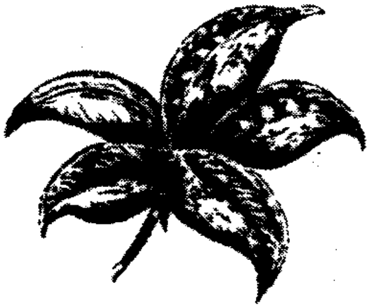


# PÆONIA

*AN INTERNATIONAL NEWSLETTER FOR PEONY HYBRIDIZERS*

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## Table of Contents:



## *MORE ON THE RECIPROCAL INTERSECTIONAL CROSS*

Donald Smith

Encouraged by my limited success with the reverse intersectional cross (see Vol. 26, No. 1), I was determined to increase my effort on this cross for 1996. I had planned to concentrate on repeating the particular cross (*Age of Gold* x *M. Wash.*) that had yielded the only plant produced thus far, but a shortage of flowers on *Age of Gold* dictated a somewhat different strategy. Fortunately, I had recently obtained a large plant of the lutea hybrid *Thunderbolt* for the express purpose of testing its fertility in the reverse cross. This plant produced 10 flowers which were all pollinated using Martha W. pollen. Six of these 10 crosses were successful, yielding 14 seeds overall. *M. W.* pollen on various other shrub (tree) peonies also produced numerous seeds. As a matter of fact, pollen from this unique plant has produced seed on nearly every woody peony on which I have used it, including several suffruticosa (Moutan) varieties. This is especially interesting considering that several p. suffruticosa pollens produced no seeds for me when used on Martha W. in the opposite cross. The viability of these various seed lots has yet to be established, but the seeds from the suffruticosa variety *Stolen Heaven* look particularly good. These seeds appear to be quite different from other tree peony seeds and more closely resemble those from the *Martha Washington* x lutea hybrid crosses. These seeds are all quite firm and fully developed and most sink in water which is unusual for reciprocal cross (RC) seeds. They are also significantly smaller and not as black in color as other tree peony and RC seeds that I have handled so far. At this point I am fairly optimistic that a few of these seeds might germinate and grow. This would be a rather significant development indeed. So stay tuned for further news. A summary of all the reciprocal crosses made during the last 3 years using *M. Wash.* pollen is given in the table below.

| Cross | No. of Crosses | No. of Seeds | Ave. Seeds/Cross | Germ. Rate (%) |
|---|---|---|---|---|
| F1 Lutea Hyb. x Martha Wash. | 44 | 33 | 0.7 | 17 |
| F2 Lutea Hyb. x Martha Wash. | 22 | 182 | 8.3 | 0 |
| A. G. Lutea Hyb. x Martha Wash. | 3 | 2 | 0.7 | ? |
| P. Suffruticosa x Martha Wash. | 4 | 25 | 6.3 | ? |
| | | | | |
| All Tree peonies x Martha Wash. | 73 | 242 | 3.3 | 0.1 |

F1 = Age of Gold, Thunderbolt, Banquet
F2 = Golden Era, A-198, Exotic Era
A. G. = Zephyrus, Nike, Leda
Suffruticosa varieties = Shintenchi, Stolen Heaven, others

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## *SPECULATIONS ON SEVERAL UNSOLVED MYSTERIES OF THE ORIENT; THE POSSIBLE ROLE OF RECIPROCAL CROSSES*

Donald Smith

Beginning around 1954 Louis Smirnow astonished the peony world with a series of remarkable discoveries from Japan. The first of these discoveries was the introduction of *Oriental Gold*, the first double yellow herbaceous peony. Then came the startling discovery of the Ito intersectional hybrids, the first known progeny from a cross between a tree peony (lutea hybrid) and a herbaceous type (lactiflora). Next came the discovery of the uniquely-colored herbaceous peony, Fan Tan. These announcements were soon followed by another extraordinary discovery of two more remarkable peony hybrids, which were introduced into the US under the names *Pink Harmony* and *Pink Symphony*. These were hailed as the progeny of the first successful crossing of a herbaceous peony with a Japanese tree peony (i.e., p. suffruticosa).

