635.652:581.169:575.1.018.6

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 74-24 (1974)

INHERITANCE OF COLOURS IN *PHASEOLUS VULGARIS* L. IV RECOMBINATION WITHIN THE 'COMPLEX LOCUS *C*'

R. PRAKKEN

Department of Genetics, Agricultural University,
Wageningen, The Netherlands

(Received 20–IX–1974)

CONTENTS

I. GENERAL INTRODUCTION ON GENE-ACTION IN *PHASEOLUS VULGARIS* COLOUR

In his last article (Prakken III, 1972b) the present author came to a 'General synthesis' on the genetics of seedcoat colour in *Phaseolus vulgaris* L., mainly consisting in the integration of the so-called 'yellow-black colours' and the 'red-black(ish) colours'. According to him the genetic scheme given there fits with the results of all main investigations.

The seedcoat colours appear to depend upon the action of about nine 'main loci', grouped below into the categories *I*, *II*, *III-a* and *III-b*, and numbered 1–9. The symbols of the loci with colour effect(s) on plant parts other than the seedcoat are printed in ***bold italics*** and those without such effects in *italics*.

I. Basic genes or groundfactors

1. ***P***, the basic gene or 'groundfactor' for seedcoat colour, all *pp*-plants being completely white-seeded.
2. **T**, the gene necessary for a completely coloured seedcoat, all *tt*-plants with coloured seed (*P*.) being but partly coloured, i.e. having seed with a (very) small to a (very) big white part, the coloured part showing accurately the same colour as the genetically corresponding totally coloured *P.T.*-plants, see below.

II. Three dominant colour genes or chromogenous factors

Each of these produces, together with the groundfactor *P*, a distinct, very pale seedcoat colour:

3. *C*, preliminary indicated here as the 'complex locus for ever-segregating and constant mottling', is a 'locus' having numerous 'alleles'. Together with *P*. only, *CC* produces a pale greenish yellow colour (*Cc* is mottled: very pale greenish yellow with white background mottling), while C^r. (or $\dot{R}$., cf. chapter II) produces a pale lilac red one, both without a (brown) hilumring. Since this 'locus' will be analysed in the present article a more extensive introduction on the 'complex locus *C*' will be given in chapter II.
4. *D*, the gene causing, together with *P*., a brown hilumring but further hardly influencing seedcoat colour, leaving it, with *P*. alone, dirty whitish. Therefore *D* is indicated as the 'hilumring factor'.
5. *J*, a gene causing, like *D*, a brown hilumring, but moreover giving the whole seedcoat a shiny pale yellowish (or better: a shiny creamish pale buff) colour, therefore called 'shine factor'. All *J*.-colours are shiny and furthermore they show an intensive '*afterdarkening*', continuing over many years. None of the *jj*-colours show this afterdarkening.

III-a. Three dominant modifying genes or intensifying factors

These genes cause, each in their specific way, a *darkening* of the pale colours produced by the combined action of *P*. together with *C*., *D*. or (and) *J*., with black or blackish as the most dominant and darkest colour:

6. *G*, the 'yellowbrown factor', changing the shiny pale greenish yellow of

P.C.J. into yellowbrown, but hardly influencing *jj*-colours.

7. *B*, the '(grey)greenish brown factor', changing the pale greenish yellow of *P.C.* into (grey-)greenish brown. 'Yellowbrown factor' and '(grey-)greenish brown factor' together, *G.B.*, produce a (dark)brown colour.
8. *V*, the 'violet factor', changing the pink anthocyanin colour of cotyledons, hypocotyl, flower (= pale lilac), fruit, etc. into violet, at the same time changing yellow to brown seecoat colours into violet to black ones. The allele V^{lae} ($=v^{lae}$) causes a pale lilac (=pale pink) flower colour and *vv* leaves it white, their only difference. Dominance for flower colour is incomplete.

III-b. One recessive modifying gene or intensifying factor

9. ***Rk***, the 'locus for recessive red". The symbol was derived, by SMITH 1939, from the variety *R*ed *K*idney, that has recessive red seed, *rk rk*; a third allel, rk^d, produces a darker red.

For further information on the combined action of these main colour genes see PRAKKEN III, 1972b: the scheme opposite p. 82 (the yellow-black colours) and the systematic enumeration on pages 72–78 (the yellow-black colours *and* the red-blackish ones).

II. THE 'COMPLEX LOCUS *C*' AND ITS VARIOUS COLOUR ACTIONS

Since the beginning of the century it has become clear that the 'complex locus *C*', cf. chapter I, is concerned with many characters:

> Dark pattern against background colour; red against non-red seedcoat; one- or selfcoloured seedcoat against a patterned one; the pattern shows many types: striping, mottling, fine dotting, etc., etc. (cf. a.o. LAMPRECHT, 1940, 1947); the pattern is often (but not always) in red or darker colour (*G*, *B*, *V*) on a very pale buff background; the mottling (and striping?) is 'constant' or 'ever-segregating'.
>
> In many cases also the colour of plant parts other than the seed coat is involved: quantity and (or) intensity of anthocyanine colour in cotyledons, hypocotyl, whole plant, flower and ripening fruit. Even a strong (absolute?) correlation between seedcoat pattern and taste of the cooked seed was suggested (sweetness; TJEBBES and KOOIMAN I, 1919).

Each of the seedcoat characters mentioned above was indicated with a genetic symbol: *C-c*, *R-r*, *M-m*, *St-st*, etc. Almost from the beginning these were realized to be (absolutely?) linked. Especially SHAW and NORTON (1918) in their important but very condensed study explicitly stated that most of their gene pairs *Y-y*, *Z-z*, *M-m*, *M'-m'* and *O-o* (only *Y-y* and *Z-z* will be discussed further on) had to be looked upon as absolutely (?) linked.

The colour of other parts of the plant (see above and the list of Literature, p. 34) was but seldom studied in direct connection with seedcoat colour;

originally the strong correlations between the two groups of colours were unknown in most cases. Therefore, throughout the bean literature, many gene symbols can be found for colour characters, ranging from seedling colour to fruit- or plant-colour, that later appeared to belong to the 'complex locus *C*'. Here they are indicated as 'accompanying colours'. The cases will not be traced now, but in chapters IV and V the strict relations will become clear, at least for one definite type of cross (cf. also Prakken III, 1972b).

Thus, the 'complex locus C' has to do with many and variable characters. The situation as it was found has caused *a high confusion* in the use of genetic symbols. At the one extreme there is the using of *a pair of symbols for each pair of characters*, in spite of the (to be sure often unknown) absolute (?) linkage. At the other extreme there is the tendency to look at the whole (esp. if only seedcoat colour and not the accompanying colours were considered, and if for the seedcoat character pairs not a single case of recombination was observed or recognized) *as one multiple allelic series:* C (dark pattern colour), C^r (red dark pattern), C^m (red mottled; strictly speaking the mottling consists in the pale background spots), C^{st} (red striped), ..., c (background colour), c^u (*u*nchangeable background, i.e. unchangeable by G, B and V), c^{ui} (with very *i*ntense stem colour), and at last c^{cr} (= *c*ompletely *r*ecessive: Cc^{cr} being one-coloured dark pattern). This point of view was (at least preliminary) taken by Feenstra (1960; introduced c^u) and by Nakayama (introduced c^{ui}, 1964, and c^{cr}, 1965), while the present author takes it as a *starting point*, and in a sense even extends the series of 'alleles' with $C^{st\prime}$ and $C^{m\prime}$.

Most investigators came to some intermediate standpoint, sometimes depending upon real or suspected cases of recombination between seedcoat colour genes belonging to the complex. Tjebbes and Kooiman first used, for the 'monofactorially' segregating cross between a 'yellowbrown dark pattern type' and a 'red striped type' but ***one symbol***, *S-s* or *B-b* (I, 1919), later ***two***, $\overset{\frown}{Bs}$-$\overset{\frown}{bS}$ (IV, 1921a), while finally (Tjebbes, 1931) ***three*** symbols were used, $\overset{\frown}{Brs}$-$\overset{\frown}{bRS}$, and crossing-over was discussed. Lamprecht (XV, 1940; 1961a), for quite analogous crosses, used but two symbols, $\overset{\frown}{Cr}$-$\overset{\frown}{cR}^{st}$, as he accepted all types of (dominant) red to belong to one multiple allelic series: R (selfcoloured red), R^m (red mottled), R^{st} (red striped), etc., ... r (non-red).

A few words have to be said on the relation between 'ever-segregating' and 'constant' mottling, both belonging to the complex. Looking away from Von Tschermack's association-dissociation theory, it was Emerson (1909a and b), following a suggestion of Spillman, who first tried an explanation. He supposed that mottling (or striping, etc.) *depends upon two dominant and (almost?) absolutely linked genes*, *Y-y* and *Z-z*. True-breeding mottled plants should be $YYZZ$ ($\overset{\frown}{YZ}\,\overset{\frown}{YZ}$), one- or selfcoloured ones $YY\,zz$, $yy\,ZZ$ or $yy\,zz$. Crossing $YY\,zz$ with $yy\,ZZ$ produces the mottled $Yy\,Zz$ ($\overset{\frown}{Yz}\,\overset{\frown}{yZ}$), segregating into $\frac{1}{2}$ mottled, $\overset{\frown}{Yz}\,\overset{\frown}{yZ}$, and $\frac{1}{2}$ selfcoloured ($\frac{1}{4}$ $\overset{\frown}{Yz}\,\overset{\frown}{Yz}$ and $\frac{1}{4}$ $\overset{\frown}{yZ}\,\overset{\frown}{yZ}$). Kooiman (1920) and Lamprecht (1932) found that, in the case of ever-segregating mottling, the half of F_2-plants with selfcoloured seed for one $\frac{1}{2}$ ($= \frac{1}{4}$ of the whole F_2) show the 'dark pattern colour' of the mottled plants and for the other $\frac{1}{2}$ the colour of the 'paler background spots'. Therefore they considered the ever-segregating mottling *directly to depend upon the heterozygosity Bb* (KOOIMAN) or *Cc* (LAMPRECHT; here *C-c* is used). PRAKKEN (1934, 1940) tried to combine the new discovery with the old theory of EMERSON-SPILLMAN, in replacing $\overset{\frown}{Yz}$-$\overset{\frown}{yZ}$ by $\overset{\frown}{Cm}$-$\overset{\frown}{cM}$ (*C* for dark pattern colour; *M* for locally suppressing it). In the present investigation this problem will again become actual.

III. MATERIAL AND METHODS

The methods are described earlier, e.g. in PRAKKEN III, 1972. Essential is that *for each individual plant all relevant colour characters were noted,* qualitatively and, if possible, quantitatively: colour of seedling (cotyledons and hypocotyl) and in some cases of the whole plant, flower colour (including red intensification of tip standard or not, and with or without red veins in the wings), colour of the ripening fruit, and at last seedcoat colour and pattern.

Colour extension (= quantity) on cotyledons, hypocotyl and fruit (and sometimes on other elements) usually was indicated with the numbers 0 (= green) to 10, depending upon the roughly estimated part of the surface covered with the colour. Also intensity and extension of red tip standard (0, 0^{+}?, 1–5) and of red veins wing were estimated, or described with a small schematic picture or otherwise.

None of the parent plants used in the crosses of the present article possessed the 'violet factor' *V* (violet flower and violet or blackviolet anthocyanin). All were either $V^{lae}V^{lae}$ ($= v^{lae}v^{lae}$; pale lilac flower and pink to violet-red anthocyanin) or *vv* (white flower, but for the rest the same anthocyanin colours as $v^{lae}V^{lae}$). See further, for the numerous evaluation-difficulties, PRAKKEN III, 1972b, p. 5–8.

The material discussed in the present article belongs to two periods: 1934–1940 and 1960–1968. During the second world war all the living material was lost, but fortunately all descriptions and analyses were saved. After the war again bean varieties were gathered (but partly the same), crossed and analysed, *giving quite analogous results as the earlier experiments,* also with respect to crossing over within the 'complex locus *C*'. It was precisely for the crossing over in C-C^{st} heterozygotes that the two (groups of) crossings used for the present article were selected from a much more extensive material.

It was in the same sort of cross, dark pattern type, *CC*, with (orange) red striped, $C^{st}C^{st}$, that the few cross-over types mentioned in the literature (and the very few not mentioned as such!) were found: TJEBBES (1931) and LAMPRECHT (XV, 1940; 1961a) – A profound discussion will not be made now.

The cross made in 1960 will be treated first, in chapter IV, because there the analysis was pushed further. In chapter V the results will be compared with those received from two diallelic crosses during the pre-war period, which old material was analysed in PRAKKEN III, 1972b, where however, the few crossover types but accidently were mentioned and not taken up in the analysis.

The numbering of the families was continued over the years. It was only once, viz. 1946, just after the war, that the numbering was restarted.

IV. RECOMBINATION WITHIN THE ‘C-LOCUS’ IN THE CROSS OF ‘CITROEN’ (CC) WITH ‘ORANGERED STRIPED’ ($C^{st}C^{st}$) (1960–1968)

1. Normal colours in parents, F_1, F_2, etc. (1960 and later).

The parent ‘Citroen’, line 139, had a pale greenish yellow seedcoat, without brown hilumring and without any afterdarkening. The ‘Orangered striped’ parent, line 162, possessed seed with orangered stripes upon a very pale buff background and with a brown hilumring; it is shiny and shows afterdarkening. The genotypes of parents and F_1 were learned to be:

Citroen (line 139) : $PP\ TT\ C\ \ C\ \ dd\ jj\ GG\ bb\ V^{lae}V^{lae}\ RkRk$.
Or. red striped (line 162): $PP\ TT\ C^{st}C^{st}\ dd\ JJ\ GG\ bb\ V^{lae}V^{lae}\ RkRk$.
F_1 (fam. 2473–2481 ’61): $PP\ TT\ C\ \ C^{st}\ dd\ Jj\ GG\ bb\ V^{lae}V^{lae}\ RkRk$, i.e.

the F_1-plants were heterozygous for C-C^{st} and J-j (shine factor pair) only. It must be mentioned here that G (the yellowbrown factor) in jj-genotypes has but an extremely little influence: the very pale greenish yellow of $CCjjgg$ is hardly or not att all changed by it.

As in all analogous cases the seed of CC^{st} F_1-plants was *threecoloured* and because of Jj with a brown hilumring, shiny and afterdarkening:

‘main colour’: shiny yellowbrown (GG!) dark pattern colour,
‘striping over it’: orangered (GG!),
‘mottling within it’: very pale buff, about like the background in line 162 (neither influenced by G, nor by B or V).

