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THE GENETICS OF CERTAIN COMMON VARIATIONS IN COLEUS¹

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Coleus are characterized by great variations in leaf color, and to a lesser degree by variations in leaf form and flower type. Genetic breeding experiments now being conducted at the Ohio State University have to date revealed at least eight sets of alleles responsible for many common variations.

Boye and Rife (1937) reported the difference between solid purple leaf color and green leaves with a brown pattern on the upper epidermis (see Fig. 1) to be due to a single pair of alleles, purple being dominant to pattern. Likewise, in the Golden Bedder strain, solid green appeared to be dominant to pattern. Another set of alleles was shown to determine whether the plant has an intense or dilute green pigmentation, the intense green being dominant to the dilute green. Later work by Boye (1941) showed that the genes responsible for solid purple, solid green and pattern belong to a single allelic series. The gene responsible for solid purple, (P) and the one responsible for solid green (p^G) are each dominant to the one resulting in pattern (p). The genes P and p^G show no dominance to each other, plants of genotype Pp^G being of a bronze gray color. The genes responsible for intense and dilute green (I, i) do not appear to be linked with the P series (see Table 6b).

Crinkly leaves have been shown to be due to a single dominant factor (C) and smooth leaves to its recessive allele (Rife, 1940). The P and C series are not linked. Deep lobed leaves were shown to be due to a simple dominant factor, and in the strain investigated by Rife (1940), were always associated with male sterile flowers.

PATTERN, MOTTLING AND SOLID COLOR

Coleus plants frequently exhibit various degrees of speckling or mottling of anthocyanin on the upper leaf surface; as contrasted with either a characteristic pattern or complete absence of anthocyanin (Fig. 1). There is great variation in the type of mottling, which would seem to indicate that multiple factors are concerned in its expression. Table 1 shows the results of selfing several mottled plants. In each instance patterned, mottled and solid colored progeny were produced. Patterned plants from such progenies always breed true, and solid colored plants usually do so. This would seem to indicate that mottling is due to the heterozygous state of the factors determining pattern versus solid color. An examination of Table 1 shows that the ratios deviate significantly from a 1 : 2 : 1, there being too few mottled and too many solid colored plants. If we test progenies for 3 : 1 ratios (three solid and mottled, one patterned), however, there is no significant deviation from the expected. Slight mottling frequently will not appear until the plants have become fairly large. Space limitations usually render it impossible to maintain complete progenies until they have reached such size, and it seems likely that when the counts were made, many potentially mottled plants were classed as solid colored. We shall henceforth use the symbols TT to designate the genotype of solid color, tt the genotype of patterned plants, and Tt that of mottled plants. The degree of mottling is apparently determined by multiple modifiers.

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When plants of genotypes tt and Tt are crossed with plants of genotype p^Gp^G all of the progeny are solid green. When plants of genotype TT are crossed with plants of genotype PP , the progeny are purple, rather than bronze gray. These observations indicate that the p factor of the purple series does not result in the