The story of the origin of the Ito hybrids is fairly well known with the exception of a few minor details (see APS Bulletin, No. 184, Mar 1967). There seems to be little question that the parentage of these hybrids is (p. lactiflora var. *Kakoden* x lutea tree peony hybrid var. *Alice Harding*). This conclusion is supported by the fact that very similar hybrids have been produced from similar crosses made by a number of hybridizers in the US. Consequently, there will be no further discussion of these hybrids here.

Unfortunately, however, much less is known about the origins of the other hybrids mentioned above. Therefore, each of these unique plants will be discussed separately below. I will begin with a discussion of the intersectional hybrids *Pink Harmony* and *Pink Symphony* since we have at least some information concerning their parentage.

## Pink Harmony and Pink Symphony

These two plants were produced in Japan and introduced into the US sometime prior to 1972 by Louis Smirnow of Brookville, New York. They were reported to be the product of crossing a herbaceous peony with a Japanese tree peony (suffruticosa). A cross that, prior to this announcement, was thought to be impossible. This was a truly remarkable discovery indeed, but was, nonetheless, quite believable, coming as it did on the heals of the introduction of the Itō hybrids. Apparently, these were not the only progeny from this cross, but were probably selected by Smirnow as the best from among a small group of similar hybrids. Unfortunately, there have been many questions concerning these two plants and after nearly 25 years, few of these questions have been answered. As a consequence, many continue to doubt whether these two intersectional hybrids ever existed at all. This, I believe, is primarily due to the fact that no one else has been able to produce similar hybrids despite many attempts over more than two decades.

First, let me address the issue of whether or not these hybrids ever existed and if they did whether they were indeed real intersectional hybrids.

The two small photographs of these varieties "published" in the Smirnow catalog remain as the only real evidence documenting the existence of these plants. However, these pictures were too small to clearly recognize characteristics that would distinguish these plants from other hybrid or ordinary lactiflora varieties. In addition, there was no other information available describing these plants that could be used to validate their identity as true intersectional hybrids. The situation was well summarized in an article by Don Hollingsworth in Pæonia (Vol. 13, No. 3, p. 2, Sep 1982) when he stated that

> "the photographs which have been published and observer statements indicate the plants have foliage which is like the Chinese peonies and not intermediate between the two species as is typical of the (Itoh) hybrids. This would be merely interesting except that both Roy Pehrson and Chris Laning have reported successful production of the hybrids using Japanese tree peony pollen. In so far as I know of Roy's and Chris' plants, their leaf form and habit is typical of the other Itoh hybrids."

This is indeed a very puzzling dilemma that has no doubt troubled many people for a very long time.

What is clear is that, if these plants existed, they are now lost, at least in the U.S. Personally, I believe that these plants existed (at least in the garden of the originator in Japan), and that Smirnow believed he had procured these plants from the originator for distribution in America. Whether the plants he photographed in Japan and later purchased ever made it to his garden in Long Island is not at all clear. I suspect that the right plants never did. It is worth noting here that it has been reported that it took three attempts (over 3 yrs.) for Smirnow to finally secure the real *Oriental Gold* from his Japanese source (APS Bulletin, No. 134, p. 31, Sep 1954). In any case it seems clear that no plants were ever distributed in the U.S. and soon after their introduction (Sept 1972) the entire supply was reported as lost (destroyed by developers in Japan).

Smirnow clearly believed that these plants were true intersectional hybrids; otherwise he would not have paid (what was probably a considerable sum) for the U.S. distribution rights for these plants. I do not question this conclusion for a couple of very good reasons that will be touched upon briefly below.

First let me say that I knew Louis Smirnow personally and he was a most honorable man. He was also a true peony expert with vast experience in collecting, growing and propagating rare species and hybrid peonies from around the world. He traveled extensively to Japan in search of rare and unusual peonies. He would not have been easily fooled into believing that ordinary lactiflora seedlings (such as those which might have resulted from a contaminated cross) were really rare (lactiflora x suffruticosa) intersectional hybrids. After all, this was the same man who had tracked down and introduced the remarkable *Oriental Gold* and the original Ito intersectional hybrids. I believe he, above all others, would have known a true benchmark peony when he saw one, and he definitely believed he had found two in *Pink Harmony* and *Pink Symphony*.

