

EXCERPT FROM "THE CONTROL OF VARIATION IN GARDEN PLANTS"

by Watkin Williams

in the Journal of the Royal Horticultural Society, Vol. 84, 1959, pp. 323-326

The development and deposition of anthocyanin pigments in plants is not confined to the petals. There are many highly prized decorative plants in which it is the leaves that provide the interest and beauty. Perhaps the best examples are *Poinsettia* and *Coleus*. The processes governing pigment formation in leaves are exactly the same in principle as those described in the flower of *Streptocarpus*. The formation of colour in leaves does however emphasise rather more spectacularly than do flowers, another aspect of the control of variation in plants, and that is patterning. Once the ability to produce pigment has been established, its distribution in various organs is then under the control of a different set of genes. Those as in *Coleus* may be capable of conditioning a bewildering array of patterns with variations both in the size and nature of the pigmented area. Each change in the pattern corresponds to some slight change in the composition of the gene itself, and this is reflected either in the location of the pigment or in the area that it covers.

One of the best-known examples of the control of patterning in the garden plants is concerned not with pigment formation but with the shape of the leaf. In *Primula sinensis* the genetics of leaf shape has been studied in great detail. There are eight genes known to be involved in the development of leaf form in this plant. These can give rise to at least 256 distinct types of leaves, each with its own shape and marginal characteristics. Of the eight genes tested, five have been known to exist in various garden varieties while the remaining three have only been found in experimental progenies. The action of five common genes when present singly gives rise to five basic leaf types as follows:

gene	leaf form
f	crimp
mp	maple
t	tongue
y	fern
o	oak

All these are recessive genes and therefore they only express themselves in the absence of their dominant counterparts. When all five are present as dominants the "type" leaf of *P. sinensis* results. Combinations of more than one gene brings about a combination of more than one pattern, and since each gene in the dominant and recessive form can condition two patterns — the normal type and the altered pattern, combinations of these five can produce 32 varieties differing in leaf shape. Not all the possible combinatorial forms are known, but those already described indicate clearly the way in which the processes that are directly concerned with growth and form are under the same genetic control as the plant pigments. Shape is the result of growth and of the relative speed of growth. Rapid growth at the apex or at the base produces an elongated or lanceolate growth form, whereas differential growth rates along leaf margins will produce a deeply serrate or incised leaf. Rate of growth in its turn depends on growth-promoting chemicals, and thus the control of shape in leaves as in *Primula sinensis* can be related to the control of growth-promoting chemicals by the gene. The basic gene function therefore is the same as that seen in the anthocyanins, except that with growth processes one is witnessing gene action at stages further removed from its basic function.

In any discussion on the genetic control of variation it must almost always be understood, even though a gene may not express itself in every cell, that all genes are present in all plant cells. The gene for red fruit in the tomato is present not only in the fruit but also in the green stem and in the colourless root tissues. The same is true of the flower colour and leaf shape genes described earlier. The fact that a gene is present in all cells, but only expresses itself in certain tissues, is a reflection of

the dependence of the gene on the right environment before its particular function can be fulfilled. For example, all green leaves have genes for the production of the green pigment chlorophylls but if kept in complete darkness, leaves that are potentially green and have genes for chlorophyll will fail to produce chlorophyll and will develop into white or cream-coloured organs.

There are however some exceptions in which the variation we utilize to beautify our gardens is not of this type and in which the patterning achieved is not the result of the differential timing or conditioning of gene action in different organs and environments. Some varieties of plants are so constructed that not all their tissues contain exactly the same genetic factors. These contain mixtures of more than one type of tissue — each tissue type having a slightly different gene complement. Plants of this kind are described as chimaeras; of these the best known are to be found among the genera *Bouvardia*, *Pelargonium* and *Solanum*.