Tjebbes and Kooiman and later Lamprecht looked upon these pale background spots as caused by the heterozygosity Bb resp. Cc, the latter symbol, of Lamprecht, being used here. Tjebbes (1931) indicated this heterozygote as $Bb\ Rr\ Ss$ ($\overparen{Brs}\ \overparen{bRS}$) and Lamprecht as $Cc\ R^{st}r$ ($\overparen{Cr}\ \overparen{cR^{st}}$). In the present article it is, as by Feenstra (1960), preliminary simply indicated as CC^{st}; cf. also page 4.

The ‘accompanying colours’ of the parent lines 139 (CC), 162 ($C^{st}C^{st}$) and their F_1 (CC^{st}) were as in the small table below, where a one-pointed arrow, ——→, indicates increasing values and a two-pointed arrow, ←——→, more or less identical values:

genotype	*cotyl.*		*hypoc.*		*flower*	*tip stand*		*veins wing*	*fruit col.*	
$C\ C$:	± pink 1	↑	pink 1–2?	↑	pale 1.	– red tip		– red v.	pink 1–2	
$C\ C^{st}$:	± pink 1		pink 0–1?		pale 1.	+ trace r.t.		– red v.	viol. red 5	
$C^{st}C^{st}$:	± pink 1	↓	green (=0)		pale 1.	+ small r.t.	↓	– red v.	viol. red 6	↓

Observe that the arrow for hypocotyl colour is *in reversed direction* with those for tip standard and fruit colour, and that for all characters F_1 is more or less intermediate, only the high fruit colour of $C^{st}C^{st}$ being subdominant. Flower colour ($V^{lae}V^{lae}$) and the lack of red veins ($RkRk$) will further be left out of consideration.

In 1962 15 F_2-families (2660–2674) were bred. Out of 651 seedlings only 347 produced ripe seeds (cause of the loss not known). Among these 347 *two plants produced seed of a deviating type,* discussed in IV-2. The remaining 345 plants, segregating for $CC^{st}Jj$, showed the expected six types, see table 1.

Table 1. Seedcoat colour in F_2 of 'Citroen' (line 139) with 'Orangered striped' (line 162), F_1 being $CC^{st}Jj$ (between brackets the numbers expected). Two deviating plants are left out.

a. *jj, without hilumring, non-afterdarkening*			
23 (21.5) $CCjj$	53 (43.1) $CC^{st}jj$	25 (21.5) $C^{st}C^{st}jj$	total
dark pattern,	*threecoloured,*	*striped*	101 (86.2)
pale green. yell. = **like Citroen**	*main col:* pale gr.y. *stripes:* pale lilac red *mottling:* white	*stripes:* pale lilac red *background:* white	
b. *J., with brown hilumring, shiny and afterdarkening*			
48 (64.7) $CC\,J.$	122 (129.4) $CC^{st}J.$	74 (64.7) $C^{st}C^{st}J.$	244 (258.8)
dark pattern,	*threecoloured,*	*striped,*	
yellowbrown (*GG*!)	*main col.:* yellowbr. *stripes:* orangered *mottling:* pale buff	*stripes:* orangered *backgr.:* pale buff	
	= **like F_1**	= **like 'Orangered striped'**	
total: CC: 71 (86.2)	CC^{st}: 175 (172.5)	$C^{st}C^{st}$: 99 (86.2)	345

Tabulation of the 'accompanying colours' in F_2 appeared rather difficult, a.o. because 'stem base' was judged and not cotyledons and hypocotyl separately. It was easy to state that no differences existed between *jj*- and *J.*-plants, but only between CC (dark pattern), $C^{st}C^{st}$ (striped) and CC^{st} (threecoloured). Therefore a short comparison will be made with line 139 (Citroen), line 162 (Orangered striped) and F_1. Cf. with the small colour table page 6.

In the $23 + 48 = 71$ CC-plants in more than half of the plants *stem base* was noted as 'green' or 'green?', but rather often it was 'pink 0^+' to 'pink 3'. – *Red tip standard* was in not a single plant observed. – *Fruit colour* was only once noted as 'green?' and for the rest as 'pink 1' to 'pink 3', the means per family varying from 1.0 to 2.0 – Thus, for all characters the CC-values were in agreement with those of Citroen (CC).

In the $25 + 74 = 99$ $C^{st}C^{st}$-plants the *stem base* was practically always 'green', a few were 'green?' and only once 'pink 0^+' was noted. – *A small red tip* was noticed in 90 of the 99 plants, while in only 9 plants it was 'overlooked' or better not observed. – *Fruit colour* in all $C^{st}C^{st}$-plants was intense violet-red, from '3' to '7', the means per family varying from 4.8 to 5.5, general mean slightly over 5 (line 162 was violet-red about 6; probably no real difference). – Thus: here too agreement with the 'Orangered striped' parent ($C^{st}C^{st}$).

In the $53 + 122 = 175$ CC^{st}-plants at last, with threecoloured seedcoat, the 'accompanying colours' were about *intermediate* between those of the parents or, like the violet-red fruit colour of $C^{st}C^{st}$, subdominant. *Stem base* was often 'green' but also 'pink 1' or 'pink 2' was observed. – *A red tip standard* was not observed in about half of the plants, while in the remaining ones it was scored as 'very small' to 'small'. – *Fruit colour* in CC^{st} at last, never was pink but always violet-red, though somewhat less extensive than in $C^{st}C^{st}$: it varied from 'violet-red 3' to 'violet-red 5', the family means from 3.6 to 4.6, in general being slightly over 4 (in F_1 it was almost 5, but the difference may mainly depend on weather and (or) evaluation). Therefore: in this case as well a good agreement with F_1-CC^{st} colours.

At any case the general conclusion must be that, *within the normal three types, CC, $C^{st}C^{st}$ and CC^{st}, probably complete linkage exists between seedcoat colour and the 'accompanying colours'* from cotyledons(?), hypocotyl, red tip standard and fruit colour.

Shortly it may be mentioned here that in the summer of 1963 two F_3-families (2734, 2735) were grown from $CC^{st}jj$ F_2-plants in which the 'pale lilac-red striping' over the 'pale greenish yellow/mottled with white' was extremely weak. F_3-segregation for seedcoat colour (and for the 'accompanying colours') was, however, quite normal: 10 CC + 21 CC^{st} + 9 $C^{st}C^{st}$.

In the summer of 1964 still four F_3-families were grown, 2824–2827, from normally threecoloured $CC^{st}J.$-plants. Leaving out J-j -segregation, the result for C-C^{st} was: 35 CC + 71 CC^{st} + 20 $C^{st}C^{st}$ (exp. 31.5 + 63.0 + 31.5). The mean values of the 'accompanying colours' for the three groups, here completely scored, were:

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
$C\ C$ (dark p.):	pink 1.0 ↑	pink 1.4 ↑	0.0 (= – red tip)	pink 1.2
$C\ C^{st}$ (threecol.):	pink 0.9	pink 1.1	1.6 (= very sm.r.t.)	violet red 4.3
$C^{st}C^{st}$ (striped):	pink 0.9 ↓	pink 0.1	2.7 (= clear r.t.) ↓	violet red 6.4 ↓

Thus, the above mentioned complete linkage seems quite corroborated.

2. Two deviating F_2-plants, their offspring and genotype: $CC^{st\prime}$, $CC^{m\prime}$.

As already mentioned (cf. p. 7) *two* of the 347 seed-bearing F_2-plants in 1962 produced seed of *a deviating type*. Both plants possessed the 'shine factor' J at least once: seed with a brown hilumring, shiny and afterdarkening. Their plant numbers were 2670-6 (indicated as *case-a.*) and plant 2672-7 (indicated as *case-b*); these indications *a.* and *b.* were also used for their F_3-offspring families. From every F_2-plant only a few ripe pods had been earned, and therefore no more than about 20 seeds were available for the breeding of F_3-*a.* and F_3-*b.* Both these F_3-families were grown in the hot house, January to May 1963. The description and analysis of F_3 will be more or less made together with that of their F_4-offspring of summer 1963. Reasons: *1.* the low number of F_3-plants; *2.* difficulties in sharply classifying (at least originally) the quite new seedcoat fenotypes; *3.* the hot house environment, that influenced the 'accompanying colours' of cotyledons, hypocotyl and tip standard; *4.* esp. in family-*a.* a good estimation of F_3-fruit colour was impossible, because of unexpectedly early and fast ripening. – At last it has to be remarked that the seed of the original F_2-plants *a.* and *b.* might have been looked at as some sort of extreme CC^{st} *J.* type. Therefore these seeds can really *best be described* in comparison with the seed of normal CC^{st} *J.* type, e.g. with the threecoloured seed of F_1.

Case-a: F_2-plant 2670-6'62 (=a.) and its offspring

Yellowbrown dark pattern (GG) was the main colour of its seed, at least principally; *red stripes were over it,* not sharply delimited however as normally, but *'flowing out' over the main colour* in a very variable degree, thus changing the yellowbrown partly into reddish brown; and, the most typical character, *the pale buff background mottling of real CC^{st}J. was completely lacking.*

The 'accompanying colours' of plant 2670–6 (= *a*) were:

base of stem	[*flower*]	*tip standard*	[*veins wing*]	*fruit colour*
pink 1	[pale 1.]	– red tip	[– red v.]	pink 2?

F_3-family *a.* (hot house; Jan.-May 1963) contained 18 seed-bearing plants: 3 *jj* + 15 *J.*, without resp. with brown hilumring. The 15 latter ones gave in the summer of 1963 15 F_4-families (2751–2765; one of them had to be discarded), and in the autumn the 3 *jj*-plants gave families 2784–2786, all plants of the latter three families lacking the hilumring.

F_3 and F_4 together learned that segregation after plant 2670–6 (*a.*) was for *J-j* (shine-factor pair) and for two alleles of the 'complex locus *C*', viz. the normal dark pattern allele *C* and a 'new allele', indicated as $C^{st\prime}$. The genotypes of 17 F_3-plants (all *GG*) are given in table 2.

Table 2. Genotypes of the 17 F_3-plants from F_2 2670-6 (a).

1. $CC \left\{\begin{matrix}JJ{:}0\\Jj{:}1\end{matrix}\right\}$:	1	**3.** $CC^{st\prime} \left\{\begin{matrix}JJ{:}3\\Jj{:}7\end{matrix}\right\}$	10	**5.** $C^{st\prime}C^{st\prime} \left\{\begin{matrix}JJ{:}2\\Jj{:}1\end{matrix}\right\}$	3	*J.*:	14
2. *CC jj*:	1	**4.** $CC^{st\prime}jj$:	2	**6.** $C^{st\prime}C^{st\prime}jj$:	0	*jj*:	3
total: *CC*:	2	$CC^{st\prime}$:	12	$C^{st\prime}C^{st\prime}$:	3	*total*:	17

Before describing the six fenotypes a few remarks. As always the colours of *jj*-types are paler than those of *J.*, they are without brown hilumring and without afterdarkening. As for the accompanying colours there is no difference between *J.* and *jj*. The six seedcoat colours, the four new ones printed in bold letter, are listed below.

First column of table 2, *CC, the quite normal dark pattern colours:*

1. *CC J.(GG)* : shiny yellowbrown dark pattern, afterdarkening.
2. *CC jj(GG)* : pale greenish yellow dark pattern; without hilumring.

Second column, $CC^{st'}$, heterozygous for the new 'allele':

3. $CC^{st'}J.(GG)$: **shiny (partly reddish) yellowbrown, with 'flowing out' red stripes** (seedcoat colour of F_2-2670-6, = *a.*).
4. $CC^{st'}jj(GG)$: **(partly reddish) pale greenish yellow with 'flowing out' red stripes; without hilumring.**

Third column, $C^{st'}C^{st'}$, homozygous for the new 'allele':

5. $C^{st'}C^{st'}J.(GG)$: **red stripes, 'flowing out' over very pale buff.**
6. $C^{st'}C^{st'}jj(GG)$: **red stripes, 'flowing out' over white; without hilumring.**

Especially in **5.** and **6.**, $C^{st'}C^{st'}$ (to a lesser degree also in **3.** and **4.**, $CC^{st'}$), the degree of 'flowing out' is so *extremely variable* that:

in some seeds there is about normal, i.e. sharply delimited, red striping, while other seeds are almost completely red, the striping being hardly visible.

Seeds from one plant can show (almost?) this whole variation, but differences between plants or families seem to depend partly upon genetical differences (see below). Within one pod there usually is a high correlation.

The F_4-segregations of 1963 used above will not be tabulated. The agreement with the expected numbers was rather good, though even in F_4 a few plants were difficult to classify. An F_5 control is shown in table 3: families 2850–2855 '64, after the six $CC^{st'}J.$-plants in F_4-family 2765 '63, nrs -1, -5, -6, -7, -8 and -10 respectively.

Table 3. F_5-segregation after the six in the text mentioned $J.\ CC^{st'}$ F_4-plants.

After $CC^{st'}Jj$ plants:	$CC\,jj$	$CC^{st'}\,jj$	$C^{st'}C^{st'}\,jj$	$CC\,J.$	$CC^{st'}\,J.$	$C^{st'}C^{st'}\,J.$	*total*
fam. 2850:	0	1	0	2	6	3	12
2851:	1	3	1	1	3	3	12
2852:	1	0	1	3	4	3	12
total	2 (2.2)	4 (4.5)	2 (2.2)	6 (6.7)	13 (13.6)	9 (6.7)	36
After $CC^{st'}JJ$-plants:							
fam. 2853:	–	–	–	3	6	3	12
2854:	–	–	–	3	7	2	12
2855:	–	–	–	4	5	2	11
total				10 (8.7)	18 (17.5)	7 (8.7)	35

After the analysis of seedcoat colour in the offspring of F_2-plant 2670-6 (= *a.*) the discussion of the 'accompanying colours' can be rather short. The descriptions on p. 7 and the small table p. 8 made clear that the influence of C^{st} compared with that of C is **very conspicuous**. Throughout the offspring of 2670–6 (= *a.*) the influence of $C^{st'}$ against that of C has been followed. *The striking conclusion has to be that, with respect to the accompanying colours, there **is no difference at all** between CC, $CC^{st'}$ and $C^{st'}C^{st'}$*, see table 4, that shows about the same mean values for the three genotypes: hypocotyl high values, tip standard and fruit colour low ones, the cotyledon values from the beginning being the same.

