin was often visible, at the base of the cotyledons). – The quantity of pink in cotyledons and hypocotyl of *CC* F_2-plants (scale from $0 =$ pure green to $10 =$ totally covered with pink) was rather variable: from 1 (or seldom 0) to 7, mean F_2-value usually being 3–4. The variation seemed mainly to depend on *temperature* (low value with high temperature, e.g. when F_1 seedlings were bred in the hot house) and on *time of observation* (cotyledons shrinking and fading with time; hypocotyl more slowly developing its full anthocyanin content). Part of the variability probably depended on *genetic differences*, but a clear analysis has not been possible. – In $C^{st}C^{st}$ the pink colour of cotyledons was about as in *CC*, but their hypocotyl was often scored as 'green', like in C^mC^m, though in a variable number of $C^{st}C^{st}$ F_2-plants a little colour was stated, pink 1–3, the average value in an F_2- or F_3-family however practically always being below pink-1. This holds good for $C^{st}C^{st}$ plants in all crosses with a $C^{st}C^{st}$ as one of the parents: 'Hinrich's Riesen', 'White J.' and 'Soldaat K.'. Quite the same observation for the hypocotyl of $C^{st}C^{st}$-plants was made by NAKAYAMA and SAITO (X, 1971).

The so called 'red tip standard' (see chapter II) was in *CC*- and C^mC^m-plants always completely lacking ('—red tip' in the table above), while in $C^{st}C^{st}$-plants it is probably always present ('+ red tip'): when in a few cases not observed in a homozygously striped $C^{st}C^{st}$ F_2-plant, it was found in their F_3-offspring. Its size is *extremely variable*, from over more than half of the standard to (almost) invisible. Like in the case of anthocyanin in the seedlings the variability is partly caused by (non-analysed) genetic differences and partly by environmental influences: by much sunlight the extension is increased, by dark weather or by a shadowed place on the plant it becomes decreased, as shown by repeated observations on the same group of plants. The red tip, if very weak, is best visible at the tip of the flower buds.

The intense violet-red fruit colour of $C^{st}C^{st}$-plants at last, usually 5–9 (scale again: 0 = green, to 10 = totally covered with violet red), average value about 6 to 7, was very conspicuous as compared with the slight pink, 0–4, of *CC* and $C^{m}C^{m}$ plants. The variation in quantity and intensity of the violet red appeared not very great, and distinguishing it from the slightly pink types was hardly ever difficult.

So far the colours connected with the three homozygous types. As mentioned above, the heterozygotes, CC^{m}, CC^{st} and $C^{m}C^{st}$, were by their seedcoat pattern and/or colour clearly distinguishable from the homozygotes. It could be stated (see the descriptions or tables regarding the 'accompanying colours' for F_2 of the crosses) that the quantity of pink colour in cotyledons and hypocotyl and the size of red tip standard were *one the average intermediate*. This meant that in many heterozygous plants the values for seedling colour or red tip standard were on the verge of zero or that colour even was quite invisible (= —), cf. e.g. F_2- and F_3-analysis in cross 2, 'Kievit' with 'Hinrich's Riesen'. Such cases of lacking of the red tip were often controlled by the next generation and always the 'red tip standard' *reappeared,* at least in (most of) the homozygously striped plants, $C^{st}C^{st}$. – The intense violet-red fruit colour of $C^{st}C^{st}$ at last, 5–9 and on the average 6 to 7, appeared to be, in CC^{st} and $C^{m}C^{st}$, not intermediate but subdominant, their fruit colour being decidedly intense violet-red but of a somewhat lower quantity, usually 4–7 and on an average 5 to 6, about one point lower than in the corresponding $C^{st}C^{st}$-plants.

The general conclusion to be drawn from my own results and from those of other authors seems to be that each allel of the 'complex locus' *C* usually has its own pleiotropic actions, but this point will not now be further delt with.

V, the violet factor, alleles (V,) V^{lae} and *v*.

Five of the seven varieties used in this study possessed a pale lilac flower, $V^{lae}V^{lae}$, the other two were white-flowered, 'White J.' being *ppTTvv* (double recessive for white flower) and 'Soldaat K.' being $PPttV^{lae}V^{lae}$. The F_1 between the two latter varieties (cross 8) therefore was *triple heterozygous for white flower,* $PpTtV^{lae}v$, and extremely pale lilac. See table 6, p. 28. The most dominant allel of the series, the 'violet factor' *V*, was not at all present in the parent varieties, therefore only pink or violet-red anthocyanin colours occurred and no violet ones, while the seedcoat colours of the yellow-black class all belonged to *columns* 1–4 of the scheme p. 82, the left half. The flower colour of $V^{lae}v$ appeared to be much paler than the pale lilac of $V^{lae}V^{lae}$. By heterozygosity *Pp* and *Tt* the $V^{lae}v$-colour becomes still paler, cf. $PpTtV^{lae}v$ mentioned above, that only with some difficulty can be distinguished from the white-flowered *vv*. From all the crosses in which the only *vv*-variety 'White J.' was the one parent (see fig. 5, crosses 8, 9 and 11) it became fully clear that the difference between V^{lae}. (pale or very pale lilac flower) and *vv* (white flower) *is in flower colour only*: neither upon seedcoat colour nor upon the anthocyanin of seedling or fruit walls has *vv* any influence, while it is of importance to know, that *vv only changes the overall colour of the flower into white*: it does not influence the particular flower characters 'red tip standard' (in C^{st}., cf. under locus *C* above) nor 'red veins wing' (in $rk^d rk^d$, cf. under locus ***Rk*** below). Rather the contrary, for the contrast and therefore the visibility of both these particular characters is more clear against the white overall colour of *vv*-flowers than against the pale lilac of V^{lae}. ones (and, according to my further experiences, in pale lilac V^{lae}.-flowers the visibility is greater or better than in violet coloured *V*.-ones).

