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GENETICS OF FLOWER COLOR

by Don Smith

In the previous issue of the newsletter I discussed the chances of producing orange peonies by using P. potaninii and its hybrid progeny. My conclusions and predictions were based primarily on empirical data and relationships. In this article I would like to take this discussion to the next level by presenting a far more detailed and scientific discussion based on my understanding of the modern theory of plant genetics and heredity. Most of what follows was taken from Verne Grant's excellent book "Genetics of Flowering Plants", Columbia U. Press, N.Y., 1975 (Chapter 9).

Flower color inheritance has been studied in a large number of plant species by several independent teams of researchers. Paris, Haney and Wilson (1960) surveyed these studies and searched for common denominators and features in the different specific gene systems for flower color. These authors concluded that flower color is one of the phenotypic characteristics that is controlled by a serial gene system. They also found that in most species the system can be described in terms of six genes with very specific types of interactions between them.

Serial gene systems are composed of two or more Mendelian genes, each controlling a different step in a developmental sequence. Generally, there are three basic modes of gene interactions in such serial systems. In the first type of gene interaction, one gene masks the effect of another, so that the phenotype is effectively determined only by the former gene whenever both genes are present. The effects are comparable to those produced by the combination of a dominant and recessive allele of one gene, but in this case the dominant character is due to the interaction between two separate genes. This dominance of one gene over another is known as epistasis. If the first gene blocks or depresses the action of genes controlling later stages in the reaction chain, then it is called an inhibitor gene. This constitutes the second type of gene interaction. In the third type, two or more genes are considered to be complementary factors if one gene provides the necessary conditions for the action of another gene controlling a subsequent step in the reaction chain. The genes form an epistatic series if the first gene switches the reaction into an alternate pathway.

The six genes as designated by a uniform gene nomenclature are W, Iv, Y, B, P, Dil. There actions are as follows: W switches color production on or off. Iv and Y control ivory and yellow colors respectively. Genes B and P produce anthocyanin pigments which have purple. blue or red colors. The gene Dil acts as an intensifier or a bleaching factor. The dominant and recessive alleles of these genes have the following phenotypic effects:

W	colored	ww	white
Iv	nonivory	iv iv	ivory
Y	nonyellow	yy	yellow
B	purple or violet	bb	blue
P	purple or violet	pp	pink, rose, red
Dil	intense color	dil dil	dilute color

The six color genes form an epistatic series running from W, the top epistatic member, to Dil, the bottom hypostatic member. The series is usually W > Iv > Y > B > P > Dil (Paris, Haney and Wilson, 1960).

In some cases, however, a slightly simpler model involving only five genes can be used to adequately describe the observed flower colors. One such case is the common garden dahlia, *Dahlia Variabilis*.

The garden dahlia is highly variable in flower color. There are white, ivory, yellow, magenta, purple, orange, and red forms, and various tones within some of these color groups. The genetics controlling the inheritance of flower color in Dahlia is complex and was first unraveled by Lawrence and Scott-Moncrieff (1935). A simplified explanation of this model can be found in Grant (1975) and is presented below:

Five main genes determine flower color in *Dahlia variabilis* --- I, Y, A, B, H. These genes fall into three categories. I and Y produce flavone pigments, Y being epistatic to I. A and B produce anthocyanins (cyanidin and pelargonidin). H is an inhibitor. The actions of the dominant alleles of these genes are as follows (Crane and Lawrence, 1938):

I	produces ivory flavone
Y	produces yellow flavone
A	produces pale anthocyanin
B	produces deep anthocyanin
H	inhibits yellow flavone

Color variation in the garden dahlia has two basic components: the flavone pigments, producing ivory and yellow colors; and the anthocyanin pigments, giving reddish to purplish colors. The total array of colors is a result of various mixtures of these components. Some examples are:

ivory background	+	pale anthocyanin	=	magenta
ivory background	+	deep anthocyanin	=	purple
cream background	+	either anthocyanin	=	crimson
yellow background	+	pale anthocyanin	=	apricot
yellow background	+	deep anthocyanin	=	scarlet

The interaction of the two flavone-producing genes (I, Y) and the two anthocyanin-producing genes (A, B) determines the mixtures of pigments and types of color expression. Additional effects are caused by the color inhibitor gene H. When both flavone and anthocyanin pigments are absent, the resulting color is white. The main genotypes and the corresponding flower colors for *Dahlia variabilis* are listed in Table 1.

