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

by Don Smith

For those who have not yet been completely discouraged by the recent articles concerning the chances of producing orange colored peony flowers, here is a little hope that relates to the lutea hybrid group.

While researching the topic of flower color inheritance for recent newsletter articles, I came across another example which seems to have several parallels to the flower color mechanism that occurs in P. lutea and its hybrids. The following paragraph is summarized from "The Genetics of Flowering Plants" by Verne Grant, chapter 19, p. 343.

Two closely related species, Mimulus lewisii and M. cardinalis, occur over a wide range in western N. America and are interfertile. One of the most conspicuous character differences between these species is flower color. M. lewisii is pink, while M. cardinalis is bright orange. It is believed that this character difference is controlled by a single allele pair. Apparently, the gene controls the presence or absence of a yellow carotenoid pigment in the epidermal cells of the corolla. The presence of this yellow pigment in combination with other underlying pigments brings about the orange color of the flowers in M. cardinalis. M. lewisii, on the other hand, has a dominant suppressor (inhibitor gene) of carotenoid pigment production in the corolla and thus it is pink and so are its F1 hybrids with M. cardinalis.

Unfortunately, we do not know what type of pigments are underlying the yellow in this case. Most likely they are either cyanidins or pelargonidins or some combination of the two. Nevertheless, this is an excellent example which demonstrates that two colors (pink and yellow) that do not mix, can still combine to create the overall effect of bright orange flower color. In this instance, pink overlaid by carotenoid yellow gives bright clear orange.

This is, of course, precisely the effect that we are hoping to achieve in the lutea hybrids. The fact that this mechanism produces good orange color in Mimulus should provide considerable hope that this same mechanism might work in the lutea hybrid group as well.

However, before we get too excited about our prospects for success, we need to investigate this issue further by studying the experimental results obtained with the F1 lutea hybrids concerning the inheritance of flower color. In this regard, it is indeed unfortunate that Prof. Saunders did not keep records on his tree peony hybrids. It would certainly be very useful to know which suffruticosa varieties were used as pollen parents for the Saunders lutea hybrids or whether P. delavayi was ever used in producing any of the dark reds (crimsons and very dark black maroons) in the "Black Pirate Group". Fortunately, we do have some pedigree information from the work of Daphnis, Henry and Lemoine that can be especially helpful here. This data is summarized in Tables 1-3. Although Table 3 has little relevance to the discussion of orange flower colors, it is included here for the sake of completeness only.

When P. lutea was crossed with the pink Japanese tree peony, *Shintenchi* (Color group II), the resulting F1 hybrids showed considerable variation in flower color. These hybrids covered the full range of colors from golden yellow (*Demetra*) to pale pink (*Redon*) and included the unique and unusual multicolor, *Gauguin*. These results are summarized in Table 1.

The suffruticosa (Japanese) tree peonies contain only two anthocyanin pigments, pelargonidin (scarlet) and peonidin (crimson). Many suffruticosa varieties (primarily those in color Groups II, III, IV and V) contain mostly pelargonidin pigment with only minor amounts of peonidin. Others suffruticosa varieties contain primarily peonidin pigment. The lutea hybrids, on the other hand, in addition to large amounts of carotenoid contain mostly peonidin with little or no detectable pelargonidin. Only a small handful of these hybrids have even minor amounts of pelargondin pigments according to pigment tests conducted by F. C. Cooper. It seems clear that Cooper was troubled by the fact that so few of the lutea hybrids showed even these traces of pelargonidin pigment and thus he concluded that "peonidin is dominant over pelargonidin". I am convinced that his concern stemmed from the belief that at least some of the Saunder's hybrids tested must have come from suffruticosa pollen parents in color groups II, III, IV, and V (i.e., those containing predominately pelargonidin pigment). He must have wondered why these pelargonidin pigments were not showing-up in the lutea hybrids. So it would appear that the combination of carotenoids and pelargonidins has yet to be made.

One thing is quite clear from Mr. Cooper's tests and analysis; the combination of yellow carotenoid and peonidin pigments <u>does not produce</u> the desired orange color effect in peonies. Therefore, the important question that remains is whether carotenoids and <u>pelargonidins</u> can combine to produce orange flowers.

This key question remains unanswered, despite the fact that Mr. Cooper tested more than a dozen lutea hybrids that contained both red and yellow pigments, because none of these hybrids contained more than mere traces of pelargonidin pigment.