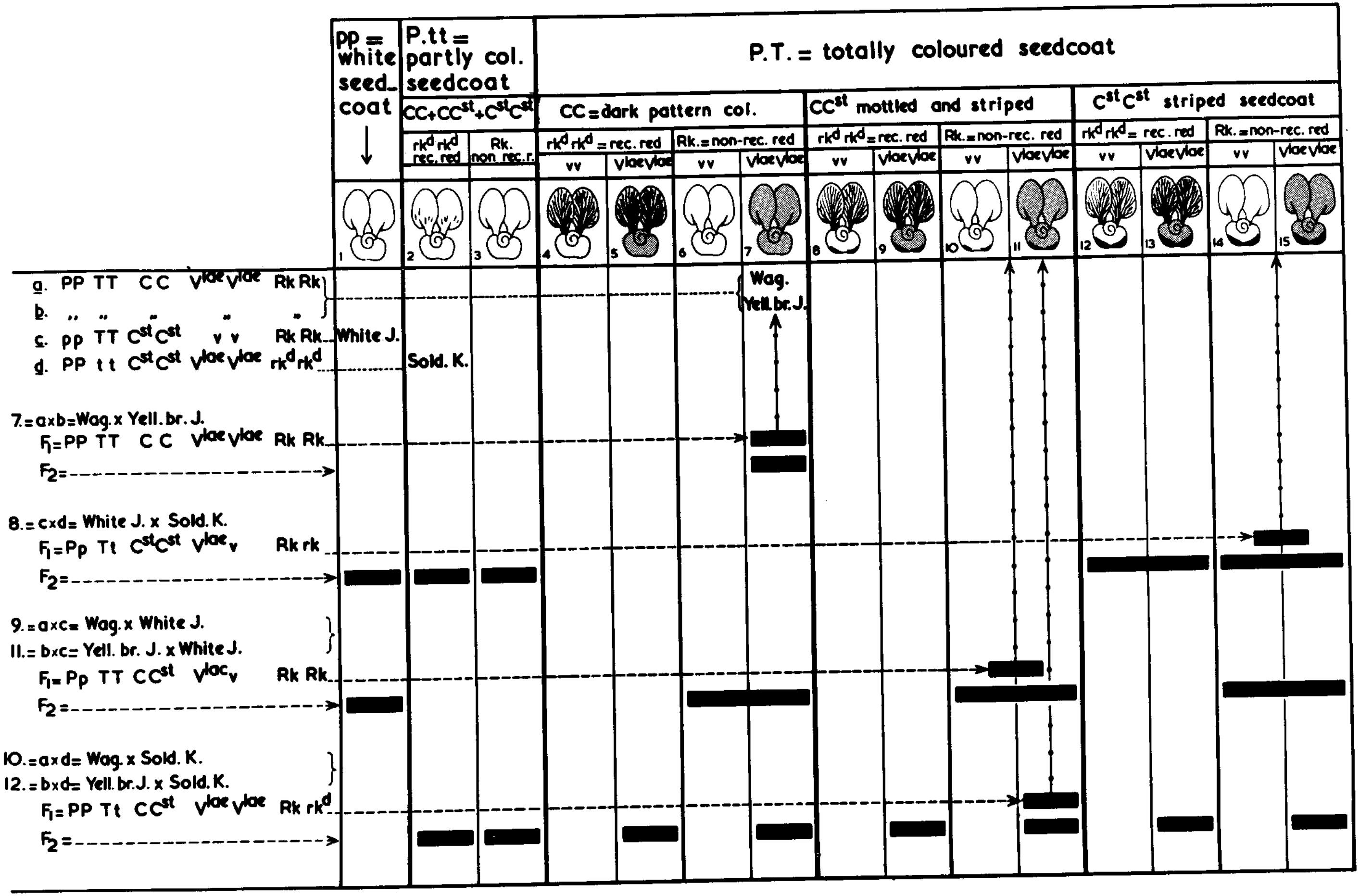
***Rk**, the locus for recessive red, rkrk* and $rk^d rk^d$.

It was only the variety 'Soldaat K.' that possessed the allele for recessive red colour, very probably that for darker red, $rk^d rk^d$ (see SMITH and BECKER MADSEN, 1948). Its white flowers (*tt*, partly coloured seed, see ***T***, p. 61) usually showed, in the lower half of the wings, fine fragments of red coloured veins, cf. fig. 9, no. 2). In the F_1 of the three crosses 8, 10 and 12 (cf. fig. 5, p. 25) no trace of red veins was found, but in their F_2-offspring the red veins reappeared: all recessive red seeded plants, $rk^d rk^d$, (usually) showed in their flower-wings more or less intense (to very pale) red veins, while none of the *Rk*. plants showed the character. In *T*. $rk^d rk^d$ plants, with totally coloured seedcoat, the red veins were over the whole length of the wings (cf. fig. 9), but in $tt\,rk^d rk^d$ plants, with partly coloured seed, there were but fragments of red veins, mainly in the lower half of the wings, like in the $tt\,rk^d rk^d$ parent variety 'Soldaat K.' or slightly more or less. In short, all F_2- and F_3-results showed that 'red veins wing' has to be looked at as *a pleiotropic action* of the $rk^d rk^d$ (or *rkrk*) genotype.

Under the discussion of *V*, just above, it was already mentioned that in white *vv*-flowers the red veins are better visible than in pale lilac $V^{lae}V^{lae}$-ones. And under the discussion of ***T*** (p. 61) the work of MIYAKE, IMAI and TABUCHI (1930) was mentioned, who first pictured the red veins, in the white flowers of *tt*-plants (1930, Pl. I, 6). It seems to me that among their *TT*-plants they only had $V^{lae}V^{lae}$-types and not *vv*, and that therefore they possibly overlooked red veins in them. LAMPRECHT (1936a, p. 165) on the ground of that picture and the 3:1 segregations mentioned by them, proposed the symbol *Lin-lin* (from lineatus), but to me the special symbol does not seem necessary (the 3:1 segregation possibly was *T.–tt*).

FIG. 9. Scheme of the *flower types* and of the *corresponding seedcoat colour types* occurring in the second group of diallelic crosses: *a.* 'Wagenaar', *b.* 'Yellowbrown J', *c.* 'White J' and *d.* 'Soldaat K'. The relevant genes are *P-p*, *T-t*, *C*-C^{st}, *Rk*-rk^d and V^{lae}-*v*. The latter pair however, changes flower colour *only*, from white (*vv*) via very pale lilac ($V^{lae}v$; not represented in the scheme) to pale lilac ($V^{lae}V^{lae}$). (The most dominant allel *V*, not represented in this group, changes white resp. pale lilac flower into violet, like anthocyanin colour in the whole plant, at the same time usually producing violet to black seedcoat colours.)

The colour genes *D* (hilumring factor) and *J* (shine factor) do not influence the flower type, nor do the modifying genes *G* (yellowbrown factor) and *B* (grey-greenish brown factor). Principally therefore, to each flower type $2^4 = 16$ seedcoat colour types belong, and, taking into account the numerous alleles of the 'complex locus' *C* and their peculiar heterozygotes, many times as much. Remark: in flower numbers 5, 9 and 13 has, by mistake, the pale lilac overall-colour of the wings been left out and therefore their red veins are too conspicuous.


PP = white seed-coat
P.tt = partly col. seedcoat
CC+CCst+CstCst
rk^d rk^d rec. red
Rk. non rec. r.
P.T. = totally coloured seedcoat
CC = dark pattern col.
CCst mottled and striped
CstCst striped seedcoat
rk^d rk^d = rec. red
Rk. = non-rec. red
vv
v^{lae}v^{lae}
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
a. PP TT CC v^{lae}v^{lae} Rk Rk
b. " " " " "
c. pp TT CstCst v v Rk Rk
d. PP t t CstCst v^{lae}v^{lae} rk^{d}rk^d
Wag.
Yell. br. J.
White J.
Sold. K.
7. = a×b = Wag. x Yell. br. J.
F$_1$ = PP TT C C v^{lae}v^{lae} Rk Rk
F$_2$ =
8. = c×d = White J. x Sold. K.
F$_1$ = Pp Tt CstCst v^{lae}v Rk rk
F$_2$ =
9. = a×c = Wag. x White J.
11. = b×c = Yell. br. J. x White J.
F$_1$ = Pp TT CCst v^{lae}v Rk Rk
F$_2$ =
10. = a×d = Wag. x Sold. K.
12. = b×d = Yell. br. J. x Sold. K.
F$_1$ = PP Tt CCst v^{lae}v^{lae} Rk rk^d
F$_2$ =

The *very variable intensity* of the red veins could not sharply be analysed genetically, but two consequences of it become clear to me.