Although the tissues that co-exist in chimaeras may differ in respect of any genetic factor, the types most frequently encountered are those showing differences in chlorophyll development. These are expressed as variegated forms in which the margin of the leaf is white and the central part of the lamina green as in the variegated form of *Solanum capsicastrum* and of *Bougainvillea*, or else where the margin is green and the central part white, as in the *Pelargonium* "Freak of Nature". In types where the leaf margin is devoid of chlorophyll and the central region is green, the two types of tissue — the white and the green, are so arranged that the white or chlorophyllous layer (or layers) of cells completely surrounds a central core of green tissue. Where the leaves show the reverse patterning of variegation, the orientation of the tissue is likewise reversed, the basic genetic control of cell processes in chimaeras is no different from that in any other plant, and the fact that a certain plant is a chimaera in no way alters the action of the genes in the individual cells.

The chimaerical nature of plants may be demonstrated by separating the different tissues and thereby producing plants which are pure for one or other of the layers. Such a separation frequently happens spontaneously during the growth of the chimaera. Thus one frequently finds, on plants of the variegated *S. capsicastrum* shoots with non-variegated, green leaves as well as shoots on which the leaves have no trace of chlorophyll. The different types of shoot result from the accidental inclusion in a bud, of cells of only one of the layers. The occurrence of three types of growth, variegated, normal green and white on one and the same plant is the sure diagnostic feature that a given variegated plant is a chimaera. It is a very rare event for a plant that is not a chimaera to show segregation into different types of growth on one and the same individual.

Apart from the accidental separation during growth of the coexisting tissues, it is possible to separate the central core region of a plant from the outer layers by taking root cuttings. It is a feature of the development of many roots, after the very first period of their development, that they cast off the outer layers of cells leaving only the inner core to form the entire cross-section of the root. The buds which form on old established roots consist entirely of the tissue type forming the inner core, and develop into plants which are no longer chimaeras but have the same genetic constitution in every cell. If the inner core is green then shoots raised from root cuttings will be green, while if the inner core is white, as in the form of SPIRAEA described by BATESON, the adventitious shoots developed on roots will be albino, and will die.

It has already been mentioned that all plant characters may be involved in chimaeras. The phenomenon is not confined to chlorophyll production and distribution. The variety 'Bridesmaid' of *Bouvardia*, which has pinkish flowers, gives rise from root cuttings to plants with red flowers resembling exactly the variety 'Hogarth'. Thus 'Bridesmaid' has a central core of tissue of the variety 'Hogarth', while in the overlying tissue the gene for red pigment has been changed to one conditioning pink colour. The typical red of 'Hogarth' has become masked by a skin of quite a different genetic constitution.

Similarly, root cuttings from the varieties 'Escot', 'Mrs. Gordon' and 'Pearl' of fancy and semi-double *Pelargoniums* are all known to give plants from root cuttings which differ in colour pattern and in the amount of crumpling of the petal when compared with the parent plant from which they were propagated. Plants raised from root cuttings of 'Mrs. Gordon' are very similar to, and are possibly identical with, the variety known as 'Cardiff', while those from 'Pearl', which is a white semi-double, produce flowers with well-developed bands of bright pinkish red colour.

The few aspects of the control of variation that it has been possible to describe are but a very small fragment of the information that is available on this fascinating subject. They do however serve to highlight the basic control that is exercised by the smallest unit of life — the gene, on each and every aspect of vital processes. Whatever the variation, however dazzling, spectacular, or complex it may be, its determination can be traced back to micro-chemical processes emanating from the gene on the chromosome. Sometime in the near future someone may be able to answer the questions what is a gene? This is the central problem in biology today.

REPRINT FROM A.P.S. BULLETIN #177 (June, 1965) by David L. Reath

The new book, "The Peonies" is certainly a fine text for reference and study. I've already spent many hours checking all the fine articles and was very pleased to find the permanent account of Prof. Saunders' work. It is well written and very useful to us.

Within the description of the Saunders hybrids there is mention of several hybrids which are capable of setting seed or have fertile pollen. These hybrids could well be the backbone of many future worthwhile breeding projects. We should try to locate all of these varieties which are available and get them distributed to as many of our hybridizer's gardens as possible to be more certain of preserving the variety as well as to give these plants a good workout in hybridizing. The following varieties are discussed in the chapter.

