

REQUIRED READING –

1. "The Peonies" by John C. Wister, \$3.50 from American Peony Society.  
250 Interlachen Rd., Hopkins, MN 55343
2. The Bulletins of the American Peony Society.

The PAEONIA is authorized by Miss Silvia Saunders.

Editors are Chris and Lois Laning,  
553 West F Avenue, Kalamazoo,  
Michigan, 49007.

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SEED DISTRIBUTION:

The list includes the following:

1. Lactiflora from Gus Sindt. We have a very good supply still to be distributed!
2. Suffruticosa — from Domoto of California. He was very generous again this past year!
3. 'Sable' x lobata F2
4. 'Serenade' F2
5. 'Rushlight' F3
6. Quad F2 x 'Moonrise'
7. *P. lobata* (slow to germinate)
8. 'Sanctus' x 'Rushlight' F2
9. Red-Pod Clone F2

This year I plan to try Prof. Saunders' method of germinating herbaceous seeds. He permitted his seeds to dry out during the winter and sowed them in the spring. This old method may have much to offer.

- Chris

## SOME ADVANCED GENERATION, INTERSPECIES HYBRID EFFECTS ON SEED PRODUCTION AND SEED GERMINATION PROGRESS IN PAEONIA.

by Don Hollingsworth

The general run of luck in peony hybridizing is that the changes achieved are more often merely interesting than they are spectacular. As a matter of fact, the notion of "spectacular" is ordinarily reserved for the flower. Conversely, the heredity systems through which hybridizing works come to bear upon virtually all of the developmental processes, not just those leading to the improvements that are being sought. Much of the changes which are realized concern dimensions of the plant which we have had no desire to change. Thus, in the pursuit of desired ends we may encounter a large measure of unwanted or negative results.

Often, many of the negative results get very little notice, so long as there are enough positive outcomes to support our continuing interest. For example, we seldom ever calculate the number of seeds that we do not get from a cross. One normal (wild type) peony carpel often shows evidence of 15-20 ovules. With adequate fertilization each of these might develop into a seed (and the seed into a plant). So, a flower with three normal pods might develop 40 to 60 seeds. However, this level of seed production is scarcely ever reached in crosses between species; in such crosses we expect to get few seeds. We are frequently quite satisfied to continue matings which we fully expect will yield less than one seed per flower pollinated.

Other outcomes of hybridizing that are often of little notice include the failure of some seeds to germinate, and the production of plants having a weak constitution. So long as there are at least some plants that become established, the associated losses seem minor. It is the positive results upon which a decision to continue a cross is ordinarily made.

Not all seed production deficits are so easily ignored. One of these is the production of so-called "soft" seeds, which may occur in dramatic proportions in certain crosses. This phenomenon is most often encountered when using advanced generation tetraploid hybrids that are of mixed species lineage as pollen parent, and the diploid Chinese peonies (*Paeonia lactiflora*) as pod parent. Roy Pehrson compared various peony hybrids on the basis of the seed production that might be expected when crossed with Chinese peonies (APS Bulletin No. 194, Sep. 1969). He found the excessive production of soft seeds to be characteristic of certain hybrid pollinators. '**Archangel**' and '**Moonrise**' are two familiar tetraploids which when crossed on Chinese peonies give very few viable seeds, but a great number of soft seeds. This is in contrast to the predominance of "good" seeds when a non-hybrid tetraploid such as *P. peregrina* is crossed on Chinese peonies.

A relatively smaller proportion of soft seeds is sometimes seen in other types of crosses, i.e., between certain Chinese peonies, in some of the interspecies crosses and in crosses between two tetraploid, advanced generation, hybrids. However, when the numbers are small and these occurrences are considered alone, it provokes little more than a passing curiosity. For example, the cross '**Moonrise**' x '**Archangel**' may give a relatively low rate of seed production, but there will not be such a predominance of soft seeds as is seen when these tetraploids are crossed on diploids.