Next, I will attempt to address the issue of the origins of these plants. Although the cross responsible for these hybrids was identified, the direction of the cross was never unambiguously stated (see for example the article in APS Bulletin, Sept. 1972, p. 16 and Smirnow's catalogs from that time) and the parentage was never firmly established, at least to my satisfaction. Smirnow reported that these plants were the result of a cross between *Kakoden* and a Japanese tree peony. At different times both *Kagura Jishi* and *Nishiki no Tsuya* were mentioned (in different reports) as being the Japanese tree peony parent used in this cross. However, when writing about these plants in the literature he was never very precise concerning the direction of the cross. I am not convinced that Smirnow ever knew the true parentage of the cross that produced these plants. He may have assumed the direction of the cross based on what was known about the Ito hybrids, where *Kakoden* was clearly used as the seed parent. Despite the general confusion regarding this issue, I am convinced that Smirnow believed that the cross which produced these plants was *Kakoden* x *Kagura Jishi* (i.e., *Kagura Jishi* pollen applied to *Kakoden*). I wonder if anyone has tried to repeat this exact cross. Maybe there is something unique about *Kagura Jishi* as a pollen parent in this cross; or possibly it is *Kakoden* that has some unique property (such as unreduced gametes). In addition, it should be remembered that not all lutea hybrids produce progeny with complete flowers when used on lactiflora varieties. In fact, *Alice Harding* and *Golden Era* may be fairly unique in this regard. We should also remember that most, if not all, of the lactiflora x suffruticosa progeny produced so far have come from lactiflora seed parents with anemone and Japanese-type flowers. It may turn out that the use of these seed parents is primarily responsible for producing the incomplete flowers found on so many of these hybrids.

In recent days, I have begun to ponder the question of whether these intersectional hybrids could have come from the reverse cross (i. e., p. suffruticosa x p. lactiflora) rather than the one normally assumed? Maybe we have been trying to repeat the wrong cross, or more precisely, we may have been making the right cross, but in the wrong direction.

It is interesting to speculate about what we might expect from a reciprocal cross of this type. The Itō type intersectional hybrids exhibit intermediate foliage (and flower type) that is strongly influenced by the tree peony side of the cross. This is most likely the result of a double dose of tree peony chromosomes due to unreduced gametes from the pollen parent. If the cross were made in the reverse direction, however, and the unreduced gametes occurred again on the pollen side, then the progeny would show intermediate foliage that would lean strongly toward the herbaceous side (the result of the progeny receiving a double dose of chromosomes from the lactiflora parent). In such a case, the $F_1$ progeny would undoubtedly exhibit lactiflora-looking foliage and herbaceous plant habit with flowers that are more double (more lactiflora-like). Such hybrids might be difficult (without close examination) to distinguish from ordinary lactiflora seedlings were it not for the fact that they had originated from a tree peony seed parent. We might expect more doubleness in the flowers even if there are no unreduced gametes involved or even if the unreduced gametes occurred instead on the female side of the cross; simply due to the fact that the lactiflora variety is the pollen parent (see article on reciprocal crosses, p. 10, this issue). Obviously there are other possibilities and combinations that could occur, but at least it is possible to envision a scenario which could produce a group of hybrids that might fit the general description we have for *Pink Harmony* and *Pink Symphony*.

*Kakoden* is described as a white double with white stamens and green pistils (The Peonies, p. 79). I assume from this description that it has pollen and is therefore, fertile both ways. This being the case I would ask the following question- How can we be sure about the direction of this cross? Since we have yet to achieve the "right" result by pursuing the lactiflora x suffruticosa cross, maybe we should also try the reciprocal cross and see what it will produce. There is a good chance that we will get something different. Even if we do not get what we want (hybrids similar to P. H. and P. S.), what we do get may still be an improvement over what we have now from the opposite cross (incomplete flowers).

