COLOUR INHERITANCE IN THE SEED COAT OF PHASEOLUS VULGARIS

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THE variation of the colour of the seed coat in the common garden bean, *Phaseolus vulgaris,* is rather great. The inheritance of these characteristics is complicated, and the factorial basis of the variation has been analyzed only to a slight extent although several papers on this subject have been published. A chief reason of this may be sought in the difficulty of making the crossings.

As to the literature on the inheritance of the seed coat colour is must be said that the mode of denominating the factors is in an annoying state of confusion. Different writers use one and the same symbol for different factors, and other use different symbols for one and the same factor. The result is that almost the whole alphabet has been employed for the denomination of only a few factors.

Furthermore, the identifying of the colour nuances referred to is very difficult. Papers on this subject are written in at least six different languages, and writers of the same language often use different denominations for the same nuance. If the variety treated is at hand the nuance in question is easily found. The confusion of the names of the commercial bean sorts, however, is very great. It is always rather uncertain whether a variety obtained from a seedsman under one name is identical with the variety treated by an investigator under the same name.

In order to lessen the difficulties it would first and foremost be necessary to denominate the colour nuances in such a manner that they could be identified by other than the writer of the paper. The most simple manner may be to add a coloured illustration or to give references to a generally known code of colour. SIRKS (1920) holds that this procedure only would create an air of scientific objectivity; even in the best hands it would be of no real value on account of the modifications during different years. It is true, the colour is rather modifiable but this way of denomination of the nuances would certainly be better than no denomination at all. The

language further, has names only for a small number of colour
nuances. The adoption of a code of colour would be an object, and
by no means an unimportant one, for the next international congress
of geneticists.

I. THE INHERITANCE OF THE STEEL BLUE COLOUR.

If a sample of seeds of »*Steninge hybrid*» — an old Swedish sort
of asparagus bean — is examined the colour of the seed coat is gene-
rally found to fall into three types. Some seeds are black and other
are mottled in black and brown (C. C. = 118) [1]. The seeds of the
third type are steel coloured (C. C. = 412—423) on a brown back-
ground. The steel colour does not quite cover the brown colour,
however; this is especially the case at the end of the seed. The inten-
sity of the colour varies for the rest rather much. In some seeds it
is to be seen only as a dark streak on the back of the seed. »*Steninge
hybrid*» is no pedigree sort. It varies also in other characters as earli-
ness, colour marking of the pods, flower colour, etc. The variation
of these characteristics, however, is not so obvious at that of the colour
of the seed coat.

A similar variation in the colour was also found in some pedigree
parcels, all descendants in the first generation from single plants.
These segregations were, unfortunately, not observed before the
treshing of the plants was over. It was therefore impossible to cal-
culate the ratios of this generation. The different colour types were
assorted and sown separately in the experimental field in 1919. In
the continuation of the experiments each plant was naturally treshed
separately.

When the plants were examined the black and the steel coloured
were found to breed true to type. The descendants of the mottled
showed segregation in 55 black, 88 mottled and 53 steel coloured; thus,
in a ratio of about 1 : 2 : 1.

As the number of plants in D_2 (accepting the terminology of
HERIBERT-NILSSON, 1920, I call the progenies of a plant D_1, D_2 etc.)
was rather small all seeds were sown next year. The results were
the same as those of the foregoing year. The descendants of the
mottled showed segregation in 255 black, 466 mottled and 220 steel
coloured, as seen in table 1. The black type bred true. One single

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[1] C. C. = 118 refers to the numero of the colour in the »Code des Coleurs»
of KLINCKSIECK et VALETTE (1908).

TABLE 1. *The segregation of the steel colour in D_2 and D_3.*

N:o 1919	D_2			D_3								
	D_1-plants mottled			D_2-plants black			D_2-plants mottled			D_2-plants steel coloured		
	Black	Mottled	Steel coul.	Black	Mottled	Steel coul.	Black	Mottled	Steel coul.	Black	Mottled	Steel coul.
2666	16	27	14	181	—	—	106	165	84	—	—	177
2671	8	7	3	90	—	—	22	27	15	—	—.	5
2674	20	41	26	221	(1)	—	106	233	94	—	(5)	289
2675	5	4	6	32	—	—	10	25	15	—	(3)	58
2680	6	9	4	28	—	—	11	16	12	—	(3)	18
Total	55	88	53	552	(1)	—	255	466	220	—	(11)	547
Obs. pro 4	1,12	1,80	1,08	—	—	—	1,08	1,98	0,94	—	—	—
Theoret.	1	2	1	—	—	—	1	2	1	—	—	—
Standard error M_k	0,124	0,143	0,124	—	—	—	0,056	0,065	0,056	—	—	—
Deviation, D.	0,12	0,20	0,08	—	—	—	0,08	0,02	0,06	—	—	—
D/M_k	0,097	1,40	0,65	—	—	—	1,43	0,31	1,07	—	—	—