The differences in the degree to which soft seeds are produced in various crosses vary from extremely high to none. Thus, there is an opportunity to logically reason what may be the causal factors. We can assume with high confidence that the soft seeds do not signify pollination failure. Fertilization must have

occurred, for if it did not we would expect no evidence of development beyond the ovule. Therefore, we can proceed with the analysis from the view that our key data has to do with failure of development. This takes us immediately to the realization that soft seeds are only one level of developmental failure. Except for those failures that are attributable to what we might term accidents of the environment, the death of a seed or death of a resulting plant anytime before flowering maturity is reached, may also be considered a developmental failure. Of course the question of how to tell the difference between death due to environmental accident and death due to developmental failure is an obvious problem for interpreting any data gathered after the seed has been planted outdoors.

Owing to my practice of germinating peony seeds indoors under controlled conditions, I have some useable data which goes beyond harvest time counts of "soft" seeds and "good" seeds. These data are included in the table below: soft seeds, death of seeds failure to develop a root and slowness of root development. Details of the rooting procedure are published elsewhere (APS Handbook of the Peony, 3) and need not be reiterated here. It should be mentioned, however, that the procedure allows one to exercise a certain amount of control over the time of rooting through manipulation of temperatures. The data in the table was collected on seeds that were withheld from rooting temperatures until about the first of December and reflect observations taken through mid-January.

Seven different matings are listed. *P. lactiflora* cv '**Gertrude Allen**' is the pod parent in each one. This is one of the most successful cultivars with difficult hybrid pollinators that I have used. The first four items are Lutea Hybrids, the Itoh cross, '**Tecumseh**' represents the Saunders Lobata of Perry (SLP) backcross. "Laning's Best" represents the advanced generation tetraploids that were implicated earlier. '**Dawn Pink**' represents a highly fertile, non-hybrid mating and serves as the control group against which to compare the other crosses.

Pollination controls which tend to assure validity of the reported crosses included the use of pollens which gave at least some germination on test. Except for the non-hybrid cross, all flowers were bagged for a couple of days against insect pollination. The '**Gertrude Allen**' flower has fully transformed stamens and normally produces no pollen.

Comparison of Seed Yield and Germination Performance of Seeds Resulting From  
Six Hybrid and One Non-Hybrid Pollinations of *Paeonia Lactiflora* cv '**Gertrude Allen**'

Pollinator <sup>1</sup>	At Harvest, 1978.				January 1979 Observations. Rooting Scores.						
	Pods	Soft	Save		Outs	Dorm	No Root	Short Root	M/L Root	Brnched	Total Germ
'Age of Gold'	5	6	52		3	18	11	17	2	1	31
'Alice Harding'	2	1	5			3		2			2
'Demetra'	8	3	2		1				2		2
'Gauguin'	2	2	5		2		1		1	2	4
'Tecumseh'	7	4	8		1	1			1	4	5
Laning's Best	11	78	4		2	1			2		2
'Dawn Pink' ( <i>P. lactiflora</i> )	4	5	175		8	18			46	121	157

<sup>1</sup>There is always a problem in interpreting hybrid cross data when the yield of seeds is low, especially so in case of the Itoh Cross. The possibility of contamination by a few grains of *Paeonia lactiflora* pollen is ever present. For this reason I have commenced recording the advancement of root growth, the early development of branched roots being thought typical of straight bred *P. lactiflora* seeds.

<sup>2</sup>The data on this cross is a little fuzzy, for three pods of the '**Tecumseh**' cross seeds were accidentally mixed with part of the '**Dawn Pink**' seeds. The un-mixed seeds of the '**Dawn Pink**' cross were handled

separately and had neither soft seeds, nor outs. Thus the values at these positions probably arise either partly or wholly from the hybrid seeds.

Explanation of selected categories: Pods = (a poor choice of terms), here used to mean the collective production of one flower. Soft = any seeds that collapse when given a firm pinch, very few have any endosperm, most are nothing but an empty seed coat. Outs = seeds that die and become invaded by mold or simply decay, usually appearing during the course of the warm incubation period. Dorm = no evidence of growth. No Root = although growth is apparent, due to bulbing and splitting in the hilum area, no root has developed; some of these are merely slow, others never make a root. Shrt Root = short root, maybe very young, but usually slow. M/L Root = medium and long roots, not yet branched. Brnched = secondary roots (branches) have appeared.

Examination of data in the table shows the following areas of differences between crosses.

