PAEONIA

Volume 14, No. 2 June, 1983

REQUIRED READING:

1. "The Peonies" by John C. Wister, $3.50 from American Peony Society, 250 Interlachen Rd., Hopkins, MN 55343
2. Bulletins of the American Peony Society.
3. History of the Peonies and their Originations.
4. The Best of 75 Years; 3 & 4 ed. by Greta Kessenich, and available from the American Peony Society.

Editors are Chris and Lois Laning,
553 West F Avenue,
Kalamazoo, Michigan, 49007.
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LETTER FROM: Ben Gilbertson, Kindred, North Dakota

Reading the article by Ms. Betty Halas in the March Newsletter brought back memories of the twenty or more years that I struggled with Mloko in my hybridizing of peonies with no success in producing a worthwhile hybrid of any kind, both ways. I got several offspring from using Tenuifolia Rubra Plena as a seed parent and Mloko pollen, which was always produced in abundance, but did not ever produce seed on lactiflora. I also got several plants from the single Tenuifolia on Mloko, but none worth keeping.

I was, however, successful in producing several crosses of both Tenuifolia and Lactiflora on the peony '**Claire de Lune**', which was a cross of Lactiflora x Mloko. '**M. Jules Elie**' x Mloko were the parents of '**Claire de Lune**' and seems like a very normal diploid. Now Tenuifolia R. P. has never set seed for me from Lactiflora pollen. I could never get a seed from Mloko pollen on '**Claire de Lune**'. What this all means, I don't know.

I also had several mature plants of '**Oriental Gold**' at that time and used Mloko pollen lavishly on '**Oriental Gold**' many times, but never produced a seed.

I believe Dr. Saunders made a number of Tenuifolia x Mloko crosses and reverse crosses and I grew many of them for many years. All were single and I doubt if any of them are in the trade today.

It will be of great interest if someone will go ahead and make some more chromosome counts and learn for sure where Mloko belongs; also '**Oriental Gold**'.

LETTER FROM: L. J. Dewey, 2617 Wyndham Drive, Richmond, Virginia, 23235

DATE: February 25, 1983

Dear Chris and Lois,

I am enclosing a copy of a paper (Johnston, S. A., and Hanneman, R.E., Jr., Science 217, 446-8 (1982) which I found rather thought provoking. In this paper the authors present further evidence supporting their "endosperm balance number" (EBN) hypothesis which they had proposed in 1980 in an earlier paper (cited as reference 2 in the present paper). As the authors point out the endosperm in seeds of angiosperms from crosses between diploids (2x x 2x) is triploid (3x) (maternal : paternal chromosome ratio - 2:1). They further point out that in almost all angiosperms (which include the peonies) the survival of the embryo is dependent on the normal development of the endosperm. The 2:1 chromosome ratio rule for the endosperm is applicable to most intraspecific and many interspecific crosses, but there are also many interspecific and intraspecific-interploidy crosses whose endosperm development does not conform to this rule. The EBN hypothesis was proposed to help explain these exceptions to the 2:1chromosome ratio rule. In this hypothesis the genome of each species is assigned an "effective ploidy" (EBN) with respect to endosperm function by crossing to a species used as a standard. Then it is the EBN's which must be in a 2:1 maternal: paternal ratio for normal endosperm development and not necessarily the ploidies. I have tried to summarize the basis for the EBN hypothesis in the above discussion but for more detail the copy of the original paper can be consulted.

In peony seeds the endosperm is a major tissue and the embryo is very small. Therefore, embryo survival in peonies is very dependent on the proper functioning of the endosperm during seed germination. The frequent occurrence of hollow seeds, which I find particularly with interspecies crosses of tree peonies, may in many cases be the result of the failure of the endosperm to develop properly. Perhaps some of the peony seeds, especially from interspecific crosses, which are firm and appear normal but fail to germinate, have defective endosperms. A defective embryo could also be a cause for germination failure.

If we accept defective endosperms as the cause for the failure of many peony seeds to germinate, what can we do to correct the problem? One answer is to culture the embryos in vitro, thus eliminating the need for the endosperm. However, this is not a practical solution for most hybridizers since few of them will be equipped to use this technique.