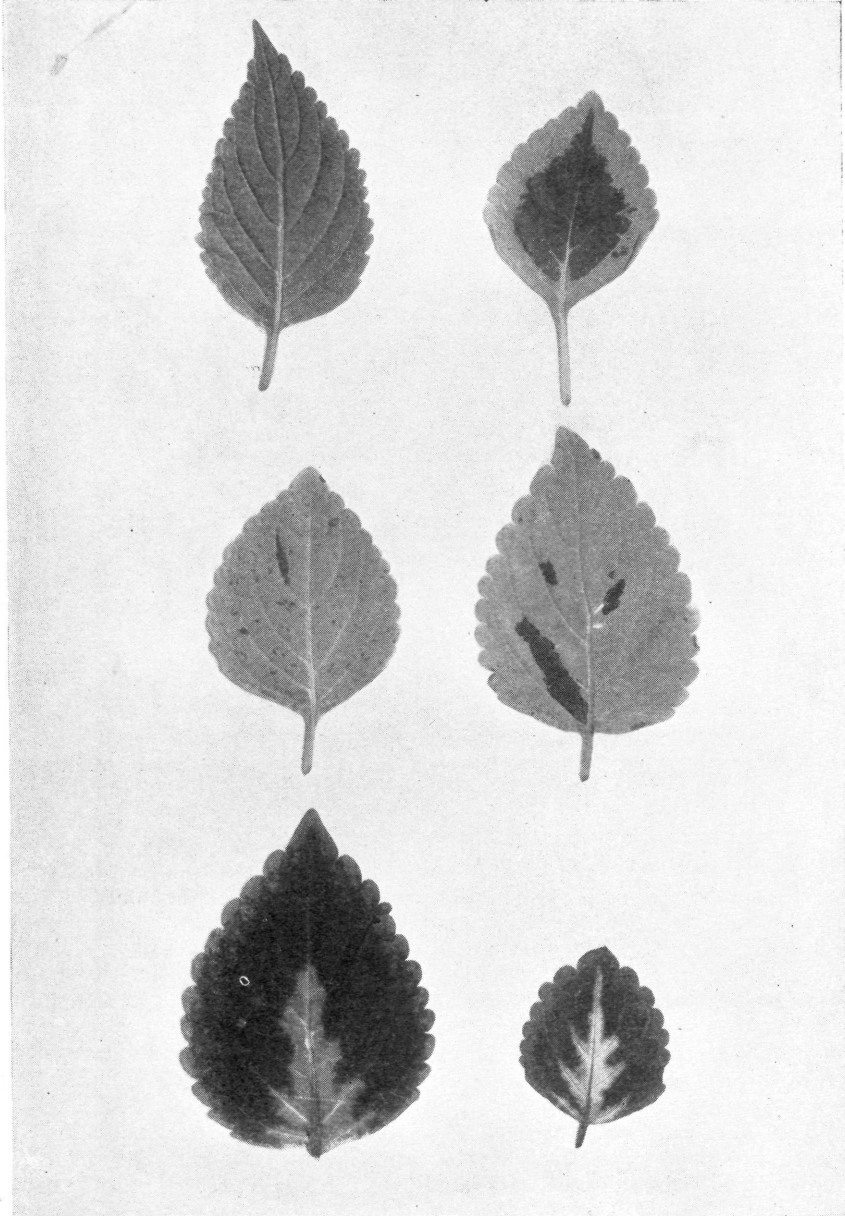


FIG. 1. Color variations in coleus leaves. Upper row, solid green on left, pattern on right. Middle row, speckling and mottling. Lower row, distinct pattern and chlorophyll deficient on left, faint pattern and chlorophyll deficient on right.

formation of a pattern, but rather is responsible for a solid green, phenotypically the same as that produced by p^G . The two types of solid green differ in breeding behavior in that p^G is epistatic to t , whereas T is epistatic to p . Apparently the plants used by Boye (1941) in the analysis of the P series were homozygous for tt , thus making it possible to differentiate between the two types of green on the basis of the presence or absence of patterns.

TABLE 1
ANALYSIS OF DATA OBTAINED BY SELFING MOTTLLED AND SPECKLED PLANTS

A.						
<i>Seed Sample</i>	<i>Pattern</i>	<i>Mottled</i>	<i>Solid</i>	X^2	<i>df</i>	<i>Probability</i>
1	25	33	42	17.340	2	very small
2	17	20	17	3.628	2	0.3-0.05
3	6	16	12	3.353	2	0.3-0.05
4	20	36	23	0.638	2	0.95-0.7
5	5	8	9	3.231	2	0.3-0.05
	73	113	103	28.190	10	very small
Deviation				Heterogeneity		
df=2				df=8		
$X^2=20.274$				$X^2=7.984$		
p=very small				p=0.5-0.3		
B.						
<i>Seed Sample</i>	<i>Pattern</i>	<i>Mottled and Solid</i>		X^2	<i>df</i>	<i>Probability</i>
1	25	75		0.0001	1	0.99
2	17	37		1.390	1	0.3-0.05
3	6	28		0.789	1	0.5-0.3
4	20	59		0.001	1	0.99
5	5	17		0.001	1	0.99
	73	216		2.181	5	0.95-0.7
Deviation				Heterogeneity		
df=1				df=4		
$X^2=0.009$				$X^2=2.172$		
p=0.99				p=0.97-0.70		