From my experience, crossing p. suffruticosa with p. lactiflora is much easier in the reverse direction (i. e., p. suffruticosa x p. lactiflora) than the opposite way (i. e., p. lactiflora x p. suffruticosa). By this, I mean more productive not easier to accomplish. Since suffruticosa varieties bloom well before even the earliest lactiflora varieties. it is neccessary to find an early source of lactiflora pollen. As mentioned in the previous article various *M. W.* x p. suffruticosa crosses have produced no seeds for me whatsoever whereas similar reciprocal crosses (p. suffruticosa x *M. W.*) have all produced some seed. The late L. J. Dewey once reported that he had never had any seeds from various suffruticosa pollens used on his superseeder *HP1-61*. I believe that Don

Hollingsworth has also reported similarly negative results as well concerning the use of suffruticosa pollen on lactiflora. Although a few others (Pehrson and Laning) have reported success with the lactiflora x suffruticosa cross, it is my understanding that all of the resulting hybrids have exhibited incomplete/malformed flowers on plants with more or less tree peony-like foliage. These results are clearly inconsistent with the photographs of *Pink Harmony* and *Pink Symphony* appearing in the Smirnow catalog.

**Fan Tan**

It has been reported that *Fan Tan* was originated in Japan around 1954 by a Japanese physician and is known there under the names *Aurea* and *Yokihi*. Much later, it was introduced and registered in the U.S. under the name *Fan Tan* by Louis Smirnow in 1975 (APS bulletin No. 216, Dec. 75, p. 32). Listed by Smirnow as a herbaceous hybrid in his catalog, the parentage of this rare peony still remains a mystery of the orient. Given below is the original catalog description of this plant taken from one of Smirnow's catalogs from that period.

> "The absolute uniqueness of Fan Tan warrants singling it out for special mention. Three colors blend to create a distinct, colorful, and beautiful flower. The basic hue is apricot-tan; but a yellow is suffused throughout each petal, and to this add an edging of pink. This makes Fan Tan the only herbaceous with a description that might fit a Lutea! It thus seems as botanically unique as it is aesthetically novel"

I would certainly agree that this description could easily fit any number of tree peony hybrids (lutea hybrids) available both then and today. Simply put, Fan Tan appeared to be a herbaceous plant with (lutea) hybrid tree peony-type flowers. At the time of it's US introduction, there were no other peonies with flowers of similar description. Despite the obvious similarities, however, it was apparently never suggested at the time that this plant might be the product of a cross with a lutea hybrid. The problem, I assume, was that the lutea hybrids are woody shrubs and Fan Tan was clearly herbaceous in foliage form and habit. Although the original intersectional hybrids (those of Itō and Higuri) had already been introduced in the U.S. (thus demonstrating the usefulness of the lutea hybrids as intersectional parents), these hybrids were quite different from *Fan Tan* in both flower color and foliage.

Since then, however, other peonies have been developed with flowers that would also fit this description, but which, in addition, also have (more or less) herbaceous plant habit. These are, of course, the new intersectional hybrids (p. lactiflora x p. lutea hybrids) developed by R. Anderson and others in the U.S. Many of Anderson's newer intersectionals have flowers that are suffused and/or edged with another color. Some are quite similar to many of the Saunders lutea hybrids from the "tea rose" color group such as *Marchioness* and *Apricot*. In addition, I have several genuine intersectional hybrids with foliage and plant habit that is convincingly herbaceous.

So, what do you think? Could *Fan Tan* be an intersectional hybrid rather than a herbaceous hybrid as previously believed? This suggestion must be given some consideration based on the information now available. Personally, I do not believe that this plant is a new species or a hybrid involving some unknown species. Thus, the question remains ---- Where could this uniquely lutea hybrid flower coloration have come from, if not from lutea itself or one of its hybrids? In the light of the most recent developments, we also need to consider the possibility that this peony might be the product of a reciprocal intersectional cross (such as p. lutea hybrid x p. lactiflora or maybe p. lutea hybrid x some other herbaceous species). Perhaps, this unique peony was the first reciprocal intersectional hybrid ever produced.