plant, however, with black and brown mottled seeds, was found among
552 black seeded. The seeds of this mottled type was quite identical
with that of the segregating mottled type. This plant represented no
doubt a spontaneous crossing with a steel coloured type; the plants
had not been isolated. All descendants from steel coloured parents
were steel coloured with the exception of some spontaneous bastards.
The intensity of the steel colour, however, varied much. In some
plants it was rather dark, and the seeds became of a deep blue colour;
even the darkest steel coloured seeds were very easy to distinguish
from the black ones. In the other extremes the steel colour was limi-
ted to the back of the seed and was to be seen only as a dark streak.
In this case, too, the rest of the seed take on a singular shiny colour
on its surface; this is especially to be seen in the middle of the seed,
and, therefore, it is easy to distinguish these seeds from other coffee-
brown varieties. Most of the seeds were of an intermediate intensity
of colour. The number of spontaneous bastards was much larger
in this type. 11 bastards were found among 547 steel coloured. Thus
it appears as would this type be more disposed to spontaneous cros-
sings than is the case with the black one. The percentage of spon-
taneous crossings in the black type is 0,18 %; in the steel coloured it

is 1,97 %. The average is about 1,1 %. This value corresponds with the average value for the spontaneous crossing in beans recorded in a previous paper (1921).

The mode of segregation in D_2 and D_1 of these colours has the character of a monohybrid one. If the black colour is assumed to depend on a factor K, and the steel colour on the absence of this factor the segregation will be explained by means of the following presumptions. The factor K shows a complete dominance as to the intensity of the black colour. As a heterozygote, however, it is not able to develop the black colour on the whole surface of the seed coat but only in spots; the seed becomes then mottled. The varying intensity of the steel colour on different plants may be explained by the assumption of modificatory factors, in the same way as the varying intensity of the black colour of the spelts in oats is explained by NILSSON-EHLE (1909). This seemingly monohybrid segregation may, however, be much more complicated.

In order to make this segregation as well as another to be treated below better understood I think it appropriate to give a summary of the most important colour factors of the seed coat. As far as possible the nomenclature of SHAW and NORTON (1918) will be used; the results here recorded are to be compared with the statements given by these authors.

SHAW and NORTON classify the seed colours in two series, viz. a yellow-black and a red one. The following factors are established:

P is the fundamental colour factor. Gives buff or ecru colour. All pp-plants have the seed coat white coloured.

In the yellow-black series the following factors are established among other:

H factor for light brown or olive brown,
C » » yellow,
F » » coffee brown,
G » » black.

LUNDBERG and ÅKERMAN (1917) have recorded a factor C which, together with the fundamental factor P, gives »chocolate brown» colour. Another factor G gives a yellow brown colour together with the fundamental factor. The factors C and G give together a dark brown colour. The factor G is perhaps identical with SHAW and NORTON's factor for yellow, viz. C. The factor for »chocolate brown», C, is probably neither identical with the factor for »coffee brown», F, of SHAW and NORTON nor with their factor for »olive brown», H. The

above mentioned gives an idea of the difficulty of identifying the colour factors of the seed colour in the garden bean.

In the red series the following factors are established:

D gives a light red colour together with the fundamental factor P.

E is epistatic to D and gives dark red colour.

The black factor G is epistatical to the other factors of the yellow-black series. The interrelation of the factors of this series seems, however, not to be quite established.

Besides the fundamental factor P SHAW and NORTON assume special fundamental factors, M and M_1, for the yellow black and the red series. When these factors are absent the colour will be buff or ecru even if the factor P and other factors of respective series are present.

