SOME BASIC HEMEROCALLIS GENETICS

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After sixteen years of breeding daylilies I have noticed, not surpris ingly to another daylily breeder, that there are a great number of genetic factors affecting the various characteristics, especially those concerned with flower quality such as color, size, form, texture, substance, ruffling and fragrance. Since Hemerocallis seems genetically complicated, often it is bred by methods involving trial and error, chance, intuition, guesses and wishful thinking. More accurate breeding would be possible if we understood more about the inheritance of the many daylily characteristics. In the future, daylily genet ics should become unraveled to the point that the unknowns that are the most evasive now will fit into place like the last remaining pieces of a jigsaw puzzle. After the basic daylily color genes are sorted out and understood, it will be possible for at least a geneticist to look at a flower and list the genes responsible for its color and form. You may wonder how this could help the majority of daylily breeders, who are not geneticists. Genetics can help any daylily breeder by giving him guidelines to foll ow to obtain certain desired results. For example, you do not need to know anything about the genetics of yellow and melon to make use of the fact, based on genetics, that crosses of melon daylilies will not produce any yellow seedlings.

My daylily breeding methods at present admittedly involve chance, intuition, guesses and wishful thinking. However, after observing many thousands of seedlings, and having kept records, I have learned some general results to expect from certain types of crosses. I thought i t might be worthwhile to summarize my interpretations of daylily genetics for several color classes. Sorting out each characteristic accurately is complicated, at least at present, by difficulties in recognition of charac ters and interpretation. For example, PRIMA DONNA is genetically a yellow (with additional color characteristics). DREAM MIST also is genetically a yellow (a very pale one, also with color overlay), which I learned by certain crosses. Errors in judgment are also possible in other color gro ups, such as red and pink, which are inherited differently. True reds are genetically different from very deep pinks, which may appear close to light red. In such cases, knowledge of a clone's parent is helpful and sometimes necessary.

You may wonder why, if I know some of the genetics of daylilies, I do not put this information to work immediately to turn out "custom made" daylilies. The answer is threefold: 1. I know about the genetics of only some characteristics while understanding little or nothing about the genetics of many other characteristics. 2. In some flowers, particularly in blends, it is difficult to interpret the genetic makeup. Daylilies have so many color shades and variations that it is not always easy to recognize even known genetic traits, especially when they may be modified by genes whose action is not yet understood. I think Mendel would have huge problems if he had used daylilies instead of peas for his pioneer work in genetics. 3. The most important reason that use of information on genetics has not enabled me to perform miracles is that, with the very large number of genes involved, as is the case in daylilies, the chance is extremely small of obtaining a certain desired genotype out of the many possibilities from a given cross. This is the reason that daylilies have been improved gradually over a period of years. Even if daylily genetics were fully understood, it still would be a matter of chance when trying to combine in one plant a selected combination of many genes. The great improvement in daylilies in the past ten years is remarkable and the improvement can continue without the use of genetics, but an understanding of basic daylily genetics can eliminate many unproductive crosses. Also, unless we first understand the genetics of diploid daylilies, it will be very difficult to figure out the genetics of the more complicated tetraploids.

My records would be much more useful if I had kept descriptions of all the seedlings of each cross (that is, entire progenies) instead of only those seedlings that I saved each year. It takes all of my time during the daylily blooming season to dig and dispose of the discards, without any time left to write descriptions of these discards. Thus any information I have learned about daylily genetics is a by-product of years of breeding for improved clones. However, certain deductions about daylily genetics are possible by examining my records, and these are given here in hopes that they can be used as a basis for future more detailed studies and also to help beginning daylily breeders select parents for crosses. It would take more than an entire issue of this journal to print all of the data from which I have drawn conclusions. Therefore, I decided to write a rather generalized account of the information that I have at present. Daylily genetics is complicated not only because there are so many inherited characteristics but also because a large percent of these characteristics are affected quantitatively by numerous gene modifiers, resulting in many degrees and shades of variation. However, several basic aspects of daylily genetics are apparent.

I think, from observing the results of crosses, that the basic colors of yellow, pink and melon are inherited as follows: There is a dominant gene for pink, which I shall label P; its recessive allele, p, is present in double dose (homozygous) in all yellows and melons. There is also a gene, which I shall label Y, that is present in all genetically yellow daylilies. I do not know whether or not the genes for yellow and melon are alleles. If they are alleles, which means that they occur in one pair of chromosomes, then yellow is dominant to melon. If they are not alleles, which means that they would occur in two separate pairs of chromosomes, then yellow is epistatic to melon, and all of our daylilies then would be homozygous for the genes for melon. In both cases, many of the results of breeding would be the same. For example a cross of a homozygous yellow with a melon would produce 100% yellows, which it does. In either case, the F_2 would be 75% yellow and 25% melon, which is the ratio obtained. Also, in either type of inheritance, crossing a heterozygous yellow (such as one having a melon parent) with a melon would produce 50% melon offspring, which it does. In order to write genotypes, using symbols for the genes, which aids in figuring out the genetic possibilities of crosses, I shall write genotypes that are correct if the genes for yellow and melon are alleles. If it is discovered that the genes for yellow and melon are not alleles, then it would become necessary to revise my present discussion and genotypes, all of which are written on the assumption that the genes for yellow and melon are alleles. All cream, pale yellow, medium yellow, gold and orange daylilies have the Y gene but do not have any gene for pink, so yellows are either YYpp or Yypp. Melon daylilies do not have the Y gene but instead have two doses of its recessive allele, which we can label y. Also, melons to not have any gene for pink. Thus all melons (whether pale, medium, or deep melon) are yypp. Many melons have pink or lavender midribs and also they may have pink toning (which is pronounced in LITTLE RAINBOW, for example); this pink in the midribs and pink toning is not due to the gene for pink, but is an intrinsic part of the melon color. A pink daylily (any shade from very pale ink to rose) has a dominant gene for pink, P, and also two doses of the gene, y, which is also present in all melons. Therefore, a pink is either PPyy or Ppyy.

The "genetically yellow" daylilies range from very pale (such as ICE CARNIVAL) through pale yellows, lemon yellow, gold and orange. All of the genetically yellow daylilies have either one or two genes for yellow. A yellow may be true-breeding, producing no melons when crossed with melons. But a yellow that is not true-breeding will produce some melons if crossed with a melon and it can produce some pinks, and in some cases also some melons, if crossed with a pink. A yellow that had a pink or melon parent is not true-breeding for yellow. The color range of yellows, from very pale (near white), through various shades of yellow, to orange, is caused by gene modifiers which vary the intensity of yellow color. Thus ICE CARNIVAL is very pale yellow while the old clone, PLAYBOY, is orange, genetically a yellow that is greatly intensified.

The "genetically pink" daylilies have either one or two genes for pink but no genes for yellow. A pink daylily that has two genes for pink is true-breeding in that it will produce 100% pinks when crossed with either pinks or melons. Or a pink may have only one gene for pink, in which case it will produce 50% pinks and 50% melons when crossed with a melon. As in the yellows, pinks vary in color intensity, ranging from very pale, thr ough various shades of medium pink, to rose (almost light red). Also, as in yellows, the variation in pink color intensity is due to gene modifiers that affect the intensity of pink color.

The "genetically melon" daylilies each have two genes for melon, an d no genes or either pink or yellow. Therefore, you will not get any pinks from a melon selfed or crossed with another melon. Also, you will not get any yellows from a melon unless you cross it with a clone that has one or more genes for yellow.

I have found much evidence that the same gene modifiers cause the color intensity variations in the three basic colors: Yellow, pink and melon. (There are other basic colors besides these three, of course.) Thus, the same modifiers that result in orange color in a genetically yellow daylily will cause a pink to be a deep pink and also will cause a melon to be a deep melon (such as GEORGE CUNNINGHAM). This information can be useful in choosing crosses to get lighter or deeper flower color. For example, you can obtain an orange daylily even if you have no orange-flowered clones to use, by crossing a yellow with a deep pink that had a melon parent.(so that it will be heterozygous for pink). Crossing a yellow with a true-breeding pink will not give orange, seedlings--but more on that later. The offspring that inherit a gene for yellow (from the yellow parent), no gene for pink, and a color intensifying gene modifier (from the deep pink parent) will be orange. You also can get some orange seedlings by crossing a yellow with a deep melon. Crossing a yellow with a pale pink (one that had a melon parent, so that it will be heterozygous for pink) will produce some yellow seedlings, most of which will be pale to medium yellow. Another example: If you want to get pinks from a genetically yellow clone that had either a pink or a melon parent, to get deep pinks choose an orange (genetically yellow) to cross with a pink. If you want medium pinks, use the medium yellows (those that had a pink or melon parent) to cross with a pink. To get pale pinks, choose pale yellows (also those that had a pink or melon parent) to cross with pinks. In all of these crosses you will not get all pink offspring, and the pinks you do get will not likely be all the same shade. But by choosing crosses as I have described, you can have some control over the color intensity in many cases.