Another approach may be provided by the EBN hypothesis presented in the Johnston and Hanneman paper. If this phenomenon is operating in peonies, we might be able to produce more viable seeds by the proper manipulation of our interspecies crosses. I personally do not have enough T. P. breeding data to test this hypothesis for Paeonia, but could it be that there is enough herbaceous peony breeding data available to make a start? What we would need to know is which species crosses take well and which do not. From a comparison of this data, we might be able to assign EBN's to the individual species. These EBN's could then serve as guides for making profitable crosses or for making "bridging" crosses on the way to difficult or impossible crosses. If nothing else, thinking about this problem may help keep us mentally alert while we are waiting for the peonies to come up.

L. J. Dewy

Manipulations of Endosperm Balance Number Overcome Crossing Barriers Between Diploid Solanum Species

Johnston, S. A., and Hanneman, R.E., Jr., Science 217, 446-8 (1982)

Abstract. *Abortion of the hybrid endosperm is the basis for the inability to hybridize many angiosperm species. This has made it nearly impossible to incorporate the valuable characteristics from several wild, diploid Solanum species into the cultivated potato Solanum tuberosum. But some wild species have "endosperm balance numbers" different from those of most Solanum diploid species, and these numbers or "effective ploidies" can be manipulated to create new hybrids.*

Endosperm, a tissue peculiar to angiosperms, is formed by the fertilization of the central cell of the embryo sac by a sperm identical to the one which fertilizes the egg. The endosperm is triploid (3x) in crosses between diploids (2x x 2x) since it receives two sets of maternal chromosomes and one set of paternal chromosomes. After fertilization, the endosperm grows rapidly, becoming the nutritive tissue for the embryo. The nature of the endosperm ranges from an ephemeral tissue, as in bean, to a major tissue in the mature seed, as in corn. However, in almost all angiosperms the survival of the embryo is dependent on the normal development of the endosperm (1). Therefore, endosperm is important not only as the major food stuff of man and his livestock, but also because its normal development is necessary to support the development of a viable embryo, thus placing a restraint on our ability to genetically improve crops through sexual hybridization. This limitation is especially important in efforts to introduce into cultivated lines valuable characteristics from wild and exotic germplasm.

There are several types of endosperm dysfunction which prevent crossing (1). One type is evident in intraspecific, interploidy crosses. For example, crosses between a diploid and its colchicine-induced tetraploid form generally fail because the endosperm aborts. The cause of this type of dysfunction has been a source of experimentation and debate for over 50 years (2). Lin (3) clarified the problem by demonstrating that in corn a 2:1 ratio of maternal:paternal chromosomes is necessary for normal endosperm development. In a 2x x 4x cross the maternal:paternal chromosome ratio in the endosperm would be 2:2 and in a 4x x 2x cross, 4:1.

The 2:1 ratio rule is applicable to most intraspecific and many interspecific crosses. However, there are many interspecific crosses whose endosperm development does not conform to the 2:1 ratio rule (2). For example, 4x (2n = 4x = 48) Solanum acaule yields aborted seed when crossed with the cultivated potato, 4x S. tuberosum Group Tuberosum. Yet, S. acaule crosses readily with 2x (2n = 2x = 24) haploids extracted from Gp. Tuberosum, producing seeds with normally developed endosperm (4). In the 4x S. acaule x 4x Gp. Tuberosum cross, the maternal:paternal ploidy ratio in the endosperm is 4:2 (= 2:1), yet the endosperm aborts, while it develops normally in the 4x S. acaule x 2x Gp. Tuberosum haploid cross where the maternal:paternal ploidy ratio is 4:1.

An "endosperm balance number" (EBN) hypothesis has been proposed (2) in order to establish a single unifying concept concerning endosperm function in intraspecific-interploidy and interspecific crosses. In this hypothesis the genome of each species is assigned an "effective ploidy" (or EBN) with respect to endosperm function by crossing to a species used as a standard. It is the EBN's which must be in a 2:1 maternal:paternal ratio (not necessarily the ploidies) for normal endosperm development. The consistency of this hypothesis has been demonstrated (5).