In cross 12, 'Yellowbrown J.' with 'Soldaat K.', the variability in intensity was greatest. After much observation in F_2-F_4 it was concluded that $Ttrk^drk^d$-plants with clearly visible red veins, in the next generation segregate *tt*-plants in the white flowers of which the red vein fragments are clearly visible, but that $Ttrk^drk^d$ plants *with very faint red veins* segregate $ttrk^drk^d$ plants the white flowers of which *completely lack* the small red vein fragments, a case not pictured in figure 9.

The second disturbing complication has been extensively discussed in chapter V, cross 15, 'Hinrich's Riesen' with 'Soldaat K.', and is connected with the occurrence of *extremely clear red veins*. From this cross it became evident that such very clear red veins, apparently being so by (a) homozygously present intensification factor(s), are not completely but *incompletely recessive*: $Rkrk^d$-plants show, in the newly opened flowers or in the buds, extremely fine red veins, especially in the upper half of the wings. For more details see p. 53. This case too is not pictured in fig. 9.

In this figure 9 all main pleiotropic actions, as far as related to *seedcoat-* and *flower colours* are, with the help of crosses 7–12 of chapter IV, pictured schematically: $\boldsymbol{P\text{-}p}$, $\boldsymbol{T\text{-}t}$, $\boldsymbol{C\text{-}C^{st}}$, $\boldsymbol{V^{lae}\text{-}v}$ and $\boldsymbol{Rk\text{-}rk^d}$.

D. *Some further results* (*new genes; linkages*).

With regard to some further results, especially the crosses 8, 10 and 12, with 'Soldaat K.' (partly coloured, *tt*, and recessive red, rk^drk^d) as one of the parents, are of importance; see fig. 5, p. 25.

Cross 8 was 'White J.' with 'Soldaat K.', the F_1 genotype being $\boldsymbol{PpTtC^{st}C^{st}}$.. $JJggBBV^{lae}v\boldsymbol{Rkrk^d}$. For the present purpose the segregations V^{lae}-v add Rk-rk^d are of no importance.

As seen in the lower lines of table 6, p. 28, the F_2-families together contained 368 whites (*pp*; exp. 346), 61 + 180 = 241 plants with partly coloured seed (*P.tt*; exp. 259.5) and 197 + 578 = 775 plants with totally coloured seed (*P.T.*; exp. 778.5). Among the 241 *P.tt* plants the greater number showed the 'Soldaat K.' type with *six colour centres*, while part of them showed five centres or less (see fig. 6 and 7). The coloured part and its centres were of a rather variable type and no sharp distinction in two or more types could be made. In none of the *P.tt* plants the coloured part was greater than in 'Soldaat K.' or consisted of more than its six centres (both parents therefore being *restr restr*, see p. 67, crosses 10 and 12).

On table 6 it is further seen that the subdivision of the 775 *P.T.*-plants is for Rk-rk^d and for V^{lae}-v. The *P.tt*-plants (all white-flowered) are, save for Rk-rk^d, also subdivided for a second pair of characters, viz. into '+ cl' and '— cl', see the table. It is a pair of characters *only visible in P.tt*-plants: '+ cl'- plants show a sharp precipitation-like line around the coloured part or each separate, even the smallest, element of it (= circumliniated), while in '—cl'-plants this line is completely lacking, as in the *PPtt*-parent variety 'Soldaat K.' (see fig. 7). F_3

colours, as the dominant and recessive 'red', or better 'red-black' colours fit in with precisely the same scheme (in which the 'groundfactor' *P* is left out).

The character of the colours in *row* **I–VIII** depends upon the action of three dominant '*colour genes*', viz. *C* (factor for ever-segregating mottling), *D* (hilumring factor) and *J* (shine factor), which, together with the '*groundfactor*' P, each individually and in their combinations, result in distinct very pale colours, those of *column* **1** in the scheme. These very pale colours of *column* **1** are by the darkening action of three '*modifying genes*' viz. *G* (yellowbrown factor), *B* (grey-greenish brown factor) and *V* (violet factor), each individually and in their combinations, in a specifical way changed (or not changed, see below) into the colours of *columns* **1–8**, the last column containing dark gray, blackish or black colours. The colour character of *rows* **I–VIII** follows here:

Row **I** : *c c ddjj* , seedcoat white, hardly or not influenced by *G*, *B* and *V* (*V* sometimes produces a pale glaucescent tinge)
Row **II** : *CCddjj* , mat 'dark pattern' colours without brown hilumring.
Row **III** : *c cD.jj* , hilumring background type, whitish, hardly or not influenced by *G*, *B*, *V*(*V*: see *row* **I**).
Row **IV** : *CCD.jj* , mat 'dark pattern' colours with brown hilumring.
The types **V–VIII**, with *J*, all have brown hilumring, they are shiny and afterdarkening:
Row **V** : *c c ddJ.* , shiny and afterdarkening 'background colour' series.
Row **VI** : *CCddJ.* , shiny and afterdarkening 'dark pattern colour' series.
Row **VII** : *c cD.J.* , as row V, because *J* is epistatic over D-d.
Row **VIII**: *CCD.J.* , as row **VI**, because *J* is epistatic over D-d.

The *Cc*-rows (left out above and in the scheme) show 'ever-segregating mottling' in the *CC*-'dark pattern colour' and the *cc*-'background colour' in the same column. The background mottling therefore is:
in Ccddjj: always *white*, as row I
in CcD.jj: always *whitish*, as 'hilumring type' colour, row III
in $Cc\genfrac{}{}{0pt}{}{dd}{D.}J.$:as the *eight shiny background colours* in row V (=VII)

A few remarks must be made here on a second background allel, c^u. In the non-shiny *jj*-types (*row* I–IV) it does not make any difference wether the background alleles *cc*, cc^u or c^uc^u are present. In the shiny J.-types however (*row* V–VIII) it makes an important difference: the *cc*(or cc^u)*J.* shiny background genotype is typically influenced by the modifying genes *G*, *B* and *V* and it shows the eight colours of *row* V (or VII), but the c^uc^u*J.* shiny background genotype is not influenced by these three dominant modifying genes, i.e. all eight genotypes for *G-g*, *B-b* and *V-v* show the colour of **V–1**, *ggbbvv*, shiny pale yellowish or (creamish) pale buff (c^u = allel for *u*nchangeable shiny *J.*-background: see FEENSTRA, 1960 p. 8 and NAKAYAMA, 1964). The background mottling of Cc^u is likewise unchangeable. The allel c^u or the genotype c^uc^u is met with in many early studies.

The darkening actions of *G*, *B* and *V* will be discussed further on (cf. also p. 4).

Integration of the 'yellow-black' system with the 'dominant red' and 'recessive red' colours (or better: 'red-blackish' colours) appeared difficult. It took a long time and many investigators took part in it. A few of the difficulties, first with respect to dominant red (LAMPRECHT: R, R^{ma}, R^{st} etc; here, preliminary: C^{r}, C^{m}, C^{st}) will shortly be discussed, without striving for completeness.