Table 4. Mean values of the 'accompanying colours' in the F_4-families after the 10 $J.CC^{st'}$ F_3-plants (cf. table 2).

	number of plants	mean values of their accompanying colours						
		cotyledons	*hypocotyl*		*tip standard*		*fruit colour*	
$C\ C$	: 36 (exp. 33.2):	pink 2.2 ↑	pink 2.6 ↑	all high	– red tip ↑	all low	pink 1.9 ↑	all low
$C\ C^{st'}$	: 58 (exp. 66.5):	pink 2.1	pink 2.7		– red tip		pink 2.6	
$C^{st'}C^{st'}$	: 39 (exp. 33.2):	pink 2.3 ↓	pink 3.1 ↓		– red tip ↓		pink 2.4 ↓	

As a general conclusion it can be stated that, compared with the original allele for red striping C^{st}, the new allele for red striping, $C^{st'}$:

1. Has *lost* the capacity of causing mottling in *C*-dark pattern colour.
2. Has *lost* the capacity of preventing the 'flowing out' of red colour.
3. Has *lost* the capacity of causing violet red fruit colour.
4. Has *lost* the capacity of causing red tip standard.
5. Has *lost* the capacity of keeping the hypocotyl green.

(6. Because of the low and about like values no change in cotyledon colour could be stated).

Case-b: F_2-plant 2672-7'62 (= b.) and its offspring.

Pure yellow-brown (GG) was the main colour of its seedcoat; in this colour was *a very pale buff background mottling* like in the threecoloured seed of $J.CC^{st}$ plants; the most typical character of real CC^{st} plants however, *the red striping, was completely lacking.* The 'accompanying colours' of the plant were:

base of stem	*flower*	*tip standard*	*veins wing*	*fruit colour*
green	pale 1.	+ trace red t.?	– red veins	violet-red 3.

(compare with the values of 2670-6'62 = *a.*, p. 9).

F_3-family *b.* (hot house; Jan.-May '63) contained 16 seed-bearing plants: 1 *jj* (pale greenish yellow with white mottling and without hilumring) + 15 *J.* (with brown hilumring), these 15 being of two types:

2 one-coloured yellowbrown dark pattern type (*CC J. GG*)

13 two-coloured, viz. yellowbrown with pale buff mottling (?? J. GG).

Here too, as in *a.*, segregation was for *J-j* and for two 'alleles' of 'locus *C*', one of the latter being the normal dark pattern allel *C*. The numbers of F_3-family *b.* however, 2 one-coloured + 14 mottled, *do not suggest an eversegregating mottling* of the type 1 *CC* + 2 *Cc* (mottled) + 1 cc (LAMPRECHT; = KOOIMAN *B-b*), as might be expected from the genotypes these investigators used for analogous parent types (cf. p. 4).

F_4 had to learn. From the 15 J.-plants, in the summer of 1963, the F_4-families 2736–2750 were obtained. The two yellowbrown *CC*-plants gave *CC*-plants only (one F_3 parent was *JJ* and one *Jj*). The 13 mottled F_3-plants behaved in two ways:

4 gave mottled-seeded plants only (together 52), while

9 segregated into 35 dark pattern (CC) + 94 mottled-seeded plants.

Therefore it certainly is no 'ever-segregating mottling' (as expected by TJEBBES and KOOIMAN or by LAMPRECHT), but a clear case of 'constant mottling' without, however, the red colour usually connected with it. LAMPRECHT indicated the 'allele' for red mottling as R^{ma} ($=C^{m}$ here). I indicate the new 'allele' for constant mottling (*without red*) analysed here, as $C^{m\prime}$, and from (F_3 and) F_4 the genotypes of the 16 F_3-plants were concluded, see table 5.

Table 5. Genotype of the 16 F_3-plants from F_2 2672-7 (= *b.*), as concluded from (F_3 and) F_4.

				total
1. $CC\left\{\begin{matrix}JJ:1\\Jj:1\end{matrix}\right\}$ 2	**3.** $CC^{m\prime}\left\{\begin{matrix}JJ:3\\Jj:6\end{matrix}\right\}$ 9	**5.** $C^{m\prime}C^{m\prime}\left\{\begin{matrix}JJ:0\\Jj:4\end{matrix}\right\}$ 4		*J.*: 15
2. *CCjj*: 0	**4.** $CC^{m\prime}jj$: 1	**6.** $C^{m\prime}C^{m\prime}jj$: 0		*jj*: 1
total: *CC*: 2	$CC^{m\prime}$: 10	$C^{m\prime}C^{m\prime}$: 4		16

The analysis of the F_4 revealed a clear cut correlation between seedcoat colour genotype and the 'accompanying colours'. The mean F_3-colour values were:

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
$C\ C$ (2) :	pink* 3.5 ↑	pink 0.6 ↑	– red tip	pink 2.0
$C\ C^{m\prime}$ (10):	pink 0.6	pink 0.3	– to + trace r.t.	viol. red 3.7
$C^{m\prime}C^{m\prime}$ (4) :	pink 0.8 ↓	green (=0.0)	(– to) + small r.t. ↓	viol. red 5.1 ↓

* (unexpectedly high, but only two plants; cf. table 7, p. 13).

The seedcoat types **1.** to **6.** of table 5 are described below, the four new ones in **bold** letter.

First column, CC, the quite normal dark pattern colours:

1. *CC J.(GG)* : shiny yellowbrown, afterdarkening.

2. *CCjj(GG)* : pale greenish yellow, without hilumring.

Second column, $CC^{m\prime}$, *heterozygous for the new 'allele':*

3. $CC^{m\prime}J.(GG)$: **shiny yellowbrown with pale buff mottling, afterdarkening;** in the pale buff part a very fine yellowbrown stippling.

4. $CC^{m\prime}jj(GG)$: **pale greenish yellow with white mottling, without hilumring;** in the white parts a very fine pale greenish yellow stippling.

Third column, $C^{m\prime}C^{m\prime}$, *homozygous for the new 'allele':*

5. $C^{m\prime}C^{m\prime}J.(GG)$: **shiny yellowbrown with pale buff mottling, afterdarkening;** (like **3**, but the pale buff parts slightly greater and with less stippling).

6. $C^{m\prime}C^{m\prime}jj(GG)$: **pale greenish yellow with white mottling, without hilumring.** (like **4**, but the white parts slightly greater and with less stippling).

The difference between $CC^{m\prime}$-mottled and $C^{m\prime}C^{m\prime}$-mottled as described above (the latter slightly *greater* pale buff resp. white spots with lesser fine yellowbrown resp. greenish yellow stippling) was found out or corroborated only by accurate comparison of F_4-segregation with F_3-fenotype, e.g. in the 13 F_4-families from $C^{m\prime}.J.$ F_3-plants, see table 6 (fam. 2738–2750).

Table 6. F_3-genotypes concluded from F_4 fenotypic segregation after $C^{m'}.J.$ F_3-plants.

number of $C^{m'}.J.$	segregation in the F_4 families				
genotypes in F_3.	*CCjj*	$C^{m'}.jj$	*CCJ.*	$C^{m'}.J.$	*total number*
6 $CC^{m'}Jj$	3(5.1)	10(15.4)	20(15.4)	49(46.1)	82
3 $CC^{m'}JJ$			12(11.5)	34(34.5)	46
4 $C^{m'}C^{m'}Jj$		15(15.2)		46(45.8)	61
0 $C^{m'}C^{m'}JJ$				–	–

The difference between seedcoat colour of $C^{m'}C^{m'}$ and $C^{m'}C$, however, is *not absolutely sharp.* For a new check upon it, and also for a more definite finding out of the correlations between seedcoat colour and the 'accompanying colours' a rather extensive program was set up, analysing F_5-families in the summer of 1964:

a. Fam. 2828–2838, from all mottled seeded plants, $C^{m'}.JJ$, of F_4-fam. 2741.
b. Fam. 2839-2848, from all yellowbr. mottl. plants, $C^{m'}.J.$, of F_4-fam. 2743.
c. Fam. 2856–2859, from four homoz. mottl. plants, $C^{m'}C^{m'}J.$, of F_4-fam. 2749.

Group a. The parent plants for families 2828–2838 were ordered and numbered from the most probable heterozygous, $C^{m'}C$ (2828) to the most probable homozygous, $C^{m'}C^{m'}$ (2838). This was done on two grounds: on the basis of seedcoat colour (viz. the character of the pale background spots, see p. 12) *and* on the basis of the accompanying colours (esp. hypocotyl, tip standard and fruit colour). Each F_5-family consisted of 12 plants. The results with respect to the 11 F_4-mother plants were very satisfying:

8 F_4 heterozygotes, $C^{m'}C$: 2828, -29, -30, -31, -32, -33, -34 and -36;
3 F_4 homozygotes, $C^{m'}C^{m'}$: 2835, -37 and -38.

The F_5-segregation after these 8 $(JJ)C^{m'}C$ heterozygotes together was 25 *CC* (yellowbrown dark p.) + 70 $C^{m'}.$ (yellowbrown mottled). Trying to classify tentatively these 8 segregating families into their three genotypes resulted in:

25 *CC* (exp. 23.7) + 49 $C^{m'}C$ (exp. 47.5) + 21 $C^{m'}C^{m'}$ (exp. 23.7) = together 95.

The groups b. and c. too gave satisfying results, which, because of size of this article, will not be discussed.

'Accompanying colours' and their correlation with seedcoat colour (CC–$C^{m'}C$–$C^{m'}C^{m'}$) were already given for the F_2-mother plant (p. 11) and for its F_3 family (p. 12). As a last analogous example the results for the just discussed 11 F_5-families from $JJ\,C^{m'}.$ F_4-plants (*Group a.*) may be given, see table 7 and its arrows.

Table 7. Mean values of the 'accompanying colours' in 11 F_5-families: 8 from F_4 $C^{m'}C$-plants and 3 from $C^{m'}C^{m'}$-ones.

		cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
8 fam. from	*C C* (25 pl):	pink 0.3 ↑	pink 0.8 ↑	– red tip	pink 1.0
$C^{m'}C$-plants:	$C^{m'}.$ (70 pl):	pink 0.3	pink 0.2	+ red t. 2.2	viol. red 3.9
3 fam. from		*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*
$C^{m'}C^{m'}$-plants:	$C^{m'}C^{m'}$ (36 pl):	pink 0.5 ↓	green (0.0)	+ red t. 2.9 ↓	viol. red 5.7 ↓

Comparison of table 7 with the small table on p. 8 shows that, with respect to the 'accompanying colours', this $C^{m'}C$-segregation corresponds rather well with the $C^{st}C$-segregation: see the various (relative) values and the one- and two-pointed arrows.

As a general conclusion it can be stated that, compared with the C-dark pattern allele, the new allele for constant mottling $C^{m'}$:

1. Has *gained* the capacity of causing mottling in the dark pattern colour.
2. Has *gained* the capacity of preventing the 'flowing out' of red colour (this point will become clear in IV-3, the cross between $C^{st'}C^{st'}$ and $C^{m'}C^{m'}$).
3. Has *gained* the capacity of causing intense violet red fruit colour.
4. Has *gained* the capacity of causing red tip standard.
5. Has *gained* the capacity of keeping green the hypocotyl.

(6. Because of the low and about like values no change in cotyledon colour can be stated).

Plaese confer these statements 1–5 (or 6) for the change of C into $C^{m'}$ with the statements 1–5 (or 6) for the change of C^{st} into $C^{st'}$ on p. 11: **loss** in the last mentioned case precisely agrees with **gain** in the first mentioned or present one.

3. Cross between the two new homozygous genotypes $C^{st'}C^{st'}$ and $C^{m'}C^{m'}$.

During 1964 and '65 homozygous lines for the new genotypes $C^{st'}C^{st'}$ and $C^{m'}C^{m'}$ were selected, controlled and crossed, by a.o. the then student Ir. VAN DEN BERKMORTEL who helped to continue the analysis. Reciprocal crosses were made between plants of the families:

2927'65, $C^{st'}C^{st'}JJ\,GG$: 'flowing out' (orange)red stripes upon very pale buff

and

2928'65, $C^{m'}C^{m'}\ JJ\,GG$: shiny yellowbrown with very pale buff mottling.

Seeds from the resulting pods were grown, in the hot house, early spring 1966, families 2972–2977, giving in total 29 F_1-hybrids. These were heterozygous $C^{st'}C^{m'}$ only. The colour of *their ripe seedcoat appeared to be exactly the same as that of the original CC^{st} hybrids, i.e. threecoloured:*

$$C^{st'}C^{m'}\ (JJ\,GG)\begin{cases}\textit{main colour:}\text{ shiny yellowbrown}\\ \textit{stripes over it:}\text{ orangered}\\ \textit{mottling within it:}\text{ very pale buff (not influenced by }GG\text{)}\end{cases}$$

Also the 'accompanying colours' of $C^{st'}C^{m'}$ were like those of CC^{st}.

This is not surprising when comparing the points 1–6 p. 11 with 1–6 p. 14: as stated just before, precisely the activities **lost** by the C^{st} 'allele' in changing to $C^{st'}$ are **gained** by the 'allele' C in its change to $C^{m'}$, or vice versa. The two new 'alleles' might be the result of *crossing-over* between the 'alleles' C and C^{st} *at the same point*, though in two independent processes, because they were found in the offspring of two different F_1-plants. See further the summarizing discussion, chapter VI.

In the summer of 1966 seed of three F_1 plants was sown:

fam. 3102, from F_1 2973–3: $C^{st'}C^{m'}$ }
fam. 3103, from F_1 2976–4: $C^{m'}C^{st'}$ } the allele from the mother plant first.
fam. 3104, from F_1 2977–2: $C^{st'}C^{m'}$ }

All three F_2 families showed segregation into the three seedcoat fenotypes that were to be expected, viz. both parent types and the F_1-type, see table 8.

Table 8. F_2-segregation after F_1 $C^{st'}C^{m'}$ *(JJ GG)*. In parentheses the numbers expected (one plant with deviating seedcoat colour, 3103–65, has been left out; see IV-4).

	(or.) red striped, the red 'flowing out' over very pale buff backgr.	threecoloured, like original F_1, i.e. not 'flowing out'	yellowbrown with pale buff background mottling	
	$C^{st'}C^{st'}$	$C^{st'}C^{m'}$	$C^{m'}C^{m'}$	*total*
fam. 3102:	12 (12.2)	23 (24.5)	14 (12.2)	49
fam. 3103:	32 (24.2)	35 (48.5)	30 (24.2)	97 (+ 1 dev.)
fam. 3104:	25 (23.0)	43 (46.0)	24 (23.0)	92
total	69 (59.5)	101 (119.0)	68 (59.5)	238 (+ 1 dev.)

'Accompanying colours' could be scored but very uncompletely. In family 3102 the mean values were as to be expected:

	cotyledons		*hypocotyl*		*tip standard*		*fruit colour*	
$C^{st'}C^{st'}$:	?	↑	?	↑	− red tip		pink 3.1	
$C^{st'}C^{m'}$:	?		?		+ red t. 0.7		violet-red 4.9	
$C^{m'}C^{m'}$:	?		?		+ red t. 1.8	↓	violet-red 5.8	↓

(for $C^{st'}C^{st'}$ cf. table 4, p. 11; for $C^{m'}C^{m'}$ cf. table 7 p. 13.