Table 1. The main genotypes for various flower colors in Dahlia variabilis (Lawrence and Scott-Moncrieff, 1935)

Genotype	Flower Color	Genotype	Flower color
iyab	white	iYab	yellow
Iyab	ivory	IYab	yellow
iyAb	rosy-magenta	iYabH	cream to primrose
iyaB	rosy-purple	iYAbh	apricot
IyAb	bluish-magenta	iYaBh	scarlet
IyaB	bluish-purple	iYaBH	crimson

In polyploid plants, each color gene is present in multiple doses (three doses in a triploid, four in a tetraploid, etc.) and consequently dosage effects of these genes can also come into play. For example, when a genotype which is constant for four color genes but varies in the number of dominant alleles of the fifth gene, where the fifth gene is I, A, or H, will give a graded series of shades within a given color class. Thus magenta pigmentation becomes progressively deeper in the series Aaaa, AAaa, AAAa, AAAA. The gene I for ivory flavone also shows a similar dosage effect. The genotype iiii has no flavone, and Iiii has only a slight trace of flavone pigment, while IIii, IIIi and IIII are fully pigmented with flavone. Dosage effects can also be exhibited by inhibitor genes as well. For example, an incomplete dominant allele of a bleaching gene in a single dose may only make a flower color one shade lighter, but flower color will progressively become lighter with increasing doses of the gene. Normally, these dosage effects are superimposed on gene interactions to produce the large array of flower colors and shades seen in Dahlias and many other species.

I believe that this five gene model can also be applied to peony hybrids with only a few minor modifications that involve changing the order of the epistatic series. Following this approach, I have used this model to attempt to explain the flower color variations observed in several groups of peony hybrids. The results of applying this model to peony hybrids are given in Tables 2 and 3. These tables list the seven main genotypes where the yellow producing gene (Y) is present. To facilitate a direct comparison, I have repeated a sub-set of the data presented in Table 1 for *Dahlia varaibilis* in Table 1a. Table 2 shows the results of the model applied to P. mlokosewitschii hybrids. The important change to note here is that the yellow gene, Y, is hypostatic to all three other color genes in the series. In this model, yellow is only expressed in the absence of the inhibitor gene and the other color genes. The combination that permits the orange (apricot) color in dahlias (iYAbh) in this case gives instead a rosy-ivory color. Moreover, there are no other combinations that can produce orange colors. I believe that this model is in excellent agreement with the experimental data for this hybrid group. Further, it is my prediction that this model can also be applied to the potaninii hybrid group as well. This prediction is based on the observed similarities between the F1 hybrids of these two groups (see related article, Vol. 28, No. 3, p. 3).

In addition to the 5 or 6 "color" genes that make-up the serial gene systems described above, there are one or more additional genes that also play an important role in flower color expression. These are inhibitor genes that turn-off or suppress the production of plastid pigments in the flower petals so that other pigments can be expressed. The most important of these plastid pigments is, of course, chlorophyll, the universal green pigment found in all leaves. However, petals are really just modified leaves, in which a genetic mechanism (inhibitor genes) has evolved to inhibit chlorophyll production. In the bud stage, petals often appear greenish, and occasionally a green tinge remains even in mature petals where chlorophyll suppression has not been complete. The greenish tinges found in P. wittmanniana and its hybrids such as *Green Ivory* and *Ballerina* are examples of such incomplete chlorophyll suppression in peonies. In some cases, there is also a gene which suppresses the production of another plastid pigment called carotenoid. This is, of course, the yellow pigment which occurs in P. lutea and its hybrids.

Table 1a. Relationship between genotype and flower color for *Dahlia Variabilis*
(after Lawrence and Scott-Moncrieff, 1935).
Y is epistatic to I (i.e., Y > I).