SHAW and NORTON (1918) considered the 'red' colours as caused quite independently from the 'yellow-black' colours, the *latter* according to them needing, besides the groundfactor P, the 'modifier' gene M and the *first* (=red) ones the 'modifier' M'. To me it seems as if their need for M and M' was connected with the fact that the only background-colour variety they used in their crosses was 'Blue Pod Butter', and that this variety, as appeared later, did not possess the genotype cc but $c^{u}c^{u}$ (or better: $c^{ui}c^{ui}$, cf. NAKAYAMA VII, 1964). Within the 'yellow-black' colours of SHAW and NORTON all three modifying genes, G, B and V, can be traced, but within their 'red' seeded types (dark mottled = mottled and light mottled = striped) they made but one colour distinction, viz. into 'medium or bright red' and 'dark or purplish red'.

SIRKS (1920) tried to analyse a genetically very complex spontaneous hybrid, apparently $PpC^{st}cJJ$, for segregation was into 24 whiteseeded plants, 19 with various cc-background colours and 37 striped seeded ones, of numerous colour types (exp. 20 + 15 + 45). The background colour types, $ccJJ$, mentioned by SIRKS gave me the impression of segregation for G, B and V, but regrettable enough, SIRKS in that case did not analyse stem-, flower- or fruit colour, while precisely for a dependable classification of *cc*-shiny background colours, and as well for that of the corresponding striped-seeded plants, the colour of flower etc. (v or v^{lae} against V) is of great importance.

This importance of stem-, flower- or fruit colour becomes very clear from a paper of TJEBBES and KOOIMAN (V, 1921), also on a spontaneous hybrid and its offspring. The segregation was into 11 whiteseeded plants and 33 striped-seeded ones (the mother plant therefore being $PpC^{st}C^{st}$), the stripes of the latter plants showing many colours, from (pale) red to black. From each individual plant not only seedcoat colour but also colour of flower and fruit was scored:

$$44\left\{\begin{array}{l} 11 \text{ white-fl. and white-seeded, } pp \left\{\begin{array}{l} 4 \text{ pale red fruit: } blbl \\ 7 \text{ pale blue-violet fruit: } Bl. \end{array}\right. \\ \quad \text{(cf. present art. p. 61)} \\ 33 \text{ striped seeded, } P. \left\{\begin{array}{l} 10 \text{ pale lilac fl. and red fruit: } blbl \\ 23 \text{ violet fl. and black-violet fruit: } Bl. \end{array}\right. \end{array}\right.$$

This Bl of TJEBBES and KOOIMAN certainly is identical with the 'violet factor' V, while $bl = v^{lae}$. The many seedcoat colours (= stripe colours) were by them first very roughly grouped into 'reddish' and 'blackish' ones, and they spontaneously supposed these types to correspond to *blbl* and *Bl.* resp. When however TJEBBES, a few months later, for each individual plant, really compared seedcoat colour with the colour of flower and fruit, he had a rather astonishing experience and he wrote (translated from Netherlands): 'From this experience it became clear that *pod colour is really correlated with seedcoat colour, though in another way than first seemed most plausible.*' The cause of the initial misinterpretation is, according to the present writer, the fact that the 'grey-greenish brown factor' *B* changes, in the striped-seeded $C^{st}C^{st}$-group, the colours 'red' (*ggbb*) and 'orangered' (G.bb) into 'greyish-violet' (*ggB.*) and 'dark (blackish) brown' (*G.B.*) respectively, colours that easily could and can be taken for *V*-colours (*Bl* of Tjebbes and Kooiman = *V*; their 'blackish violet' fruit colour certainly is the very dark violet of $V.C^{st}C^{st}$-fruits). – This analysis is very instructive, but I would hardly have discussed it at length if not *Bl-bl* (symbol from Tjebbes and Kooiman) had been used by various investigators, sometimes for the 'violet factor' *V* as by the authors, sometimes for the 'grey-greenish brown' factor *B* (Nakayama VI, 1961, p. 53; there he still supposed that *Bl-bl* acts upon the dominant 'red' colours only and not on the 'yellow-black' ones), and sometimes probably for both (Smith, 1939). This gave much confusion and interfered with the identification of the genes of the 'yellow-black' with those of the 'red-black' group.

Various other complicating mistakes, as e.g. looking upon (pale or very dark) two-coloured seeds as one-coloured, or upon three-colouredness as two-colouredness, will only be mentioned.

Smith (1939) in his first important article on red seedcoats in *Phaseolus vulgaris* (dominant red and especially the recessive red, *rkrk*) was handicapped by the abundance of 'red' colours and their genetic background, but his main task, the analysis of recessive red, was made sharply, like later the analysis of the triple allely, Rk-rk-rk^{d}, by Smith and Becker-Madsen (1948). As mentioned above *Bl-bl* probably was sometimes used in both senses, for *V-v* and for *B-b*, while the action of the 'yellowbrown factor' *G* was not clearly seen, though segregation for *G-g* certainly accurred, as appears from the coloured pictures and colour descriptions in Smith, 1939. In that material there was, in my opinion, segregation for various alleles of the *C* (or *R*)-locus (C-c^{u}-C^{m}-C^{st}), for *Rk-rk* and moreover for *G-g*, *B-b* and *V-v* (or V^{lae}), but partly because of lack of information on flower- or fruit-colour a complete re-analysis appeared difficult.

Smith (1939) mentioned Gloyer (1928) as the first describer of 'recessive red' colour. In trying to re-analyse Gloyer's F_1-, F_2- and F_3-results I came to the conclusion that the genotype of his relevant F_1 at all probability was $\boldsymbol{PpTTCc^{u}}$ $..JJGgBBV^{lae}$ *(or v)* $\boldsymbol{Rkrk^{(d)}}$ (dark brown mottled upon pinkish buff). In F_2 it viz. gave the *CCJJRk.* shiny dark pattern colours grey-greenish brown (*ggBBvv*; scheme: **VI–3**) and dark-brown (*G.BBvv*; scheme: **VI–4**); by $rk^{d}rk^{d}$ the first colour was changed into the rather easily distinguishable 'seal colour', the latter in a much less easily distinguishable very dark brown. In these colour regions a few mis-classifications are quite understandable. Of the F_2 $^1/_4$ further was of the 'unchangeable background' type $c^{u}c^{u}$, resp. pinkish buff ($c^{u}c^{u}Rk.$) or recessive red ($rk^{(d)}rk^{(d)}$), and $^2/_4$ was of the Cc^{u}-mottled type: in *Rk.* upon pale pinkish buff and in $rk^{(d)}rk^{(d)}$ upon recessive red.