1. Number of fertilizations that developed beyond the ovule stage.
2. Proportion of soft seeds produced.
3. Proportion of seeds that evidenced non-viability by rotting (Outs).
4. Slowness of root growth rate as compared to the control group.
5. Proportion of seeds which started root growth.

Generally, it is seen that soft seed production tends to be accompanied by a suppression in seed viability.

The control group, by '**Dawn Pink**', sets a high standard of performance, high even among other crosses of its type (within the species). Seed yield averaged more than 40 per flower, root germination was 90% and none of the roots is clearly slow. Even if we don't discount the Soft and Out values (see table footnote 2), the percentage of loss is very low.

Pollinations by the advanced generation tetraploid hybrid "Laning's Best" gave results that are typical of the more extreme occurrences of soft seeds production. About 95% of the seeds which developed were judged to be soft. Of the four remaining, two initiated root growth and one rotted.

Data values for the '**Tecumseh**' cross fall well within the range of other pollinators of my experience in the triploid SLP backcross. They tend to yield a moderate proportion of soft seeds and the seeds which initiate roots often complete germination successfully.

The remaining seed lots are all of the Itoh cross, *P. lactiflora* x (*P. lutea* x *P. suffruticosa*, lutea hybrids). The seed production rate obtained from the '**Age of Gold**' cross is extraordinarily high in my experience with this cross and I associate it partly with the unusually good rate of pollen germination for an F<sub>1</sub> Lutea Hybrid which was obtained when this pollen was tested. This unusual occurrence is detailed as part of an article scheduled to appear in the March 1979 Bulletin of the American Peony Society.

Although the focus of discussion is here directed mostly to differences observed by type of cross, the range of differences among the reported four pollinators of the Itoh Cross serves to remind that each pollinator is an individual and can be expected to show individual differences.

The data presented above is not in conflict in its implications with similar observations which I have made on my hybrid crosses over the past several years. All of these observations tend to support the view

that there is a suppression of seed production and seed viability which is magnified when using parent plants having a greater extent of mixed species origins. Thus I am persuaded to conclude that what we are seeing is, at least partly, a consequence of the degree to which the chromosome pairs of the hybrid parent do not precisely match in structural makeup. Elsewheres I have termed this to be "chromosome mismatches."

To do more than to hint at the manner in which chromosome mismatches may come to bear on the developmental viability of a given fertilized ovule is beyond the limits of this space. I shall try to convey it in a general way. High fertility of a plant demonstrates that the chromosome half sets which it received from its two parents are well enough matched not to cause a serious degree of failure during reduction division as its own germ cells (gametes) are produced. Not only is it producing a satisfactory proportion of functionally complete germ cells but they must also be containing a well balanced half set of the genetic information that is critical in order for a mature plant to develop. The chromosome complement of each species has its own characteristic differences from other closely related species. This is one of the ways in which the species are kept from interbreeding or forming fertile progeny in nature. While within a breeding population of a species there may exist a great deal of genetic variation among all the individuals taken together, the chromosome complement will tend to be precisely matched throughout the breeding group. Failure of this within one or more members of a group tends to define the progeny of those members out of the breeding population due to lowered fertility, unless some associated survival advantage is conferred.

In domestic breeding we work to reduce the fertility consequences of chromosome mismatches. Through the often simple expedients of controlled pollination and asexual reproduction techniques we keep lineages in existence that would have dead-ended at the next generation under natural conditions. By so doing, we have been able to eventually create what some people have called synthetic species — new, freely interbreeding groups that are not entirely like any of the parent species from which they descended. What happens is that a compatible and complete enough half set of chromosomes emerges as the functioning genome. (Unless a highly inbred strain is produced, the "functioning genome" will be only approximately identical, but it need only be approximately so for satisfactory fertility.)

During the early generations of a breeding program which involves combining two or more species, especially while we are still bringing in new chromosome sources through out-crossing, there tends to be a maximization of the potential for incomplete or unbalanced gene complements to occur in the germ cells (gametes). When a pair of unbalanced gametes that come together in fertilization happen to offset the inherent deficiencies of one another, there may be obtained a successful individual that, nevertheless, has a low potential for putting forth gametes having well balanced half sets of chromosomes.