Often crosses of yellows produce seedlings in various shades of yellow. However, an apparently "stable" shade of yellow is one that appears lemon yellow to me. By stable, I mean that this color of yellow, when selfed or crossed with another lemon yellow, has produced offspring in which all of the yellows are lemon yellow. An explanation for this stable shade of yellow is that a lemon yellow is homozygous (true-breeding) for a certain color intensity modifier that when present in double "dose" results in lemon yellow. Crossing two different shades of yellow will give yellows, some of which may be the shade of one of the parents, or some may be either lighter or darker than either parent. Therefore, there must be either a cumulative effect of certain gene modifiers of yellow or else recessive genes from each parent may be expressed when they are combined, resulting in a double dose of the recessive, in the progeny. An example of this is that you can obtain some golds by crossing a pale yellow with a yellow. I have obtained both pale yellow and lemon yellow from crosses of gold with pale yellow. Yellow crosses with gold can produce a wide range of shades from pale yellow to orange. From orange crossed with gold I have obtained mostly orange and gold seedlings. Pale yellow crossed with orange can produce yellows in shades intermediate between the parents. I concluded that DREAM MIST is genetically a yellow (a very pale yellow), the additional overlay of color being inherited separately, because DREAM MIST crossed with a deep pink produced some orange offspring. These orange offspring inherited a gene for yellow from DREAM MIST, as the pink parent could not have a gene for yellow. Also; these orange seedlings inherited a color intensifying modifier from the deep pink parent. The resulting combination of a gene for yellow plus one or more color intensifying genes resulted in orange. PRIMA DONNA also is genetically a yellow with an overlay of added color, a conclusion based on the fact that PRIMA DONNA crossed with melons produced some gold seedlings. These seedlings could have inherited the gene for yellow only from PRIMA DONNA since melons do not have any gene for yellow. One gold seedling from PRIMA DONNA crossed with PEACE RIVER (a deep melon) had a slight overlay of darker color on the petals. This overlay of color may have been inherited from PRIMA DONNA (there is no color overlay in PEACE RIVER), in which case a different combination of modifiers of the overlying color resulted in a subdued overlay compared with that of PRIMA DONNA. Thus it appears that, at least in the blends that I have studied, the basic color and the overlying color are inherited separately.

The melon daylilies are somewhat more predictable than yellows and pinks because crosses of two melons always produce 100% melon offspring. Misinterpretation of color in melons is possible because some clones that are genetically melon have considerable pink toning, especially after a day in the hot sun, and such melons could be mistaken for pinks. A very pale pink could be mistaken for a melon, too. For example, ANNIE WELCH, which I have seen listed as "pinkish melon," is genetically a pink, which I know because it has produced offspring having pink when it was crossed with clones that do not have any gene for pink. The common term "melon pink" is confusing (it usually refers to a melon with considerable pink toning) and one that should not be used in a discussion of daylily genetics. All melons have two doses of the recessive gene, y. Since some yellows have one dose of y and all pinks have two doses of y, some melon offspring are obtained by crossing a melon with either a yellow that carries melon or with a heterozygous pink (a pink that had a melon parent would be heterozygous for pink). Also crossing two yellow clones (both of which carry melon) will produce 25% melon offspring. Likewise, crossing two pink clones (each of which is heterozygous for pink) will produce 25% melons and 75% pinks. Medium colored melons selfed or crossed with other medium melons produce all medium melons. I think that the medium-colored melons are homozygous for the same color intensifying modifier that is present in lemon yellows. Crossing. two different shades of melons produces melon offspring in varying. shades. Sometimes you will get seedlings that are either lighter or darker than either of their parents. Crossing a melon with a yellow produces 100% yellow offspring (if the yellow parent is YY) or 50% yellows and 50% melons (if the yellow parent is Yy).

Pink daylilies crossed with inks will produce either 100% pinks (if at least one parent is homozygous for pink) or else 75% pinks and 25% melons (if both parents are heterozygous for pink). A pink crossed with a melon will produce 100% pinks (if the pink parent is PP) or else 50% pinks and 50% melons (if the pink parent is Pp). Some pinks also can be obtained by crossing a pink with a yellow that had either a pink or melon parent. Pink color can vary from pale pink to deep pink (rose), which appears almost light red. Crossing two pinks can produce seedlings in which the pink ones are the same shade of pink as one of the parents, or some may be lighter or darker than either parent. Since the same color intensity modifiers affect the depth of color of yellows, melons and pinks, then a deep pink (rose) has the same complement of these modifiers as are present in both orange and deep melon. Thus one could develop deep pinks from medium-colored pinks by first crossing a medium-colored pink with either orange or deep melon and then selecting the deep-colored offspring to cross with pinks to obtain deep pinks.

I have not mentioned the colors that result when the genes for yellow and pink are combined. First it is necessary to understand how yellow, pink and melon are inherited, which I have discussed. A clone having genes for both yellow and pink is not yellow and it is not pink, but it is some shade of apricot, peach or copper, in which the color intensity can vary (as in yellows, pinks and melons) from pale peach bright copper-orange. All of these are genetically Y-P-, the color intensity variation among clones being due to the same modifiers that also are responsible for the color intensity variations that occur in yellows, pinks and melons.

In order to understand some other colors of daylilies, you need to know about a color-dulling dominant gene, which I shall call "drab" and label D. The gene for drab is wide-spread among cultivated daylilies, and makes possible some additional colors when in combination with various other genes. I think that the gene for drab occurs in "muddy" pink, buff, tan, and brown daylilies. MARY ANNE is an example of a muddy pink, which has the gene for drab. Thus the genotype of MARY ANNE is yyP-D-. A clear pink daylily, which has a double dose of the recessive allele of d, has the genotype yyP-dd. Brown, such as my BROADMOOR AUTUMN, which came from LIMONERO (yellow) crossed with MARY ANNE (muddy pink), inherited a gene for yellow from LIMONERO (and a gene for melon from MARY ANNE), a gene for pink from MARY ANNE (and a recessive gene for not pink from LIMONERO), and the gene for drab from MARY ANNE (plus a recessive gene for not drab from LIMONERO). Thus I know the genotype of BROADMOOR AUTUMN, which is YyPpDd. Since BROADMOOR AUTUMN has produced some melon seedlings when crossed with melon-carrying pinks and yellows, and since a melon daylily inherits one recessive gene for melon from each parent, then this test cross proves that BROADMOOR AUTUMN does have a gene (y) for melon. Also I have found that BROADMOOR AUTUMN has a gene for yellow, since it has produced some gold (genetically yellow) seedlings when crossed with pink. The pink parent does not have any gene for yellow, so the gene for yellow in the gold seedlings had to come from BROADMOOR AUTUMN. I know that BROADMOOR AUTUMN also has a gene for pink because it has produced some pink seedlings when crossed with yellows that were heterozygous for yellow. The gene for pink in these pink seedlings must have been inherited from BROADMOOR AUTUMN as no gene for pink could come from the yellows, since yellows do not have any gene for pink. From BROADMOOR AUTUMN I have obtained seedlings that are copper and orange-copper (having yellow plus pink plus color intensifying modifiers, and without the gene for drab: Y-P-dd), orange-tan (maybe similar genetically to BROADMOOR AUTUMN with different color intensity modifiers), maroon (probably deep pink with the gene for drab: yyP-D-), deep pink and rose (yyP-dd), orange (Y-pp), peach (Y-P-dd with intensity modifiers that cause pale color) and browns in several shades.

From the results of certain crosses, I concluded that the gene for yellow and the gene for pink probably are not alleles, but instead they belong to two separate sets of genes. My peach-colored seedling, 68-7, which has genes for both yellow and pink, came from a melon (which could not have genes for either yellow or pink) crossed with a seedling (64-84) that has genes for both yellow and pink. If the genes for yellow and pink were alleles, then the peach seedling could not have inherited both of these genes from 64-84, unless there was a chromosome crossover resulting in a chromosome carrying both genes. Since the peach seedling did inherit both yellow and pink, both of which could come only from 64-84, then I conclude tentatively that the genes for yellow and pink are not alleles. Because of the possibility of chromosome crossover, I need the results of more test crosses to be certain that the genes for yellow and pink are not alleles.

The genes for pink and melon are not alleles, a conclusion I based on the following: LIMONERO (a yellow) crossed with pinks never produced any pink or melon offspring; therefore, LIMONERO does not have any genes for either pink or melon. BROADMOOR AUTUMN, which came from LIMONERO crossed with MARY ANNE (a pink), was tested by crosses and found to have genes for both pink and melon, as I have explained. Since BROADMOOR AUTUMN could not have inherited genes for either pink or melon from LIMONERO (which does not have these genes), then it must have inherited a gene for pink and a gene for melon from MARY ANNE, which would not be possible if the genes for pink and melon were alleles. The possibility of crossover does not influence my conclusion in this case because I know that the genes for pink and melon in BROADMOOR AUTUMN are on separate chromosomes, since BROADMOOR AUTUMN has produced both pink and melon seedlings when crossed with melons. Thus the genes for pink and melon are not alleles, which means that they occur in two separate sets of genes.