A logical extension of the EBN hypothesis is that EBN differences could act as incompatibility barriers between diploid species. We present evidence, from a simple crossing experiment, that such barriers do exist between diploid Solanum species and that manipulation of the EBN ratios in the endosperm can overcome these incompatibilities to produce new and potentially useful interspecific hybrids.

Most of the wild and cultivated dipioid species in the subsection Potatoe are intercrossable (6). However, there are several species and species groups (series) which seem to be strongly isolated from the majority of diploid species. Representatives of some of these isolated species were used to test the applicability of the EBN concept.

The Mexican diploid S. cardiophyllum was used as a representative of the Series Pinnatisecta. There has long been an interest in using the disease resistance of this and the related Series Bulbocastana in potato improvement (7). However, there has been very little success in crossing S. cardiophyllum and related species with cultivated diploids or other "bridge" species that could in turn be crossed with cultivated diploids (8).

The closely related diploids, S.fernandezianum and S. brevidens, are in the Series Etuberosa, which is one of the two series in subsection Potatoe that do not bear tubers (6). The species in this series have extreme resistance to frost (9) and leaf roll virus (10). Interestingly, the only substantiated successful interseries cross involving an Etuberosa species was with a Series Pinnatisecta species (11). This suggests that, even though the species in these two series are geographically and evolutionarily widely separated (6), the same mechanism may underlie their isolation from other diploids.

Diploid S. commersonii is considered to be closely related to and is assigned to the same series, Commersoniana, as S. chacoense (6) which crosses readily with most diploids. However, there have been no substantiated successful crosses of 2x S. commersonii with S. chacoense or other diploids.

We performed interspecific crosses using standard techniques in the crossing and identification of hybrids (Table 1). Both S. chacoense and S. verrucosum had been assigned EBN's of 2 in previous experiments (5) and were used as standards in the crosses we report. From the results of crosses 1, 2, 3, and 4 (Table 1) it is clear that S. curdiophyllitm crossed with 2EBN diploids only when it contributed two genomes as a male, not the usual single one, either in the artificially produced 4x form (cross 3) or through the functioning of 2n (= 2x) pollen (cross 4); 2n pollen is pollen which through the functioning of 2n (= 2x) polic ploidy (2n) rather than the normal reduced ploidy (n) of the gamete. Therefore, S. caerdiophyllum must be assigned an EBN of 1. This demonstrates that effective ploidy (EBN) differences can function as a barrier to hybridization between diploid species.

Crosses 5 and 6 (Table 1) indicate that the non-tuber-bearing species S.fernandezianum can also be assigned an EBN of 1 (12). Crosses 7,8, and 9 demonstrate that S. commersonii is also 1EBN. This is especially remarkable because S. commersonii is sympatric and considered closely related to 2x (2EBN) S. chacoense (6).

To demonstrate the potential usefulness of the EBN concept we applied the knowledge of the EBN assignments stated above to create a new hybrid. Diploid (2n = 2x = 24) S. brevidens is a non-tuber-bearing species of Series Etuberosa which crosses readily with S.fernandezianum; therefore, it should also be 1EBN. In crosses of 2x (1EBN) S. brevidens x 2x (2EBN) S. chacoense, the hybrid seeds were abortive and the embryos could not be rescued by embryo culture (cross 10, Table 1). However, when colchicine-induced 4x (2 EBN) S. brevidens was crossed with 2x (2EBN) S. chacoense the seeds were much better developed (cross 11, Table 1). Without special treatment, one hybrid seed germinated, producing a vigorous plant that was clearly hybrid (12) (Fig. 1). Since the hybrid seeds did not have completely normal endosperm development in the 4x (2EBN) S. brevidens x 2x (2EBN) S. chacoense cross, either the EBN assigned S, brevidens is not precisely 1 or there are other factors involved in endosperm development. Employing a meiotic mutant of 2x (1EBN) S. commersonii, which produces 2n pollen and therefore delivers 2EBN to the egg and central cell, we have also produced hybrids between 2x (1EBN) S. commersonii and 2x (2EBN) S. chacoense.

We have demonstrated that effective ploidy (EBN) barriers exist between diploid Solanum species and that, with knowledge of EBN's, ploidies can be manipulated (13) to produce new and potentially useful hybrids. Since the EBN concept is probably applicable to many other angiosperm genera (2), it could be employed to break crossing barriers between other crops and their wild relatives.