This could be the result of the specific suffruticosa varieties used by Saunders and others as pollen parents or possibly it is the result of the presence of an inhibitor gene in P. lutea that inhibits the production of pelargonidin pigment. If the latter is the case, then orange flower colors can only be obtained by breeding-out the "offending" inhibitor gene. This will take several generations to accomplish.

Unfortunately, the only hybrid with known parentage that was tested by Cooper is the Daphnis hybrid, *Gauguin*. This variety is included in Table 1. Its pollen parent is listed as *Shintenchi* which is in color group II (Pink). Other members of this color group tested by Cooper showed a predominance of pelargonidin pigment, but unfortunately *Shintenchi* was not one of the varieties that was pigment tested. If *Shintenchi* contains mostly pelargonidin pigment like other members of this color group, then I believe that a dominant pelargonidin inhibitor gene must be at work here.

However, other possibilities also exist. One of these possibilities is that separate genes control the production of peonidin and pelargonidin pigments in P. suffruticosa and its hybrids. For example, gene A might control production of peonidin and gene B the production of pelargonidin pigment; and A could be epistatic to B (A > B). This would agree with Cooper's conclusion that "peonidin is dominant over pelargonidin". Simply stated, pelargonidin colors can not be expressed in the presence of peonidin. But, Y may also be epistatic to B (i.e., Y > B), so that pelargonidin pigment can not be produced in the presence of carotenoid pigment. This can be more easily explained by using the five gene model discussed in my earlier article (Vol. 28, No. 4). Only one minor revision is required to update this model for the discussion at hand. According to this revised model, the actions of the dominant alleles of these genes would be as follows:

I	produces ivory flavone
Y	produces yellow carotenoids
A	produces peonidin pigment
B	produces pelargonidin pigment
H	inhibits or bleaches yellow carotenoids

Even if carotenoids and pelargonidins do combine to produce orange, this does not address the more important question; can we actually combine these two pigments in a single peony hybrid? The obvious answer would seem to be yes, but I am not at all sure that this answer is right. We have no evidence from the pigment tests of Cooper to suggest that pelargonidin can exist along with other pigments in anything but trace amounts. Cooper's studies would suggest that pelargonidin can exist only by itself. This is probably the result of its controlling gene being hypostatic to the genes that control other pigments (i.e., I, Y, A). Of the 28 varieties of tree peonies (both suffruticosa and lutea hybrids) tested by Cooper, all fell into one of two categories with regard to flower pigment. These two groups were:

1. Peonidin with little or no pelargonidin

2. Pelargonidin with only minor amounts of peonidin.

There were no other combinations observed. The varieties tested represented 7 of the 9 (non-white) color groups that have been used to classify tree peonies. Only the Purple (VI) and Lilac rose (VIII) color groups were not represented in these tests. Cooper's results can be summarized as follows:

> Peonidin or pelargonidin alone, but never large doses of both pigments together. Carotenoids and peonidins together, but never carotenoid and pelargonidin pigments in the same flower.

It would. of course, be extremely helpful to have additional flower pigment data from a much larger number of tree peony varieties. This is especially true in the case of the "orange-colored" varieties such as *Tessera*. In the absence of such data, however, we are forced to draw conclusions and base our predictions only on the information that we currently have.

Table 1. Summary of experimental results obtained from crosses involving P. lutea and pink Japanese tree peonies

Seed parent	Pollen parent (P. suffruticosa)	F1 hybrid name	Seed parent flower color	Pollen parent flower color	Color of F1 hybrids
P. lutea	x Shintenchi (II)	= Demetra	yellow	x pink	= Golden yellow
P. lutea	x Shintenchi (II)	= D. H. Lawrence	yellow	x pink	= Pink w/ purple streaks

P. lutea	x Shintenchi (II)	= Gauguin	yellow	x pink	= Multicolor (red and yellow)
P. lutea	x Shintenchi (II)	= Redon	yellow	x pink	= Pale pink

Table 2. Summary of experimental results obtained from crosses involving P. lutea and dark pink or red Japanese tree peonies

Seed parent	Pollen parent (P. suffruticosa)	F1 hybrid name	Seed parent flower color	Pollen parent flower color	Color of F1 hybrids
P. lutea	x Ubatama (V)	= Kronos	yellow	x Dark crimson	= Dark red
P. lutea	x Ubatama (V)	= Persepolis	yellow	x Dark crimson	= Good red
P. lutea	x Reine Elizabeth (III)	= Mme. L. Henry	yellow	x Lilac rose	= Yellow, blendec w/red
P. lutea	x La Ville de St. Dennis (VIII)	= Souv. de M Cornu	yellow	x Rose red	= Yellow, blendec w/red