Moonrise (p. 49)	Nosegay (p. 56)
Serenade (p. 49)	Gwenda (p. 56)
Archangel (p. 49)	Daystar (p. 56)
May Lilac (p. 49)	Roselette (p. 56)
No. 4992 (p. 49)	Rushlight (p. 56)
Halcyon (p. 52)	F1 of Mloko x Macrophylla (p. 56)
Ladybird (p. 54)	Nova (p. 56)
Good Cheer (p. 54)	Picotee (p. 59)
Little Dorrit (p. 54)	No. 14400 (p. 59)
Scarlet Tanager (p. 54)	No. 14414 (p. 59)
Eclipse (p. 54)	Silver Dawn (p. 59)
Diantha (p. 54)	

SEED DISTRIBUTION - Chris Laning

Parentage of seeds sent out:

1. Roy Pehrson's description of one batch of seed he sent: "Mixture of open pollinated seeds from a number of hybrid allotetraploids. Most will be inter-fertile and pollen good. The pollens, however, if used on lacti will make mostly hollow seeds. Bee pollination perhaps best."
2. 'Roy Pehrson's Best Yellow' = Moonrise F2 x Quad F2.
3. Roy's 2nd Best Yellow = Lactiflora x Quad F2. .
4. 'Rushlight' F2 = Seedlings of 'Rushlight' which is a triple hybrid - albi x (tenui x mloko)
5. 'Roselette' F2 = same type of seeds as is #4.
6. 'Petite Renée' x 8969 - carmine pink jap x Saunders' #8969.
7. Number 12128 = (albi x macro) x officinalis (Otto Froebel)
8. 'Vista' x 'Archangel' = 'Vista' - lacti pink jap, with center that is large, made up of many yellow staminodes.
9. 'Archangel' = Saunders albi x macro, and is an F2
10. Quad F2 x 'Roselette' = just what it says.
11. 'Battle Flag' x 'Red Red Rose', F2 = plants have hybrid appearance - set seed easily and flowers are dark red - single ; also pods stay bright red until early fall.
12. Michau's lactiflora mix .
13. Michau's other seeds - their labels explain the parentage.
14. Roy's "Mauve Bomb" F2, unknown parentage.
15. Suffritocosa = tree peony seeds from Mr. Domoto of California.
16. Suffruticosa = tree peony seeds from John Simkins of Canada.
17. Other batches of seeds are of crosses that are self-explanatory, but if you have a question regarding your seeds, drop me a card and I'll answer.

Most of the seeds sent out are of open pollination; that is, not protected from stray pollen. This is not as serious as you may think since these hybrids come into bloom early in the season — before lactiflora clones are in bloom.

Persons that made this seed distribution project possible with their contribution of seeds are as follows?

Mrs. Leo Armatys

Don Hollingsworth

Roy Pehrson

Toichi Domoto

Chris Laning

Silvia Saunders

Mr. and Mrs. Goldsmith

Ed Michau

John Simkins

p.s. If seeds did not arrive in good condition, let me know. The method of packaging may not have proved adequate, though easy.

LETTER TO: Chris Laning
FROM: L.J. Dewey, 2617 Wyndham Drive, Richmond, Va. 23235
DATE: November 19, 1976

Dear Chris:

Thank you so much for your shipment of peony seeds which I received November 5. The crosses sound very interesting to me, and I am delighted to have the seeds. I was especially pleased to have some seed from Roy Pehrson (mloko x mloko and mloko x daurica). This is the first time I have had any of his seed.

The seeds from the herbaceous crosses you sent are "incubating" now, I am trying Don Hollingsworth's germination technique -- he sent me detailed directions. I have access to an environmentally controlled room where the temperature is maintained around 78°F and will try holding the seeds in damp vermiculite at this temperature initially. I'll keep you informed from time to time on the progress of the germination of those seeds.