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Table 1. Interspecific crosses which establish that four dipioid Solanum species have an endosperm balance number (EBN) of 1. Crosses were made on cut stems in a greenhouse, or on intact plants grown in an insect-proof screenhouse. Seeds were extracted from the fruits 5 months after pollination, treated with gibberellic acid (1500 parts per million), and grown in a greenhouse. Six to 15 plants from each cross were grown to maturity, except for cross 11. Hybridity was established by morphological comparisons, and in crosses 3.4, and 11 triploidy (2n = 3x = 36) was also diagnostic. Chromosome counts were done on root-tip and pollen mother cells. In cross 6, hybridity was confirmed by an irregular meiosis, averaging only 7.9 bivalents per pollen mother cell. All plants were obtained from the Inter-Regional Potato Introduction Station, Sturgeon Bay, Wisconsin.

Experiment number	Cross *		Pollinations (No.)	Fruit (No.)	Avg # of seeds per fruit.	Condition of endosperm	Ploidy of offspring	Endosperm maternal: paternal ratio	
								Ploidy	EBN
1	2x (2EBN) S. verrucosum	x 2x S. cardiophyllum	7	6	34	Abortive		2:01	2:1/2
2	4x S. cardiophyllum	x 2x S. cardiophyllum	5	3	41	Abortive		4:01	2:1/2
3	2x (2EBN) S. verrucosum	x 4x S. cardiophyllum	17	9	27	Good	3x	2:02	2:01
4	2x (2EBN) S. chacoense	x 2x S. cardiophyllum	4	4	38	Good	3x	2:02	2:01
5	2x S. fernandezianum	2x (2EBN) S. chacoense	8	8	106	Very abortive		2:01	1:01
6	2x S. fernandezianum	x 2x S. cardiophyllum	1	1	60	Poor to good	2x	2:01	1:1/2
7	2x S. commersonii	2x (2EBN) S. chacoense	12	9	26	Abortive		2:01	1:01
8	2x S. commersonii	x 4x S. cardiophyllum	10	10	25	Abortive		2:02	1:01
9	2x S. commersonii	x 2x S. cardiophyllum	21	14	17	Good	2x	2:01	1:1/2
10	2x S. brevidens	2x (2EBN) S. chacoense	5	4	75	Abortive		2:01	1:01
11	4x S. brevidens	2x (2EBN) S. chacoense	5	3	38	Poor to fair	3x	4:01	2:01

* The plant introduction (PI) numbers of the species used were: S. brevidens, PI 218228; S. cardiophyllum, PI 255519 or PI 275215 (with 2n pollen); S. chacoense, PI 217451; S. commersonii, PI 243503; S. fernandezianum, PI320270; and S. verrucosum, PI 161173.

LETTER FROM: "Father Joe" Syrovy, Vining Iowa - March 9, 1983

TO: Chris and Lois Laning

From the enclosed newspaper clipping you can see that records have been broken here in Iowa for the warmest winter we've had for 50 years! "IT'S OFFICIAL: WINTER OF '82-83 WARMEST IN IOWA IN 51 YEARS!"

Last fall it was not only warm but very wet. The herbaceous peonies kept their green foliage until very late. The tree peonies, too, kept their foliage on and only a few began to drop their leaves, so we stripped the remaining foliage hoping in this way that the stems would mature more rapidly. Besides, we wished to trim them and cut out dry or diseased stems. We hoped also to give them a Bordeaux mixture both before winter set in, which we did between rains. We also applied a dressing of wood ashes.

We had some winter weather during the first few weeks of February but then it turned very warm, temperatures going from the 40's to 70°. It was also dry so we burned off our herbaceous peony beds. We were able to resume our tree peony trimming, cutting off branches with borer damage, poking a wire down the rest of the stem and sealing it afterwards with an asphalt paint.

We were alarmed in the meantime, because the weather became warmer especially in February, reaching from 60° to 70°! The buds on the tree peonies began to swell and on some showing green tips. The temperature then dropped to below freezing and finally to 21°. Will the blossom bud survive?