An important observation was made by miss BOSMA in studying the seedcoat colour of the individual plants. – To begin with I must remind of a phenomenon known to all who work with red striped beans, $C^{st}C^{st}$ (Lamprecht: $R^{st}R^{st}$). In some plants not all seeds are red *striped*: in part of the seeds a high '*extension*' of the red colour (often pod-wise) has occurred, to almost completely red, leaving from the pale background colour no more than a spare (but still sharply delimited) *mottling*, and with the original striping still being visible in the red as darker bands. I will here not discuss these and other 'extension' phenomena, but general experience has learned (see e.g. KAJANUS, 1914, and TJEBBES, 1923): *firstly* that 'normally red striped seeds' and 'seeds with extended red', from the same plant, produce quite the same offspring, viz. plants that (mainly) produce red striped seed; *secondly* that the 'tendency for red-extension' can be different for different lines. – Experience during the present investigation made clear that both these points also apply to the degree of 'flowing out' of the red colour in $C^{st'}C^{st'}$. Miss BOSMA now, in accurately studying the seeds of every plant, observed a clear difference between family 3102 on the one hand and 3103 plus 3104 on the other, in two respects: in 3102 the homozygously striped plants $C^{st'}C^{st'}$ showed a much higher degree of 'flowing out' of the (orange) red, while at the same time the, non-flowing-out, (orange) red stripes of the threecoloured heterozygotes $C^{st'}C^{m'}$ showed a much higher degree of 'extension' of the red stripes, the red then covering most of the yellowbrown main colour and leaving from the pale background mottling but little points, sharply delimited. – A causal connection between both phenomena seems probable, but a complete explanation cannot yet be given.

This paragraph IV-3 has learned that the seedcoat colour of the new F_1, $C^{st'}C^{m'}$, is exactly the same as that of the original F_1, CC^{st}; that F_2-segregation was as to be expected, and that the 'accompanying colours' here too show a practically complete linkage with seedcoat colour type, though *in reversed direction* with respect to e.g. the red striping.

4. One reverse cross-over plant in F_2 of $C^{st'}$ $C^{m'}$; its offspring and its genotype

One plant was left out in the F_2-analysis made in IV-3, viz. 3103-65 '66, because of his deviating seedcoat colour, not fitting in with $C^{st'}C^{st'}$–$C^{st'}C^{m'}$–$C^{m'}C^{m'}$-segregation of the 238 normal F_2-plants.

When looked at superficially, this plant might belong to the $C^{st'}C^{st'}$ group with its extremely variable 'flowing out' of the (orange)red stripes. The seeds of 3103-65 '66, however, *did not show the slightest 'flowing out'*, therefore being precisely like the seed of the original parent 'Orangered striped'. Also the accompanying colours of 3103-65 pointed in that direction: *Not* '–red tip' and 'pink-3 fruit colour' like red striped $C^{st'}C^{st'}$, *but* '+ red tip standard 1' and 'violet-red 4 fruit colour', colours connected with the C^{st} or the $C^{m'}$-allele (cf. the small tables p. 6 and p. 15).

The plant might have originated from *a stray seed* $C^{st}C^{st}$, but that seemed improbable (and was excluded by its offspring, cf. below). It might also have arisen through fertilisation of its F_1-mother plant 2976-4, $C^{st'}C^{m'}$ (cf. p. 15) by *an alien pollengrain*, C^{st}, but when F_1 was grown in the hot house, early spring 1966, no C^{st}. plants or 'alleles' C^{st} were present. Possibly *a new crossover in* F_1 *2976-4*? F_3 might learn.

For further study 60 seeds of F_2 3103-65 '66 were handed over to the then student Ir. J. A. VAN ITTERSUM, together with seeds from other plants, in total 478 seeds, giving the families 3209–3221'67. The mother plants were chosen so that Mr. Van Ittersum could control, repeat or reconstruct the whole history of the alleles C, C^{st}, $C^{st'}$ and $C^{m'}$.

Family 3221, from the deviating F_2-plant 3103-65 '66, segregated into two types for seedcoat colour, ratio 1:3:

16 (exp. 14.5): seedcoat with (orange)red 'flowing out' stripes: $C^{st'}C^{st'}$

42 (exp. 43.5): seedcoat like the parent 3103-65, i.e. like the original 'orangered striped parent', genotypes $C^{st}C^{st'}$ and $C^{st}C^{st}$. Now it looks quite certain that the parent plant 3103-65 possessed the genotype $C^{st}C^{st'}$, and that the gamete C^{st} arose in F_1-plant 2976-4, $C^{st'}C^{m'}$, *by a reverse crossing-over*, i.e. a crossover in exactly the same region by which in the original hybrid CC^{st} the gametes $C^{st'}$ and $C^{m'}$ arose, found in plants 2670-6 '62 (*case-a*) and in 2672-7 '62 (*case-b*). With this hypothesis the 'accompanying colours' of the 58 plants of family

3221'67 agreed quite well:

	cotyledon	*hypocotyl*	*tip standard*	*fruit colour*
16 $C^{st'}C^{st'}$:	pink 0.9 ↑	pink 1.1 ↑	— red tip	pink 2.3
42 C^{st}. :	pink 1.1 ↓	pink*0.5	+ red t.*0.5 ↓	viol. red*3.1 ↓

* (homo- and heterozygotes together).

From the careful analysis by Mr. VAN ITTERSUM, who generally noted rather low colour values, I further only take over the mean values for the accompanying colours of his *five* heterozygous genotypes, each one placed between the values of the two corresponding homozygotes (Table 9 p. 18, sub 1–5; for origin of 9 sub 6 see next chapter: 5, *4*, p. 19). I think this table is worthwhile, because all values per individual plant and therefore the means are taken up by *the same person* and *in the same summer* (except for sub 6).

Conclusion of IV-4; by a reverse crossing over in F_1-$C^{st'}C^{m'}$ the original allele C^{st} was reconstituted.

5. Crosses between the two original types and the two new homozygotes.

$$\left.\begin{array}{l}(JJ)CC(GG)\text{: yellowbrown dark p.}\\ \qquad\qquad\text{and}\\ (JJ)C^{st}C^{st}(GG)\text{ orangered striped}\end{array}\right\} \times \left\{\begin{array}{l}(JJ)C^{st'}C^{st'}(GG)\text{ (or.) red striped, 'flowing out'}\\ \qquad\qquad\qquad\text{and}\\ (JJ)C^{m'}C^{m'}(GG)\text{ yellowbr. with pale mottling.}\end{array}\right.$$

This part, IV-5, will be treated very shortly, as three of these four F_2-segregations are analogous to the segregations already treated in foregoing parts of the article.

1. CC ($JJGG$) with $C^{st'}C^{st'}$ ($JJGG$), F_1 $CC^{st'}$ ($JJGG$).

The genotype of F_1, $CC^{st'}$, is the same as that of the deviating plant 2670-6 '62 = *a* (which, however, was *Jj*). Its seedcoat colour and accompanying colours, and its offspring too (F_2-families 3083-3085'66) therefore are analogous to those of 2670-6'62 and its offspring (except for the lack of *jj*-plants):

genotype and number	*cotyledons*		*hypocotyl*		*tip standard*		*fruit colour*	
$C\ \ C$, 50 (exp. 46.5):	? ↑		pink 3.4 ↑	all high	— red t. = 0.0 ↑	all low	pink 1.7 ↑	all low
$C\ \ C^{st'}$, 87 (exp. 93.0):	?	?	,, 2.9		— ,, ,, = 0.0		,, 1.3	
$C^{st'}C^{st'}$, 49 (exp. 46.5):	? ↓		,, 3.0 ↓		— ,, ,, = 0.0 ↓		,, 1.1 ↓	

(cf. with table 4, p. 11 and with table 9, sub 3, p. 18; the relative values between the three genotypes are more important than the absolute ones)

2. CC($JJGG$) with $C^{m'}C^{m'}$ ($JJGG$), F_1 $CC^{m'}$ ($JJGG$).

The genotype of this F_1, $CC^{m'}$, is the same as that from the deviating type 2672-7 1972 = *b*. (which, like *a*., was *Jj* too). Therefore it is not surprising that also in this case seedcoat colour and accompanying colours, and the characters of the F_2 offspring too (F_2-families 3086, 3089, 3090 '66), were analogous to the characters of the deviating plant *b*. and its offspring (except for the lack of *jj*):

Table 9. 'Accompanying colours' of the six heterozygous genotypes (for the four 'alleles' C, C^{st}, $C^{m'}$ and $C^{st'}$), each of the six between the values of its two homozygous parent types. – Compare the arrows, $\longrightarrow$: they allways point to the higher values. The *hypocotyl*-arrow always points in the opposite direction of the arrows for *tip standard* and *fruit colour*, i.e. the three characters are *exchanged together* (probably *hypocotyl colour* too, but that is in all cases about 1.0). In two of the six groups of three, sub 3 and sub 6, therefore the values for 'hypocotyl', for 'tip standard' and for 'fruit colour' are the same for the three genotypes, indicated by a two-pointed arrow: $\xleftrightarrow{\text{all low}}$ for low values and $\xleftrightarrow{\text{all high}}$ for high ones.

* behind the family number indicates a segregating family;

fig. 9 sub 2 : the only case where the extension of mean 'pink' fruit colour (3.0) reaches the 'violet-red) value of the heterozygotes (2.9);

fig. 9 sub 5 : mean values for $C^{st}C^{st'}$ and $C^{st}C^{st}$ *together*;

fig. 9 sub 6 : mean values for hypocotyl colour of the three genotypes (slightly) higher than the usual (almost) green.

		cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
1. The two 'original alleles', C and C^{st}:					
$C\ C$	(3210, -11*, 12*):	pink 0.8 ↑	pink 1.4 ↑	– red t. = 0.0 |	pink 1.4 |
$C\ C^{st}$	(3211*, -12*) :	„ 1.0 |	„ 0.7 |	+ „ „ 0.8 |	viol. r. 3.2 |
$C^{st}C^{st}$	(3209, -11*, -12*):	„ 0.8 ↓	„ 0.1 |	+ „ „ 1.7 ↓	„ „ 4.5 ↓
2. The two 'new alleles', $C^{st'}$ and $C^{m'}$:					
$C^{st'}C^{st'}$	(3220*):	pink 0.6 ↑	pink 0.6 ↑	– red t. = 0.0 |	pink 3.0 |
$C^{st'}C^{m'}$	(3220*):	„ 0.5 |	„ 0.5 |	+ „ „ 0.3 |	viol. red 2.9 |
$C^{m'}C^{m'}$	(3220*):	„ 0.5 ↓	„ 0.0 |	+ „ „ 0.6 ↓	„ „ 3.9 ↓
3. C with 'the one new allele', C and $C^{st'}$:					
$C\ C$	(3213*, -15):	pink 0.5 ↑	pink 1.1 ↑ all high	– red t. = 0.0 ↑ all low	pink 2.0 ↑ all low
$C\ C^{st'}$	(3213*) :	„ 0.7? | ?	„ 1.1 |	– „ „ = 0.0 |	„ 3.0 |
$C^{st'}C^{st'}$	(3213*, -14, -16):	„ 1.3 ↓	„ 1.3 ↓	– „ „ = 0.0 ↓	„ 2.7 ↓
4. C with 'the other new allele', C and $C^{m'}$:					
$C\ C$	(3217*, -18*, -19):	pink 0.4 ↑	pink 0.8 ↑	– red t. = 0.0 |	pink 2.9 |
$C\ C^{m'}$	(3217*, -18*) :	„ 0.7 |	„ 0.2 |	+ „ „ 0.2 |	viol. red 3.7 |
$C^{m'}C^{m'}$	(3217*, -18*) :	„ 0.7 ↓	„ 0.0 |	+ „ „ 0.5 ↓	„ „ 4.5 ↓
5. C^{st} with 'the one new allele', C and $C^{st'}$:					
$C^{st'}C^{st'}$	(3221*) :	pink 0.9 ↑	pink 1.1 ↑	– red t. = 0.0 |	pink 2.3 |
$C^{st}C^{st'}$ } $C^{st}C^{st}$ }	(3221*) :	„ 1.1 ↓	„ 0.5 |	+ „ „ 0.5 ↓	viol. red. 3.1 ↓
6. C^{st} with 'the other new allele', C^{st} and $C^{m'}$ (see IV-5, 4, p. 19):					
$C^{st}C^{st}$	:	pink 1.1 ↑	pink 0.6 ↑ all low	+ red t. 2.4 ↑ all high	violet red 4.7 ↑ all high
$C^{st}C^{m'}$	:	„ 0.9 |	„ 0.5 |	+ „ „ 2.2 |	„ „ 4.8 |
$C^{m'}C^{m'}$	:	„ 1.2 ↓	„ 0.6 ↓	+ „ „ 2.1 ↓	„ „ 4.7 ↓

genotype and number	*cotyledons*	*hypocotyl*	*tip stand.*	*fruit colour*
$C\ C$, 48 (exp. 41.2):	? ↑	pink 3.7 ↑	— red t. = 0.0 |	pink 1.3 |
$C\ C^{m'}$, 77 (exp. 82.5):	? | ?	„ 2.2 |	+ „ „ = 1.5 |	viol. red 5.3 |
$C^{m'}C^{m'}$, 40 (exp. 41.2):	? ↓	„ 0.1 |	+ „ „ = 2.5 ↓	„ „ 6.2 ↓

(cf. with accompanying colours small tab. p. 12, tab. 7 p. 13, and tab. 9, sub 4).

3. $C^{st}C^{st}(JJGG)$ with $C^{st'}C^{st'}(JJGG) = F_1\ C^{st}C^{st'}(JJGG)$.

The F_1, $C^{st}C^{st'}$, produced seed exactly like that of 'orangered striped' parent

$C^{st}C^{st}$ (cf. IV-4). F_2-families 3094, 3095 and 3096 '66, segregated into 1 $C^{st'}C^{st'}$ (with 'flowing out' orangered stripes): 3 C^{st}. (with sharply delimited stripes). The 'accompanying colours' were as below:

genotype and number	*cotyledons*	*hypocotyl*	*tip standard*	*fruit colour*
$C^{st'}C^{st'}$, 43 (exp. 43.0):	? ↑	pink 4.6 ↑	— red t. = 0.0	pink 1.0
$C^{st}C^{st'}$ $C^{st}C^{st}$ } 129 (exp. 129.0):	? ↓ ?	,, * 2.6	+ ,, ,,** 1.2 ↓	violet red** 4.2 ↓

* high, because of the included heterozygotes
** low, because of the included heterozygotes

This whole situation for F_1, $C^{st}C^{st'}$, and its F_2-offspring is parallel to that in F_2 plant 3103-65 '66 and its offspring, family 3221'67 (see chapter IV-4). It therefore fits with the hypothesis that 3103-65 '66, in F_2 of $C^{st'}C^{m'}$, resulted from *a reverse cross-over* within these two 'new alleles', in such a way that a pure C^{st}-gamete was reconstituted, that, together with an unchanged $C^{st'}$-gamete, the F_2 plant 3103-65 did arise, with its offspring family 3221 (cf. table 9, sub 5).