As to the heredity of mottling of the seeds two different mode of behaviour are found. In the first form the characteristic of mottling is constant. When crossed with a self coloured variety mottling proves to be dominant, and F_2 shows the ordinary 3 : 1 segregation. The second form of mottling is not constant but shows always segregation in 2 mottled : 2 self coloured. The mottled type segregates in the same manner in the following generations; the self coloured becomes constant. As to the phenotype both are similar.

The opininons differ as to the factorial basis of mottling. EMERSON (1909), suggested by SPILLMAN, has advanced the hypothesis that mottling is due to two factors, Y and Z, which both must be present for the bringing about of mottling. These factors are absolute coupled in the true-breeding varieties. If a plant has the factor Y and another the factor Z the bastard, having both factors, becomes mottled. The segregation in F_2 will be: 2 $YyZz$: 1 $YYzz$: 1 $yyZZ$ as the factors are absolute repulsed in this case. Thus, the ratio becomes 2 mottled : 2 self coloured. EMERSON (1909) has, however, set forth still another theory. The true breeding mottling is due to one factor and the ever segregating type to another factor, which has effect only as a heterozygote. The latter should be identical with the factor for mottling established by SHULL (1908). KOOIMAN (1920) has given us another theory. Constant mottling is brought about by one factor, V. Another factor, B, causes a total colouration of the seed coat with the exception of the hilum ring. In its heterozygous stage it causes the ever segregating type of mottling. Whether or not any of these theories covers the fact is still unsettled. It is possible that mottling needs quite another factorial scheme to be understood.

The segregation in the »*Steninge hybrid*» resembles some of the segregations recorded by SHAW and NORTON, viz. in their crosses with »Blue Pod Butter». This is especially the case in the crossings between this variety and »Black Wax». The seeds of »Blue Pod Butter» are of a buff or ecru colour. Furthermore, this variety is distinguished by deeply coloured flowers and purplish foliage.

The seeds of the F_1-generation of this cross were black mottled. F_2 showed segregation in black, mottled and buff coloured in the ratio 1 : 2 : 1. The buff coloured had all the deeply coloured flowers and the purplish foliage of »Blue Pod Butter». The self coloured bred true in F_3, and the mottled showed the segregation mentioned above.

SHAW and NORTON think that »Blue Pod Butter» lacks the determiner M of the yellow-black series and the factor for mottling, Z, while it has the black-factor, G, and the other factor for mottling, Y. »Black Wax» has the black factor, G, and the other factor for mottling, Z. The factors Z and M are absolute coupled. The genetical formulae of these varieties would then be: $PyZMG$ for »Black Wax» and $PYzmG$ for »Blue Pod Butter». The segregations recorded agree well with these presumptions.

There is apparently 'a great similarity between this cross of SHAW and NORTON's and the heredity of the steel colour in »Steninge hybrid». However, the segregation cannot be due to the absence of the determiner M in the steel coloured plants; in this case the ground colour should be buff and not chocolate brown. It is necessary to assume that the steel coloured plants lack a factor, K, which results in the dilution of the black colour to steel colour. The chocolate brown colour may be due to at least one factor C, besides the fundamental factor P; this factor C is perhaps identical with the factor C of LUNDBERG and ÅKERMAN. Furthermore, it is necessary to assume that the black and the steel coloured plants have each one a factor for mottling, and that an absolute coupling is at hand between the factor K and one of the factors for mottling. The formula of the steel colour will then be $PCGkYz$ and of the black $PCGKyZ$. It is possible, however, that other hypostatical colour factors are present.

SHAW and NORTON have found plants with seeds of a »smoky black or brown colour» in the cross between »Blue Pod Butter» and »Black Wax. They assume that this colour is a mere modification and have not investigated its genetics. It is very probable, however, that it is identical with the steel tinge that is to be seen on plants lacking the factor K. The other plants noted as buffs should then

also be steel coloured.   As is mentioned above the steel tinge is very modifiable, and it is very often limited to a dark streak close to the hilum.   If this assumption is right the segregation would be explained if »Blue Pod Butter» had the formula $PYzkG$ and »Black Wax» $PyZKG$, K and Z being absolutely coupled as before.

As far as I can judge from their somewhat scanty communication it is the result from this cross that has lead SHAW and NORTON to the assumption of still another ground factor besides P.   The assumption of a factor K with the above mentioned effect explains, however, the both segregations as well as the appearance of the smoky black or brown seeds in the cross with »Blue Pod Butter».   I therefore doubt the existence of a ground factor M, nor do I think such a factor necessary for the explanation of the segregation.