As for the reasons that I think the same color intensity modifiers are responsible for the color depth variations in yellows, pinks and melons, this conclusion was made from the results of certain crosses, of which I shall give some examples: (1) A pale yellow (LIME PAINTED LADY) was crossed with a pink. Some of the offspring were gold, which is a deeper color of yellow than LIME PAINTED LADY, the yellow parent. A gold from this cross got one gene for yellow from LIME PAINTED LADY, but it did not get any gene for yellow from its pink parent since a pink has no genes for yellow. The gold color of the progeny must be due to the gene for yellow (from LIME PAINTED LADY) plus a combination of gene modifiers (from both parents) that increased the yellow to gold. The results cannot be explained on the basis of multiple alleles for yellow being responsible for different shades of yellow, since the gold progeny of this cross could have only one gene for yellow, the same gene for yellow that is present in the pale yellow LIME PAINTED LADY. (2) First, a gold seedling was obtained from LIME PAINTED LADY crossed with a pink. The gold seedling from this cross could have only one gene for yellow, which came from its yellow parent. This gold seedling then was crossed with a pink (GRECIAN GIFT). One of the offspring that I saved from this cross was yellow, which had to have the same gene for yellow that was present in its gold parent. The genetic difference, then, between the gold and its yellow progeny was a difference in the complement of color intensity modifiers of yellow. (3) A cream (DREAM MIST) was crossed with a deep pink, giving some orange progeny. An orange from this cross would have one gene for yellow from DREAM MIST, as its pink parent could not have a gene for yellow. The orange color resulted when there was a combination of one gene for yellow plus one or more color intensity modifiers, either a cumulative effect of modifiers from both parents or the effect of a color enhancing modifier from the deep pink parent. (4) A deep melon (PEACE RIVER) was crossed with a pale yellow (LIME PAINTED LADY). One seedling that I kept from this cross was orange. This orange could have only one gene for yellow (from LIME PAINTED LADY) but obviously it had a combination of modifiers from the yellow and melon parents that resulted in a deeper yellow color than that of its yellow parent. Since many times I have obtained some orange offspring from a yellow or gold crossed with either deep pink or deep melon, I suspect that a dominant gene modifier is responsible for intense color in all three (yellow, pink and melon) as well as in the daylilies that have both pink and yellow (resulting in copper). (5) In a similar example, a gold was crossed with a deep melon, producing an orange. This orange, having the same gene for yellow that was present in its gold parent, had at least one added modifier from the melon parent that intensified the genetic yellow, making it orange. (6) A deep melon, crossed with a pale yellow, produced a gold seedling. This gold seedling, as in the above cases, would have the same gene for yellow that was present in its pale yellow parent. Since it appears that the same color intensity modifier is present in deep melon, deep pink and orange, then crossing a yellow with either a deep melon or a deep pink (heterozygous for pink) is likely to intensify the color of at least some of the yellows in their seedlings, resulting in some of the genetic yellows in the progeny being gold or orange. Crossing a yellow with a pale melon or pale pink (one heterozygous for pink) likely will give you seedlings in which the yellows are mostly in the lighter shades. Since some crosses produce seedlings that are darker than either parent, or lighter than either parent, expect such variations. For example, the pink FIRST FORMAL (not a deep pink) has given me many deep-colored seedlings even when crossed with a medium-colored clone. In general, though, crossing with pale-colored clones tends to give lighter seedlings than crossing with deep-colored clones. I also think that other colors such as brown, tan, buff, copper and apricot are influenced by the same color intensity modifiers that affect depth of color in yellows, pinks and melons. It will take further effort to find out how many color intensity modifiers there are that cause color intensity variations in yellows, pinks, melons, combinations of pink and melon, and all of these colors that are affected by the gene for drab. However, it is possible by genetic studies to find out how many modifiers there are and exactly how they are inherited. At present, using yellow as an example, I know that color intensity modifiers are responsible for at least these distinctly different shades of yellow: near white (ICE CARNIVAL), very pale (WHITE FORMAL), pale yellow (PRAIRIE

MOONLIGHT), yellow (CONVENTION QUEEN), gold (CARTWHEELS) and orange (PLAYBOY).

Arisumi (1) discussed breeding and genetics of red daylilies, mentioning the early "reds" (the "THERON" class developed by Stout). I have not seen these early reds so am not able to judge whether or not they were true reds. However, reading Stout's description, in the 1949 Hemerocallis Yearbook (the first yearbook), I notice that he described the THERON class (a group of dark daylilies) as "mahogany red, maroon, Mars violet and almost, if not, black." From this description, it appears that the THERON class did not include any true bright reds. My conclusions about the genetics of red are based on results of crosses that I have made. First I want to compare notes with Arisumi: (1) Arisumi found that a non-red crossed with a non-red produced 100% non-reds. I have obtained identical results from hundreds of crosses of non-reds. (2) Arisumi concluded : "in daylilies red flower is dominant over non-red flower." I agree with this conclusion. (3) Arisumi also concluded: "The intensities of red are determined quantitatively by many genes controlling the amount of pigment produced, and genes that complement or modify their action." I also agree with this conclusion.

The point that needs to be made, concerning inheritance of reds, is that every bright red (not muddy) daylily has not only one or two dominant genes for red but also two recessive genes for clear color. There is a dominant gene, which I shall call muddy (M) that occurs in all muddy red daylilies. Using the symbol R for red, and using m for the recessive gene that occurs in double dose in clear reds, we can write the genotype of a clear red daylily: R-mm. A muddy red is R-M-. The M gene is prevalent in many daylily clones. The M gene makes a red daylily muddy but does not show in a yellow, so it does not make a yellow dull or muddy. Most of my crosses of red with yellow have produced muddy red seedlings. A muddy red that had a clear (mm) red parent has one dose of the recessive gene, m, for clear color, so is Mm. When this muddy red (Mm) is crossed with a clear red (mm), 50% of the red offspring will be clear red and 50% of them will be muddy red. The reason that Arisumi got muddy reds from NOONTIDE crossed with SUMMER INTERLUDE is that the red offspring inherited the R gene (from SUMMER INTERLUDE) and the M gene (from NOONTIDE), so they were RrMm. I do not know whether the dominant gene for muddy, which dulls the color of reds, is the same as the dominant gene for drab that is present in muddy pink, buff, tan and brown. Until we find out whether or not M and D are the same gene I shall use different symbols for each of them.

Arisumi listed eight crosses of reds (both parents red), all of which produced 100% red offspring. I have seen all of the clones that he used for these crosses and think all but one are true reds (a true red being defined as one having red color that is due to the gene, R). The true reds that he used are SUMMER INTERLUDE, HEARTS AFIRE and ALAN. But KANAPAHA, which Arisumi listed as red, is a clone that I think is deep pink, not red. I recall, in 1959, standing in the yard of a friend. She was looking at her first flower on her new plant of KANAPAHA, and she said to me that she liked the deep rose color of KANAPAHA. Probably KANAPAHA is genetically a deep pink, without any gene for red. I do not think that the dominant gene for pink (P) is the same as the dominant gene for red (R) since in hundreds of crosses of pinks with other colors I have never obtained any reds whose color intensity compares with reds such as PRAIRIE CHIEF and CHIPPER CHERRY. The only color approaching red that has come from pinks is a light red, actually deep rose, which I think is a highly intensified pink. When Arisumi crossed KANAPAHA with HEARTS AFIRE (a red), he got 100% red seedlings. This is the expected result of crossing a pink with a homozygous red. I also conclude from the results of this cross that KANAPAHA does not have the gene (M) for muddy. KANAPAHA, since it has clear color, also does not have the gene (D) for drab, so perhaps M and D are the same gene, although we need more information to decide this.