4. $C^{st}C^{st}(JJGG)$ with $C^{m'}C^{m'}$ $(JJGG)$, F_1 $C^{st}C^{m'}$ $(JJGG)$.

The seedcoat of F_1, $C^{st}C^{m'}$, appeared to be *threecoloured:*
main colour: yellowbrown dark pattern colour,
striping over it: (orange)red, like in the $C^{st}C^{st}$-parent, i.e. sharply delimited,
mottling in it: pale buff, like in the $C^{m'}C^{m'}$-parent.

The seed-fenotype therefore is much like that of the original F_1 $CC^{st}Jj\,GG$, or like that of the F_2 plants $CC^{st}J.GG$. With one (inconspicuous) difference however: the pale buff background spots in $C^{st}C^{m'}$ are slightly larger than those in the original CC^{st} and in $C^{st'}C^{m'}$ (see Discussion). F_2-segregation after F_1-$C^{st}C^{m'}$ was, for the three F_2-families together:

F_2-fam.	*genotype and number*	*cotyledons*	*hypocotyl*		*tip stand.*		*fruit colour*	
3097	$C^{st}C^{st}$ 49 (44.2):	1.1 ↑	pink 0.6 ↑	all low*	+ red t. 2.4 ↑	all high	viol. red 4.7 ↑	all high
3098	$C^{st}C^{m'}$ 76 (88.5):	0.9	,, 0.5		+ ,, ,, 2.2		,, ,, 4.8	
3099	$C^{m'}C^{m'}$ 52 (44.2):	1.2 ↓	,, 0.6 ↓		+ ,, ,, 2.1 ↓		,, ,, 4.7 ↓	

(* hypocotyl value higher than normal (about green = 0.0), possibly because of late observation)

These values have been used in table 9, sub 6. There are no clear differences between the values of the three genotypes, no more than in table 9, sub 3. But the *high* values in sub 3 (hypocotyl) are *low* in sub 6, while the *low* values in sub 3 (tip standard, fruit colour) are *high* in sub 6.

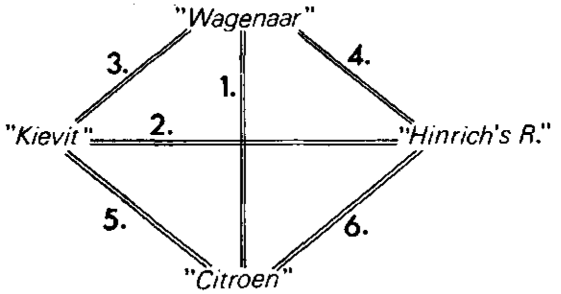
From the above crosses 3 and 4 it becomes clear at once why, in the original F_2-families after F_1-CC^{st}, fam. 2660–2674 '62 (cf. p. 7) only the two crossover individuals $CC^{st'}$ (= *a.*) and $CC^{m'}$ (= *b.*) were found and not a single $C^{st}C^{st'}$ or $C^{st}C^{m'}$: $C^{st}C^{st'}$ (cross 3 above) has a seedcoat *like normal* $C^{st}C^{st}$-plants, while $C^{st}C^{m'}$ (cross 4 above) is very much *like normal* CC^{st}, viz. threecoloured.

This situation appeared to be the same in the old material to be discussed below in chapter V: in those F_2's only combinations of cross-over gametes $C^{st'}$ or $C^{m'}$ with C were discovered and not a single one with C^{st}.

V. RECOMBINATION WITHIN THE 'C-LOCUS' OF THE OLD DIALLELIC CROSSES
(1934–1939, PRAKKEN III, 1972)

In PRAKKEN III (1972) two diallelic crosses between four varieties each were analysed. For sake of convenience both diallelic groups and the numbers (fat) under which the crosses were analysed, **1–6** and **7–12**, are pictured below as figures 1 and 2.

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



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

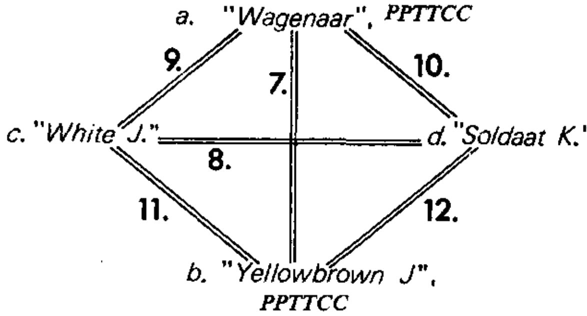
seedcoat:
shiny red striped,
$C^{st}C^{st}$
flower: pale lilac

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

Figure 1. Scheme of the first diallelic cross between four varieties. Main part of genotypes:

a. 'Wagenaar': $PP\ TT\ C\ C\ DD\ JJ\ gg\ bb\ V^{lae}V^{lae}\ Rk\ Rk$
b. 'Citroen': $PP\ TT\ C\ C\ dd\ jj\ GG\ bb\ V^{lae}V^{lae}\ Rk\ Rk$
c. 'Kievit': $PP\ TT\ C^mC^m\ dd\ JJ\ gg\ bb\ V^{lae}V^{lae}\ Rk\ Rk$
d. 'Hinr.R.': $PP\ TT\ C^{st}C^{st}\ dd\ JJ\ gg\ bb\ V^{lae}V^{lae}\ Rk\ Rk$

flower: pale lilac
seedcoat: shiny pale greenish yellow dark pattern (scheme: **VIII–1**)



seedcoat:
white, $ppTTC^{st}C^{st}$,
flower: white

seedcoat:
$PPttC^{st}C^{st}$, partly col.
flower:
white, with trace red veins

seedcoat: shiny yellowbrown dark pattern (scheme **VIII–2**)
flower: pale lilac

Figure 2. Scheme of the second diallelic cross between four varieties. Main part of genotypes:

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

As can be seen in figures 1 and 2 most of the parent varieties were CC (dark pattern) or $C^{st}C^{st}$ (C^{st} = 'allele' for red striped), while only one of the varieties possessed the allele C^{m} (red with very pale buff mottling). Of the 12 F_1's six had the genotype CC^{st} and therefore the typical threecoloured seedcoat:
main colour: dark pattern (greenish yellow or darker),
striping over it: red stripes (or darker),
mottling in it: very pale buff.

In the F_2-families after F_1-CC^{st} the segregation usually was 1 CC: 2 CC^{st}: 1 $C^{st}C^{st}$, while *a few (5) plants with deviating seedcoat colour were found.* These F_2 plants are mentioned in PRAKKEN III (1972) but were not discussed then, because the present article was already planned. A review of these deviating plants is given in table 10, were they are numbered *as cases 1–5* (last but one column in the table). Three of them had a seedcoat like *a.* in chapter IV and two like *b.*, while all five, like *a.* and *b.*, as normal allele appeared to possess C.

Table 10. Number of plants with a *normal* and with a *deviating* seedcoat colour in the six F_2-groups after CC^{st} F_1-plants.

number of the cross (fig. 1 and 2)	number F_2-plants with a normal seedcoat colour	number F_2-plants with a deviating seedcoat colour	discussed below under the number	colour of the deviating seedcoat
4	505	2	*1* and *2*	like *a* (both)
6	148	1	*3*	like *a*
9	266 (*P.*, not *pp*)	1 ?	*5*	like *b*
10	138 (*T.*, not *tt*)	0	–	–
11	344 (*P.*, not *pp*)	1	*4*	like *b*
12	388 (*T.*, not *tt*)	0	–	–
total	1789	total 5		

Case-1: Cross **4**, *'Wagenaar' with 'Hinr.Riesen', F_2-plant 1506-8 '37.*

Segregation in cross **4** (PRAKKEN III, 1972, p. 16–19) was for C–C^{st} only, all plants having the colour gene JJ (shine factor), all being recessive for the dominant modifying genes (thus: gg, bb, $V^{lae}V^{lae} = v^{lae}v^{lae}$) and dominant for the recessive-red factor, i.e. RkRk. For the F_2-segregation into 1 CC (shiny pale greenish yellow): 2 CC^{st} (threecoloured): 1 $C^{st}C^{st}$ (red striped on pale buff) see PRAKKEN III, 1972, table 4 p. 17, and for a detailed tabulation of the 'accompanying colours' in F_2 see table 5 p. 18 there. The latter table might be summarized as follows, *the arrows again pointing from the lower to the higher or (and) more intensive values:*

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
$C\ C$:	pink 4.0–4.5 ↑	pink 2.0–3.0 ↑	all-red tip	pink 1.0–2.0
$C\ C^{st}$:	„ 3.0–4.0	„ 1.5–2.5	most–, few +trace	violet red 5.0
$C^{st}C^{st}$:	„ 2.0–3.0	„ 0.1–1.0	few–, most +slight ↓	„ „ 5.5–6.0 ↓

This is the normal picture here: a rather high cotyledon colour, highest in *CC*, the remaining characters about like those in chapter IV.

The seeds of F_2-plant 1506-8'37 superficially looked like the normal CC^{st}-heterozygote but, precisely as in *case-a.* of chapter IV (p. 9): *the very pale buff background mottling was completely lacking, while the red striping was rather pale and more or less 'flowing out' over the greenish yellow main colour.*

Seeds of this deviating plant were sown as family 1722'38. Its segregation was analogous to that of *a.* (see chapter IV, table 2 p. 9; here, however, all plants are *JJ*) and therefore the same symbols, *C* and $C^{st'}$, are used:

5 *C* *C* (exp. 5.5): shiny greenish yellow dark pattern (like Wagenaar).
9 *C* $C^{st'}$ (exp. 11.0): greenish yellow with 'flowing out' red stripes (= like the mother plant).
8 $C^{st'}C^{st'}$ (exp. 5.5): 'flowing out' red stripes over very pale buff (almost whitish) background; the homozygous new type.

The 'accompanying colours' are, unfortunately, but partly known, see table 11.

Table 11. The accompanying colours of F_2 1506-8'37 and of its F_3-offspring, family 1722 '38 (cf. with table 4 p. 11).

	cotyledon		*hypocotyl*		*tip standard*		*fruit colour*	
F_2 mother plant:	pink 5		pink 3		— red tip		pink 1	
F_3 offspring (fam. 1722):								
C C :	?	↑	?	↑	— red tip	↑	pink 2.0	↑
C $C^{st'}$:	?	± 4?	?	± 3?	— red tip	all low	pink 1.5?	all low
$C^{st'}C^{st'}$:	?	↓	?	↓	— red tip	↓	pink 1.3	↓

Seedling colours in F_3 were not noted. Because of the high values in the F_2-mother plant (table 11: pink 5 and pink 3) it might be supposed that in F_3 the values of the three genotypes were of the same (rather high) level. Therefore, behind the F_3-values of cotyledon and hypocotyl the bipointed arrows ←——→ with a question mark have been placed, making the whole of the 'accompanying colours' with the arrows quite analogous to table 4 p. 11 or to table 9 sub 3, p. 18 (with higher seedling values however).

This means that in this *case-1* the change of C^{st} to $C^{st'}$ was in all respects analogous to the change in the *case of plant-a:*

1. *Loss* of the capacity of causing mottling in the dark pattern colour.
2. *Loss* of the capacity of preventing the 'flowing out' of the red colour.
3. *Loss* of the capacity of causing intensive violet red fruit colour.
4. *Loss* of the capacity of causing red tip standard.
5. (Probably *loss* of the capacity of keeping the hypocotyl about green).
6. (Probably *loss* of the capacity of keeping the cotyledon colour rather low).

From this *case-1* (= plant 1506-8'37) unfortunately no F_4-families were bred.

*Case-2: Cross-***4**, *'Wagenaar' with 'Hinr.R.', F_2-plant 1503-5 '37.*

The second plant in the same cross-**4** with a deviating seedcoat colour was of the same type as *case-1*(1506-8): the *pale buff background mottling lacking* and the (pale) *red stripes 'flowing out'* over the dark pattern colour.

Why it, according to its lower family number, is not indicated as *case-1*, but as *case-2*, will soon become clear. Its F_3-segregation for seedcoat colour too was quite analogous and therefore the same gene symbols, C and $C^{st'}$, will be used. F_3 (fam. 1721'38) contained:

7 $C\ \ C$ (exp. 6.0): shiny greenish yellow dark pattern (like Wagenaar),
8 $C\ \ C^{st'}$ (exp. 12.0): greenish yellow dark p. with 'flowing out' red stripes (like mother plant),
9 $C^{st'}C^{st'}$ (exp. 6.0): 'flowing out' red stripes over very pale buff. (The 'flowing out' here too was very variable).

These rather deviating F_3-numbers made an F_4-control desirable. From the eight $CC^{st'}$-plants and from the nine $C^{st'}C^{st'}$-ones F_4-families were bred: 2633–2640 and 2641–2649 '38. All heterozygotes really segregated, together into:

37 CC (exp. 39.2) + 73 $CC^{st'}$ (exp. 78.5) + 47 $C^{st'}C^{st'}$ (exp. 39.2) = 157. The nine $C^{st'}C^{st'}$ homozygotes produced the homozygote type only, again with a high variability in the extension and intensity of the 'flowing out'.

The 'accompanying colours' of F_2 1503-5 '37 (= *case 2.*) and its F_3-offspring are given in table 12.