The variation of the size and the shape of the seeds in the material, here recorded, was rather great, just as is the case of the commercial samples of »Steninge hybrid».   I was under the impression that the steel coloured seeds were smaller, thinner and more decidedly kidney-shaped than the black ones.   A statistical investigation showed, however, that there was no correlation at hand between these characteristics and the seed colour.

II. THE GENETICS OF DOUBLE MOTTLING.

When assorting a commercial sample of brown bean in 1916 some differing types were found.   They were sown in the experimental field the following year, and the plants were treshed separately.   In 1918 the pedigree parcels, descendants from these plants, were all treshed together by a mistake.

One of these showed segregation in three different kinds of mottling, viz. in violet (C. C. = 571) and brown (C. C. = 151) on a yellowish white (C. C. = 0221) ground colour (double mottling), brown violet (C. C. = 57—58) on yellowish white and violet (C. C. = 571) on the same back ground.   On examining the material the yellowish white plants were found to be constant.   The brown violet and the violet mottled showed segregation in resp. brown violet or violet mottled and yellowish white.   The brown self coloured segregated in brown and yellowish white.   These types were not investigated further.   The descendants of the double mottled showed segregation in 48 double mottled (and brown violet mottled), 7 violet mottled, 7 brown self coloured and 3 yellowish white.   Seeds from these plants

were sown in the following year, and the segregation was similar to that obtained in 1918 and 1919.

Table 2 shows the segregation in D_3, and table 3 the correspondence of the theoretical and the observed ratios in the segregating D_3-lines. It is rather satisfactory as is seen from the table.

TABLE 2. *The segregation in D_3.*

The seed colour of the D_2-plants	The genetical formula of the D_2-plants	Number of plants in D_2	D_3			
			Mottled		Self coloured	
			Double mottled	Violet on yellowish white	Brown	Yellowish white
Double mottled	*PPBBDDYYZZ*	15	175	—	—	—
»	*PPBbDdYyZZ*	10	71	18	16	7
»	*PPBbDDYYZZ*	4	30	11	—	—
»	*PPBBDdYyZZ*	8	77	—	31	—
Violet mottled	*PPbbDDYYZZ*	4	—	64	—	—
»	*PPbbDdYyZZ*	3	—	35	—	13
Brown self col.	*PPBBddYYZZ*	3	—	—	63	—
»	*PPBbddYyZZ*	3	—	—	30	7
Yellowish white	*PPbbddyyZZ*	3	—	—	—	56

The segregation may be due to the following factors:

P, a fundamental factor. Causes the yellowish white colour.

B, a factor for brown colour. Whether or not it is identical with SHAW and NORTON's factor for yellow (*C*) is impossible to decide. Perhaps it is identical with KOOIMAN's factor for brown, *C.*

D, a factor for violet colour. It is probably identical with SHAW and NORTON's factor for light violet, *D.*

Y and *Z* are factors for mottling. They are coupled reciprocally and with the factor for violet, *D.*

The factors *B* and *D* together with the factors for mottling give a bean mottled in violet and brown on yellowish white back ground, the double mottled bean. The segregation in F_2 of a plant heterozygous in all factors (with the exception of the fundamental factor, *P*) will theoretically be: 9 double mottled (*PBDYZ*), 3 brown (*PBdyz*), 3 violet mottled *(PbDYZ)* and 1 yellowish white *(Pbdyz).* The segregations obtained in D_2 and D_3 correspond with the theoretical demands. It is possible, however, that the double mottled type is heterozygous

only as to one of the factors for mottling, Y and homozygous in the other, Z, and that there is coupling only between the factor Y and the factor for violet, D. This latter factorial scheme may be the most plausible, judging from the experiments of SHAW and NORTON's, and it is therefore used in the tables 2—4. When all the factors B, D and Y are present in a heterozygous state the seed coat becomes di-