The Japanese are very clever and persistent people especially when it comes to hybridizing their favorite flower, the peony. Once having succeeded with the original intersectional cross (i.e., the Itō hybrids), they (others) surely would have continued their work beyond their initial breakthrough. And indeed, it would appear that they did, since there is evidence that they soon thereafter also succeeded in crossing p. suffruticosa with p. lactiflora to develop other new hybrids. It seems fairly obvious to me that they would also have at least attempted the cross in reverse. They may have even started with the reciprocal cross. The lack of much more fertile advanced generation lutea hybrids (which are now widely available) would not have been a serious barrier to success with this cross, since it appears that the $F_1$ hybrids are the most useful parents in the reciprocal case. All things considered, it seems highly likely to me that they would have produced, at least, a few reciprocal intersectional hybrids during that time as well.

I would be very interested in hearing from anyone who has ever grown this unique peony or is otherwise in a position to comment on these suggestions.

**Oriental Gold**

*Oriental Gold* is yet another of the great unsolved mysteries of the orient. It was first introduced into the U.S. by Louis Smirnow in 1954 (APS Bulletin No. 134, p. 32), as the first and only truly yellow double herbaceous peony. The flower is described as bright golden yellow, not pale yellow or cream, and is fully double. The roots are also yellow and the new shoots emerging from these roots are a unique yellow-green color which matures to a bright green. The foliage resembles lactiflora, but is somewhat smaller. This plant was originated in Japan and is undoubtedly a herbaceous hybrid. *Oriental Gold* has shown some fertility both ways and has been used successfully as a seed parent to produce the outstanding light yellow double *Goldilocks*. Unfortunately, the parentage of this unique plant remains a mystery.

Based on the lactiflora-like foliage form and the doubleness of the flowers, I believe that we can safely assume that *Oriental Gold* has one lactiflora parent. The yellow flowers and roots therefore, coming from the other (non-lactiflora) parent. Interspecies crosses where lactiflora has been the pollen parent seem to be significantly more likely to produce double-flowered progeny than when these crosses are made in the opposite direction (see article on reciprocal crosses, this issue, p. 10). Generalizing these results to the present case would suggest that it is more likely that lactiflora was the pollen parent of *Oriental Gold* rather than the seed parent. Thus, the mystery reduces to one of identifying the seed parent. This parent must be the source of the yellow flowers and roots and also the yellow-green stems. Here, I believe we have but three reasonable choices: 1) p. mlokosewitschi, 2) the newly discovered p. stevenianna (see APS Bulletin No. 293, Mar 95, p. 30) or 3) an unknown herbaceous species with bright yellow flowers and yellow roots and stems.

Were it not for the yellow roots and yellow-green stems, mlokosewitschi would be the clear and obvious choice as the pod parent of *O G.* This suggestion was first made by Betty Halas in the early 1980's (Pæonia, Vol. 13, No. 4, Dec 1982, p. 8) and cannot be entirely ruled out. Possibly, there is an unknown variety of p. mlokosewitschi or close relative with yellow roots. On the other hand, p. stevenianna is decribed as a plant similar to p. wittmanniana except that it has true yellow flowers (instead of pale yellow) and grayish-green foliage that is not glossy like p. wittmanniana. Little else is known at present regarding this "new" species. However, it should be noted that p. mlokosewitschi, p. wittmanniana, and p. wittmanniana var. macrophylla (i.e., p. macrophylla) are all closely related species that make up the wittmanniana group of the foliolatae sub-section of the section Pæon. P. stevenianna is undoubtedly also a member of this group which includes all the yellow flowered species indigenous to the Caucasus and northern Persia. Therefore, hybrids produced by crossing p. stevenianna with p. lactiflora might be expected to have certain similarities with those produced by crossing p. wittmanniana with p. lactiflora. The only known progeny of the cross p. wittmannina x p. lactiflora is the very lovely greenish yellow double *Ballerina* produed by Prof. Saunders. Betty Halas has previously pointed out the similarity of the leaf patterns of Ballerina and *Oriental Gold* (Pæonia, Vol. 14, No. 3, Sep 1983, p. 9) and suggested that they probably share a similar origin. The fully double flowers of both hybrids is another striking similarity as is the fact that both are yellow. In addition, neither plant is especially vigorous. It is also interesting to note that *Oriental Gold* 's only known offspring (*Goldilocks*) did not inherit any of the unique root characteristics of its famous parent. Possibly, these characteristics are passed along as (non-permanent) maternal effects (see article on Maternal Inheritance, this issue) and are lost after the first generation.