Also found a seedling T.P. on the north side of the house close to the foundation which was one inch high, already in February. I covered it with leaves and sawdust perhaps too late!

We've had some of the tree peonies for at least 25 years. Most of them have been planted deep according to the old directions, a big hole and wide enough with enriched good black dirt. That is why they have survived and blossomed some each year. It will be interesting, and we hope not sad, to see what this "June in January weather" has done to them! No doubt many of you in this "Midwest area" have experienced the same problems I have and comments on how all this has affected your peonies should be forthcoming. Our "weathermen" have reported that "our peculiar weather" was the result of the storms they had in California as they moved eastward. What next?

Regard to you both! What happened up your way?

"Father Joe" Syrovy

Dear Father Syrovy: Our Michigan winter was unusually mild; pretty much like you have experienced. Plants and trees were dormant and remained so until March. Along about the 15th of April, after three weeks of good growing weather, a cold wave (down to 9° F) killed the advanced growth on herbaceous and tree peonies. Also killed were the expanding magnolia flower buds. Magnolia stellata, M. Dr. Merrill, and M. soulangeana were a complete wash-out. But now things in general are A-OK.

Chris

LETTER FROM: Dr. P. E. Hughes, M.D., B.S., Ph.D.
70 Studley Park Road, KEW, Victoria, Australia 3101

DATE: 9th February, 1983

Dear Chris,

In your latest Issue of Paeonia you mentioned that in Australia we did not seem to be interested in herbaceous peonies; this is not so. A nurseryman, Mr. Brian Tonkin, actually has about 90 varieties which he has imported over the years from Wilds. He grows them commercially for cut flowers. Each year he digs up about three or four varieties and subdivides and replants them. He sells a few divisions of the varieties he divides that particular year — to obtain his full range would take many many years.

The reason why a lot of herbaceous peonies have not been imported to Australia by various amateurs is due to our quarantine regulations. We are restricted to 250 plants of any one genus. This applies both to an importer and to a quarantine house. The Government of each State runs a quarantine house and it is very hard to get more than a dozen or so plants into the government quarantine house. Because of this reason I built my own glass house. I have had a glass house for many many years and decided to bring this up to quarantine standard. This involves siliconing the glass inside and out at all joints. Insect proofing the glassing bars with silicone and plastic foam. Putting in a concrete floor. The drainage trap from the concrete floor has to be covered with 40 per inch metal mesh. All ventilation of the house has to be covered with similar insect proof mesh and there has to be an area with two doors so that no insects can escape from the house. Both doors have to have springs to make sure they are closed and the door has to be kept locked. Quarantine officers keep one key and the person who owns the quarantine house keeps another key. Any fan has to be boxed up and covered, with similar 40 per square inch mesh - insect proof screening.

As you can see this requires quite a lot of work and the original house needed quite a lot doing to it to bring it up to quarantine standards. It was then inspected by two officers of the Department very thoroughly and finally passed.

I installed four commercial refrigerators to acclimatise the plants but when the plants arrived those from David Reath were so large that I had to go out and get another four refrigerators. So I ended up having eight refrigerators in the quarantine house. There was some trouble getting some of them in - one in particular was a little bit wider than one of the doors and I had to take off the door of the refrigerator to get it through and the plate on. which the hinges were screwed fell down and I had to take off the lining of the door and replace it, but I finally got it through all the rubber insect proofing on the doors and got it installed.

The plants subsequently arrived, and were subject to the quarantine restrictions as are imposed here. In brief you are allowed to import 250 plants in total per genus per year as a maximum. This applies either to the house or the person, two people cannot use the same house and get 250 each, it becomes additive and if one gets 150 the other can only get 100 in the house. There is no limitation on what you can import into the government house but it is very hard to get any space there.

All plants have to be container grown until they are released from quarantine. As you can see if we are collecting peonies it is probably better to get the tree peonies first and the herbaceous peonies later.

The other restriction is that any plant commercially available in Australia cannot be re-imported. When the plants arrive you have to go through the usual quarantine procedures at the Airport Customs and then take them unopened to the quarantine office in the city. There the plants are counted and inspected and fumigated with methyl-bromide for a prescribed period. The quarantine officers then deliver the plants into the Quarantine House where nothing is allowed to be removed without their approval. This also applies to any soil, containers, or soil that is mixed.