Of much importance for my present purpose of gene-homologisation was the paper of Smith (1961) in which he analysed the crosses of six of his own varieties with a 'tester race', Line 214, that he had received from Lamprecht. Line 214 was *PP* but whiteseeded, i.e. recessive for all colour genes, while it also was recessive for all dominant modifying (= darkening) genes, and appeared to be dominant *RkRk*. The F_2-families were difficult to classify accurately, and Smith's analysis mainly depended upon his numerous F_3-families. From the genes that Smith needed for the explanation of the crosses the loci *P*, *M* (= allel of the complex locus *C*) and *Rk* can be left here out of discussion. He further found two genes that produce a brown hilumring. In their action *the first one accurately agrees* with that of the 'hilumring factor' *D*, making a brown hilumring and for the rest leaving the seedcoat whitish. The action of *the second one as accurately agrees* with that of the 'shine factor' *J*, producing, as the first one, a brown hilumring and moreover making the seedcoat shiny, while being epistatic over the first one; he further stated that *Rk-rk* worked only when this latter gene was present. In trying to coördinate his own results with those of Lamprecht (who ascribes to *five* genes a hilumring-producing action: *J*, *G*, *B* *Ins* and *Can*), Smith unfortunately choose for the first one Lamprecht's symbol *B* and for the second one *G*, genes that, as explained in Prakken II (1970) *are purely modifying genes and do not produce a brown hilumring.* In my opinion it should have been ***D*** (hilumring-factor; = *Ins* = *Can* of Lamprecht) and ***J*** (shine factor). With the latter choice both Feenstra (1960) and Lamprecht (1966) agree, in pointing out that recessive red *rkrk* or rk^drk^d colours are only produced if the 'shine factor' *J* is present. – No wonder that Smith met difficulties in trying to homologise his genes with those of Lamprecht. The homologisation of Smith's symbols with the genes as used in the present article (i.e. mainly the symbols used by Lamprecht) is according to me:

Smith, *1961*		*Present article*
P,	represents the 'groundfactor'	***P***
M,	is an allel of the 'complex locus'	***C***
B,	corresponds with the 'hilumringfactor'	***D***
G,	corresponds with the 'shine factor'	***J***
…,	a third modifying gene, 'needed' by Smith in addition to *Br* (for brown) and *Bl*, must be the 'yellowbrown factor'	***G***
Br,	corresponds with the 'grey-greenish brown factor'.	***B***
Bl,	corresponds with the 'violet factor'	***V***
Rk,	is the now generally recognized locus for recessive red,	***Rk***(-*rk*-rk^d)

As a strong additional argument for the identification of Smith's 'brown factor' *Br* with the 'grey-greenish brown factor' B of the present article the *linkage relations* can be mentioned:

Smith (1947) stated linkage *Br-Rk*, recombination percentage 37.5.

Prakken (pres. art.) stated linkage *B-Rk*, recombination percentage 38.8±3.8.

Smith, as shown above, started from the supposed hilumring-action of *G* and *B*, like Lamprecht did and also Nakayama. Both latter authors have given valuable analyses of the relation between 'yellow-black' and 'red' colours, especially in shiny *JJ*-material. When it was *Jj* and therefore segregating mat, non-afterdarkening *jj*-types, they too were liable to be played tricks by the supposed hilumring producing action of *G* and *B*.

I will now end the article by giving a review of the integrated system. It will be done *in a rather general way*, often using comparative descriptions, based upon the general specific action of most genes or alleles. By this way of description the use of colour names or indications is restricted to a minimum.

Of the 'yellow-black' system the alleles *C*, *c* and c^u will be used, of the dominant 'red-black' system C^{st} (= R^{st}, red striped) only, and of the recessive 'red-black' system (*Rk* and) $rk^d rk^d$.

As the clearest distinctions and also the most extensive and detailed knowledge are in the field of the shiny *J*-colours (*dd* or *D.*, indicated by ..) it is with this group that the review begins: ***A***, an extremely complicated group. Group ***B***, *D.jj*, is much less complicated, while group ***C***, *ddjj* paralleles group ***B*** and therefore is very easy to describe.

In the scheme opposite p. 82 the eight colours depending on the combined action of the three modifying genes *G*, *B*, *V* are *in a row*, e.g. *row* **VI, 1–8.** In the review that follows these eight types are always found *above each other*, also numbered from 1–8.

A. The J. colours, shiny and strongly afterdarkening.

I. ***The shiny yellow-black colours*** (*C-c-*c^u; all *Rk.*), cf. lower half of the scheme, in which however c^u is not included; first the three homozygotes, thereafter the three heterozygotes. The two dots (. .) mean *dd* or *D.*

The three homozygotes.

a. CC..J., the shiny dark pattern colours (scheme: *row* **VI, 1–8**):

1. CC..J.ggbbvv: pale greenish yellow (shamois to canary yellow)
2. ,, ,, ,, *G.bbvv*: yellowbrown (bistre)
3. ,, ,, ,, *ggB.vv*: grey-greenish brown (buffy citrine; 'münzbronze')
4. ,, ,, ,, *G.B.vv*: dark brown (mineral brown)
5. ,, ,, ,, *ggbbV.*: dark (blackish) violet (dark violet purple)
6. ,, ,, ,, *G.bbV.*: dark brown violet (maroon)
7. ,, ,, ,, *ggB.V.*: black
8. ,, ,, ,, *G.B.V.*: black

b. cc..J., the shiny background colours (scheme: *row* **V, 1–8**):

1. cc..J.ggbbvv: pale (yellowish) buff (Cartridge buff, Rohseidengelb)
2. ,, ,, ,, *G.bbvv*: pale yellowbrown (maize yellow)
3. ,, ,, ,, *ggB.vv*: grey brown (snuff brown)
4. ,, ,, ,, *G.B.vv*: (pale) brown (buckthorn brown)
5. ,, ,, ,, *ggbbV.*: pale yellowish buff tinged with plumbagoviolet
6. ,, ,, ,, *G.bbV.*: pale yellowbrown tinged with ageratumblue
7. ,, ,, ,, *ggB.V.*: grey brown tinged with slate blue
8. ,, ,, ,, *G.B.V.*: dark brown tinged with greyish indigo (very variable)

c. $c^uc^u..J.$, *the shiny 'unchangeable' background colour*

1. $c^uc^u..J.ggbbvv$:
2. ,, ,, ,, *G.bbvv*

etc, to

8. ,, ,, ,, *G.B.V.*

} all eight like *b.1*, i.e. pale (yellowish) buff (Rohseidengelb) (= not or hardly influenced by *G*, *B* and *V*)

The three heterozygotes.

d. *Cc..J., mottled; dark pattern **I** a, 1–8 /upon background **I** b, 1–8*:

1. *Cc..J.ggbbvv*: pale greenish yellow / pale (yellowish) buff
2. ,, ,, ,, *G.bbvv*: yellowbrown / pale yellowbrown (maize yell.)
3. ,, ,, ,, *ggB.vv*: grey-greenish brown / grey-brown.
4. ,, ,, ,, *G.B.vv*: dark brown / (pale) brown.
5. ,, ,, ,, *ggbbV.*: dark violet / pale yell. buff t.w. plumbagaviolet.
6. ,, ,, ,, *G.bbV.*: dark brown violet / pale yell. brown t.w. ageratumblue.
7. ,, ,, ,, *ggB.V.*: black / grey-brown t.w. slate blue.
8. ,, ,, ,, *G.B.V.*: black / brown t.w. greyish indigo.

e. $Cc^u..J.$, *mottled; dark pattern **I** a, 1–8 / upon pale yell. buff **I** c*:

1. $Cc^u..J.ggbbvv$: pale greenish yellow / pale (yellowish) buff.
2. ,, ,, ,, *G.bbvv*: yellowbrown / ,, ,, ,,
3. ,, ,, ,, *ggB.vv*: grey-greenish brown / ,, ,, ,,
4. ,, ,, ,, *G.B.vv*: dark brown / ,, ,, ,,
5. ,, ,, ,, *ggbbV.*: dark violet / ,, ,, ,,
6. ,, ,, ,, *G.bbV.*: dark brown violet / ,, ,, ,,
7. ,, ,, ,, *ggB.V.*: black / ,, ,, ,,
8. ,, ,, ,, *G.B.V.*: black / ,, ,, ,,

f. $cc^u..J.$, shiny background colours:

1. cc^u..J.ggbbvv:
2. ,, ,, *G.bbvv*:

etc. to

8. ,, ,, *G.B.V.*:

} colours like ***I** b, 1–8* = shiny background colours, but all eight segregating $^1/_4$ c^uc^u (shiny pale buff)

II. ***The shiny 'dominant red' colours**,* obtained by replacing *CC*, *cc* or c^uc^u above by two one allele(s) C^{st} (all *Rk*).