At the tetraploid level there is twice as much genetic material available to provide the opportunity for buffering the deficiencies of the other gamete partner at fertilization. Thus when tetraploid advanced generation hybrids having a high degree of chromosome mismatches are mated together there is a better chance of reaching an off setting balance of genetic material in the fertilized ovule (zygote) than there is when mated with diploids such as the Chinese peonies.

When vital deficiencies obtain in a particular fertilization, development will fail at some point. The stage at which development will be blocked will depend on the specific deficiencies that are present. In some instances the seeds may never be developed. In others an apparently normal seed will form, as we have seen, but the deficit will show up at a later point as, for example, an outright failure or a disruption of germination timing.

The key implication of the foregoing for peony hybridists is that crosses which lead to a high incidence of developmental failures probably are also crosses that test new combinations of peony chromosomes. In some ways, these may have the greatest long term potential of any crosses that can be made. This is not to discount the potential of working with those lines in which good fertility has been already regained. Only persistence in working with a particular breeding group over time will reveal the real worth of the effort. However, the slow breeders may pay off a little better for the application of skill and patience, in the long run.

Another implication is that continued outcrossing to the more distantly related lineages will have a tendency to perpetuate chromosome mismatch problems. The best chances of finding functional genomes and restored fertility are found in breeding individuals of similar lineage. In line matings (between individuals considered to be members of the planned breeding program) we test the potential of the variability within the group as progenitors of the wanted variations. Outcrossing, on the other hand, tests only the question of what may be obtained in the next generation. Very close inbreeding has the highest potential for finding fertile genomes, and is also the quickest way to exclude in the progeny a lot of the genetic variability which is present among individuals of the breeding group taken as a whole. When inbreeding leads to something promising, great opportunity for breeding improvement has been obtained. It is the most promising avenue toward new breeding achievements in the longer term.

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Letter to: Chris Laning  
From: Roger Anderson  
Fort Atkinson, WI 53538

Date: Dec. 5, 1973

Dear Chris:

Well how was your year for hybridizing? It's probably the best year I've ever had. Made 97 different crosses (which is way too many), 66 of them gave me seed which is mostly all sprouted and in the ground. Most of my crosses were 'Good Cheer' pollen used on those tets I received from you in '75 and on lacti.

Don Hollingsworth sent me some pollen, one of which was from "Laning's Best," so I used it on lacti and have gotten just a few good seeds. My biggest surprise was 'Age of Gold'. Using Reath's #199 pollen on it, I made 35 crosses and ended up with 21 seeds. Sixteen of these have sprouted and are in the ground, 3 rotted, and the other 2 are still in damp moss. I find that I have much better luck sprouting seed in milled sphagnum moss than I do in vermiculite. What do you use?

Regards,

Roger

ED: I use vermiculite for sprouting seeds. I have tried using sphagnum moss but the seeds became moldy.

## SYNTHETIC TETRAPLOIDS

(Syn-tets)

Roy Pehrson

I don't hesitate to declare that at sometime in the future these plants and their derivatives will be used, almost to the exclusion of everything else, in peony breeding. Someone of more scholarly bent will, hopefully, use this information to write a more definitive treatment for publication in the Bulletin. In this account I will give only a "bare bones" step-by-step outline of how it works.

### Step No. 1

Gather pollen from a tetraploid species, or from any other tetraploid in the genesis of which the species *lactiflora* has played no part. Use this pollen on seed-bearing *lactis*. If seeds are obtained, the resulting seedlings will be very sterile triploids.

EXAMPLES: The Saunders' *lobata* hybrids, the Quads, etc.

### Step No. 2

Such a sterile triploid may very rarely produce a well formed self-set seed. When grown on it may very well produce a fertile tetraploid of great breeding promise. For the purpose of this account I have dubbed these "syn-tets" because of that unorthodox origination as  $F_2$  plants from triploid parents. They also behave in an odd manner when an attempt is made to backcross them to *lactis*.

EXAMPLES: '**Moonrise**', Quad  $F_2$ , '**Archangel**', '**Sanctus**', etc.