TABLE 3.   *The correspondence between the theoretical and the observed ratios.*

Genetical formula of D_2-plants	Double mottled		Violet on yellowish, white		Brown self coloured		Yellowish white	
	Obs.	Theoret.	Obs.	Theoret.	Obs.	Theoret.	Obs.	Theoret.
PPBbDdYyZZ	10,14	9 + 0,750	2,57	3 ± 0,590	2,29	3 ± 0,590	1,00	1 ± 0,366
PPBbDDYYZZ	2,93	3 ± 0,271	1,07	1 ± 0,271	—	—	—	—
PPBBDdYyZZ	2,85	3 ± 0,167	—	—	1,15	1 ± 0,167	—	—
PPbbDdYyZZ	—	—	2,92	3 ± 0,250	—	—	1,08	1 ± 0,250
PPBbddyyZZ	—	—	—	—	3,24	3 ± 0,285	0,76	1 ± 0,285

stinctly double mottled. The violets spots are then much smaller than the brown and the yellowish white. When all factors are homozygous the violet colour seems to run together with the brown, and the seed appears to be mottled in brown violet on a yellowish white ground. Individuals, heterozygous in the brown factor B and homozygous in the factor group DYZ, are of the same appearance. The anatomical cause of these differences is that the anthocyan carrying cells are lying together in larger groups in the heterozygotes; in types which are homozygous in the factors DYZ they are scattered among the cells carrying brown pigment.

In the violet mottled type the homozygotes are also easily distinguished from the heterozygotes. The violet spots are much larger in the former type, and it seems to be phenotypically identical with the »dark mottled» type of SHAW and NORTON. In the latter type the violet spots are much smaller. It is probably phenotypically identical with the »light mottled» type of these writers. The difference between these types is quite discontinuous and there was no difficulty to distinguish them, just as is the case with the dark and the light mottled types. Their genetics is, however, quite different. The dark mottling described by SHAW and NORTON is due to a factor O, whose

absence results in light mottling. In the segregation here recorded, the dark mottling is due to the fact that the factors are in the homozygous state, the light mottling, on the other hand, because of their presence in a heterozygous one.

When the factor B is homozygous and the factors DYZ heterozygous the violet and the yellowish white spots become much smaller than when all these factors are heterozygous (brown double mottling). This type, however, is rather easily confounded with the one hetero-

TABLE 4. *The observed and the theoretical values of mottled types in D_3.*

Genetical formula of D_2-plants	Brown violet mottling $PPBBDDYYZZ$ $PPBbDDYYZZ$		Brown double mottling $PPBBDdYyZZ$		Double mottling $PPBbDdYyZZ$		Violet mottling			
							Dark mottl. $PPbbDDYYZZ$		Light mottl.	
	Obs.	Theoret.	Obs.	Theoret.	Obs.	Theoret.	Obs.	Theoret.	Obs.	Theoret
$PPBbDdYyZZ$	20	23,67	13	15,78	38	31,55	—	—	—	—
$PPBBDDYYZZ$	30	30,00	—	—	—	—	—	—	—	—
$PPBBDdYyZZ$	20	25,67	57	51,34	—	—	—	—	—	—
$PPbbDdYyZZ$	—	—	—	—	—	—	13	11,67	22	23,53

zygous in all factors. The cause of this may be the rather great power of modification of the violet colour.

On the contrary, it is not possible to distinguish between the brown homozygotes and the brown heterozygotes.

Thus it is possible to distinguish more groups of colours than is shown in table 2. They are found, however, in table 4, together with the theoretical values. As seen, the correspondence is rather good.

The original plant has probably been a bastard between a brown bean of the formula $PPBBddyyZZ$ (or . . zz) and a true breeding violet mottled of the formula $PPbbDDYYZZ$.

The segregation here recorded resembles that found in some crossings of SHAW and NORTON between types of the red and the black series. In these cases F_1 became doubled mottled in colours of both series. F_2 showed segregation in types similar to F_1 and in mottled patterns of the yellow-black colours and of the red. Furthermore self coloured brown types were obtained but neither self coloured red nor any true breeding mottled type. The crossings recorded by these writers were made between types of the formula $PYZmM_1$ . . . (the red series) and $PyZMm_1$ . . . (the yellow-black series). The fac-

tors M and Z should be absolutely coupled. The experimental facts do not agree quite well with this factorial scheme. It is necessary in either case to assume a coupling between the mottling factor Y and the ground factor M_1, or between the factors of the red series. The absence of the true breeding red type will otherwise be difficult to understand.

The segregation of the double mottled type is easily understood without the assumption of a ground factor M_1. Whether or not the segregations recorded by SHAW and NORTON require the assumption of this ground factor cannot be ascertained with certainty on account of their too scanty records.

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