The plants are counted and the 250 actually is the number of plants that arrive so that if any die they are still counted in the 250; you cannot get more as it doesn't go on the number that have survived but on the number you obtained. If a herbaceous peony comes and is divided each division counts as a plant so if you get a whole clump it only counts as one plant, so I understand that among the commercial growers if they are importing any they prefer to get clumps rather than divisions. Even a one eye division would be one off the quota.

The quarantine people fumigate them with methyl-bromide and deliver them to the quarantine house where they look pretty dried up and miserable. The quarantine officer told me to let them stand dry for at least two days "to let the gas out." The plants arrived in September and October when our weather was in the Spring time and we had days up to the 80's. This summer being hotter than the one before, and it seemed very hard to just leave the plants there dry. However, I followed out their instruction and let the plants stand for two days, then soaked them for a couple of hours and after this they looked very revived. I then packed them in the refrigerators at 5 degrees centigrade - that is about 40 degrees Fahrenheit - and held them for eight weeks.

Apparently this is most important to let auxins in the buds be destroyed so you will get good shooting. It certainly paid dividends as the results have been excellent. After eight weeks the plants were planted into plastic containers in a soilless mix of old pine bark, sand and scoria and a little coal dust and I added about a matchbox full of Osmocote to each container. You are only allowed, one plant in a container and the plants are not to touch each other. As my house is 50 square yards which is apparently in the commercial range of size, I have to crowd them in a bit and some were cleared before the last lot were planted out.

The results have been most encouraging. I did not lose a single plant from David Reath nor Roy Klehm and most of the smaller plants have done very well. I lost two or three small plants which were broken in transport at the site of grafting, presumably through rough handling somewhere in the airways. The other plants all shot I lost one or two with the herbaceous root stock rotting and the other losses surprisingly enough were among the Chinese Conquest collection. These all shot but at a subsequent date two or three of them wilted. I will mention this again later.

After the pots had been planted for two weeks they had to be treated with Nemacur P. The government officer came out and I donned a respirator and Wellington boots, gloves and protective clothing and each plant was treated with a liberal dose of a solution of Nemaeur P. After this the house was sealed for 24 hours became of the danger. It didn't seem to hurt the plants in the slightest. The plants have made excellent growth, practically all of David Reath's plants flowered and one of his tree peonies actually had eight flowers in the container in the first year which I found rather amazing. Several of the plants formed buds which aborted. A lot of the herbaceous material from Roy Klehm formed buds which aborted, but the plants remain quite healthy.

This summer as I mentioned has been particularly warm and in late November and early and throughout most of December we had several days over 100 degrees. I noticed a little bit of wilting and put 50 percent shade cloth all over the house. It still seemed a bit hot inside so I put another layer of 75 per cent shade cloth over the house which kept it much cooler. However, there was still a bit of wilting so I sprayed them all again with anti-fungal material. I have been spraying them at fortnightly intervals with Benlate, Captan, and other commercial preparations. When the wilting first occurred I watered them liberally and this seemed to make the wilting worse. Peter Rafferty suggested cutting down on the watering which I did and the results have been quite an improvement. I think the wilting is basically what happens with spring planting in your southern states, where the plants are forced into rapid growth by the warm weather before they have had a chance to form adequate roots, and you get this wilting syndrome. Certainly there was no suggestion it was botrytis.

Overall I have got 90 per cent survival rate which exceeded my wildest expectations. As mentioned, I lost some of the Chinese Conquest (title of a Smirnow marketing promotion) - tree peonies . In this connection Peter Rafferty tells me that several years ago a nurseryman named Craig, who has since died, became friendly with a communist union leader on the waterside and somehow managed to get a large shipment of tree peonies out of China. These subsequently were sold mainly to the Melbourne City Council. Peter .Rafferty acquired a collection of about a dozen plants from the Craig Estate. These plants were almost all infected with Fusarium. Whilst he kept spraying the plants he kept them alive but when the hot weather came and the spraying programme was ceased, they promptly all died. I am wondering if the Chinese method of propagation of division of plants perhaps with faulty hygiene has released some plants with fungal infections onto the market. It seems strange that the own root plants should be the only ones to suffer in this way. The Chinese herbaceous peonies I obtained from Mr. Smimow have survived well. I hope to build up a comprehensive collection over the next few years as quickly as my quota will allow.