I have not crossed pinks with reds, so have no opinion as to whether or not the same series of gene modifiers that are responsible for color intensity variations in other colors (yellow, pink, melon, combined yellow and pink) also cause the color intensity variations that occur in reds, or even whether these modifiers are partly responsible for the different shades of red. I do know, however, that a daylily with only one gene for red can be a deep or dark red. The reason for this conclusion is that, when I crossed some reds (ROYAL CRIMSON, SUMMER INTERLUDE, red seedlings) with CARTWHEELS (a gold that had a red parent), I got a number of deep reds and bright reds. These red seedlings could have only one gene for red (R) since they inherited this R gene from their red parent but could not have inherited an R gene from CARTWHEELS, since it is non-red. Since the crosses of CARTWHEELS with reds also produced some muddy reds, I concluded that CARTWHEELS is heterozygous for the dominant gene for muddy, so it has one recessive gene for clear color, which it inherited from its red parent. Thus the genotype of CARTWHEELS is Y-pprrMm. Some orange-reds have come from CARTWHEELS crossed with reds. I have not done genetic tests to find out if an orange-red has a gene for red (R) plus a gene for yellow (1), but I suspect this is the case since I have obtained orange-reds from crosses of yellow with red but not from crosses of reds. If orange-red is due to the presence of genes for both red and yellow, then I think that orange-red can occur only when the gene for muddy is absent. My reason for thinking this is that I have obtained predominantly muddy reds by crossing red with yellow. At least half of these muddy reds would have a gene for yellow, and yet their color is not orange-red. Further evidence that a muddy red can carry a gene for yellow is that I got an orange-red from a muddy red crossed with a red. Probably this orange-red inherited red, plus a gene for yellow (from its muddy red parent), plus two recessive genes for clear color (one from each parent). Also, a red crossed with CARTWHEELS (genetically a yellow, carrying the recessive gene for clear color) produced an orange-red. This orange-red probably inherited two genes for clear color (one from each parent), plus red, plus a gene for yellow (from CARTWHEELS).

Arisumi got 100% reds from all crosses using two red parents. There are some reds that would not produce 100% red offspring, but in each cross of reds that Arisumi made he happened to use at least one homozygous red (RR). If he had crossed two heterozygous reds (Rr) he would have obtained 75% reds and 25% non-reds.

The practical value of understanding the inheritance of reds, including the inheritance of the gene for muddy, is that one can know how to cross reds with other colors (to improve such characteristics as flower size, form, ruffling, throat color) and then recover good reds in the second generation by crossing the red offspring (even if muddy red) among each other, or by selfing them, or by crossing them with any other clone that is either a clear red (mm) or a muddy red (Mm) that had a clear red parent. In other words, a muddy red that had even one clear red parent is capable of producing clear red seedlings. Likewise you can get some clear reds by crossing a clear red with another color (yellow, for example) if this other clone had a clear red parent. Another practical value of genetic information on reds is that from crosses of two clear (not muddy) red parents you will not get any muddy red offspring.

It is not hard to understand why tetraploids have more shades of each color, including some that are more intense (vibrant) than in diploids, because there are more possible combinations of the basic color genes (yellow, pink, red and lavender) as well as more possible combinations of the color intensity modifiers in tetraploids than in diploids. I seldom see a really new color in diploids as most colors of new introductions have appeared in my seedlings. However, I expect to see in tetraploids many additional shades, although they will result mostly from combinations of genes that already exist in diploids. Some of the diploid daylily colors that are not covered in this article will be discussed in a future article.

(1) Arisumi, Tort. The inheritance of red flower color in Hemerocallis. The Hemerocallis Journal 24:9-14. 1970.

SOME BASIC HEMEROCALLIS GENETICS - PART 2

by Joanne Norton

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In a previous article (The Hemerocallis Journal 26(2): 29-39. I discussed the genetics of several daylily colors including melon, yellow, pink, peach, apricot, copper, buff, tan, brown and red. The present article will add the information that I have on lavender, purple, lavender-pink, rosy-purple (wine) and maroon. In both articles my discussion deals with the basic colors (melon, yellow, pink, yellow-pink combinations, red, lavender and lavender-pink). I am not including in these two articles any information on characteristics such as bicolor, bitone, dusting, eyezone, dark or light edging, and dark veining, all of which are subjects for other discussions.

I did not include lavender in my last article because this adds not just one additional color but also other colors in which lavender is involved. Therefore, the first article would have been too long if I had included the material of the present article. However, since an understanding of the inheritance of melon, yellow and pink is necessary before you can understand the genetics of lavender and lavender combinations, the present article should be read only after you have read my previous article on daylily genetics.

The first thing that I noticed about the genetics of lavender is that it involves a gene that is dominant to both melon and yellow. Many crosses of melon X melon, yellow X yellow, and yellow X melon have never produced any lavender offspring. I noticed, however, that lavenders could be obtained from crosses of yellow X lavender or from melon X lavender. Some lavenders came from these crosses of yellow X lavender:

LAVENDER FLIGHT (lavender) X 66-35 (yellow)
66-35 (yellow) X BROADMOOR FANTASY (purple)
BLUE JAY (deep lavender) X 66.35 (yellow)
66-1 (yellow) X lavender seedling
BURIED TREASURE (yellow) X LAVENDER FLIGHT (lavender)
LIMONERO (yellow) X Spalding 58-13 (lavender)
63-17 (gold) X Spalding 58-13 (lavender)

Melon X lavender crosses that produced some lavender offspring are:

62-41 (melon) X STEPHAN BLUE (lavender)
62-41 (melon) X 64-84 (lavender)

Crossing a pink with a lavender also can produce some lavender offspring in some cases. Some lavenders have come from these crosses of pink X lavender:

PICTURE (pink) X Spalding 58-13 (lavender)
pink seedling X Spalding 58-13 (lavender)
SATIN GLASS (pink) X 64-64 (lavender)
SATIN GLASS (pink) X Spalding 58-13 (lavender)
SATIN GLASS (pink) X 64-84 (lavender)
DEANE SADLER (pink) X LAVENDER FLIGHT (lavender)
LAVENDER FLIGHT (lavender) X PRAIRIE MAID (pink)
LAVENDER FLIGHT (lavender) X ANNIE WELCH (pink)

Pink is dominant to melon (see previous article). Concerning the relationship between pink and lavender, both of which appeared dominant to melon, three possibilities occurred to me: (1) lavender dominant or epistatic to pink, (2) pink dominant or epistatic to lavender, or (3) pink and lavender due to the same gene but each the result of a different modifier. Having only remnant records of crosses, in the form of descriptions of only those few seedlings that I had saved each year, and having no records of the many seedlings that I had discarded, I therefore had access to no ratios. As explained in my previous article, my interpretation of daylily genetics was a recent afterthought, so no records were taken with a genetic study in mind. Therefore, I drew conclusions by examining the records of seedlings that I had kept, and in this way discovered that the results of my crosses fit explanation number 3.

First I shall state how lavender is inherited and then give reasons for my conclusions. A lavender (any shade from pale lavender to purple) has the same gene, P, that occurs in pink and all yellow-pink combinations (which include peach, apricot, copper, buff, tan and brown). Pink and these additional colors involving pink not only have a gene for pink, P, but they also have a gene that influences the P gene to make pink color. I shall label this pink-influencing gene I^P. A lavender has the same gene, P, that occurs in a pink. But a lavender, instead of having the I^P gene, has instead a lavender-influencing gene, which I shall label I^L. The genes I^P and I^L are modifying genes (both affecting P) which show when present with P. Thus in melons and yellows (neither of which have P) the I^P or I^L genes, one or both, are present but do not affect the color of melon or yellow. Lavender-pink combinations (any shade from pale lavender-pink to rosy-purple) have the P gene as well as both I^P and I^L.

Another difference between pink and lavender is that a pink has genes for melon (yy) but no gene for yellow (Y), as discussed in my first article. A lavender however may have either genes for melon or yellow. It is possible to find out by test crosses whether a lavender has genes for yellow or melon. For example, PEACE RIVER (melon) X LUXURY LACE (lavender) is a cross from which I saved a melon seedling. Since a melon has two genes for melon (yy), the melon seedling must have inherited a gene for melon (y) from each of its parents. Therefore this seedling must have inherited the y gene from LUXURY LACE, which means that LUXURY LACE has the y (melon) gene. A second example: seedling 62-41 (melon) X STEPHAN BLUE (lavender) produced a yellow seedling. Since this seedling could not have inherited the gene for yellow (Y) from the melon parent (which has no gene for yellow—see first article), it must have inherited the Y gene from STEPHAN BLUE. Thus STEPHAN BLUE has a gene for yellow. A third example: 64-112 (a gold that had a melon parent, therefore being Yy) X LAVENDER PARADE (lavender) produced a melon seedling. One of the two genes for melon in this melon seedling must have come from LAVENDER PARADE, since a gene for melon came from each parent. Thus LAVENDER PARADE has a gene for melon.

Lavenders come from crosses in which at least one parent has the P gene and at east one parent has the I^L gene. Daylilies that have the P gene include these colors: pink, peach, apricot, copper, buff, tan, brown, lavender, lavender-pink, purple, wine and “non-red maroons” (the maroons will be discussed later in this article). The I^L gene is present in lavenders and lavender-pinks of all shades. But also the I^L gene can be present (without having any visible effect) in melons and yellows. That is, some melons and yellows have the I^L gene while others do not. This explains why sometimes lavenders are obtained from crosses of yellow X pink and melon X pink. In my first daylily genetics article I stated that the cross pink X melon will produce either 100% pink offspring (if the pink parent is PP) or 50% pinks (if the pink parent is Pp). This is true if the melon parent does not have the lavender-influencing gene, I^L. But in the present article I am adding another type of melon, one that does have the I^L gene. As will be seen below, it is possible to get some lavender and lavender-pink offspring from certain pink X melon crosses, although you could not count on it unless you knew that the melon parent had the I^L gene. A melon that had one lavender parent would have at least 50% chance of having the I^L gene.