Taken together, these facts suggest that Oriental Gold is the likely progeny of the cross p. stevenianna x p. lactiflora or some similar cross with a closely related species. Similar to the related p. wittmannina x p. lactiflora and p. mlokosewitschi x p. lactiflora crosses, it is probably an exceedingly difficult cross.

| Hybrid Name | Suggested Probable Parentage |
|---|---|
| Pink Harmony and Pink Symphony | p. suffruticosa x p. lactiflora |
| Fan Tan | p. lutea hybrid x p. lactiflora |
| Oriental Gold | p. stevenianna x p. lactiflora |

## *MATERNAL INFLUENCES IN RECIPROCAL CROSSES*

Donald Smith

Mendel (1866) found that the products (offspring) of reciprocal crosses in peas were alike irrespective of which way the crosses were made. These results combined with those of Hertwig (that fertilization involves the union of the nuclei of sperm and egg) lead to the conclusion that the nucleus is the chief organ of heredity. This conclusion has been widely accepted since the 1880s. Since then the similarity of the products of reciprocal crosses has been confirmed in many other organisms.

However, many cases have also been found where reciprocal hybrids differ from one another and resemble their respective maternal parents in some phenotypic character. When these differences do occur, they can be attributed to the effects of maternal influences. Such phenomena are most commonly found in reciprocal hybrids between species. Maternal influences can be classified into two broad categories; Maternal effects and Maternal inheritance. In either case, these terms refer to inherited traits that are transmitted by factors outside of the nucleus on the female side only. Therefore, some have also referred to this type of inheritance as extra-nuclear inheritance.

Many authors[1,2,3,4,5,6,7] have written on the subjects of maternal influence and inheritance, however most of what follows here was taken from Verne Grant's fine book "Genetics of Flowering Plants" (Chapter 12, Pg. 210-227).

In the vast majority of sexual organisms, fertilization entails the union of two morphologically differentiated gametes, sperm and egg. When the two parents have the same ploidy level, these dissimilar gametes carry the same amount of nuclear genetic material but different quantities of cytoplasm. Consequently, the amount of chromosomal material contributed to the zygote by the male and female parents is the same or nearly so; but the female parent contributes in addition a large amount of cytoplasm to the zygote, whereas the male parent contributes little or none.

As mentioned above, there are two main types of maternal influences 1) Maternal effects and 2) Maternal inheritance.

In the first type, the nuclear genotype of the mother determines certain conditions in the cytoplasm of the eggs, and thereby predetermines some particular trait in the hybrid offspring, irrespective of the genes contributed by the father. In such cases the cytoplasmically determined characteristics are non-permanent and only persist for one or two generations.

In the second type, we have true maternal inheritance. In this case, inherited characteristics are not transmitted in the usual manner by chromosomal genes located the nuclei of the sperm and egg, but are instead transmitted (from generation to generation) by genes existing outside of the nucleus in the cytoplasm of the female parent. Thus, this type of inheritance is also often referred to as non-chromosomal or cytoplasmic inheritance. These cytoplasmic genes have been identified with certain particular cell organelles, the plastids (chloroplasts) and mitochondria, and consequently they have also been called "organelle" genes. These genes are permanent components of the cytoplasm and the traits determined by them persist indefinitely through successive generations. Cytoplasmic inheritance has been established in various groups of animals, plants, fungi, and protistans.