## SOME OBSERVATIONS

Thus far, whenever an attempt has been made to backcross one of these original  $F_2$ 's to *lactiflora*, the result has always been the same. Large, apparently well-filled seed pods are formed, but when these are opened at harvest time they are found to contain hollow seeds, with only an occasional good one among them. This trait does not disappear in succeeding generations, whether these result from selfing or from intercrossing. Even the use of pollen from a more conventional type of tetraploid, ('**Silver Dawn**'  $F_3$ ) did not eliminate or dilute this trait.

This peculiarity should be no obstacle. The influence of lactiflora's genes will remain constant from generation to generation in any event. Considered as a single strain, these syn-tets possess an easy growing habit which has never before been realized in any tetraploid strain or in the diploids either. Hybridizers should pay them their fullest attention.

DON'T FORGET! MAKE THE CROSS — MIKADO x GOOD CHEER  
IT'S THE CROSS OF THE CENTURY.

Take a look at the list of seeds offered for distribution in the September PAEON IA. Numbers 1, 2, 3, 4, 6, 7, 8, 9, 10, 13, 16, 17 and 19 are all "syn-tets".

That's 13 of the 19 or 2/3 of the total. If 12, 13 and 14 are eliminated from consideration because they are not hybrids at all, the proportion rises to 13 of 16 — even more impressive. I think you will agree that this little exercise illustrates in a dramatic way how hybridizers are being led, unintentionally, to the conversion of a large segment of the herbaceous peony list to the tetraploid condition. This is really a remarkable development, even though it has been completely unplanned.

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NEWS FROM OREGON  
December, 1978

I suffer from a severe problem of not being acquainted with what plant material is available — never being able to time my Eastern trips to peony season. Thus just what some of the advanced plants and flowers really look like is unknown.

One Project: is to get representative plant material so that I can work with it and observe it daily.

Second Project: is to obtain and help preserve some of the rarer Saunders hybrids. Keith and Peggy Goldsmith have really helped me here, and I was able to get 99 different varieties from them this fall (many only a small planting piece). Perhaps 20 of these I may try to propagate commercially. Dot and I are trying to get a small mail order nursery business going with peonies, hemerocallis and Jap iris, to have an interest developed when I retire from the Medical School faculty some six years hence. My Puritan upbringing (30 miles N. of Boston) is such that to do what you enjoy doing is sinful — unless there is a profit intended with at least part of it. I don't subscribe to this mentally, but it's a hard upbringing to completely dispense with. But, if I have part of my operation commercial, some other things (I'm particularly interested in breeding in fragrance in amaryllis and hemerocallis) will be forgiven. At any rate, the commercial part will not consume all my peony interests.

Lutea ludlowii blooms well here and I'm desperately trying to get some to pollinate Rocks and other suffruticosas I have started. So far Reath and Smirnow both have been unable to supply. I will be able to get pollen from the Washington Arboretum next year.

Obviously my interest in peonies is new, but I'm generally regarded as a "sticker" and hope to continue it for many years. The help you've given me with seeds and all the advice from PAEONIA will prove most useful.

To go back to interests though, I suppose the third one would be to develop or select clones that are excellent landscape prospects. Disease resistance, plant shape, foliage, length of flowering, etc. are all important to me -- as well as uniqueness of flower or color.

Fourth: to try to find all I can about the inheritance of fragrance (medicinal as well as sweet smelling ), and see if it can't be added — sundae topping perhaps — to make some of the existing varieties more appealing.

In the meantime, lunch is over and I'll put back my hat as Director of Animal Care where I'm particularly active in dog and goat research.

Have a happy holiday.  
Allan L. Rogers  
15425 SW Pleasant Hill Rd.  
Sherwood, Oregon, 97140

P. S. We have daughters in Louisville, KY and Champaign, IL. Trying to see if we could take our vacation at peony meeting time and see everything and everybody. Any chance you and Lois would be there? (ED: Yes, we plan to attend the peony show in May. )

P. P. S. If PAEONIA wants to start a list of Hard to Find Plants, I'd be glad to compile it if people would send lists of what they had. (Lactifloras, hybrids, tree peonies) I really think it important information to make available and would write it up — and keep it up to date for PAEONIA. Should we insert some sort of a questionnaire? (ED: Good idea, Al — would you draw up a questionnaire and send it to me??)