Crosses that can produce offspring including a portion that are some shade (pale to deep) of lavender or lavender-pink are:

Always:	lavender X lavender
	lavender X lavender-pink
	lavender-pink X lavender-pink
Usually:	lavender X melon lavender X pink
	lavender X yellow
	lavender-pink X melon
	lavender-pink X pink
	lavender-pink X yellow
	lavender or lavender-pink X peach, apricot or copper
	lavender or lavender-pink X buff, tan or brown
Sometimes:	pink X yellow or melon
	peach X yellow or melon
	apricot X yellow or melon
	buff X yellow or melon
	tan X yellow or melon
	brown X yellow or melon

My conclusion that both pinks and lavenders have the same gene, P, was based on the following results of crosses:

(1) A lavender-pink seedling, 69-105, came from BROADMOOR SUNSET (melon) X PRAIRIE MAID (pink). BROADMOOR SUNSET does not have the P gene, since P does not occur in melons (see previous article). Therefore, the same gene, P, that is present in the *pink* PRAIRIE MAID is in the *lavender-pink* seedling. The I^L gene in the lavender-pink seedling must have come from BROADMOOR SUNSET.

(2) A rosy-purple (a deep shade of lavender-pink) seedling, 68-29, came from 64-112 (gold) X LAVENDER PARADE (lavender). The P gene must have come from LAVENDER PARADE since a gold (genetically a yellow) does not have P (see previous article). In LAVENDER PARADE the P is modified by I^L. But in the rosy-purple seedling the same P gene is modified by both I^L (from LAVENDER PARADE) and I^P (from 64-112).

(3) A peach (yellow-pink combination) seedling, 68-7, came from 62-41 (melon) X 64-84 (lavender). The gene, P, in the peach seedling must have come from the lavender parent, since a melon does not have P. Thus the gene, P, produced *lavender* color in 64-84 because the I^L gene was present. This same P gene produced *peach in* the 68-7 seedling, which inherited I^P from its melon parent and the gene for yellow (Y) from 64-84.

(4) A purple seedling, 70-26, came from 67-6 (pink) X 66-35 (yellow). The purple seedling must have inherited P from its *pink* parent, since yellows do not have P. The I^L gene in the purple seedling was inherited from 66-35.

(5) A pink seedling, 69-58, came from BURIED TREASURE (yellow) X LAVENDER FLIGHT (lavender). The *pink* seedling must have inherited the P gene from its *lavender* parent and I^P from BURIED TREASURE.

(6) A lavender-pink seedling, 70-61, came from 66-7 (pink)

X LAVENDER FLIGHT (lavender). The seedling inherited P, plus I^L from LAVENDER FLIGHT, plus I^P from 66-7.

(7) A rosy-lavender, 68-35, came from LAVENDER PARADE (lavender) X PRAIRIE MAID (pink). The seedling inherited P from one or both parents, I^L from LAVENDER PARADE, and I^P from PRAIRIE MAID.

(8) A rosy-purple (a deep shade of lavender-pink), 70-43, came from LAVENDER PARADE (lavender) X PRAIRIE MAID (pink). This seedling has P, I^L from LAVENDER PARADE, and I^P from PRAIRIE MAID.

(9) A lavender-pink, 67-13, came from SATIN GLASS (pink) X 64-84 (lavender). This seedling has P, I^P from SATIN GLASS, and

I^L from 64-84.

(10) A rosy-lavender (a deep lavender-pink), 67-25, came from SATIN GLASS (pink) X 64-84 (lavender). This seedling has P, I^P from SATIN GLASS, and I^L from 64-84.

(11) A lavender-pink, 67-36, came from 62-41 (melon) X STEPHAN BLUE (lavender). This seedling inherited P from STEPHAN BLUE, I^L from STEPHAN BLUE, and I^P from 62-41.

(12) A pink, 65-3, came from 62-47 (melon) X Spalding 58-13 (lavender). The *pink* seedling must have the same gene, P, that is in *lavender* Spalding 58-13, since P does not occur in a melon. The pink seedling inherited P from Spalding 58-13, I^P from 62-47, but did not inherit I^L from Spalding 58-13. This also means that Spalding 58-13 has only one I^L gene, not two.

(13) A rosy-purple (deep shade of lavender-pink), 65-4, came from NEYRON ROSE (pink) X Spalding 58-13 (lavender). The seedling has P, I^P from NEYRON ROSE, and I^L from Spalding 58-13.

(14) A rosy-lavender (deep shade of lavender-pink), 68-44, came from 62-2 (deep pink) X 65-18 (lavender). The seedling has P, I^P from 62-2, and I^L from 65-18.

(15) A lavender-pink, 69-117, came from LAVENDER FLIGHT (lavender) X PRAIRIE MAID (pink). This seedling has P, I^L from LAVENDER FLIGHT, and I^P from PRAIRIE MAID.

(16) A lavender-pink, 69-142, came from 66-35 (yellow) X EXALTED RULER (pink). The *lavender-pink* seedling must have the same gene, P, that is present in its *pink* parent. The I^L gene in the lavender-pink seedling came from 66-35.

(17) A lavender seedling, 69-127, came from BROADMOOR SUNSET (melon) X PRAIRIE MAID (pink). The P gene in the *lavender* seedling must have come from its *pink* parent.

As I already stated, lavender involves a dominant gene. Also pink is due to a dominant gene, as explained in my previous article. By dominant, I mean that lavender is dominant to melon and yellow, and pink is dominant to melon. Knowing that a dominant gene is involved in both pink and lavender, and examining the above seventeen crosses, it may occur to you that all of these crosses could be explained on the basis of separate dominant genes for pink and lavender, the different colors obtained being due to various recombinations of modifiers. However, because of some other evidence, I know that this is not the case. Instead, pinks and lavenders all have the same gene, P. The other evidence is this: From certain crosses I found that there is only one dose of the dominant gene that could cause either pink or lavender in the pink PRAIRIE MAID and also in the lavenders LAVENDER PARADE, 64-84, LAVENDER FLIGHT and STEPHAN BLUE- These clones were used in some of the above seventeen crosses. Two of those crosses (2 and 5) were yellow X lavender, the lavender in each case being one that has only one dose of the gene for either pink or lavender (so these lavender parents could not have a gene each for pink and lavender). In cross no. 5, the pink seedling would have to have the same dominant gene that is in its lavender parent. In two crosses (3 and 11), a melon was crossed with a lavender having only one gene for pink or lavender, so the lavender parent could not have separate genes for pink and lavender. Cross no. 3 produced a peach and cross no. 11 produced a lavender-pink, both of which must have the same dominant gene present in their lavender parents. In cross no. 1, a lavender-pink seedling came from a melon crossed with a pink (PRAIRIE MAID) having only one dose of the dominant gene for pink or lavender. The pink parent and its lavender-pink progeny must have the same dominant gene for pink or lavender. Another melon X pink cross (no. 17) produced a lavender seedling, which must have the same dominant gene that resulted in pink in its parent.

To draw the above conclusions about the six crosses, I would have to know that the pink (PRAIRIE MAID) and lavenders (LAVENDER PARADE, 64-84, LAVENDER FLIGHT and STEPHAN BLUE) that were used in those crosses do indeed each have only one dose of the gene that occurs in both pink and lavender. First, I know that PRAIRIE MAID and STEPHAN BLUE each have only one dose of the gene for pink or lavender because a yellow seedling, 68-84, came from STEPHAN BLUE (lavender) X PRAIRIE MAID (pink). This yellow seedling could not have the dominant gene that occurs in pink or lavender, so neither of its parents could be homozygous for this gene. Second, LAVENDER PARADE (lavender) X BROADMOOR AUTUMN (brown) produced a yellow, 70-29. Since this yellow does not have a gene for pink or lavender (if it did, it would show), then its lavender parent (LAVENDER PARADE) could not have a double dose of this gene. Also, a melon seedling, 68-72, came from 64-112 (gold, genetically a yellow) X LAVENDER PARADE. A melon does not have a dominant gene for pink or lavender, so the lavender parent (LAVENDER PARADE) could not be homozygous for this gene. Third, a yellow, 68-62, came from DREAM MIST (genetically a yellow with color overlay—see previous article) X 64-84 (lavender). By the above reasoning, I know that 64-84 is heterozygous for the gene for pink or lavender. Fourth, I know that LAVENDER FLIGHT could not have two doses of the gene for rink or lavender because the following three crosses produced seedlings that could not have the gene for pink or lavender:

BURIED TREASURE (yellow) X LAVENDER FLIGHT (lavender):
yellow seedlings 68-1 and 68-4
CONVENTION QUEEN (yellow) X LAVENDER FLIGHT:
yellow seedling 68-14
LAVENDER FLIGHT X DREAM MIST (genetically a yellow with color overlay):
yellow seedling 69-8

If LAVENDER FLIGHT were homozygous for the gene for pink or lavender, then all of its seedlings from the above three crosses would have this gene and therefore would show pink or lavender color. Since the listed seedlings do not show pink or lavender, then I conclude that LAVENDER FLIGHT is heterozygous for the gene that occurs in both pink and lavender.