The classic investigations of Michaelis (1954) were the first to firmly establish the existence of "invisible" cytoplasmic genes from the results of breeding experiments with Epilobium. Michaelis found striking reciprocal differences in the first-generation hybrids derived from crossing *Epilobium hirsutum* and *E. luteum.* The hybrids of *E. luteum x hirsutum* had reclining branches, broad green leaves, large flower petals (10.7 mm long by 9.2 mm wide), and normally developed anthers, which produced 15-20% good pollen. By contrast, the $F_1$s of the reverse cross (*E. hirsutum x luteum*) had erect pyramidal branches, narrow yellow-mottled leaves, small flower petals (4.6 mm long by 3.4 mm wide), and abortive and sterile anthers. In general, the products of crossing *hirsutum x luteum* showed inhibited growth in different parts of the plant, as compared with the more normal progeny of the reciprocal cross, *luteum x hirsutum* (Michaelis, 1954). By producing and comparing backcross progeny through numerous generations (as many as 24 generations in one direction), Michaelis was able to show that the observed phenotypic character differences were transmitted from generation to generation through the cytoplasm.

Michaelis also recognized that cytoplasmic genes do not act completely independent of chromosomal genes and that cytoplasmic genes can be affected by chromosomal genes, and vice versa. Although cytoplasmic genes can transmit a definite character, more often they simple modify the action of the chromosomal genes. Cytoplasm and nucleus form an integrated system within any given race. The normal balance between the two components is upset in hybrids and may lead to some altered state course of development (Michaelis, 1950,1954)

There are likely to be more noticeable reciprocal differences (see next article) when the parents being crossed do not have the same number of chromosomes (i.e., are not at the same ploidy level). Presumably, the parent with the greater number of chromosomes will also carry a larger number of cytoplasmic genes due to an increased amount of cytoplasm (from a larger egg cell). This being the case, more genetic material will be transmitted to the progeny when the plant with the higher ploidy level is used as the seed parent than the other way around.

It may not always be easy to separate the effects of maternal influences from other effects which cause reciprocal differences. For example, the whole situation is much more complicated in reciprocal crosses where unreduced gametes are involved. In such cases, important reciprocal differences can occur that are unrelated to maternal influences or cytoplasmic genes. It is fairly common for plants to produce unreduced gametes on one side only (i.e., only on the pollen side or only on the female side). Reciprocal crosses involving such a parent effectively become different crosses in each direction. For example, a reciprocal cross where one parent produces unreduced pollen (but not unreduced egg cells) is effectively a 2n x 4n cross in one direction, but a normal 2n x 2n cross in the opposite direction. Such crosses would produce triploid progeny in the one direction and diploid offspring in the other. Clearly, these two sets of hybrid offspring would exhibit considerable differences. However, these differences would be due predominately to the large difference in the number of chromosomal genes between the two sets of hybrids and not to any maternal influences.

It is also possible for both parents in a cross to produce unreduced pollen (or unreduced eggs). In this case the reciprocal sets of offspring might be expected to show even greater differences than in the previous example. Once again these reciprocal differences would be mostly unrelated to maternal effects. Each set of triploid progeny would be dominated by a different parent as a result of the double dose of chromosomes from the male side of the cross in both directions. Many other combinations that would likewise result in large reciprocal differences are, of course, also possible. Although these examples are unrelated to maternal inheritance, they provide strong additional rational for pursuing as many crosses as possible in both directions.

In addition, there are many examples of plants that are known to produce unreduced gametes on both sides. Reciprocal crosses involving just one parent of this type would be similar to a normal crossing of a diploid with a tetraploid. In this case the unreduced gametes would stay with the same parent and thus, would switch from the male side of the cross to the female side with a change in the direction of the cross. As a result, both sets of progeny would be dominated by the same parent and we would expect to see less obvious reciprocal differences that are once again caused by maternal influences alone.