It was a great pleasure for me to get the tree peony seeds. I assume they are from named varieties of suffruticosa. They will come in handy for a number of reasons. I am experimenting with the chemical treatment of peony seeds to see if the germination process can be speeded up. One chemical I have tried already shows some promise, but it needs further checking. In addition I want to treat T.P. seedlings with colchicine (and perhaps other chemicals) to try to induce tetraploidy. Finally, I hope to grow many of the plants to the flowering stage just to see what we can get. So you see, I have big plans for the T.P. seeds. My own T.P. seed harvest was rather meager this year.

I am still looking for T.P. species seed, especially potanini and delavayi. Smirnow sent me some seed from suffruticosa varieties (spontanea and Rock's variety) and I got some lutea Ludlowii from the University of Washington Arboretum. So you see, I have a modest beginning. Don Hollingsworth also sent me a plant of Ludlowii which he had grown from seed. It never bloomed for him, and he thought it might be worth trying to see if it would take to the Richmond climate.

Don also sent me some valuable herbaceous divisions and one other T.P. plant. He was most generous with the extras and is so willing to share his fund of information

A number of seeds from some of my crosses, which I started in late August according to your directions, are producing roots and go into the refrigerator as they get ready. Those are from herbaceous seed parents as the T.P. seeds seem to be much slower.

Again, many thanks for your generosity in sending so many seeds.

Best regards, L. J.

EDITOR (or ED.): This fellow Dewey seems to have access to facilities and equipment that we dream about. Also he knows how to use facilities. We may hear great things from his endeavor.

Hi L. J., Happy to have had the opportunity of visiting with you. I'll write soon (maybe).

-Chris

TRY FOR YELLOW

Chris Laning

P. mlokosewitschi, an herbaceous plant from the Caucasus Mountains, which has good yellow flowers, is a weak grower -- and I suppose that means not completely hardy in southern Michigan. Also, it has a very uncooperative disposition that distresses the hybridizer. Now, if the problem rests with our inability to understand its requirements, let's study new techniques. I would propose thinking in this line:

Is there a gene, or group of genes, in mloko pollen for yellow? I doubt it! And probably not in any chromosome of the ovum either. We have thought of our problem as a matter of dealing with recessives, but if the yellow is not a product of some gene, then what?

The yellow could be due to the workings of the cytoplasm, so therefore not present in any mloko hybrid where mloko is the pollen parent. If this is true we will have to take into account cytoplasm as a factor in our hybridizing. This, then, would mean mloko could be only used as a seed parent if yellow flowers is the goal.

'**Nosegay**' is an F2 of mloko x *tenuifolia*. Will backcrossing onto mloko present us with yellow flowers? (if possible to cross)

Would *P. daurica* pollen onto mloko give yellow? — or a step in that direction?

From whence comes the cream color of '**Moonrise**' which is *lactiflora* x *lobata* (Perry) — color drop-out. See June '76 issue of *Paeonia*. And of '**Prairie Moon**' which comes from '**Laura Magnuson**' x '**Archangel**'. '**Laura Magnuson**' = *lacti* x *lobata* (Perry). '**Archangel**' = *lacti* x *macrophylla*. Again, color drop-out. Note also that in both cases the flower will fade to white, not so with the mloko yellow. Roy's Best Yellow is '**Moonrise**' F2 x Quad F2. This one too fades to white.

'**Claire de Lune**' is another matter — it comes from *lactiflora* x mloko. Its flowers fade to white. Is this another case of color-drop-out? Yes!, Could its pollen back-crossed onto mloko give true yellow flowers? This we don't know. But if a back cross of this type would be successful, there is a good possibility that any hybrid with color drop-out would give similar results.

Note: Not any of those thoughts have been borne out experimentally, so help is needed from you for verification,

Following are some suggestions to assist in your thinking on this matter of cytoplasm.

In "THE PEONIES, page 56: "Oddly enough, the colors in the first generation, whichever way the cross was made, derived entirely from the Tenui side of the family: never a tea-rose or an ivory, to say nothing of a yellow; but instead, etc."