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#### Seed Characteristics and Plant Coloration Potentials

Among the early yellow peony breeding plants which I now have for pod parents there are some interesting differences in the seeds they produce. Some produce fat, round seeds that are reminiscent of those seen from the Macro Hybrids. These sometimes have very wrinkled seed coats when dry and some remain wrinkled after the seeds become fully plump during germination. The "Macro type" seeds generally have quite black seed coats. Others have seeds with more of a "top" shape, roundish but tapering some toward the hilum. These are very shiny when plump and have a silvery overcast, somewhat gunmetal blue in overall effect. Of the latter type, I currently have seeds from Moonrise F<sub>2</sub> and an advanced generation Quad that are early yellows. Of the early yellows currently represented among my germinating seeds, there are 'Roselette's Child', 'Roselette's Child' F<sub>2</sub>, 'Rushlight', an advanced generation 'Rushlight', 'Nova', and a batch of seedlings from ('Roselette's Child' F<sub>2</sub> x 'Cream Delight').

I think it is obvious that these variations in seed shape offer clues to the species sources represented, as do other attributes of the hybrid plants. We have previously discussed the season-long persistence of foliage in some Early Hybrids which is much more desirable than foliage of the midseason Hybrids that characteristically goes off shabby in midsummer. This good foliage is comparable to that of the Macro Hybrids and very likely comes from them. Chris Laning has pointed out that the Macro Hybrids have an easily divided root system. We see that a large proportion of the Early Yellows show characteristics which point to Macro as the source.

All this suggests that Macro genetic material is quite compatible with the expression of yellow in the flowers of certain early flowering herbaceous peonies. Conversely, the white of Macro appears to override the red pigments of the *Officinalis-Peregrina-Lobata* and *Lactiflora* groups, leaving little more than a purplish blush or nothing at all of the anthocyanins, in most instances. We might expect to exchange genetic material among the Early Hybrids whites and yellows or pastel pinks without losing entirely the creamy and yellow effects among the current generation seedlings. On the other hand, if we want to bring desirable Macro qualities into hybrids also having the highly desirable red color effects that are characteristic of the mid-season Hybrids, it will probably require two or more generations to achieve the genetic recombinations that will give Macro plant qualities with the wanted red pigments.

I believe that we should expect the white of Macro to also override the yellows, at least partly, among some of the seedlings when one of the parents is free of yellow or creamy effect in the flower color. However, currently available Macro Hybrid breeding materials have been shown to have among them the ability to deliver the wanted pastel colors in their progeny. (Notably '**Archangel**' as well as some of those having yellow pigments.) Thus one can now make planned crosses with high confidence of retaining the wanted colors while seeking to refine plant and flower form characteristics.

We may be very close to establishing a highly appealing strain of early pastel flowering peonies. Such a strain should be highly marketable.

- Don Hollingsworth  
5831 N. Colrain  
Kansas City, MO 64151

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#### SUFFRUTICOSA

Tree peony propagation is a tricky proposition in colder parts of the country (as in Kalamazoo, Michigan). By following the same techniques as used in producing herbaceous seedlings, we have run into serious difficulties.

Rooting T.P. seeds indoors is a simple matter! This is done exactly as with herbaceous seeds. And this is wrong! With this method the sprouted T.P. seeds must then be planted out of doors, and this, the seeds consider to be transplanting and they don't like it! Another thing they don't like is prolonged freezing weather. Only the very strongest of seedlings will survive this treatment; alas, the strongest ones are usually the singles.

If, after one years growth you find that they need to be transplanted because they are becoming crowded — you goofed! They don't want to be transplanted! ! ! ..and most of them will die. Or maybe you'll wait 'til after the second year with the transplanting. Not more than half of the seedlings will survive. Three year olds, if given winter protection along with summer care will offer a good percentage of survival. Could we have a "tap root" problem here?

Probably Paeonians living in California, Washington, and Oregon can plant T.P. seeds directly in the open garden thereby sidestepping our problems. Mild climates and T. P.'s get along together very well.

- Chris Laning