However, it should be mentioned that, except for rare cases, only a small percentage of the total gametes produced in these cases are unreduced. Consequently, in many cases the resulting sets of reciprocal progeny will be of mixed types with a high percentage of the offspring being produced by normal (reduced) gametes. In other cases however, the unreduced gametes could be the only ones to result in viable seeds/progeny and thus nearly all of the offspring would be of one type. I raise these issues to emphasize an important point that is relevant to several popular peony crosses including the intersectional crosses. The point is that unless we understand why a certain cross has been successful (for example, were unreduced gametes responsible for the results or not), it is very difficult, if not impossible, to even guess what the reverse cross might produce. Fortunately, this lack of knowledge does not prevent us from making the cross to find out what it will produce. However, we should be prepared for some interesting surprises.

When analyzing the results of prior crosses and using these results in planning for subsequent crosses, we should always try to account for the possible influence of maternal inheritance. In addition, we should also consider the possible role of unreduced gametes on the products of these crosses. Taken together these two effects provide clear justification for trying every cross in both directions whenever possible. Try also to remember that, the wider the cross we are making the more likely it is that we will see noticeable differences in the reciprocal progeny. Therefore, we should take every opportunity to make every cross in the both directions and be ready for some unexpected and interesting results.

To help with the process of including the possible effects of maternal inheritance in the planning of your future hybridizing programs, I have assembled a short list of some of the most common phenotypic characteristics that are sometimes partially or mostly under the control of cytoplasmic genes.

**Phenotypic Characteristics Which May be Controlled or Partially Controlled by Cytoplasmic Genes**

1. Foliage color (especially variegation effects)
2. Leaf shape
3. Flower size and form
4. Male fertility
   a) Anther development
   b) Pollen fertility
5. Plant growth habit
6. Heterotic effects (Heterosis; i.e., hybrid vigor)

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## *RECIPROCAL CROSSES; OBSERVATIONS AND PATTERNS*

Donal Smith

Professor Saunders has been reported as saying that "a given cross usually yields entirely different hybrids when made in the opposite way" (The Peonies, J. Wister, p. 44). As an example of these differences, he pointed-out that in the macrophylla x lactiflora cross there was a "strong tendency to doubleness" whereas the cross in reverse (lactiflora x macrophylla) gave only single-flowered progeny (The Peonies, J. Wister, p. 50). Such differences seem especially common when the species that are being hybridized do not have the same number of chromosomes. Saunders made a number of different diploid - tetraploid crosses in both directions. Of particular interest amoug these crosses are those with lactiflora as one of the parents. When studing the results of such crosses it is interesting to look for systematic patterns which might be evident in the data. After a careful study of the results of four such diploid - tetraploid crosses, I believe that one can draw a couple of general conclusions based on on what appeares to be two systematic patterns evident in the results. These conclusions are: 1. The crosses take better when the diploid species (lactiflora) is the seed parent and 2. The crosses produce a much higher percentage of double-flowered progeny when the diploid species (lactiflora) is the pollen parent. A summary of the data supporting these conclusions are given in table below.

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| Lactiflora x Officinalis (2n x 4n) | Officinalis x Lactiflora (4n x 2n) |
| Takes fairly well (~6 s/c) | Somewhat more difficult (~4 s/c) |
| Mostly single progeny | High percentage of dble-SD progeny |
| Lactiflora x Lobata (2n x 4n) | Lobata x Lactiflora (4n x 2n) |
| Takes extremely well (~17 s/c) | Probably more difficult |
| Mostly single progeny | 1 of 2 named progeny-double |
| Lactiflora x Macro (2n x 4n) | Macro x Lactiflora (4n x 2n) |
| Takes fairly well (~3 s/c) | Takes poorly (~0.5 s/c) |
| Nearly all single progeny | Strong tendency for doubleness |
| Lactiflora x Wittmanniana (2n x 4n) | Wittmaniana x Lactiflora (4n x 2n) |
| Overall results poor (many seeds-poor germ.) | Takes very poorly (hardly at all) |
| Progeny all singles | Only known progeny-Double (*Ballerina*) |