LEAF LOBES AND MALE STERILITY

In addition to the strain of plants in which deep lobes are associated with male sterility reported by Rife (1940), deep lobes have subsequently been discovered in two other strains. In one of these the male flowers are completely fertile, and the degree of lobing is indistinguishable from that in the strain characterized by male sterility. In the other strain there is variability in the degree of lobing in the heterozygous plants, which usually show lobes not so deep as do plants homozygous for deep lobing. Homozygous deep lobed plants are almost completely male sterile, although a few seeds have been obtained from them. The heterozygous plants show a fair degree of fertility, much less than do the shallow lobed plants. This type of deep lobing appears to be semilethal in the homozygous state, as such plants develop only rarely. Selfed heterozygous plants give ratios among their offspring approaching two deep to one shallow, more closely than three deep to one shallow (see Table 2c). Thus we have the following four types of plants in regard to deep lobing and male fertility; deep lobed and male sterile, deep lobed and partially male sterile which are semilethal in the homozygous state, deep lobed and male fertile; and shallow lobed and male fertile. No shallow lobed male sterile plants have been obtained.

There are at least three possible explanations for this breeding behavior. There may have been three independent mutations at different loci, one of which resulted in deep lobes with no effect on sterility, another which resulted in deep lobes and partial male sterility, and a third which resulted in deep lobes and complete male sterility. If true, plants heterozygous for any two of the three types of deep lobing should give three types of offspring when crossed with shallow lobed, male fertile plants. Two of such crosses have been made, as shown in Tables 2a and 2b.

TABLE 2
ANALYSIS OF DATA ON LEAF LOBING AND MALE STERILITY

A.

Deep ♂ sterile x heterozygous deep ♂ fertile.

12 deep ♂ sterile;
7 deep ♂ fertile;
8 shallow ♂ fertile.

Five of the deep ♂ sterile were crossed with shallow ♂ fertile.

One gave 30 offspring, all deep.
" " 32 " 17 deep, 15 shallow.
" " 17 " 8 deep, 9 shallow.
" " 5 " all deep.
" " 8 " 6 shallow, 2 deep.

B.

Deep ♂ sterile x heterozygous deep partially ♂ sterile.

2 deep completely sterile.
3 deep partially ♂ sterile.
2 deep ♂ sterile.
2 shallow ♂ fertile.

Two of the deep partially ♂ sterile, and one of the deep completely ♂ sterile were crossed with shallow ♂ fertile plants, and in each case produced offspring in the ratio of approximately 1 deep to 1 shallow.

C.

SEGREGATIONS OBTAINED BY SELFING HETEROZYGOUS DEEP LOBED PARTIALLY
♂ STERILE PLANTS

Sample	Deep	Shallow
1	10	5
2	11	3
3	8	3
4	25	12
5	28	15
6	10	2
Total	92	40

						P
1 df	X ²	value	of	deviation	from	3 : 1 ratio = 1.979
X ²	"	"	"	"	"	2 : 1 " = 0.544
						0.3-0.05
						0.5-0.3

In no instance were more than two types of offspring produced from such, definitely indicating that independent mutations cannot account for the variations.

It is possible that a single pair of alleles may be responsible for deep and shallow lobes, and another set of alleles responsible for variations in male sterility. If so, these two sets of alleles are so closely linked that they rarely, if ever, cross over. The other alternative is that the variations in both leaf lobes and male sterility are due to a single set of four multiple alleles, which may be represented as follows: L-deep male sterile, 1^P-deep, partially male sterile, 1^F-deep, male fertile and 1 shallow, male fertile.

Which of these latter two hypotheses is correct could be established only by the appearance of a shallow lobed male sterile plant or a new mutation affecting both lobes and male sterility. It is apparent, however, that the genes affecting lobing and male sterility are at the same or almost the same chromosome locus.

TABLE 3
DATA ON PURPLE VS. GREEN LOWER EPIDERMIS

A.			B.		
			Backcross Segregations		
Sample	Purple	Green	Sample	Purple	Green
1	21	8	1	16	17
2	135	41	2	16	14
3	33	11	3	38	43
4	14	7			
	<hr/>	<hr/>			
Total	203	67	Total	69	74

TABLE 4
F₂ SEGREGATIONS GREEN VS. WHITE OR PINK AREAS

Sample	Green	White or Pink Areas
1	132	44
2	22	5
3	71	27
4	67	15
	<hr/>	<hr/>
	292	91

TABLE 5
HETEROZYGOUS FAINT PATTERN SELFED

Faint	Dark	X ²	df	P
35	8	0.843	1	0.5-0.3

LOWER EPIDERMIS, CHLOROPHYLL DEFICIENCY AND FAINT PATTERNS

Lower leaf surfaces may be either purple or green. Purple lower leaf surfaces are usually associated with reddish stems and leaf veins. As shown in Table 3, backcrosses of purple x green lower epidermis give 1 : 1 ratios, and F₂ segregations of 3 purple to 1 green. Apparently, then, purple lower epidermis (B) is dominant to green (b).