Genotype	Flower color
iYabh	Yellow
IYabh	Yellow
iYabH	Cream
iYAbh	Apricot
iYAbH	Crimson
iYaBh	Scarlet
iYaBH	Crimson

Table 2. Presumed relationship between genotype and flower color for mloko and potaninii peony hybrids. Here, it is assumed that I, A and B are all epistatic to Y (i.e., I > Y, A > Y, B > Y).

Genotype	Flower color
iYabh	Yellow
IYabh	Ivory
iYabH	Cream
iYAbh	Rosy-ivory
iYAbH	Rosy-pink
iYaBh	Rosy-pink
iYaBH	Rosy-purple

For the sake of comparison, a similar model was also applied to the lutea tree peony hybrids. The results of this exercise are shown in Table 3. The model used in this case is very similar to the one describing *Dahlia variabilis* (Table 1a) where Y is epistatic to I, except that here it is also assumed that Y is epistatic to A. Another significant difference is that the yellow pigment in P. lutea (carotenoid) is a plastid pigment (similar to chlorophyll) and thus does not mix with other "normal" pigments because it occupies a different cell layer within the petal (Cooper, 1970). As a result of this effect, the anthocyanin pigments are underlaid beneath the yellow pigments from lutea. H is used here to represent an inhibitor gene for the yellow carotenoid pigment, rather than the yellow flavone pigment. These two factors combine to give a very different array of flower colors than is observed in the dahlias.

Table 3. Presumed relationship between genotype and flower color for lutea tree peony hybrids. It is assumed here that Y is epistatic to both I and A but not B (i.e., Y > I, Y > A).

Genotype	Flower color
iYabh	Brilliant yellow
IYabh	Brilliant yellow
iYabH	Light yellow
iYAbh	Yellow, pink undertones
iYAbH	Tea rose ∅ cream
iYaBh	Yellow, red undertones
iYaBH	Red , light yellow overtones

Once again it appears that the model does a fairly good job of describing the range of flower colors observed in the lutea hybrid group.

This model has helped us to understand why red and yellow genes do not always combine to produce orange. This same model can also help us to understand why sometimes white and yellow does not give yellow as we might normally expect and why, in some crosses, it appears that white is dominant to yellow. To look at this issue more closely, we must examine the genotypes that yield white or near white color. These genotypes are listed in Table 4. It was stated above that when all four color genes are absent (iyab) we get white flowers as shown in Table 1. In this case, the condition of the inhibitor gene, H, was not specified, because it does not really matter in the expression of the flower color (i.e., iyabh and iyabH both give the same result). However, in the final analysis, it does matter whether a genotype carries a gene which inhibits the expression of yellow color or not, as this gene can be passed-on to its progeny. The three genotypes in Table 4 will all exhibit white flowers, but two of these three also carry a gene that inhibits yellow. Crossed with a yellow individual (iYabh), only one of these genotypes (iyabh) will give another yellow. In the other two cases, we will get only white offspring due to the presence of the inhibitor gene. This is what is meant when it is said that white is dominant over yellow. Once the inhibitor gene is present, we can only restore the good yellow color of the original yellow parent by breeding-out the yellow inhibitor gene. Otherwise, the yellow color cannot be fully expressed in the resulting offspring. I believe that a yellow inhibitor gene is present in P. macrophylla and is responsible for the non-yellow (ivory and cream) colors in the F1 (mloko-macro) hybrids. It appears that some white lactiflora and white suffruticosa varieties also carry this dominant yellow inhibitor gene as well.

Table 4. Relationship between genotype and white flower color.

Genotype	Flower color
iyabh	white
iyabH	white
IyabH	off-white

Another very interesting possibility concerning the mixture of yellow and red pigments was mentioned some time ago by F. Cooper (APS Bulletin, No. 197, 1975). He pointed-out that in some cases red and yellow can "mix" to create violet rather than orange. In this article he states:

"we find that a mixture of yellow flavones with crimson anthocyanidin causes a shift in color, as one would expect, towards orange. .... Paradoxically we find that the flavones also participate in the color shift from crimson to purple. In this instance flavone and anthocyanidin combine chemically to, in effect, produce a new pigment which is essentially violet in color".

This may be the explanation for what happened in the Anderson intersectional hybrid, *Unique*.