From the results of crosses I have found that both I^P and I^L are present in certain clones that I thought looked like lavender-pinks. For example, MAY HALL, which has color more strongly pink than lavender but does have a lavender cast, produced a definite lavender-pink seedling when crossed with a pink (65-105). This lavender-pink seedling did not get the I^L gene from the pink parent (which does not have any lavender color), so it must have inherited I^L from MAY HALL. I stated earlier that the I^L and I^P genes also exist in yellows and melons although they do not influence the colo r of yellow or melon. By certain crosses I found that the yellow, 66-35, has both I^L and I^P. I know that 66-35 has the I^L gene because the cross 67-6 (pink) X 66-35 produced a purple seedling, which is genetically a deep lavender. This purple could not have inherited I^L from 67-6 (which has no lavender color) so it must have inherited I^L from 66-35. I know also that 66-35 has I^P, since a pink seedling, 69-50, came from LAVENDER PARADE (lavender) X 66-35 (yellow). The I^P gene was not inherited from LAVENDER PARADE, which has no pink color, so I^P must have come from 66-35-

Crosses of pink X lavender produce some lavender-pinks and often also some pink and lavender seedlings, or sometimes all three of these colors, in addition to other colors. Some pink X lavender crosses from which I have obtained both pink and lavender seedlings are:

LAVENDER FLIGHT (lavender) X ANNIE WELCH (pink)
LAVENDER PARADE (lavender) X PRAIRIE MAID (pink)
LAVENDER FLIGHT (lavender) X PRAIRIE MAID (pink)

The results of my crosses can be explained on the basis that: (1) The P gene occurs in all pinks, lavenders and lavender-pinks. (2) A pink daylily has a pink-influencing modifier, I^P. (3) A lavender daylily (pale lavender to purple) has a lavender-influencing modifier, I^L. (4) A lavender-pink daylily has both I^P and I^L.

A question arises: In lavenders, does a double dose of the P gene make a clone (PP) have deep-colored flowers? The answer is no. I have obtained purple seedlings that are heterozygous for P, so they are Pp. Examples of crosses that produced Pp purples are:

62-41 (melon, pp) X 64-84 (lavender, P-): purple seedling (Pp)
67-6 (pink, P-) X 66-35 (yellow, pp): purple seedling (Pp), 70-26

The purple seedlings from the above two crosses could have only one dose of the P gene since in each cross only one parent had the P gene. The deep color of purple and rosy-purple (deep shade of lavender-pink) is not due to a double dose of the P gene, but is due instead to color intensity modifiers.

In my first daylily genetics article I explained why I think there are color intensity modifying genes that are responsible for the range of shades in melons, yellows, pinks and yellow-pink combinations, the same series of modifiers affecting color intensity in all of these color groups. Melons range from very pale to deep (such as GEORGE CUNNINGHAM). Yellows range from very pale (such as ICE CARNIVAL), through various shades of yellow, to orange. Pinks range from very pale (such as SATIN GLASS) to rose. The yellow-pink combinations (those having a gene for pink and a gene for yellow) range in shades from pale peach, through apricots, to copper. Yellow-pink combinations that have the gene for drab, D, vary from buff, to tan, to brown.

I think that the same color intensity modifiers that cause the many shades of melons, pinks, yellows and yellow-pink combinations also cause the range of shades in lavenders and lavender-pinks. This means that the same one or more modifiers occurring in deep melon, deep pink and orange (genetically a deep yellow) also occur in purple (a deep shade of lavender) and deep lavender-pink (producing rosy-purple or wine). Therefore, in general, you can obtain some seedlings having deep lavender (purple) colored flowers by crossing a lavender with a daylily that has deep flower color, such as purple, deep pink (rose), deep melon, or orange (deep shade of yellow). Examples of such crosses that I have made are:

NEYRON ROSE (deep pink) X Spalding 58-13 (pale lavender):
rosy-purple seedling
66-42 (deep pink) X LAVENDER FLIGHT (medium lavender):
purple seedling
LAVENDER FLIGHT (medium lavender) X 68-24 (purple):
purple seedling
64-112 (gold - a deep shade of yellow) X LAVENDER PARADE (medium lavender):
rosy-purple seedling
LAVENDER PARADE (medium lavender) X MAY HALL (deep shade of lavender-pink):
deep lavender-pink seedling
67-49 (deep pink) X EMPERORS ROBE (medium lavender-pink):
deep rosy-purple seedling
62-2 (deep pink) X SOUTHERN HERITAGE (lavender):
deep wine (a deep lavender-pink) seedling

Although deeper shades of lavender and lavender-pink can be obtained by using at least one deep-colored parent, often a range of shades is obtained, some deep and some lighter shades. Also, as is true in melons, yellows and pinks, certain crosses involving lavender can produce some seedlings that are darker or lighter than either parent. Darker seedlings, which have a combination of color intensity modifiers from both parents, have come from these crosses:

(1) LAVENDER PARADE (medium lavender) X LAVENDER FLIGHT (medium lavender): one purple, one lavender having a deeper shade than either parent
(2) 64-84 (lavender) X LAVENDER FLIGHT (lavender): purple seedling
(3) LAVENDER FLIGHT (lavender) X DREAM MIST (pale yellow with color overlay): one light purple, one purple
(4) 66-7 (pink) X LAVENDER FLIGHT (lavender): rosy-purple seedling
(5) LAVENDER FLIGHT (lavender) X 66-35 (pale yellow): lavender

seedling having deeper color than LAVENDER FLIGHT
(6) DREAM MIST (pale yellow, with color overlay) X BLUE JAY (deep lavender): purple seedling
(7) LAVENDER PARADE (lavender) X PRAIRIE MAID (pink): rosy-purple seedling

I also concluded from the results of some of the above crosses that deep shades of lavender are not due to a double dose of the I^L gene, since the seedlings from crosses 4 and 7 could each have only one dose of the I^L gene (because only one parent in each cross had the I^L gene).

Usually you will not be able to get all deep shades in seedlings from a cross in which one parent has deep-colored flowers, and you will not be able to get all pale shades by using a parent with pale-colored flowers. However, you can direct the color range toward pale or deep shades in at least some of the seedlings by using a pale-flowered parent (if you want pale seedlings) or a deep-colored parent (if you want deep shades in the seedlings).

In my previous article I discussed the gene for drab (D) which is present in muddy pink, buff, tan and brown daylilies. The genetic symbols that I used were:

Y: yellow
y: melon
P: pink
P: not pink
D: drab
d: clear, not drab

A muddy pink (such as MARY ANNE) is yyP-D-, while a clear pink (such as EDNA SPALDING) is yyP-dd. The gene for drab does not affect the color of a yellow, which may be either Y-ppD- or Y-pedd. A peach, apricot or copper-colored clone is Y-P-dd, each having a different combination of color intensity modifiers. When these have the gene for drab added (Y-P-D-), they are buff, tan and brown, respectively. The D gene also affects the color of lavenders. For example, EMPERORS ROBE is a lavender-pink with the D gene, so its genotype is I^LI^PP-D-. By crossing EMPERORS ROBE with a deep clear pink (P-P-dd), I obtained a seedling (70-33) that is exactly the color of CHARLE-MAGNE. It is interesting that EMPERORS ROBE is a parent of both CHARLEMAGNE and my 70-33, these two clones having the same color. CHARLE-MAGNE is genetically the same as EMPERORS ROBE with the D gene eliminated and with increased color intensity. Thus the genotype of CHARLEMAGNE and my 70-33 is I^LI^PP-dd. In the above genotypes I have listed I^L and I^P as if they are alleles. I want to make it clear that I do not know whether they are alleles or whether they occur in two separate sets of genes, but I listed them because they are an essential part of the genotypes.