Both replaced, i.e. homozygously striped.

a. $C^{st}C^{st}..J.$, *shiny homozygously ('red–blackish') striped colours, upon pale buff background:*

1. $C^{st}C^{st}..J.ggbbvv$: red striped / upon pale (yell.) buff.
2. ,, ,, ,, *G.bbvv*: orange red striped / ,, ,, ,, ,,
3. ,, ,, ,, *ggB.vv*: greyish-violet striped / ,, ,, ,, ,,
4. ,, ,, ,, *G.B.vv*: dark (blackish) brown str./ ,, ,, ,, ,,
5. ,, ,, ,, *ggbbV.*: (dark reddish) purple str. / ,, ,, ,, ,,
6. ,, ,, ,, *G.bbV.*: slightly more brownish purple str. / ,, ,, ,, ,,
7. ,, ,, *ggB.V.*: grey-bluish black str. / ,, ,, ,, ,,
8. ,, ,, *G.B.V.*: blackish striped / ,, ,, ,, ,,

One replaced.

b. $C^{st}C..J.$, *shiny heterozygously striped, three-coloured:*

1. $C^{st}C..J.ggbbvv$: 'main colour': shiny dark pattern, like ***I** a, 1–8.*
2. „ „ $G.bbvv$: '*striping*': about like ***II** a, 1–8.*
   etc. to
8. „ „ $G.B.V.$: '*backgr. mottl.*': always pale yell. buff, like in IIa.

c. $C^{st}c..J.$, *shiny heterozygously striped, two-coloured:*

1. $C^{st}c..J.ggbbvv$:
2. „ „ $G.bbvv$:
   etc. to
8. „ „ $G.B.V.$

'*striping*' about like ***II** a, 1–8* (somewhat less bright)
'*shiny backgr. colour*' like ***I** b, 1–8* (but tinging in *5–8* less strong)

d. $C^{st}c^{u}..J.$, *shiny heterozygously striped, two-coloured:*

1. $C^{st}c^{u}..J.ggbbvv$:
2. „ „ $G.bbvv$:
   etc to
8. „ „ $G.B.V.$:

striping: about like ***II** a, 1–8*
background: in all pale yellowish buff
(very near homoz. striped, ***II** a, 1–8*, but all eight segregating $^{1}/_{4}\ c^{u}c^{u}$)

III. The shiny 'recessive red' colours, obtained by replacing, in ***I** a-f, Rk.* by $rk^{d}rk^{d}$.

In the three homozygotes.

a. $CC..J........rk^{d}rk^{d}$, *'recessive red' over the shiny dark pattern colours:*

1.	$CC..J.ggbbvvrk^{d}rk^{d}$:	completely 'rec.red' (over pale greenish yellow).	great change by $rk^{d}rk^{d}$
2.	„ „ „ $G.bbvv$ „ :	almost 'rec.red' (over yellowbrown).	
3.	„ „ „ $ggB.vv$ „ :	dark (reddish) haze (over dark grey-greenish br.).	less great change bij $rk^{d}rk^{d}$: darker.
4.	„ „ „ $G.B.vv$ „ :	dark (reddish) haze (over dark brown).	
5.	„ „ „ $ggbbV.$ „ :	slight haze (over dark violet).	
6.	„ „ „ $G.bbV.$ „ :	slight haze (over dark brown violet).	
7.	„ „ „ $ggB.V.$ „ :	slight haze? (over black).	
8.	„ „ „ $G.B.V.$ „ :	slight haze? (over black).	

Therefore: from 1–8 the influence of $rk^{d}rk^{d}$ becomes less and less conspicuous.

b. $cc..J.......rk^{d}rk^{d}$, *'recessive red' over the shiny background colours*:

1. $cc..J.ggbbvvrk^{d}rk^{d}$:
2. „ „ „ $G.bbvv$ „ :
   etc. to
8. „ „ „ $GG.B.V.$ „ :

influence of $rk^{d}rk^{d}$ about like under ***III** a*;
1. (and *2*) become (rather) recessive red;
in *3* to *8* the reddish haze is less and less visible.

c. $c^{u}c^{u}..J.......rk^{d}rk^{d}$, *recessive red over 'unchangeable background colour'*:

1. $c^{u}c^{u}..J.ggbbvvrk^{d}rk^{d}$:
2. „ „ „ $G.bbvv$ „ :
   etc. to
8. „ „ „ $G.B.V.$ „ :

all eight completely recessive red, like ***III** b, 1*
(= hardly or not influenced by *G, B, V*)

[It was in this region of $c^uc^u..JJ$-colours that SMITH and BECKER MADSEN (1948), in making the diallelic cross between a 'Buff' variety, a 'Red Kidney' type, and 'Michigan Dark Red Kidney', proved the existence of the triple alleles *Rk*, *rk* and rk^d, in homozygous condition resp. '(pale shiny) buff', 'testaceous' and 'garnet brown'; $rkrk^d$ appeared intermediate: 'dragon's blood red' (for colours see RIDGWAY, Color standards and color nomenclature, 1912). – Also crosses with the one-coloured 'dominant red' variety 'Commodore' (oxblood red; in the genes used here probably: $C^rC^r..JJggbbvvRkRk$) were involved, but in the present article C^rC^r has been left out of consideration.]

In the three heterozygotes.

d. $Cc..J......rk^drk^d$, *'recessive red' over heterozygote Cc-colours*:
  1. $Cc..J.ggbbvvrk^drk^d$: 'recessive red' *over both colours,*
  2. ,, ,, ,, *G.bbvv* ,, : *dark pattern* and *background*;
  etc., to for effect cf. ***III a*** and ***III b***:
  8. ,, ,, ,, *G.B.V.* ,, : clearest 'rec.red' effect in *1* and *2*.

e. $Cc^u..J......rk^drk^d$, *'recessive red' over heterozygote Cc^u-colours*:
  1. $Cc^u..J.ggbbvvrk^drk^d$: 'recessive red' *over both colours*:
  2. ,, ,, ,, *G.bbvv* ,, : *dark pattern*, clearest effect in *1* and *2*, see *d*.
  etc., to *background*, in *1–8* typical rec.red.
  8. ,, ,, ,, *G.B.V.* ,, : (unchanged by *G*, *B*, *V*).

f. $cc^u..J......rk^drk^d$, *'recessive red' over the shiny background colours*:
  1. $cc^u..J.ggbbvvrk^drk^d$: colours precisely like ***III b***, *1–8*,
  2. ,, ,, ,, *G.bbvv* ,, : i.e. rec. red shiny backgr. colours,
  etc. to but all segregating $^1/_4$ c^uc^u,
  8. ,, ,, ,, *G.B.V.* ,, : i.e. typical recessive reds.