The plants from Roy Klehm - he sent several herbaceous peonies and he sent them in duplicate and triplicate. Of course this involved quite a bit of the quota, so Peter Rafferty took over twelve of the plants. These went to the government quarantine office where they have a new girl graduate running the establishment. She is most conscientious and is getting much better results than her predecessors. She also has refrigeration facilities.

Peter told me that at the end of last week he received a letter from the Quarantine Authority that they were releasing 11 of the 12 plants. I don't know whether one has succumbed but at least the survival rate there is also very good. These are, of course, plants from Roy Klehm and herbaceous peonies.

I find Paeonia most informative and interesting. I don't know when the next subscription is due but could you let me know and I can send you the draft. As I mentioned earlier, my interest in the past has been in roses. I read with particular interest the interest in "Ihe Best of 75 Years" on the pigments in peonies. In roses pelargonidin does not occur in nature. Paeonidin occurs in Rosa rugosa which has been largely neglected by rose breeders and they consider it causes bluing of the flowers. Cyanidin which is only present to any marked extent in P. lobata in some of its varieties is the predominant pigment in roses and of course roses have the yellow pigments as do the various peonies. Pelargonidin has occurred as a mutant in roses, presumably in 'Baby Chateau' and 'Independence'. This has been developed by Kordes and we now have many with pelargonidin. Most of the garden reds like 'Chrysler Imperial' do contain at least one gene of pelargonidin. The movement towards the blue end of the spectrum can be achieved by of course adding hydroxyl groups to produce delphinidin or by conjugation with metalic ions or with our various other pigments as apparently occurs in the variety 'Kamada Fuji'.

In this regard cyanidin should be much more efficient than paeonidin in producing such complexes so if the cyanidin could be bred into a type of hybrid, perhaps with 'Kamada Fuji', the bluer end of the spectrum could be more closely approximated in peonies. It is also interesting to note that pelargonidin occurs in the tree peonies but not in the herbaceous.

In roses the pelagonidin containing varieties appear to be much more weak constitutionally than the non pelagonidin ones and crossing pelagonidin containing varieties with very robust roses like 'Queen Elizabeth' has resulted in much more robust pelagonidin predominant varieties. It is interesting that of the few Japanese varieties that have flowered in the quarantine house, they have been predominantly pink with the occasional purple. None of the varieties suggested among the Japanese varieties as containing pelagonidin in "The Best of 75 Years" or anything like it has flowered. Perhaps I have not got any of these varieties or if so, they follow the same pattern in the roses in that they are weak growers.

The same patterns of inheritance and dominance of genes appear to be common throughout the animal and plant kingdoms, thus in horses and cows, etc., black is dominant over the red of the Hereford or the brown or bay of the horse over the chestnut. Similarly in the flowers delphinidin is almost universally dominant over cyanidin and pelargonidin. The increased degree of hydroxylation is dominant. I am not quite sure if the methoxy group is dominant over a hydroxyl group, but I would strongly suspect it would be. It would seem that if the gene to methylate the hydroxyl group to produce a methoxy group and paeonidin perhaps be lost and the mutants contain pure cyanidin, but such does not appear to be the case. Perhaps if tetraploid forms of a tree peony could be obtained by Dr. Reath's method with culture seed and these crossed with various tetraploid lobata hybrids, we could obtain a. peony with cyanidin and the ability to approach the yellow end of the spectrum.

Such hybrids would, of course, have a double dose of the herbaceous as well as the tree peony entities and so would probably contain sufficient heat material to be much more viable and fruitful than most of the present Itoh crosses except for those involving '**Alice Harding**' gender. I have had no practical experience at all of peony hybridizing and these are just a few ideas which I somehow hope to put into practice in the next few years.