Dr. Toru Arisumi reported that red color in daylily flowers is inherited as a dominant (The .Hemerocallis Journal 24:9-14. 1970). In my last article (The Hemerocallis Journal 26:29-39. 1972) I added the information that a muddy red has a dominant gene for red (R) plus a dominant gene (M) that makes the color muddy, while a clear red has the gene for red (R) plus a double dose of recessive genes (mm) that make the color clear. I suspect that the M gene in reds is the same as the D gene in non-reds (such as pink), but have not done genetic tests to find out if this is true. A muddy red (R-M-) might be described as maroon. But certain non-red clones (those without the R gene) also appear maroon. The non-red maroons have the gene for pink (P), along with color intensity modifiers producing deep pink, plus the gene for drab (D). Thus a maroon that is genetically a "drab deep pink" (yyP-D-rr) is genetically different from a maroon that is a muddy red (----M-R-). It can be difficult to distinguish between these two kinds of maroons, but probably the drab deep pink is in many cases a lighter shade of maroon than the muddy red. However, I would not be sure I could distinguish between these two types of maroon by phenotype. Probably some drab deep pink types of maroon have the I^L gene, resulting in a "drab deep lavender-pink", which could be difficult to distinguish, by phenotype, from a drab deep pink (without I^L). Some maroons that are not muddy reds but that must be drab deep pinks (either with or without I^L) came from the following crosses in which both parents were non-red:

BROADMOOR GOLD (gold) X BROADMOOR AUTUMN (brown)
HORTENSIA (yellow) X PRAIRIE MAID (pink)
BURIED TREASURE (yellow) X SOUTHERN HERITAGE (lavender)
LIMONERO (yellow) X MARY ANNE (pink)
DREAM MIST (yellow with color overlay) X 64-64 (lavender)

It should be kept in mind that correct interpretation of daylily genetics is possible only if identification of flower colors is accurate. Therefore, one must learn to recognize at least a good portion of the basic colors to be able to use genetic information as an aid in breeding daylilies. Thinking of daylily flower color in terms of its genotype takes experience because of the many phenotypes, some of which may be difficult to interpret. However, in most cases it is possible to know at least part of the genotype by observing the phenotype. Knowing the parentage of a clone also can help you to fill in some of the genotype. Summarizing the information from this article and my previous article, I shall list first the genes involved in the main color types:

Y: yellow y: melon
P: pink or lavender
p: not pink or lavender
I^P: pink-influencing modifier
I^L: lavender-influencing modifier
D: drab
d: clear, not drab
R: red
r: not red
M: muddy (may be the same as D)
m: clear, not muddy (may be the same as d)

Second, I shall list the genotypes of the main daylily colors:

melon: yypprr
yellow: Y-pprr
clear pink: yyP- I^P-ddrr
muddy pink: yyP- I^P-D-rr
peach, apricot and copper: Y-P- I^P-ddrr
buff, tan and brown: Y-P- I^P-D-rr
lavender and purple: Y-P- I^L-ddrr or yyP-I^L-ddrr
lavender-pink and rosy purple (wine): Y-P- I^LI^Pddrr or yyP- I^LI^Pddrr
muddy-lavender-pink: Y-P- I^LI^PD-rr or yyP- I^LI^PD-rr
clear red: R-mm
maroon (muddy red): R-M-
maroon (drab deep pink): yyP- I^P-D-rr, with color intensity modifier(s) causing deep color

As mentioned in my first article, perhaps an orange-red has genes for both yellow (Y) and red (R), but this is not definitely known and is offered as a possibility to be tested. In addition to the above genes , there is a series of color intensity modifiers causing the numerous shades of each color. There is evidence that the same color intensity modifiers occur in the pale shade of each basic color, other combinations of mod ifiers occurring in the intermediate shades of each basic color, still another complement of modifiers in the deep shade. For example, the genotype for color intensity modifiers is the same in deep melon, orange (deep shade of yellow), rose (deep shade of pink), copper (deep shade of yellow-pink), brown (deep shade of drab yellow-pink), purple (deep shade of lavender) and rosy-purple (deep shade of lavender-pink).

For those daylily breeders who panic and run at the sight of genetics, I include the following practical information that can be used without any knowledge of genetics:

(1) Lavender and purple are alike genetically except for color intensity. Therefore, crosses of lavenders and purples will produce a high percentage of lavender and purple seedlings.

(2) Lavender-pink and rosy-purple (wine) are alike genetically except for color intensity.

(3) A cross of lavender X pink is likely to produce some lavender-pink seedlings.

(4) Crossing a lavender or lavender-pink (any color intensity from pale lavender-pink to rosy-purple) with lavender, melon, yellow, pink, peach, apricot, copper, buff, tan or brown can produce many possible colors, including lavender and lavender-pink. To get fewer muddy colors, avoid using muddy pink, buff, tan, brown and maroon.

(5) Sometimes lavenders and lavender-pinks are obtained from crosses in which neither parent is lavender or lavender-pink. Such crosses are listed elsewhere in this article.

(6) No lavenders are produced by these crosses: melon X melon, yellow X yellow, melon X yellow, pink X pink, pink X peach, pink X apricot, or pink X copper.

(7) You can breed for deeper shades of lavender and lavender-pink by making crosses in which at least one parent has deep color. For example, you can get some purple offspring from lavender X deep melon, lavender X rose (deep pink), or lavender X orange (deep yellow). This is useful if you want some purple seedlings but have no purple parent to use, or if you want to develop a purple with certain characteristics that are present in an available melon, pink or yellow.

(8) You can breed for pale shades of lavender and lavender-pink by crossing a lavender with a pale yellow (such as ICE CARNIVAL), pale

melon, or pale pink (such as SATIN GLASS).

(9) Therefore, if you have only one lavender (any shade from pale lavender to purple), you can get seedlings having flowers in any other shade of lavender by crossing your lavender with clones having pale or deep-colored flowers, depending on whether you want pale or deep lavender seedlings. This breeding method is helpful in tetraploid breeding since purple and lavender tetraploids are still relatively scarce and high-priced. When I buy a lavender or purple tetraploid, the shade of lavender will be of least importance. Instead I would choose one with high quality (size and form of flower, height of scape, bud count, vigor, etc.). Then I could use this one lavender to get tetraploid seedlings in any shade of lavender, including purple.

SOME BASIC HEMEROCALLIS GENETICS - Part 3

by Joanne Norton

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In my first two genetics articles (2, 3) I discussed the basic flower colors: melon, yellow, pink, lavender, lavender-pink, yellow-pink combinations, colors involving the D (drab) gene, and red. I did not discuss the patterns in which these colors occur. Many daylily flowers, of course, are not solid colored. It is the various color patterns that I shall discuss in this article. Before reading further you should be familiar with the material in my first two articles, including the symbols that I use for the various genes.

The patterns that I list below are the ones that I have seen many times in daylilies, but I do not mean to imply that they are the only patterns that exist. If there are other patterns, then either I have not seen them or else I have not recognized them. The patterns that I shall discuss, however, are the ones most often encountered in daylilies. They are:

(1) solid (petals and sepals about the same color)

(2) eyezone (circular pattern just outside the throat)

(3) dusted (flower appears finely sprinkled or dusted with pink, lavender or lavender-pink)

(4) bicolor (petals are some shade of pink, lavender or lavender-pink;

sepals are without or mainly without this color)

(5) bitone (sepals are more strongly colored than petals with pink, lavender or lavender-pink)

(6) edged (flower segments are edged with pink, lavender or lavender-pink)

A pattern that I am not including in the present discussion because I do not have enough information about it is one in which a solid colored flower (such as red, pink, apricot and others) has either pale or yellow edges on the petals and sepals.

I have never seen a red daylily in a bicolor or bitone. Also, I have never seen one edged with red or dusted with red. Some red flowers have a band of deeper red just outside the throat, which perhaps is an eyezone. Some flowers have a pattern (dusted, bicolor, bitone or edged) in deep rose, which I think is genetically deep pink, not red. Therefore, I think that a flower having the dominant gene for red (R) has red all over, except for the throat in some cases. Thus the patterns, except perhaps for eyezone, have not been visible in any red that I have seen, although I think it most likely that reds can carry genes for these patterns that do not show because the entire flower has red pigment.

For the patterns to be expressed, there are genes present that cause the patterns. In addition, and this must be kept in mind, the patterns are expressed only when the P gene is present. This is the gene that occurs in the following colors:

pink, all shades from pale pink to rose (yyP-I^P-dd)

lavender, all shades from pale lavender to purple (yyP-I^L-dd)

lavender-pink, all shades from pale to rosy-purple (yyP-$I^L I^P$-dd)

drab pink or lavender-pink (yyP-D-)

peach, apricot and copper (Y-P-dd)

buff, tan and brown (Y-P-D-)

Since the patterns are not expressed when P is absent, they never appear in a melon (yypp). This is the reason there is no melon with an eyezone.

Much of the genetics of color patterns is not known, but these things I have found:

1. All of the patterns (eyezone, dusted, edged, bicolor and bitone) are expressed only if the P gene is present.

2. The color of the pattern is influenced by the same modifiers of P (IL and IP) that affect the color of a solid colored flower involving P.

3. More than one pattern can appear in the same flower. I have seen these combinations:

solid plus eyezone	bicolor plus eyezone
solid plus edged	bitone plus eyezone
dusted plus eyezone	edged plus eyezone

I do not know if other combinations are possible, but do know that I have observed the above combinations.