IV. ***The shiny 'dominant' and 'recessive red' colours***, $C^{st}. rk^drk^d$, obtained from ***II***, *a-d*, in replacing *Rk*. by rk^drk^d.

a. $C^{st}C^{st}..J......rk^drk^d$, *shiny recessive red, homozygously striped colour*:
  1. $C^{st}C^{st}..J.ggbbvvrk^drk^d$:
  2. ,, ,, ,, *G.bbvv* ,, : *striping*:
  3. ,, ,, ,, *ggB.vv* ,, : *1–8* is parallel with ***II a***, *1–8*, but somewhat
  4. ,, ,, ,, *G.B.vv* ,, : darkened by rk^drk^d.
  5. ,, ,, ,, *ggbbV.* ,, : *background colour*:
  6. ,, ,, ,, *G.bbV.* ,, : not pale buff as in ***II a***, *1–8*, but all typical
  7. ,, ,, ,, *ggB.V.* ,, : rec. red.
  8. ,, ,, ,, *G.B.V.* ,, :

b. $C^{st}C..J......rk^drk^d$, *shiny rec. red, heteroz. striped, three-coloured*:
  1. $C^{st}C..J.ggbbvvrk^drk^d$:
  2. ,, ,, ,, *G.bbvv* ,, : *'main dark pattern colour'*: like ***III a***, *1–8*
  etc. to *'striping'*: about like ***IV a***, *1–8* just above
  8. ,, ,, ,, *G.B.V.* ,, : *'background mottling'*: all typical recessive red

c. $C^{st}c..J.......rk^drk^d$, *shiny rec. red, heteroz. striped, two-coloured*:
1. $C^{st}c..J.ggbbvvrk^drk^d$:
2. ,, ,, ,, *G.bbvv* ,, : ‘*striping*’: about like ***IVa**, 1–8* above.
etc. to ‘*background colour*’: like ***IIIb**, 1–8.*’
8. ,, ,, ,, *G.B.V.* ,, :

d. $C^{st}c^u..J.......rk^drk^d$, *shiny rec. red, heteroz. striped, two-coloured*:
1. $C^{st}c^u..J.ggbbvvrk^drk^d$: *striping*: about like in ***IVa**, 1–8* above
2. ,, ,, ,, *G.bbvv* ,, : *background*: all typical rec. red like that in IVa,
etc. to 1–8 (therefore about like ***IVa**, 1–8*, but all
8. ,, ,, ,, *G.B.V.* ,, : segregating $^1/_4$ $c^uc^urk^drk^d$).

B. The D.jj-colours, mat and non-afterdarkening, but with a brown hilumring.

In this colour group there is no difference between *c* and c^u (the latter is left out), nor exists a visible difference between *Rk.* and rk^drk^d (which both are left out). Only the yellow-black group (*CC, cc, Cc*) and the group with dominant red ($C^{st}C^{st}$, $C^{st}C$, $C^{st}c$) need to be described.

I. The mat yellow-black colours with brown hilumring (*C-c*).

a. *CCD.jj, the mat dark pattern colours with brown hilumring* (scheme: *row* **IV, 1–8**).
1. *CCD.jj ggbbvv*: pale greenish yellow
2. ,, ,, ,, *G.bbvv*: pale (greenish) yellow, with yellowbr. car. str.
3. ,, ,, ,, *ggB.vv*: grey-greenish brown
4. ,, ,, ,, *G.B.vv*: soft (mat) brown
5. ,, ,, ,, *ggbbV.*: dark grey violet
6. ,, ,, ,, *G.bbV.*: mat brown grey
7. ,, ,, ,, *ggB.V.*: mat greenish black
8. ,, ,, ,, *G.B.V.*: mat blackish or dark mouse gray

b. *ccD.jj, the ‘hilumring type’ background colour group* (scheme: *row* **III, 1–8**)
1. ccD*.jjggbbvv*:
2. ,, ,, ,,*G.bbvv*: with a brown hilumring, but further seedcoat whitish,
etc. to *G*, *B* and *V* (almost) without influence
8. ,, ,, ,,*G.B.V.*:

c. *CcD.jj, the mat colours like in a, 1–8, mottled upon whitish background.*
1. *CcD.jjggbbvv*: pale greenish yellow
2. ,, ,, ,,*G.bbvv*: pale (greenish) yellow all with whitish
etc. to background mottling
8. ,, ,, ,,*G.B.V.*: mat blackish (dark mouse grey)

II. The mat colours with ‘dominant red’, obtained by replacing *CC* or *cc* by two or by one allele(s) C^{st}.

a. $C^{st}C^{st}D.jj$, *mat homozygously (‘red’) striped colours, with brown hilumring*:

1. $C^{st}C^{st}D.jjggbbvv$: pale lilac str.
2. „ „ *G.bbvv*: pale lilac str.
3. „ „ *ggB.vv*: grey-lilac str.
etc. to
8. „ „ *G.B.V.* mat grey-blackish str.?
} all upon whithish background

Therefore: parallel the ***A IIa*** shiny homoz. striped colours, but paler, mat, i.e. not shiny, and non-afterdarkening.

b. *$C^{st}CD.jj$, mat heterozygously ('red') striped, three-coloured:*
1. $C^{st}CD.jjggbbvv$:
2. „ „ *G.bbvv*:
etc. to
8. „ „ *G.B.V.*:
'main colour': like ***B I** a, 1–8*
'striping': like ***B II** a, 1–8*
'background mottling': all whitish

c. *$C^{st}cD.jj$, mat heteroz. ('red') striped, two-coloured:*
1. $C^{st}cD.jjggbbvv$
2. „ „ *G.bbvv*
etc. to
8. „ „ *G.B.V.*
striping: much like *a, 1–8*
background: whitish, like in *a*

C. The ddjj-colours, mat, non afterdarkening, without brown hilumring.

This whole group ***C*** is completely parallel with group ***B*** above: ***C I** a, b, c* and ***C II**, a, b, c*.

The differences are:

absence of the brown hilumring;

colours usually somewhat paler;

background or background mottling purely white (*ccddjj*-types, scheme: *row* **I, 1–8,** of course are completely white, only *V* sometimes producing a slight pale glaucescent tinge).

VI. SUMMARY

After chapter I (Introduction; 'yellow-black' and 'red' colours) and chapter II (Material and methods) *two diallelic crosses* between four varieties each are analysed, not only for *seedcoat colour* but also, per individual plant, for the '*accompanying colours*': of seedling (cotyledons and hypocotyl), flowers (including red tip standard and red veins in the wings) and fruits. These diallelic crosses are treated in chapters III and IV, while in chapter V three 'connecting crosses' are given.

Chapter VI, Discussion and conclusions, begins with a short Introduction, A.

In VI B the crosses are discussed with respect to *seedcoat colour inheritance*: segregation for all nine main loci (see below) occurred.

In VI C the *pleiotropic actions* of the loci printed below in ***bold letter*** are described, while those printed in *normal letter* appeared to be without such actions: ***P***, ***T***; ***C***, ***D***, ***J***; *G*, *B*, ***V*** and ***Rk***. On basis of the crosses in chapter IV a scheme for the relations between flower- and seedcoat colour is constructed: figure 9 p. 65.