Table 3. Summary of experimental results obtained from crosses involving P. lutea and white Japanese tree peonies

Seed parent	Pollen parent (P. suffruticosa)	F1 hybrid name	Seed parent flower color	Pollen parent flower color	Color of F1 hybrids
P. lutea	x White Empress	= Aphrodite	yellow	x white	= Pale creamy yellow to white
P. lutea	x White Empress	= Artemis	yellow	x white	= Light yellow
P. lutea	x White Empress	= Avra	yellow	x white	= Light yellow to white
P. lutea	x White Empress	= Marie Laurencin	yellow	x white	= Pink to purple
P. lutea	x White Empress	= Persephone	yellow	x white	= Very pale yellow
P. lutea	x White Empress	= Themis	yellow	x white	= Light pink
P. lutea	x Yaso-okima	= Alice Harding	yellow	x white	= Yellow

The color groups referred to in the above tables (given in parenthesis) are those used to classify tree peonies in *The Peonies*, p. 206. They are as follows:

I = White, II = Pink, III = Rose Red, IV = Scarlet, V = Crimson, VI = Purple, VII = Magenta, VIII = Lilac Rose, IX = Yellow, X = Yellow with red markings.

Before some of you become totally discouraged again, let us look at the progress that has been made in the direction of orange so far. Of approximately 170 named varieties of lutea hybrids there are only a handful that have flowers that are "orangy" in color. These varieties are listed below in Table 4 along with an unnamed seedling grown in Australia that was mentioned in a recent article by Bill Seidl (*Pæonia*, Vol. 28, No. 2). Also given in Table 4 are the seed and pollen parents for each of these varieties. Note that *Chinese Dragon* appears twice and *Golden Era* three times in the parentage of these varieties.

Table 4. The parentage of the "orange" tree peony hybrids.

Variety Name	Color	Seed parent	x	Pollen parent
Tessera (D-4)	Peach/Orange	P. lutea	x	Unknown
Ariadne (D-304)	Peach	Unnamed BC2	x	Impomon (Moutan)
Nike (D-368)	Coral peach	Unnamed BC2	x	Guardian of the Monastery
Brassy Lady (SH-127)	Amber tan/harvest	Golden Era	x	(G. Era x Chinese Dragon)
Chow/Seidl Sdlg	Orange	(A-198 x Chinese Dragon)	x	Golden Era

(Golden Era x Chinese Dragon) = Seidl seedling (SH-39)
(A-198 x Chinese Dragon) = Seidl seedling (SH-16) which is described as flesh colored blended rose

Although, none of the flowers listed in Table 4 can truthfully be described as having really "good" orange color, they do represent a good starting point for orange colored tree peonies. If I were trying to develop orange tree peonies, I would start by attempting to acquire some of the above varieties and then try inter-breeding them. *Tessera* has produced seedlings and *Nike* has pollen of more than adequate fertility. *Brassy Lady* is said to be fertile both ways. Unfortunately, several of these peonies may be very difficult to obtain. *Nike* is listed in the 1998 Klehm catalog (at $75.00) but is probably the least orange of the entire group. By selecting and crossing the best of the offspring from such crosses, a race of orange colored tree peonies might be developed in two or three generations. Personally, I am far from convinced that really "good", clear orange colors will ever come from this line of breeding, but it is probably our best shot for orange and thus should certainly be pursued by those in a position to do so.

SPECULATIONS ON THE ORIGIN OF YELLOW AND GREEN FLOWER COLOR IN THE CHINESE TREE PEONIES: PART II

by Don Smith

Tree peony cultivation in China goes back about 1,400 years or more. Originally a relatively unimpressive mountain bush, the tree peony has been bred and refined by generation after generation of chinese horticulturists so that today more than 400 distinct varieties are in cultivation in China. These varieties come in at least 8 different flower forms and no less than 17 separate flower colors including white, maroon, purple, "black", various shades of red, pink, and magenta as well as pale yellow and green.