Table 12. The 'accompanying colours' of F_3 1503-5 and its F_3-offspring.

	cotyledons	*hypocotyl*	*tip standard*		*fruit colour*	
F_2 mother plant:	pink 5	pink 0	— red tip		(?; ripe)	
F_3-offspring (fam. 1721):						
C C (7)	?	?	— red tip	↑ all low	pink 2.2 (?)	↑ all low
C $C^{st'}$ (8)	?	?	— ,, ,,		,, 3.8	
$C^{st'}C^{st'}$ (9)	?	?	— ,, ,,	↓	,, 3.7	↓

The means of the 'accompanying colours' in the eight segregating F_4-families together (2633-2640 '38, see above) were:

	cotyledons		*hypocotyl*		*1st* stem leaf*		*tip stand.*		*fruit colour*	
$C\ \ C$ (37):	pink 3.4	↑	pink 3.1	↑	trace pink	↑	— red tip	↑ all low	ripe	↑ ?
$C\ \ C^{st'}$ (73):	,, 2.0		,, 2.0		trace ,,		— ,, ,,		ripe	
$C^{st'}C^{st'}$ (47):	,, 0.3		green (= 0.0)		all green		— ,, ,,	↓	ripe	↓

* (the colour of first stem-leaf is but seldom noted)

Comparing again the points of change with the turn-over of C^{st} into $C^{st'}$ in this *case-2* with those in *cases-a*(page 9–11) and – *1*(p. 22) it can easily be stated that:

1.
2. } the *loss* of seed-coat colour capacities is similar, and

3.
4. } the *loss* of fruit- and of tip standard colour capacities is also similar,

but that:

5. }the capacities for hypocotyl- and for cotyledon-colouring *have not*
6. }*changed at all.* The colour of cotyledons in $C^{st\prime}C^{st\prime}$ is extremely low, but also in $CC^{st\prime}$ and CC above, p. 23, it is much lower than in the original F_2, cf. the small table on p. 21. See the one- and the two-pointed arrows.

Case-3: Cross 6, *'Citroen' with 'Hinr. R.', F_2-plant 1528-77 '37.*

For parents, F_1- and F_2-segregation (F_2-families 1527 and 1528'37; together 148 plants with 'normal' seedcoat type) see **PRAKKEN** III, 1972, p. 22. Segregation there was not for C–C^{st} only, but also for J-j and G-g, the F_1 being $CC^{st}JjGg$.

F_2 contained one plant with a deviating seedcoat: *yellowbrown with 'flowing out' pale (orange-) reddish stripes; the pale buff background mottling again was completely lacking.*

[The sentence in the upper part of p. 24 in **PRAKKEN**, 1972, 'Therefore in a sense .... but *lacked* the red mottling of normal CC^{m}', was written without close enough contact with the *cases 1–5* analysed here; it is mixing up the cases and contains another mistake: viz. CC^{m} instead of CC^{st}; it better had been left out.]

The description above suggests that the deviation in seedcoat colour again is analogous to the *cases-a.*, *-1.* and *-2.*, and therefore here too, after the F_3-analysis, the alleles C and $C^{st\prime}$ were used. The F_3 offspring, family 1940'38, 20 seedbearing plants, was as follows (genotype 1528-77 '37 = $CC^{st\prime}JJGg$):

4 C C (exp. 5): shiny yellowbrown dark pattern.
11 C $C^{st\prime}$(exp. 10): { 10 shiny yellowbrown, with pale 'flowing out' red stripes (like the mother plant: *JJG.*).
  1 shiny greenish yellow with pale 'flowing out' red stripes (JJgg, like in *case-1.* and *-2.*).
5 $C^{st\prime}C^{st\prime}$ (exp. 5): 'flowing out' orange red stripes over very pale buff background.

The 'accompanying colours' of the F_2-plant and its F_3 family 1940 '38 are given in table 13 and were rather surprising.

Table 13. 'Accompanying colours' of F_2-plant case-3 and its F_3-family.

	cotyledons			*hypocotyl*			*tip standard*		*fruit colour*	
F_2 plant 1528-77:	pink 3			pink 2			out of flower		violet red 4	
F_3 fam. 1940 '38										
4 CC :	?	↑		?	↑		— red tip	|	pink 2.0	|
11 $CC^{st\prime}$:	?	|	?	?	|	?	— or + trace r.t.	|	violet red 5.0	|
5 $C^{st\prime}C^{st\prime}$:	?	|		?	|		+ small red tip	↓	violet red 5.0	↓

Fortunately an extensive F_4 was bred, families 2671–2682 '39, from 2 CC, 5 $CC^{st\prime}$ and 5 $C^{st\prime}C^{st\prime}$ F_3-plants.

Families 2671 and 2672, from *CC(JJG.)* gave dark pattern plants only; both segregated for G-g and together they gave 7 gg (shiny greenish yellow) + 17 G.

(shiny yellowbrown). Their 'accompanying colours' were, on the mean, quite normal:

cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
pink 1.9	pink 2.4	— red tip	pink 1.2

Families 2678–2682, from $C^{st'}C^{st'}$-plants ('flowing out' orange red stripes over very pale buff), were ordered according to the F_3-mother plants: from very 'little flowing out', i.e. much like $C^{st}C^{st}$, to 'highly flowing out', i.e. the red stripes hardly distinguishable from the (then also red) background. The degree of 'flowing out' in F_4 again was very variable, but *on the whole more or less parallel with that in the F_3-mother plants.* Their mean 'accompanying colours' were:

cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
pink 0.9	pink 0.1	+ small red tip	violet red 5.1

Families 2673–2677 at last came from $CC^{st'}$-plants (one appeared to be *GG*, three *Gg* and one *gg*, but the influence of G. is sometimes small). For C–$C^{st'}$ the five families (each of 16 plants) together gave:

22 *CC* (exp. 20.0) + 44 $CC^{st'}$ (exp. 40.0) + 14 $C^{st'}C^{st'}$ (exp. 20.0) = 80 plants. In these 80 plants the 'accompanying colours' were:

	cotyledons		*hypocotyl*		*tip standard*		*fruit colour*	
C C (22):	pink 1.8	↑	pink 2.4	↑	— red tip		pink 1.2	
$C\ C^{st'}$ (44):	,, 1.2	?	,, 1.8		{ — r.t. most + r.t. few		} violet red 4.1	
$C^{st'}C^{st'}$ (14):	,, 1.2		,, 0.2		{ — r.t. few + r.t. most	↓	} ,, ,, 4.3	↓

From F_2, F_3 and F_4 the following conclusions about this change from C^{st} to $C^{st'}$ in plant *case-3.* can be drawn:

1. }
2. } that there was *loss* of seedcoat colour capacities like in *cases-a.*, *-1.* and *-2.*;

but that, at all probability,

there has been *no change at all* in the capacities numbered 3–6
3. for fruit colour,
4. for tip standard,
5. for hypocotyl colour and
6. for cotyledon colour

Case-4: Cross **11**, *'Yellowbrown Jansen' with 'White Jansen', F_3 plant 712-1,* 1935.

The one plant with a clearly deviating seedcoat colour in this cross did in fact not belong to the 344 *P.* F_2-plants analysed in PRAKKEN III, 1972 (76 *CC* + 171 CC^{st} + 97 $C^{st}C^{st}$), but it came from an earlier cross by the chief-gardener JANSEN who, in 1934, put the seeds of a number of F_2-plants at my disposal. For the genotype and characters of parents, F_1, etc. see PRAKKEN III, 1972, p. 41–44. Of importance is:

'Yellowbrown J.': *PP (TT) C C (JJ)* GG *bb* .... etc.
'White J.' : *pp (TT)* $C^{st}C^{st}$ *(JJ)* gg *BB* .... etc.
F_1 therefore : *Pp (TT) C* C^{st} *(JJ)* Gg *Bb* .... etc.

F_2-segregation was extremely complicated and therefore I began 'exercising' by sowing seeds of 70 F_2-plants from Jansen, grouped according to their seedcoat colour: families 706–775'35. Families 706–733 came from CC^{st} (three-coloured) F_2-plants. Their 'main colour' was *G.B.* (brown), *ggB.* (greenish brown), *G.bb* (yellowbrown) and *ggbb* (greenish yellow). There indeed were many things to learn or to investigate further. In 1936 therefore F_3- and F_4-families 1196–1224 were sown, coming from F_2- of F_3-plants that gave some problem or that (possibly) showed or seemed to show some deviating character in seedcoat colour or in 'accompanying colours'.

In this way the families 1196–1204 came from F_2- or F_3-plants that seemed to be heterozygous CC^{st}, *but in which the red (or darker) striping, normally belonging to it, was either totally invisible* (1196–1200) *or almost so*, e.g. but a trace in one of many seeds (1201–1204). Nevertheless, eight of these nine families showed the normal segregation into 1 *CC*: 2 CC^{st}: *1* $C^{st}C^{st}$, with the normal 'accompanying colours' (though 'seedcoat colour' and also the 'red tip standard', were sometimes very weak). It was only family 1200 '36 that for seedcoat colour behaved in another way, viz, precisely like plant *case-b.*, in chapter IV-2, see p. 11. Its mother plant, 712-1'35, was therefore denoted as $CC^{m'}$; its seed was shiny greenish yellow with pale buff mottling and *without any trace of red striping*, genotype (*P.TT*) $CC^{m'}$(*JJggbb.....*). The monofactorial segregation of family 1200 '36 was into:

10 *C C* (exp. 9): shiny greenish yellow dark pattern, and
$26\begin{cases} C\ \ C^{m'} \\ C^{m'}C^{m'} \end{cases}$ (exp. 27): shiny greenish yellow with very pale buff mottling.

In 1937 from all 36 F_4-plants F_5-families were bred: 8 seeds from each *CC*-plant and, as far as possible, 16 seeds from each mottled-seeded $C^{m'}$.-plant. Result:

the 10 *CC* (fam. 1446–1455 '37) gave one-coloured greenish yellow-seeded plants only (= dark pattern);
the 26 families after $C^{m'}$. (1456–1481'37) gave:
15 segregating families, after $C^{m'}C$ F_4-plants, together 58 greenish yellow dark pattern + 167 mottled.
11 non-segregating families, after $C^{m'}C^{m'}$ F_4-plants (constant mottling, without red!).

Now, the genotypes of all 36 plants in family 1200'36 being known, the following table of the mean values of their 'accompanying colours' could be constructed:

	cotyledons		hypocotyl	tip standard	fruit colour
10 CC-plants	: pink 2.9 (1–4)	↑	pink 4.0 (2–6)	— red tip	pink 4.3 (4–5)
15 $C^{m'}C$-plants	: „ 2.8 (1–4)	?	„ 2.0 (1–4)	most — r.t. few + trace	violet red 6.5 (6–8)
11 $C^{m'}C^{m'}$-plants	: „ 2.5 (0–4)	↓	„ 0.2 (gen. 0)	+ small r.t.	„ „ 7.2 (6–8)

The conclusion in this *case-4.* might be that, like in *case-b.* of chapter IV (p. 14), $C^{m'}$ has arisen from a *C*-'allele' by *gaining*, from a C^{st}-'allele', the following abilities:

1. To make pale buff background spots in the dark pattern colour.
2. To prevent the 'flowing out' of red colour (not proved).
3. To produce a highly coloured (violet-red) fruit.
4. To produce a red tip standard.
5. To (almost) prevent the production of colour in the hypocotyl.

(6. On seedcoat colour, like in case *b.* of chapter IV (cf. p. 14) no sure statement could be made (because of the likeness).) Cf. with points 1–6 on p. 14.

Case-5: Cross 9, 'Wagenaar' with 'White J.', F_2-plant 1641-115 '38.

For genotype and colour characters of parents, F_1, F_2, etc. see PRAKKEN III, 1972. The four F_2-families, 1493–1495'37 and 1641'38 contained 94 white-seeded *pp*-plants and 266 normal *P.*-ones with coloured seedcoat: 55 *CC* + 132 CC^{st} + 61 $C^{st}C^{st}$, in each group *ggbb* and *ggB*. – Moreover in family 1641'38 one plant with a deviating seedcoat colour occurred: plant-115 showed a greenish brown (*B.*) main colour, with very pale buff background-mottling, but *absolutely without any trace of dark grey-violet striping* as belonging to threecoloured normal CC^{st}(*JJggB.*). Its offspring, however, was incompletely studied, so *case-5* remains uncertain.

VI. SUMMARIZING DISCUSSION AND TENTATIVE STRUCTURE OF THE 'COMPLEX LOCUS C'

In chapter I, *General Introduction*, the action of nine 'main factors' for colour in *Phaseolus vulgaris* was reminded of.

Chapter II, *The complex locus C*, pictured the extremely intricate situation with respect to this 'locus'. – Some investigators (esp. those who studied seedcoat colour only or who did not meet any 'recombination' within *C*, e.g. FEENSTRA, 1960, and in a sense the present author too) tried to meet the situation, at least preliminary, by providing a longer and longer series of alleles, all inspired upon *C*, the 'allele' for (yellow–black) dark pattern colour: C-C^{r}-C^{m}-C^{st}-C^{rho} ....c-c^{u}-c^{ui}-c^{cr}. – Other investigators looked upon the 'complex' as consisting of strongly linked individual loci, usually two or three. So did at an early stage EMERSON (1909) and SHAW and NORTON (1918), later e.g. TJEBBES and KOOIMAN (1919–1931) and LAMPRECHT (from 1931–1964). – In the present article the author follows up both (contradicting) lines: *on the one hand* he extends the long series of 'alleles' with (at least) two, $C^{st'}$ and $C^{m'}$, while *on the other hand* he extends the number of (sub-)loci in the 'complex' to at least six, including the accompanying colours too.

In chapter III, *Material and methods*, the methods of description are shortly mentioned and also the two groups of material that were studied:

in chapter IV *one cross*, intensively studied from 1960–1970, and
in chapter V *two diallelic crosses*, each between four varieties, studied from 1934–1940 (see Prakken III, 1972).

In chapter IV the *Recombination within the 'C-locus' in the cross of Citroen (CC) with 'Orangered striped' ($C^{st}C^{st}$)* is treated.

Chapter IV-1 deals with the *Normal colours in parents, F_1, F_2, etc.* – The genotypes of parents and F_1 were:

'Citroen' (line 139, dark p.) : $PP\ TT\ C\ \ C\ \ dd\,jj\ \ GG\ bb\ V^{lae}V^{lae}\ RkRk$.
'Orangered striped' (line 162): $PP\ TT\ C^{st}C^{st}\ dd\ JJ\ GG\ bb\ V^{lae}V^{lae}\ RkRk$.
F_1 (CC^{st}, threecoloured) : $PP\ TT\ C\ \ C^{st}\ dd\ Jj\ GG\ bb\ V^{lae}V^{lae}\ RkRk$.

The seeds of F_1 showed the wellknown threecoloured type:

$$\left.\begin{array}{l}\textit{main colour: }\text{yellowbrown}\\ \textit{striping over it: }\text{orangered}\\ \textit{mottling in it: }\text{pale buff}\end{array}\right\}\text{ genotype }\left\{\begin{array}{l}\text{here (P}\small{\text{RAKKEN}}\text{): } CC^{st}.\\ \text{T}\small{\text{JEBBES}}\text{ and K. } \overset{\frown}{Brs}\ \overset{\frown}{bRS}\,(= Bb\ Rr\ Ss).\\ \text{Lamprecht: } \overset{\frown}{Cr}\ \overset{\frown}{cR^{st}}\ (= Cc\ R^{st}r).\end{array}\right.$$

(*B-b* of TJ. and K. = *C-c* of LAMPR. = locus for ever-segregating mottling).