In VI D *some further results* are discussed: new genes and linkages.

In VI E, finally, '*A complete synthesis of seedcoat colour inheritance*', a rather incomplete analysis of the historic development of the studies on 'red' or better 'red-blackish' colours, of the difficulties involved, and of the ultimate complete integration of the 'yellow-black' with the 'red-blackish' colours is given. It ends with *a systematic survey of the integrated system*, that seems to be in conformation with the results of all investigators (p. 73–79).

A number of details on the 'complex locus *C*', partly from the literature and partly from the own crosses, have been left out of discussion. I hope to be able to discuss the real character of this 'locus' in (a) coming (articles).

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COLOUR SYSTEMS

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Scheme for the inheritance of the group of yellow-black seedcoat colours in *Phaseolus vulgaris* L.

The *horizontal rows* **I–VIII** represent the 'colour groups' casued by the action of the (complementary) 'colour genes' *C, D* and *J*, together with the 'basic gene' *P* (left out); to the left are the genotypes (in **bold letter**) and above in each row is the general character of the group.

Within the groups are (except for I and III) more or less '*parallel series*' of principally eight colours, *vertical columns* **1–8**, caused by the action of the 'modifying genes' *G, B* and *V* (the latter sometimes having a slight action as colour gene, see **I, 5–8**); at the top of each column is the genotype (in **bold letter**), together with an attempt to a general colour description.

Below the genotype in bold letter is the genotype written in KOOIMAN's symbols A, B, C, D, E, F, (G); the colours occurring in his analysis, columns 2, 4, 6 and 8, are indicated with a dot.

Uppermost in most of the 64 compartments is a colour describing name, mainly derived from the results of KOOIMAN and PRAKKEN; in the lower half of each compartment is, between quotation marks, the corresponding (according to the present author) german colour name of LAMPRECHT, together with, between brackets, his english translation; in the right upper quarter (*jj V.*) the correspondence is uncertain in some cases.

The 'ever-segregating' mottled types (*Cc*) are not represented in the scheme: they are mottled in the colours of I and II, III and IV, V and VI, VII and VIII.

Abbreviations: K. = KOOIMAN; yell. br. f. = yellowbrown factor; t.w. = tinged with; car. str. = Caruncula Strich (caruncula stripe).

					vv(or V^{lae}(V^{lae})		
					bb		B. (gre
					gg	G. (yell. br. f.)	gg
					gg bb vv	**G.bb vv** (K.: [GG] ee ff)	**gg B. vv**
					pale creamish buff or pale greenish yellow	**pale yellowish to yellow brown**	**grey-brown to greenish brown**
					1	**2**	**3**
jj: mat and non-afterdarkening	dd: without h.r.	background colour: cc	**cc dd j j** (K.: bbddcc)	**I**		seedcoat quite white ●	
		dark pattern colour: CC	**CC dd j j** (K.: BB dd cc)	**II**	pale greenish yellow 'geschwefeltes weiss' (primrose yellow)	● pale (greenish) yellow 'gelblich weiss' (yellowish white)	**mat** grey-greenish brow 'russgrün' (bistre green)
	D.: with hilumring	background colour: cc	**cc D. j j** (K.: bb D. cc)	**III**		● seedcoat whitish	
		dark pattern colour: CC	**CC D. j j** (K.: BB D. cc)	**IV**	pale greenish yellow 'ambra' = 'steinfarbig ohne car.str.' (light colonial buff)	● pale (greenish) yellow (lemon coloured) 'steinfarbig' (mit caruncula str.) (stone colour)	**mat** grey-greenish brow 'mat münzbronze' (dull buffy citrine)
J.: shiny and afterdarkening, always brown hilumring	dd	background colour: cc	**cc dd J.** (K.: bb dd C.)	**V**	(creamish) pale buff (pale yellowish) 'rohseidengelb' (cartridge buff)	● (pale) yellowbrown 'maisgelb' (maize yellow)	**shiny** grey-brown 'havannabraun' (snuff brown)
		dark pattern colour: CC	**CC dd J.** (K.: BB dd C.)	**VI**	pale greenish yellow (to canary yellow) 'schamois'and'kan.gelb' (shamois and canary y.)	● yellowbrown 'bister' (yellowish brown)	**shiny** grey-greenish brow 'münzbronze' (buffy citrine)
	D.	background colour: cc	**cc D. J.** (K.: bb D. C.)	**VII**		●	**shiny** seed
		dark pattern colour: CC	**CC D. J.** (K.: BB D. C.)	**VIII**		●	**shiny** seed

		V. (violet factor)			
	enish brown factor	bb		B. (greenish brown factor)	
	G. (yell. br. f.)	gg	G. (yell. br. f.)	gg	G. (yell. br. f.)
	G.B. vv (K.: [GG] E. ff)	**gg bb V.**	**G.bb V.** (K.: [GG] ee F.)	**gg B. V.**	**G.B.V.** (K.: [GG] E.F.)
	pale soft brown to dark hard brown	**diverse violet colours**	**brown grey to dark brwon violet**	**dark greenish to black**	**mouse grey to black**
	4	**5**	**6**	**7**	**8**
white background colour group, non-afterdarkening					
	●	white or tinged with pale glaucescens	●		●
ark pattern colour group without hilumring, non-afterdarkening					
n	● soft brown ‘hell lohfarben’ = ‘hell antiquabraun?’ (clay colour)	grey-violet (violet blue) ‘purpurgrau’ (purplish grey)	● mat brown grey ‘umbra?’ (Brussels brown)	mat greenish black (dark olive grey) ‘dunkel grün-grau’ (dark greyish green)	● mat blackish grey (mouse gey) ‘sepia’? (sepia)
hilumringtype background colour group, non-afterdarkening					
	●	whitish or tinged with glaucescens	●		●
ark pattern colour group with brown hilumring, non-afterdarkening					
n	● soft brown ‘lohfarben’ = ‘antiquabraun’? (dark clay colour)	dark grey violet ‘dunkel bräunl. drab’? (deep brownish drab)	● mat brown grey ‘dunkel umbra’? (dark Brussels brown)	mat greenish black ‘schwarzgrün’ (blackish green)	● mat blackish (dark mouse grey) ‘warm sepia’? (warm sepia)
background colour group (always brown hilumring; afterdarkening)					
	● (pale) brown ‘rhamninbraun’ (buckthorn brown	pale yellowish buff t.w. plumbagoviolet ‘eisenhutviolett’ (bluish violet)	● pale yellow brown t.w. ageratum blue ‘ageratum blau’ (ageratum blue)	grey brown t.w. slate blue ‘dunkles indigo’ (dark indigo)	● brown t.w. greyish indigo ‘graulich indigo’ (greyish indigo)
dark pattern colour group (always brown hilumring; afterdarkening)					
	● dark brown ‘mineralbraun’ (mineral brown)	dark violet ‘dunkel veilchenviolett’ (violet purple)	● dark brown violet ‘kastanienbraun’ (maroon)	black ‘reinschwarz’ (black pure)	● black ‘reinschwarz’ (black pure)
background colour group (always brown hilumring; afterdarkening) at colour as *row* V, but because of D. usually slightly darker					
	●		●		●
ark pattern colour group (always brown hilumring; afterdarkening) at colour as *row* VI, but because of D. usually slightly darker					
	●		●		●