History books claim that during the Sung Dynasty (960-1279 A.D.), every household in the capital city of Luoyang (Loyang) grew tree peonies. According to these reports, local residents considered other plants beneath their diginity and there was a saying that "the peony is the only real flowering plant under heaven." Whenever, a famous specimen blossomed in Luoyang, everyone in the capital went to look, so that the stream of viewers and carriages often caused traffic jams. The price for a rare variety was said to be more than the amount of taxes paid by 10 households of moderate income. Probably, the rarest and most famous of these rare varieties was a variety called *yao huang* (Yao's Yellow or Yao's Family Yellow). This pale yellow variety was bred by the Yao family in Baisimaban at the foot of Mount Mangshan near Luoyang in central China. One author writing during the Sung Dynasty wrote the following:
"The Yao Family Yellow and Wei Purple are a thousand cash for a single stem. (However,) No one will sell me a Yao Yellow."

The ancient Chinese not only revered the tree peony (which they regarded as "the king of flowers"), they also invested considerable time and energy to the task of improving their favorite flower by developing new and better varieties. Developing new flower forms and colors was clearly one of their prime objectives. In this regard, yellow and purple varieties were probably the most treasured of all. Greens and "blacks" were undoubtedly also ranked among the most prized group as well. I believe that the ancient Chinese were quite obsessed with the idea of creating yellow, green, black, and blue tree peonies. After all, it was undoubtedly a surefire road to fame and fortune in ancient China. With this in mind, it is interesting to note here, that the very rare pale yellow double herbaceous peony, *Oriental Gold/Golden Wheel* is now also believed to have originated in the imperial gardens of China more than two hundred years ago (*Pæonia*, Vol. 27, No. 3, p. 6).

But, the question remains, where did these unique tree peonies come from? At this point, the answer should be obvious. From the hands of ancient Chinese hybridizers.

I am convinced that these rare tree peonies are merely advanced generation hybrids that were created by Chinese hybridizers from crosses of Chinese tree peonies (Moutan) with several different species of wild tree peonies such as P. potaninii and P. delavayii. Although these other species were not discovered by western explorers until the late 1890's, it seems extremely unlikely that at least some of these wild tree peony species (other than P. suffruticosa) were not known to ancient Chinese gardeners, plant collectors and explorers much earlier. After all, we must remember that these species are native to the mountains of southwestern China, not very far from the city of Luoyang.

To my knowledge, there are only two known species of tree peonies with yellow flowers, P. lutea and P. potaninii (var. Trollioides and/or Tall Yellow). Consequently, it is reasonable to assume that one of these two species is the source of the yellow pigment in *yao huang* and the other yellow Chinese tree peonies. However, the pale yellow color exhibited by the yellow Chinese varieties is very different than the bright yellow seen in the many lutea hybrids now in existence. With this evidence in hand, I believe we must conclude that P. potaninii (Trollioides/Tall Yellow) is the probable source of the yellow seen in the Chinese tree peonies. If this is indeed the case, then we already know the answer to another important question raised in several recent newsletter articles; what is the breeding potential of P. potaninii (Trollioides) and its hybrids for yellow and orange flower color?

Therefore, if we wish to know what flower colors can be expected in the hybrid offspring of P. potaninii (Trollioides) crossed with Moutan, I suspect that all we need do is look at the colors exhibited by the Chinese tree peony group.

LETTERS TO THE EDITOR:

received 8/20/98

Once Upon A Dream

by Harold Entsminger

Yellows are basically color intensifiers. Chalcones are miscible with flavones and anthocyanidins. Whites are pigmented by flavones, thereby making their otherwise translucent state white. White x Yellow, as in Trollioides, potaninii x *Gessekai*, would be expected to produce pale yellow; enter *Hélène*

Martin. *Martha Washington* x Potaninii would be expected to intensify the light pink of *Martha Washington*; enter the darker pink, *Unique*, with an unusual hue, yellow spread. *Tessera*, copper-orange, intensified can give orange? We know chalcones are miscible, not recessive, to anthocyanidins and flavones, but not to carotenoids. So we can have yellow and orange together like Gauguin's red and yellow effect, and also purple and yellow. Lavender? *Mons. Antoine Rivieres'* Cyclamen pink-purple with chalcones present can be magificent Indigo. *Hélène Martin* x Potaninii can give Apricots, Lilacs and Blues? Imagine purples as "blacks". Imagine *Coral Charm*, *Good Cheer*, *Frances* and *Nancy* , all as oranges!!! They can be feathered, flecked, striped, or laced in multi-colors, and various colors. It is happening. You will be part of it. Imagine...A peony with Je ne sais quoi, chalcones!