SPECULATIONS ON THE ORIGINS OF YELLOW AND GREEN FLOWER COLORS IN CHINESE TREE PEONIES

by Don Smith

One of the best known of all the Chinese tree peonies is a pale yellow variety known as *Yao's Family Yellow (Yao Huang)*. This variety has been written about since the Sung Dynasty (960-1274) and is still available today along with several other light yellows such as *Imperial Yellow Robe (Yu Yi Huang)* and *Golden Silk Passes through to the Top (Jin Si Guan Ding).* Clearly, these can not be compared to the bright, intense yellows found in the lutea hybrid group, but they are true yellows nonetheless.

This being the case, I wonder how many of you have ever thought about where these yellow flower colors came from (i.e., what is the origin of these unique yellow peonies)?

Both Chinese and Japanese tree peonies are generally regarded as pure races (of P. suffruticosa) of intraspecies hybrids that have been cultivated and improved through interbreeding for at least a thousand years. Although, this may be true for the Japanese tree peonies, I believe that it is unlikely to be the case for the Chinese tree peony group. To support this assertion I list the following observations:

1. The Chinese tree peony group contains flower colors and types not seen in the Japanese tree peony group.

2. Some of these colors are also not present in any of the wild species that are thought to make-up the suffruticosa group.

3. These flower colors include light yellow, light green, cream and apricot.

4. These flower colors imply the presence of one or more yellow pigments.

5. Many of these colors are very similar to those found in the herbaceous hybrids with mloko and/or wittmanniana "blood".

6. These colors are very different from those found in the lutea tree peony hybrids.

These observations lead to the obvious question.

1. Where do these unusual (non-suffruticosa) flower colors in the Chinese tree peony group come from?

Possible Answers:

1. Color breaks caused by genetic mutations due to radiation, chemicals or other sources.

2. Yellow genes introduced into the race through crosses with other species such as P. potaninii trollioides.

Additional Observations and Information:

1. P. suffruticosa and P. potaninii are both native to western China.

2. The yellow pigments found in P. potaninii Trollioides (chalcones) and P. mlokosewitschii (flavones) are related and might be expected to behave similarly in crosses with other species that contain different (anthocyanins) but also related pigments.

LETTERS TO THE EDITOR:

Letter from Theresa Griesbach
received 24 Aug. 98

T. A. Griesbach
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Dear Mr. Smith

As always your latest issue of <u>Pæonia</u> proved quite interesting. While I appreciate your rumbles of thunder, it's too soon to rain on the parade of those avid orange seekers.

As you mention in your article, there have been only two known hybrids involving P. potanini trollioides. *Hélène Martin* is of great interest in breeding, but doesn't tell us how its chalcones might interact with anthocyanidins. *Unique* speaks to this regarding peonidin creating your "deep, dark unusual pink". An article by Robert Geneve in the July/August 1996 <u>The American Gardener</u> states " These (chalcones, aurones and flavones) are not as important as carotenoid pigments for creating the yellow colors found in flowers, but they do act in tandem with anthocyanidins to increase depth or intensity of color". This statement, while predicting the color of *Unique* does not explain the shift toward coral created by the interaction of flavones with the normally crimson cyanidin. How then, can we predict how flavones or chalcones will react with scarlet pelargonidin or how chalcones will react with cyanidin? Each combination should be tried even if the hoped for orange is not the result. I only wish I had *Hélène Martin* in order to try a few combinations myself!

I did try my first I-hybrid cross. From the thirty six flowers pollinated, there were fifty six intact and sixty six ruptured seeds. Many of the ruptured seeds had begun to mold, ten of which were beyond hope of saving and were disposed of. Wish me luck on bringing the others to bloom!

sincerely,

Theresa Griesbach

IN THE NEXT ISSUE OF PÆONIA:

1. ***THE POTENTIAL FOR ORANGE FLOWER COLOR FROM P. LUTEA AND ITS HYBRIDS***

2. ***SPECULATIONS ON THE ORIGINS OF YELLOW AND GREEN FLOWER COLORS IN THE CHINESE TREE PEONIES: PART II***

3. Brief article/comments by Harold Entsminger on the role of yellow pigments and the potential for orange progeny from P. potaninii Trollioides and its hybrids.