For the 'accompanying colours' F_1 (and generally CC^{st}) was *intermediate* between both homozygous types (only 'violet-red fruit' *subdominant* over 'pink'); see the arrows: $\xrightarrow{\text{low to high}}$ and $\xleftrightarrow{\text{about same values}}$; summer 1964 e.g.:

	cotyledons	*hypocotyl*	*tip standard*	*fruit colour*
$C\ \ C$ (dark p.):	pink 1.0 ↑	pink 1.4 ↑	— red tip (0.0)	pink 1.2
$C\ \ C^{st}$ (threecol.):	„ 0.9	„ 1.1	+ trace r.t. (1.6)	violet red 4.3
$C^{st}C^{st}$ (striped):	„ 0.9 ↓	„ 0.1	+ clear r.t. (2.7) ↓	„ „ 6.4 ↓

F_2 gave 71 CC + 175 CC^{st} + 99 $C^{st}C^{st}$ = 345 normal seeded plants, with their normal accompanying colours, *plus two plants with seed of deviating type: case-a.* and *case-b.*

Chapter IV-2 deals with these *Two deviating plants, their offspring and their genotypes.* Compared with the threecoloured CC^{st} it appeared that:

plant-a. *lacked* the pale buff background mottling, and that its red striping was 'flowing out' over the dark pattern colour
plant-b. *lacked* the red striping over the dark pattern colour with its pale buff mottling.

Leaving J-j here out of consideration, the next generations (F_3–F_4) learned that both, *case-a.* and *case-b.*, were heterozygous for '*unchanged C*' and a '*new allele*', indicated resp. $C^{st'}$ and $C^{m'}$.

Case-a, $CC^{st'}$ (= *a.*), gave segregations like in table 4 p. 11 (arrows!):

	cotyledons	*hypocotyl*		*tip standard*		*fruit colour*	
$C\ C$ (36):	pink 2.2 ↑	pink 2.6 ↑	all high	— red tip ↑	all low	pink 1.9 ↑	all low
$C\ C^{st'}$ (58):	„ 2.1	„ 2.7		— „ „		„ 2.6	
$C^{st'}C^{st'}$ (39):	„ 2.3 ↓	„ 3.1 ↓		— „ „ ↓		„ 2.4 ↓	

The new homozygous type, $C^{st'}C^{st'}$, is *(orange)red striped, the red stripes 'flowing out' (extremely variably!) over very pale buff background.* Its 'accompanying colours' are like those of *CC* (cf. the bipointed arrows).

Case-b, $CC^{m'}$ (= *b*), segregated according to its F_3 (and F_4) into:

		cotyledons		*hypocotyl*	*tip standard*	*fruit colour*
	$C\ C$ (2) :	pink* 3.5 ↑		pink 0.6 ↑	— red tip	pink 2.0
hardly	$C\ C^{m'}$ (10):	„ 0.6	?	„ 0.3	(-to) + trace r.t.	violet red 3.7
disting.	$C^{m'}C^{m'}$ (4) :	„ 0.8 ↓		green (0.0)	(-to) + small r.t. ↓	„ „ 5.1 ↓

(* unexpectedly high, but only two individuals; cf. small table p. 12 and also table 7 p. 13).

The new homozygous type, $C^{m'}C^{m'}$, shows *dark pattern colour with pale buff mottling* and it hardly differs from the heterozygote $CC^{m'}$: a clear case of *dominant constant mottling (without red)*. Its accompanying colours are like those of $C^{st}C^{st}$ (cf. the one-pointed arrows).

A careful study of the actions of both 'new alleles' reveals that a change from C^{st} into $C^{st'}$ can be described as '**losses**', point by point corresponding with '**gains**' in a change from *C into* $C^{m'}$, cf. pages. 11 and 14:

1. *Loss (gain)* of the capacity for causing pale mottling in C-dark pattern colour.
2. *Loss (gain)* of the capacity or preventing the 'flowing out' of red colour (for point 2 see chapter IV-3).
3. *Loss (gain)* of the capacity for causing violet red fruit colour.
4. *Loss (gain)* of the capacity for causing red tip standard.
5. *Loss (gain)* of the capacity for keeping the hypocotyl (almost) green.
6. (Because of like cotyledon colour no exchange can be stated, only supposed).

Points 3–6 together might be considered as a 'change over' of *all* 'accompanying colours', but results in chapter V make the subdivision necessary).

On the basis of the facts described so far, esp. the strict correspondence between 'loss' and 'gain', one may conclude that the two 'new alleles' both *originated by crossing-over at a corresponding place within the 'complex locus-C'.* Looking at points 1. and 2. above as separate actions and, preliminary, at points 3–6 as one '*Acc*ompanying colour action', *the exchanged (= lost) part of* C^{st} *seems to contain:*

M (from: *m*ottling; locally suppressing the action of *C*);

Pr (from: *pr*eventing the 'flowing out' of red colour);

Acc (from: *acc*ompanying colours; point 3–6 above).

Seeking for probably separate actions *in the remaining part of the original allele* C^{st} results in:

c^u (from: c^u, the symbol for *u*nchangeable background colour;

R (from: producing *r*ed color);

St (from: restricting the red colour to *st*ripes).

Continuing this reasoning for the original 'allele' C and for the 'alleles' $C^{st'}$ and $C^{m'}$ one comes to sub-structures as pictured in figure 3, in which not only the points of exhange in chapter IV-2, *case-a.* and *-b.* are given, but also those in *cases-1,. -2., -3, -4. (and -5.)* of chapter V (see below, p. 32–33).

Chapter IV-3, *Cross between the two new homozygous genotypes*, served as a proof on the hypothesis developed before: the F_1 between $C^{st'}C^{st'}$ and $C^{m'}C^{m'}$, i.e. $C^{st'}C^{m'}$, *was in all respects like the original F_1*, i.e. CC^{st}: threecoloured seed. Its F_2 segregated into:

$\frac{1}{4}$ (69) $C^{st'}C^{st'}$: flowing out orangered stripes over very pale buff.

$\frac{1}{2}$ (101) $C^{st'}C^{m'}$: the wellknown threecoloured seedcoat

$\frac{1}{4}$ (68) $C^{m'}C^{m'}$: yellowbr. dark pattern colour with pale buff constant mottling.

Each genotype showed its specific 'accompanying colours': $C^{st'}C^{st'}$ those of CC, $C^{m'}C^{m'}$ those of $C^{st}C^{st}$ (small table p. 15). One plant with deviating seedcoat colour (and accompanying colours) occurred, see IV-4 below.

In Chapter IV-4, *One reverse cross-over*, this deviating F_2-plant was described and analysed (Ir. Van Ittersum). Its seedcoat colour was precisely like that of the original $C^{st}C^{st}$-parent: orangered striped (not flowing out). Being an *admixture* seemed improbable and was in fact contradicted by its offspring: $\frac{1}{4}$ (16) $C^{st'}C^{st'}$ (flowing-out red stripes) + $\frac{3}{4}$ (42) $C^{st}C^{st'}$ and $C^{st}C^{st}$, see table top p. 17. *Conclusion:* in the F_1-mother plant, $C^{st'}C^{m'}$, *a reverse cross-over has taken place, in the same region as the original one*, thus reconstituting the original 'allele' C^{st} (accompanying colours included), which gamete combined with an unchanged $C^{st'}$–gamete. It must be mentioned here that F_1-$C^{st'}C^{m'}$ was grown in the hothouse, winter-spring 1967, *without* any $C^{st}C^{st}$-plants or C^{st}-'alleles' being present. – For having an impression of the 'accompanying colours' *in the four homozygous types*, of C, C^{st}, $C^{st'}$ and $C^{m'}$, and *in their six heterozygotes*, it is of importance to study table 9 (p. 18): values and arrows (all, except for table 9 sub 6, taken in *one* summer by *one* person).

Chapter IV-5 at last treats *Crosses between the two original types and the two new genotypes*. These four crosses,

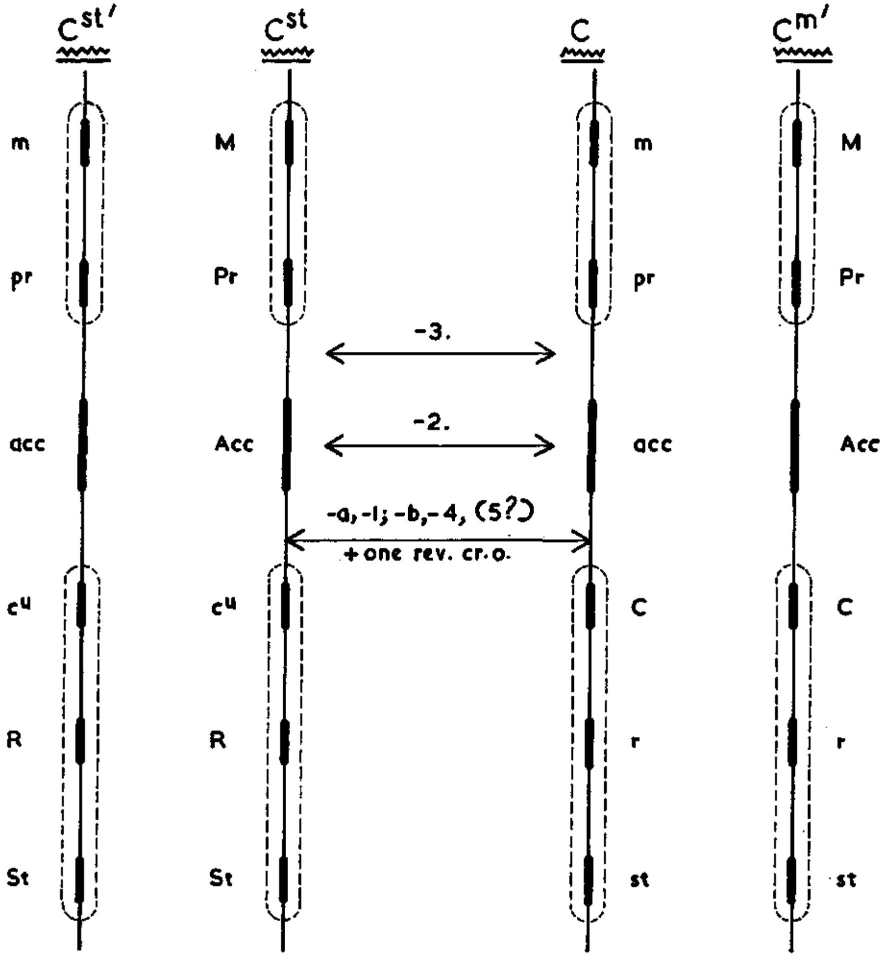
$$\left.\begin{array}{c} CC \\ \text{and} \\ C^{st}C^{st} \end{array}\right\} \text{with} \left\{\begin{array}{l} C^{st'}C^{st'} \\ \text{and} \\ C^{m'}C^{m'} \end{array}\right.$$

made understandable, why only the deviating types $CC^{st'}$ (= *a.*) and $CC^{m'}$ (= *b.*) were found and not a single one $C^{st}C^{st'}$ or $C^{st}C^{m'}$:

$C^{st}C^{st'}$ does not differ from $C^{st}C^{st}$ (both orangered striped), while

$C^{st}C^{m'}$ looks very much like CC^{st} (both threecoloured): a slight difference

Figure 3. Tentative linear scheme of the 'complex locus C'.



(..............................) : sub-loci of which, in the present investigation, separability and (or) order has not been proved. – With respect to the figure in 'Annual report of the Bean Improvement Cooperative' (1974, 17, p. 71) a few changes have been made:

a. $C^{st'}$ and $C^{m'}$ have changed place.

b. *Acc* (for *Acc*ompanying colours) came instead of *Col.*

c. The middle arrow (for *case-2.*) had to be added.

Origin (meaning) of the symbols for the sub-loci:

$M-m$ = causing resp. non-causing *m*ottling in dark pattern colour.

$Pr-pr$ = *pr*eventing resp. non-preventing the 'flowing out' of red colour.

$Acc-acc$ = influencing the '*Acc*ompanying colours' in the one or the other direction (probably a complex sub-locus).

$C-c^u$ = producing resp. non-producing dark pattern colour.

$R-r$ = producing resp. non-producing *r*ed colour.

$St-st$ = restricting resp. non-restricting the red colour to *st*ripes.

is that in the first, $C^{st}C^{m'}$, the pale buff background spots are slightly greater and more clear than in the latter, CC^{st} (because of *MM* against *Mm*, see fig. 3, p. 31).

Chapter V deals with '*Recombination within the 'C-locus' of the old diallel crosses*', analysed 1934–1940 (PRAKKEN III, 1972). See figures 1 and 2 (p. 20), table 10 (p. 21) and figure 3 (p. 31). In this material, like in that of chapter IV, only deviating plants $CC^{st'}$ (= like *case-a.* in chapter IV: *cases-1.*, *-2.* and *-3.*) and $CC^{m'}$ (= like *case-b.* in chapter IV: *cases-4.* and *-5.*) were discovered.

Cases-1., *-2.* and *-3.* each segregated into F_3-families consisting of:
$\frac{1}{4}$ C C (dark pattern),
$\frac{1}{2}$ C $C^{st'}$ (like the F_2 mother: dark pattern with 'flowing out' red stripes),
$\frac{1}{4}$ $C^{st'}C^{st'}$ (the new homoz. type: 'flowing out' red stripes over very pale buff).

This means that, *in all three cases, -1., -2.* and *-3.*, a change of 'allele' C^{st} into $C^{st'}$ at least consists in the loss (by C^{st}) of the seedcoat colour capacities mentioned under point 1. and point 2., see p. 29. *The complex of 'accompanying colours'* (*Acc-acc* in fig. 3) *however, behaved in different ways,* and precisely on the ground of this behaviour *Acc-acc* received its place in fig. 3.

Case-1.

The 'losses' by C^{st} in its change to $C^{st'}$ enclosed both seedcoat colour points (1, 2) and the complete 'accompanying colour' complex (3–6), i.e. *the whole series 1–6*, p. 29. Therefore, in figure 3, *case-1* belongs to the big arrow, cf. also table 11 p. 22, and table 4 p. 11.

Case-2.

In this case the 'loss of capacities' in the change of C^{st} into $C^{st'}$ again contained points 1. and 2. for seedcoat colour, but with regard to the 'complex of accompanying colours', *Acc*, the losses were restricted to point 3. (loss intensive violet-red fruit colour) and 4. (loss of red tip standard), while in the characters point 5. (green hypocotyl) and point 6. (low coloured cotyledons) no change could be stated: *the complex Acc seems to be sub-devisible.* See table 12 p. 23 and especially the small table below it, values and arrows. – In figure 3. the *case-2* may be represented by the middle (short) arrow.