On the market here is a plant called '**Fire King**'. It looks like lobata, and blooms very early and the foliage dies down in the summer or early fall or autumn, as we call it here. However, I have two plants and Peter Rafferty has one and all the pods are empty, so if it is a species we really do expect some seed but we are just hoping that it in turn is fertile.

I hope this answers your query as to our lack of interest, or our apparent lack of interest, in herbaceous peonies, as you will now understand is not the case.

Yours sincerely,

Peter Hughes

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LETTER FROM: T.Person (Grower), La Houguette, St. Lawrence, Jersey, C.I.

DATE: April 5, 1983

Dear Mr. Laning:

It is with interest that I have read, your article "Peonies" in the March issue of the A.P.S. Bulletin. I'm certain that growing plants from seedlings would encourage more people to grow peonies. It is so slow to grow the seed that amateurs like me give up too quickly. The first seeds that you sent me two years ago are only coming through the ground now. The first year half a dozen came through but were cut by some insects in the autumn, (the fall) — last year I saved a dozen and this year already another dozen. The problem is that the weeds grew so fast that I pulled all the sticks to mark the varieties and now I don't know what I'm growing.

With seedlings there is the satisfaction to see something above the ground. Unfortunately I don't think that seedlings would pass through customs clearance without all the usual certificate for plants to enter Europe.

Last year's seed that you sent me are just coming through. They were covered with black polythene up to six weeks ago so no trouble with weeds. All my peonies are through now and some in bud. One '**Paula Fay**', planted six months ago, from Mr. K. Crossley, Minnesota, is 18" tall with four buds.

We had a mild winter, but it is much too wet now.

Yours sincerely,
T. Person

ED. NOTE: Seed distribution is a grand success. Interest in it grows year by year. Now is the time to provide an additional service, namely seedling distribution. This year I am offering one year old seedlings, mixed parentage, at $5.00 per dozen and two year old seedlings at $10.00 per dozen. Orders will be limited to not more than one dozen of each.

Chris

SUBJECT: Additional information on P. californica

FROM: Don Hollingsworth, 5831 N. Colrain Ave., Kansas City, MO 64151

Due to inversions of segments of chromosomes and exchanges of segments between different pairs of chromosomes, some of the chromosomes pair in blocks of four, six, or eight. This is seen as a ring structure with the paired chromosomes lapping one another which holds the ring together. As I recall, the analysis of why this might contribute to the survival of the species was that it would tend strongly to prevent segregation. Different geographical populations of the California peony were found to have different numbers of pairs involved in the ring formation phenomenon. Presumably, this assured that certain advantageous combinations of genetic material would be preserved during germ cell formation. Don't hold me to the "due to" statement that started this sentence. I didn't go back to the references and mean only to relate this in a general way and I intend not to redo the references unless someday I get to the point of wanting to hybridise the California peony with some other species. In that event, I will want to understand as much as possible about this unusual pattern of pairing before taking up time in the effort. I don't see any reason now why we should expect this species to breed with other species, at least, to be able to intermingle the genetic material with that of a second species in the formation of fertile descendants. (Graduate students under Stebbins at Berkley did the above studies.)

Taxonomically, multiple flowers per stem has been considered to be the older or more primitive condition -- in terms of evolution of the species. This comes out of the studies done by Stebbins using the Saunders peonies. I have not seen that Saunders did not agree with Stebbins, and since they collaborated on part of the writing that came out of the study, I presume that Saunders had no strong feelings against it. Stern does not concern himself with the philogenetic organization of the species, except to say which tetraploids came from which diploids. Stebbins' conclusions didn't agree with Stern in this area at all, and is probably more nearly correct in that he used information that Stern simply ignored or did not take into account in his explanation.

In number of flowers per stern, the more specialized form is considered to be one flower, or the absence (or suppression) of axillary flowers. In this context *tenuifolia* is among the most advanced while *californica* is one of the most primitive in its characters. The Delavayanae species are believed by someone I read, maybe Stebbins, to be more closely related to the Western American species. Both have multiple flowers and make a second break of growth from axillary vegetative buds without chilling requirement (to break; dormancy). All other species we know have a very strong suppression or dormancy of the axillary vegetative buds, only releasing them for growth if the terminal dominance is removed by pruning (or, giberellin will do it).