In the same book (page 50), "Professor Saunders early noted that a cross usually gives different results when made in reverse. It was found that when a flower of macro was crossed by pollen of an albiflora (presumably imported from the south, in late May) there is a strong tendency to doubleness. And another difference appears: the cross in this direction takes very badly: "1929: 27 crosses, 14 seeds; average .5 seeds per cross." Note by Chris: Is the gene for doubleness only on the pollen parent?

Same book - page 116 - "The frequent tendency of seedling peonies to resemble their maternal parents more than the paternal may well be due to the influence of cytoplasmic factors, for while both parents contribute equally of the nuclear elements and units of heredity, the cytoplasm of the new organism is derived only from the female parent to the extent that those little understood factors supplement the influences of the genes, the maternal influence becomes apparent. Important though they obviously are, there is reason to believe that genes are not the sole architects of many plant phenotypes."

Hey team! are you still with me? O.K. then, I shall proceed.

We would, like to see a dominant gene for yellow on a chromosome of an herbaceous peony plant, and mloko for this may not be the route to take. In that case, we are left with the option of borrowing from the lutea or lutea hybrid. This has been done for us with the Itoh hybrids. Our problem doesn't end here, however, seeing that the plants produce neither seed nor pollen apparently. Repeating this extremely difficult cross and obtaining similar results still will not give us the pleasure of mixing red and yellow to get orange.

Any comments you have on this subject could be put in a future issue of Paeonia. Let me hear from you!

This is a letter from C. Graham Jones
November 14, 1976
"Redgarth", the Pioco
Churchdown, Gloucester
ENGLAND GL3-2EX

Dear Chris,

Many thanks for your two letters, one containing seed, which arrived in good condition. All these seeds are in a mixture of moist peat and vermiculite and am looking forward to some growth within the next 10 days. I have enclosed a selection of all the species seed I have at the moment, some you will see are in very short supply, but hope next autumn to obtain further supplies. My big problem now is, you may have heard, the Head Gardener at Highdown, where these seeds come from died in August, so the only way I will be able to identify the plants will be when they are in flower as there are very few labeled.

Don't bother about payment as I am sure with the service I have received in the past and what I may request in the future will more than outweigh the postage.

The weather here has settled for a few days, after 2 months of heavy rain, which has made the ground unworkable, but with slight night frosts, 2°, we are having short but sunny days.

Yours sincerely,
"Cliff"

ED: their reservoirs should be filling up .-- with all the rain!

ARTICLE FROM: J. ROYAL HORTICULTURAL SOCIETY, Vol. 84 (1959)9 PP 326-328
A NEW SPECIES OF PAEONY

Paeonia steriana

H. R. Fletcher

On July 21, 1938, Mr. Frank Ludlow and Dr. George Taylor were collecting in the Tsangpo Valley in the Kongbo Province of South-East Tibet. Near Gyala, under the dense shade of QUERCUS ILEX forest, they stopped for a wayside lunch and soon realized that they were sitting on a fruiting paeony. The fruits were green and immature and although flowers were not to be seen, the natives affirmed that these were white. Two months later, when Ludlow and Taylor returned to collect mature fruits, they found that all the seeds had been shed.

Nine years later, on April 18, 1947, Mr. Ludlow and Col. H. H. Elliot, at a place called Tamnyen, found the plant again, just coming into flower, and a week later, April 24, they gathered beautiful flowering specimens at the spot where Ludlow and Taylor had found it originally in 1938. As the natives had affirmed, the flowers were white. Finally, at Tamnyon, on August 5, 1947, Ludlow and Elliot collected mature indigo-blue seeds from the bright red capsules.