Case-3.

Like in *case-1*, and *-2.*, also in *case-3.* the change of C^{st} into $C^{st'}$ consisted, for the seedcoat colour, in the 'loss of capacities' 1. and 2. (and therefore again the same symbol $C^{st'}$ was used!). *The 'complex of accompanying colours', however, was not changed at all,* i.e. points 3–6 (p. 29) remained the same as in C^{st}: 3. intensive violet-red fruit colour, 4. red tip standard, 5. (almost) green hypocotyl and 6. low coloured cotyledons. See table 13 p. 24 and the small table in centre p. 25. – In figure 3 the case is represented by the upper (short) arrow.

Case-4. and *case-5.*

In both these cases the seedcoat colour of the deviating plant was like that of *case-b.* in chapter IV: dark pattern colour with pale buff mottling, the *red striping lacking*. In case 5. the offspring was too incompletely studied and therefore it is mentioned here but very short.

Case-4.

For the complex history of this case see *Prakken* III, 1972, p. 43–44, and (or) the present article p. 25–27. It is known that the '(in)visibility' of the red striping in normal CC^{st} is highly influenced by: *a.* the presence of modifying (=darkening) genes, *b.* probably by microgenes influencing the striping itself, and *c.* by external conditions. In some cases the stripes therefore are practically invisible, especially in genotypes *jj*.

In this *case-4*, however, the disappearence of striping certainly did not depend upon *a.*, *b.* or *c.*, mentioned above, but (like in *case-b* of chapter IV) on *crossing-over*. Segregation after this plant, *case-4*, was into:

$10\ C\quad C$ (dark pattern) and

$$26\ C^{m'}.\ \left\{\begin{array}{l} 15\ C^{m'}C \\ 11\ C^{m'}C^{m'} \end{array}\right\} \text{both mottled (= constant mottling).}$$

Also the behaviour of the 'accompanying colours' in this change of C into $C^{m'}$ was quite analogous to that in *case-b* of chapter IV: '*gain*' of the whole complex contained by points 1–6, p. 29. Therefore *case-4* is, together with cases *-a.*, *-b.* and *-1* (and the one reverse crossing-over), placed near the same big arrow in figure 3.

Case-5.

This case of mottling without striping has, like *case-4*, also been placed, in fig. 3 p. 31, near the big arrow, though with a question mark, as the description of its offspring was lacking.

VII. SUMMARY (cf. figure 3 p. 31).

The author studied, in two groups of material (Ch. IV and Ch. V), the 'complex locus C' of *Phaseolus vulgaris L.*, viz. in crosses between CC (= non-red dark pattern) and $C^{st}C^{st}$ (= red striping on very pale buff). – F_1, CC^{st}, showed always the wellknown *threecoloured* seedcoat:

dark pattern main colour, *red striping* over it and *pale buff mottling* within it, the latter usually ascribed to heterozygosity Cc. – The F_2 (about 2000 plants) segregated (pseudo-) monofactorially into $\frac{1}{4}\ CC + \frac{1}{2}\ CC^{st} + \frac{1}{4}\ C^{st}C^{st}$, each of the three types with its own special 'accompanying colours', for cotyledons, hypocotyl, tip standard and ripening fruit, CC^{st} generally being intermediate for them.

Among those about 2000 F_2 individuals, *seven plants* with a *deviating and quite new* seedcoat colour occurred (Ch. IV: *cases -a.* and *-b.*; Ch. V: *cases*

-1., *-2.*, *-3.*, *-4.* and *-5.*). Compared with normal threecoloured CC^{st}, *four* of them (*-a.*; *-1.*, *-2.* and *-3.*) *lacked the pale buff mottling* and their red stripes were 'flowing out' over the main colour, while *three* of them (*-b.*; *-4.* and *-5.*) *lacked the red striping*, thus showing dark pattern with pale buff mottling.

The deviating types were, according to F_3 etc., *heterozygous*, all for the 'normal allele' C and a 'new allele', indicated as $C^{st'}$ and $C^{m'}$ respectively.

[Later, see Ch. IV–5, it appeared that the combinations of the two new alleles with C^{st} are indistinguishable in F_2: $C^{st}C^{st'}$ being like $C^{st}C^{st}$, and $C^{st}C^{m'}$ almost being like CC^{st}.] The homozygous $C^{st'}C^{st'}$ showed red stripes 'flowing out' over pale buff, while $C^{m'}C^{m'}$ showed dark pattern with pale buff mottling (*constant:* $\overset{\frown}{CM}\ \overset{\frown}{CM}$, cf. p. 5, and fig. 3 p. 31).

Five of the seven cases, were such that the 'flowing out red striped ones', $C^{st'}C^{st'}$ (*cases-a.* and *-1.*) possessed the accompanying colours of original CC, while the constant mottled ones, $C^{m'}C^{m'}$ (*cases -b.*, *-4.* and *-5*?) showed those of the original $C^{st}C^{st}$. These five cases can be described (see p. 29) by saying that

the losses, point 1–6, by C^{st} in its change to $C^{st'}$, correspond with

the gains, point 1–6, by C in its change to $C^{m'}$, both changes at all probability depending on exchange (cross-over) at the same point within the 'complex locus C', cf. the large arrow in figure 3 p. 31.

The two remaining cases are *-2.* and *-3.*, both $C^{st'}C^{st'}$. In *case -3.*, C^{st} in its change to $C^{st'}$ certainly *lost* the two seedcoat colour capacities (point 1. and 2. p. 29), but it *kept* the whole complex of accompanying colour capacities, unchanged (point 3–6). *Case-2.* is intermediate: together with points 1. and 2. (seedcoat) it also lost 3. and 4. (high fruit colour and red tip standard), but apparently the seedling characters (points 5. and 6.) did not change.

After this analysis it need not wonder that after crossing $C^{st'}C^{st'}$ (*case -a.*) with $C^{m'}C^{m'}$ (*case-b.*) the characters of F_1, $C^{st'}C^{m'}$, were *quite the same as those of the original hybrids* CC^{st}*:* threecoloured seedcoat etc.; and that, among the offspring of F_1-$C^{st'}C^{m'}$, one plant $C^{st'}C^{st}$ did occur, the second gamete of it being reconstituted by a new (reverse) cross-over (Ch. IV-4).

In fig. 3 a tentative attempt is made to 'explain' the phenomena and to localize the points of exchange, assuming the 'complex locus C' to contain *six subloci*, of which at least one, the sub-locus for the accompanying colours, *Acc-acc*, in its turn appeared to have a complex structure.

A critical discussion of the literature has not been made now. Starting in 1965, a program of crosses including the two 'new alleles' and some 'old' ones has been extended to a complete diallelic cross, including eight of the most characteristic 'alleles', C-C^{r}-C^{m}-C^{st}-$C^{st'}$-$C^{m'}$-c and -c^{u}, in total 28 (or 56) crosses, the analysis of which may give some further or better insight.

LITERATURE

EMERSON, R. A. (1909a). Factors for mottling in beans. Am. Br. Assoc. **5**: 368–376.

EMERSON, R. A. (1909b). Inheritance of color in the seeds of the common bean, *Phaseolus vulgaris*. Ann. Rep. Nebr. Agric. Exp. St. **22**: 65–101.

FEENSTRA, W. J. (1960). Biochemical aspects of seedcoat colour inheritance in *Phaseolus vulgaris* L. Meded. Landbouwhogeschool. Wageningen **60** (2): 1–53.

KAJANUS, B. (1914). Zur Genetik der Samen von *Phaseolus vulgaris*. Zschr. f. Pflanzenz. **2**: 378–388.

LAMPRECHT, H. (1932a). Beiträge zur Genetik von *Phaseolus vulgaris*. I. Hereditas **16**: 169–211.

LAMPRECHT, H. (1933). Zur Genetik von *Phaseolus vulgaris*. VI. Vierter Beitrag zur Vererbung der Testafarbe. Hereditas **17**: 249–316.

LAMPRECHT, H. (1936a). Zur Genetik von *Phaseolus vulgaris*. XII. Über die Vererbung der Blüten- und Stammfarbe. Hereditas **21**: 129–166.

LAMPRECHT, H. (1940). Zur Genetik von *Phaseolus vulgaris*. XV. Über die Vererbung der Mehrfarbigkeit der Testa. Hereditas **26**: 64–99.

LAMPRECHT, H. (1947). The seven alleles of the gene R of *Phaseolus*. Agri Hortique Genetica **5**: 46–64.

LAMPRECHT, H. (1948). Die Terminalverstärkung der Blütenfarbe von *Phaseolus vulgaris* und ihre Vererbung. Agri Hortique Genetica **6**: 49–63.

LAMPRECHT, H. (1951a). Die Vererbung der Testfarbe bei *Phaseolus vulgaris* L. Agri Hortique Genetica *9*: 18–83.

LAMPRECHT, H. (1951b). Über die Vererbung der roten Hülsenfarbe bei *Phaseolus vulgaris*. Agri Hortique Genetica **9**: 84–87.

LAMPRECHT, H. (1960). The synonymy of the genes Sh and D with J and B for the seed coat colour of *Phaseolus vulgaris*. Agri Hortique Genetica **18**: 205–208.

LAMPRECHT, H. (1961a). Weitere Koppelungsstudien an *Phaseolus vulgaris*. Agri Hortique Genetica **19**: 319–332.

LAMPRECHT, H. (1961b). Die Vererbung der rezessiv roten Testafarbe von *Phaseolus* sowie Bemerkungen zur Manifestation und Symbolik von Testafarbgenen. Agri Hortique Genetica **19**: 344–359.

LAMPRECHT, H. (1964). Die Vererbung eines neuen Typs von Marmorierung der Samen von *Phaseolus vulgaris*. Agri Hortique Genetica **22**: 256–271.

MIYAKE, K., Y. IMAI & K. TABUCHI, (1930). Contributions to the genetics of *Phaseolus vulgaris*. Journ. Coll. Agric., Imp. Univ. Tokyo **11**: 1–20.

NAKAYAMA, R. (1961). Genetical studies on kidney beans (*Phaseolus vulgaris*). VI. Genetical behavior of plant color, with special reference to seed-coat colour in the hybrids between White Kidney and other varieties. Bull. Fac. Agric., Hirosaki Univ. **7**: 37–65.

NAKAYAMA, R. (1964). Genetical studies on kidney beans (*Phaseolus vulgaris*). VII. A modifier of flower color and its relation to c^u gene. Bull. Fac. Agric., Hirosaki Univ. **10**: 1–13.

NAKAYAMA, R. (1965). Genetical studies in kidney beans (*Phaseolus vulgaris*) VIII. A new allel at the *C*-locus. Bull. Fac. Agric. Hirosaki Univ. **11**: 55–58.

NAKAYAMA, R. and K. SAITO (1968). Genetical studies on kidney beans (*Phaseolus vulgaris*). IX. Inheritance of a type of marbling on seed-coat in a variety Contender. Bull Fac. Agric., Hirosaki Univ. **14**: 9–15.

NAKAYAMA, R. and SAITO (1971). Genetical studies on Kidney beans (*Phaseolus vulgaris*). X. On the inheritance of hypocotyl colour (3). Bull. Fac. Agric., Hirosaki Univ. **17**: 114–125.

PRAKKEN, R. (1934). Inheritance of colours and pod characters in *Phaseolus vulgaris* L. Genetica **16**: 177–294.

PRAKKEN, R. (1940). Inheritance of colours in *Phaseolus vulgaris* L. I. Genetica **22**: 331–408.

PRAKKEN, R. (1970). Inheritance of colour in *Phaseolus vulgaris*. L. II. A critical review. Mededelingen Landbouwhogeschool, Wageningen **70**–23: 1–38.

PRAKKEN, R. (1971). Inheritance within the yellow – black seedcoat colour group of *Phaseolus vulgaris* L. Annual report of the Bean Improvement Cooperative **14**: 49–52.

PRAKKEN, R. (1972a), Seedcoat colour in *Phaseolus vulgaris* L. Attempt to a general synthesis. Annual report of the Bean Improvement Cooperative **15**: 74–79.

PRAKKEN R. (1972b). Inheritance of colours in *Phaseolus vulgaris* L. III. On genes for red seedcoat colour and general synthesis. Mededelingen Landbouwhogeschool, Wageningen, **72**–29: 1–82.

PRAKKEN, R. (1974). Recombination within the 'Complex locus *C*' of *Phaseolus vulgaris*. Annual report of the Bean Improvement Cooperative **17**: 67–71.

SHAW. J. K. & J. B. NORTON (1918). The inheritance of seed coat colour in garden beans. Bull. Mass. Exp. Stat. **185**: 59–104.

SMITH, F. L. (1939). A genetic analysis of red seed-coat color in *Phaseolus vulgaris*. Hilgardia **12**: 553–616 (with two col. plates).

SMITH, F. L. (1947). Inheritance of seed-coat color in derivatives of Pinto beans. Journ. Am. Soc. of Agron. **49**: 1039–1052.

SMITH, F. L. and Cath. BECKER MADSEN (1948). Seed color in beans. Interaction of the alleles at the *R*, *Rk* and *Bl* loci in *Phaseolus vulgaris*. The Journal of Heredity **39**: 191–194.

SMITH, F. L. (1961). Seed-coat color genes in six commercial varieties of beans. Hilgardia **31**: 1–14.

TJEBBES, K. (1923). Ganzfarbige Samen bei gefleckten Bohnenrassen. Ber. d. D. Bot. Ges. **41**: 217–224.

TJEBBES, K., 1931. Two linkage groups in the garden bean. Hereditas **15**: 185–193.

TJEBBES, K. and H. N. KOOIMAN (1919). Erfelijkheidsonderzoekingen bij boonen. I. Kruising van kievitsboon en bruine boon. Genetica **1**: 323–332.

TJEBBES, K. and H. N. KOOIMAN, 1921a. IV. Over den streepingsfactor. Een geval van volkomen afstooting tusschen twee factoren. (On the striping factor. A case of complete repulsion between two factors). Genetica **3**: 28–34.

TJEBBES, K. and H. N. KOOIMAN (1921b). Erfelijkheidsonderzoekingen bij boonen. V. Analyse eener spontane kruising van de stok-kievitsboon. Genetica **3**: 34–49.

TJEBBES, K. and H. N. KOOIMAN (1922). Erfelijkheidsonderzoekingen bij boonen. VII. Bloemkleur en zaadhuidkleur. Genetica **4**: 447–453.

To people especially interested in the problem a copy with a colour-photograph of the main seedcoat types will be sent on demand.