White or pink spots, due to the absence of chlorophyll, are frequently found in the center of coleus leaves. The extent of these spots is variable, ranging from a narrow stripe along the midribs of the leaves, to areas covering almost the entire leaf surface. Crosses between solid green and chlorophyll deficient strains give solid green progeny, and in the F₂ ratios of approximately 3 solid green to 1 chlorophyll deficient, indicating that solid green (A) is dominant to this type of chlorophyll deficiency.

Faint patterns, as contrasted with distinct patterns shown in Figure 1, are sometimes found. Whether the pattern is distinct or faint apparently is independent of the type of green, and is determined by the type and distribution of anthocyanin. A faint patterned plant when selfed, produced offspring in the ratio of approximately 3 faint to 1 distinct, (Table 5), suggesting dominance of the faint pattern (O) to the distinct (o).

LINKAGE

At least eight sets of alleles are indicated as being responsible for the variations discussed in this paper. Of the 28 possible linkage relationships 11 have been tested, as shown in Table 6. In none of these tests do the ratios obtained deviate significantly from what one should expect on the basis of random assortment, thus giving no indication of linkage.

TABLE 6
TESTS FOR LINKAGE

				X^2	<i>df</i>	<i>P</i>
A						
Backcross, P and L allelic series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
29	34	23	20	4.537	3	0.3-0.05
B						
Backcross, P and I allelic series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
22	23	30	21	4.075	3	0.3-0.05
C						
Backcross, I and L allelic series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
26	32	17	31	5.959	3	0.3-0.05
D						
Backcross, B and L series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
22	23	19	17	1.826	3	0.7-0.5
E						
Backcross, A and L series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
20	14	19	28	4.924	3	0.3-0.05
F						
Backcross, A and B series.						
<i>Non-crossovers</i>		<i>Crossovers</i>				
25	18	15	23	2.986	3	0.5-0.3
G						
F ₂ segregation, A and I series—Test for deviation from 9 : 3 : 3 : 1 ratio.						
<i>A_I_</i>	<i>A_ii</i>	<i>aaI_</i>	<i>aa ii</i>	X^2	<i>df</i>	<i>P</i>
107	25	34	10	2.704	3	0.5-0.3
H						
F ₂ segregation, B and I series—Test for deviation from 9 : 3 : 3 : 1 ratio.						
<i>B_I_</i>	<i>B_ii</i>	<i>bbIi</i>	<i>bbii</i>	X^2	<i>df</i>	<i>P</i>
110	25	31	10	2.379	3	0.5-0.3
I						
Cross of IiI1 x IiI1—Test for deviation from 3 : 1 : 3 : 1 ratio.						
				X^2	<i>df</i>	<i>P</i>
27	12	30	12	1.070	3	0.95-0.7
J						
Selfed plant of genotype OoLl—Test for deviation from 6 : 3 : 2 : 1 ratio.						
				X^2	<i>df</i>	<i>P</i>
24	11	4	4	1.982	3	0.7-0.5

SUMMARY

1. Leaf patterns in coleus are due to the homozygous state (tt) of a pair of alleles. The heterozygous state (Tt) produces mottling or speckling, and the other homozygous state (TT) results in solid green. Solid green due to p^G is epistatic to both Tt and tt , while Tt and tt are epistatic to p .

2. Four genes, either closely linked or belonging to the same allelic series, are responsible for variations in leaf lobes and male sterility.

3. Purple lower epidermis of leaves is dominant to green, solid green leaf color is dominant to white or pink spots, and faint leaf patterns appear to be dominant to distinct leaf patterns.

4. Tests gave no evidence for linkage between P and I , P and C , P and L , B and L , B and A , B and I , A and I , A and L , I and L , and O and L .

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