Although the collectors had stated in their field notes that the paeony reminded them of the beautiful white-flowered *P. emodi* Wall, of Kashmir, yet the flowering specimens (Ludlow, Sherriff and Elliot 13543), in spite of their white flowers, were identified with the rose-flowered *P. mairei*, a species described by Leveille in 1915 from material collected by Marie at So-chan in Yunnan, but which also is present in Szechwan, where Pere Farges gathered it near Tchen-Kovu-Tio, and Wilson near Tatsionlu. However, when the white-flowered paeony became established in cultivation (raised from seeds of Ludlow, Sherriff and Elliot 14231) in the garden of Major and Mrs. Knox Finlay, Keillour Castle, Methven, Perth, and in the Royal Botanic Garden, Edinburgh, and probably elsewhere, and when the cultivated and wild materials were studied together, it was obvious that the Kongbo plant was neither *P. mairei* nor *P. emodi*, but was in fact a species new to science which it pleases me to name in honour of Sir Frederick C. Stern, who has not only monographed the genus but who for many years has successfully cultivated a great number of Paeony species and raised some splendid hybrids.

PAEONIA STERNIANA = A perennial herb with glabrous stems 30-90 cm. high. Leaves alternate, biternate, including the petiole up to 30 cm. long; leaflets glabrous deeply cut into many narrow elliptic or narrow oblong-elliptic acuminate or acute segments up to 10 cm. long, and 2 cm. broad, dark green above, glaucous below. Flowers solitary up to 8 cm. across. Sepals 4, the exterior lanceolate, foliaceous, longer than the petals, the interior ovate, apiculate up to 105 cm. long and broad. Petals white, obovate up to 3.5 cm. long, 2 cm. broad, thin and papery. Stamens with white filaments and yellow anthers. Carpels 3-4, glabrous, pale green. Follicles scarlet when mature, 2.5 cm. long, 1 cm. broad, seed indigo-blue.

S.E. Tibet, Kongbo, Tsangpo Valley, between Tripo and Gyala, alt. 2,830 m., (9000 ft.). Growing amongst shrubbery in stony places, like *P. emodi*, although not so big and anthers not so golden. This paeony matures its seeds very early, much earlier than *P. emodi* of Kashmir, which it superficially resembles.

P. mairei and *P. emodi* sit comfortably in Section Paeon, subsection Foliolatae F.C. Stern. In this subsection the species are all herbaceous and the lower leaves are cut into distinct leaflets all of which are entire. *P. mascula* Miller is typical of the subsection. *P. sterniana*, on the other hand, has

its leaflets very deeply lobed or toothed and is quite clearly a member of Section Paeon, subsection Dissectifoliae Stern. In this subsection its nearest of kin is *P. anomala* L., widely distributed from the Ural Mountains to Lake Baikal in Central Asia. The phenotype of the two species is very similar, though *P. sterniana* lacks the lines of very short hairs along the veins on the upper leaf surface, which are so characteristic of *P. anomala*, *P. veitchii* Lynch, which Wilson introduced from Szechwan for Veitch in 1907, also is closely allied but is at once distinguished by having two or more flowers to a stem, whereas the flowers of *P. sterniana* always are solitary.

This was a bad year for peonies where Mr. Louis Smirnow lives. Here is a portion of two of his letters:

Dear Chris October 12, 1976

You have no idea how much harm was done here by the hurricane in August — it did most damage to the most important hybrids and tree peonies. All Itohs were flooded and damaged - 'Oriental Gold' - new introductions of tree peonies also damaged. Water here was eighteen inches high and just could not get rid of it before all roots were damaged.

Would it be possible, as suggested by Father Syrov, to place an "ad" or memo in the next issue of your scholarly bulletin that I am seeking Itoh hybrids and 'Oriental Gold'. If so, it will help me greatly. Again, Chris, I will never forget your assistance.

Cordially,
Louis Smirnow

Dear Chris October 24, 1976

Thank you for your kind letter. I have only one plant of Coreacea - growing here for over two years. Since you do much more hybridizing than I do and because you are so nice a person, it is being mailed to you at once.

Thanks for writing in December issue about items I am seeking. I forgot to tell you that in the hurricane I lost several outstanding seedlings - really outstanding varieties. I did manage to save one which will be introduced next year — will call it Dr. Martin Smirnow - huge white, fullest double I have ever seen.

Will write when shipping season is over.

Louis

ED: I suppose he also needs Fan Tan.

His address is: Louis Smirnow

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Brookville, N.Y. 11545