4. Although two patterns may be expressed simultaneously, many clones have only one pattern visible.

5. I do not have enough information to know whether three patterns can be expressed at once, but do have records of seedling 69-58 which was pink with a deeper pink eyezone and deeper pink on the edges of the flower segments.

Fifteen years ago Dr. Philip G. Corliss (1) stated that eyezone is due to a dominant gene. I think that he probably was right, as I have found that using a parent with an eyezone usually (perhaps always) gives seedlings in which some have eyezones. If eyezone were recessive, then crossing eyed X not-eyed would only sometimes give some eyed offspring. I think, however, that one of Dr. Corliss' reasons for thinking eyezone is dominant was erroneous. He incorrectly assumed that his GOLDEN PINAFORE (registered as a cadmium orange self) had no eyezone because its parents (which had eyezones) must have been heterozygous, each having one dominant gene for eyezone and one recessive gene for no .eyezone. He did not realize that the eyezone pattern is not expressed in yellows (without the P gene), and therefore that his GOLDEN PINAFORE might actually have a dominant gene for eye-zone, not being expressed because the P gene was not present. He thought that two parents without eyezone would never produce any seedlings with eyezone. This is not the case. If either a melon, or a yellow without the P gene, is crossed with a daylily having the P gene (such as pink, lavender, lavender-pink, peach, brown), in some cases you will get some seedlings with an eyezone, depending on whether or not the melon or yellow parent has the gene for eyezone. Four examples from my records are:

LAVENDER FLIGHT (lavender) X 66-35 (yellow): 70-4 (lavender with a deeper lavender eyezone)

BROADMOOR SUNSET (melon) X MAY HALL (lavender-pink without eyezone): 71-32 (pink with deep pink eyezone)

BURIED TREASURE (yellow) X LOVE THAT PINK (pink without eyezone): 68-9 (peach with deep pink eyezone)

BROADMOOR SUNSET (melon) X MAY HALL (lavender-pink without eyezone): 69-137 (pink with deeper pink eyezone)

In the above four examples, I think that the gene for eyezone in the seedlings came from their melon or yellow parent.

Dr. Corliss (1) thought that bicolor was due to a recessive gene, even though he noted, "I rarely use bicolors in breeding unless the bicolor has a greatly desired characteristic other than the color, for the offspring are usually bicolors,—" He again was thrown off in his reasoning by the fact that the bicolor pattern is not expressed unless P is present, which he did not know. He stated, "—you get bicolors from many crosses not involving parents that are bicolors. Thus, my EVERMORE is a bicolor whose parents are (red) and (yellow)—BLANCHE HOOKER and AMUR VALLEY." From my recollection of the color of BLANCHE HOOKER, I do not think it was a true red (with the R gene) but that instead it had the P gene. I think that EVERMORE inherited P from BLANCHE HOOKER and the gene for bicolor (which I think is a dominant) from the yellow parent in which this gene was not expressed because the yellow parent did not have P. The remainder of his article (page 112) is incorrect, based on erroneous conclusions. I have obtained bicolors from two non-bicolors, but only when one of the parents was either yellow or melon. Crossing two non-bicolors that both have P has never produced any bicolor offspring. I think that bicolor is dominant to solid color involving P, and that you will get many bicolors if one or both parents are bicolors. The reason that you sometimes get bicolors from two non-bicolor parents is that the gene for bicolor is not expressed unless P is present, and therefore the dominant gene for bicolor can be present without showing in a yellow or a melon. This of course does not mean that the gene for bicolor is present in all yellows and melons. I obtained bicolor seedlings from the following crosses, which in all cases used one parent that was either yellow or melon:

COSETTE (yellow dusted rose) X yellow seedling: 61-69 (pink and yellow bicolor)

LIME ICE (yellow) X 59-29 (lavender-pink): 61-76 (pink and yellow bicolor)

MADRIGAL (apricot blend) X FRANCES FAY (melon): 63-11 (pink bicolor)

59-23 (buff) X LIME PAINTED LADY (yellow): 65-15 (buff and yellow bicolor)

BROADMOOR SUNSET (melon) X LOVE THAT PINK (pink): 70-17 (deep pink and apricot bicolor)

BRIGHT LIGHTS (pink) X 66-35 (yellow): 70-21 (pink and cream bicolor)

KINGS GRANT (apricot) X 66-35 (yellow): 70-32 (pink and cream bicolor)

In a solid colored flower involving the P gene (pink, lavender, lavender-pink, peach to copper, buff to brown) and also having the dominant gene for eyezone, the eyezone color is always the same basic color as the petal color. For example, a pink flower can have a deeper pink eyezone, but not a purple eyezone. A lavender flower can have a deeper lavender eyezone but never an eyezone in any shade of pink. The I^L and I^P modifiers of P thus affect the basic color of not only the petals and sepals but also the eyezone color. Therefore, there is no point in trying to breed for a pink flower with a purple eyezone, or a lavender flower with a rose (deep pink) eyezone. Examples of my solid-colored (this solid color involving P) seedlings that have the same basic color in petals, sepals and eyezone are:

65-42 (rose with deeper rose eyezone)

65-35 (buff with deeper buff eyezone)

67-55 (lavender-pink with deeper lavender-pink eyezone)

68-9 (pink with deeper pink eyezone)

68-23 (deep pink with deeper pink eyezone)

68-24 (purple with deeper purple eyezone)

68-33 (lavender with deeper lavender eyezone)

68-66 (deep buff with deeper buff eyezone)

68-74 (apricot with deeper apricot eyezone)

68-83 (pink with deeper pink eyezone)

68-85 (pink with deeper pink eyezone]

69-6 (drab pink with deeper drab pink eyezone)

69-22 (pink with deeper pink eyezone)

69-32 (maroon with deeper maroon eyezone)

69-45 (lavender with purple, deep lavender, eyezone)

69-57 (rosy-purple with deeper rosy-purple eyezone)

69-59 (deep pink with deeper pink eyezone)

69-62 (pink with deeper pink eyezone)

69-64 (brown with deeper brown eyezone)

69-66 (pink with deeper pink eyezone)

69-69 (pink with deeper pink eyezone)

69-70 (maroon with deeper maroon eyezone)

69-75 (pale pink with deep pink eyezone)

69-78 (pale pink with deep pink eyezone)

69-95 (pale pink with deep pink eyezone)

69-105 (deep lavender with deeper lavender eyezone)

69-110 (deep drab pink with deeper drab pink eyezone)

69-117 (lavender-pink with deeper lavender-pink eyezone)

69-121 (lavender with deeper lavender eyezone)

69-123 (lavender-pink with deeper lavender-pink eyezone)

69-137 (deep pink with deeper pink eyezone)

69-138 (pink with deeper pink eyezone)

70-4 (lavender with deeper lavender eyezone)

71-32 (pink with deeper pink eyezone)

72-1 (purple with deeper purple eyezone)

72-4 (pale drab pink with deeper drab pink eyezone)

The seedlings listed above, which are all of the eyed seedlings for which I recorded the eyezone color, all have solid color involving the P gene. There are no exceptions, in my records, to the rule that the eyezone and petals (when P is involved in petal and sepal color) are the same basic color, differing in color intensity, the eyezone being darker than the petals and sepals. The same rule holds true for the pattern combinations of dusted plus eyezone, bicolor plus eyezone, bitone plus eyezone, and edged plus eyezone. Examples of my seedlings with these combinations are:

Dusted plus eyezone:

65-37 (lavender dusting, deep lavender eyezone)

68-37 (deep lavender dusting, deep lavender eyezone)

69-46 (lavender dusting, deeper lavender eyezone)

Bicolor plus eyezone:

65-50 (lavender and cream bicolor with lavender eyezone)

65-65 (pale lavender and cream bicolor with deeper lavender eyezone)

Edged plus eyezone:

64-84 (cream with lavender edging and lavender eyezone)

Bitone plus eyezone:

67-18 (lavender and yellow bitone with deeper lavender eyezone)

It is not possible to get mixed colors in any of these pattern combinations. Therefore, we will not be able to get such combinations as a pink dusted flower with a lavender eyezone or a lavender bicolor with a pink eyezone.

There are genes in daylilies that affect the distribution, or patterns, of color caused by the P gene. When the P gene is expressed throughout the flower, we get a solid color in any of the many colors excluding melon, yellow, and those having the gene for red (R). However, if the gene causing overall expression of P (solid color pattern) is not present or is suppressed by a gene dominant or epistatic to solid color (I do not know how these genes are inherited), then P will be expressed in a pattern that does not entirely cover the petals and sepals. These other patterns (eyezone, bicolor, bitone, dusted and edged) each have P expressed in different areas of the flower. In eyezone, P is expressed in a band, of varying width and color intensity, just outside the throat. In a bicolor,

is expressed in the petals but little or none in the sepals. In a bitone, P is expressed mainly in the sepals and not as strongly in the petals. In dusted, P is expressed as fine dots or sprinkling of color on the petals and sepals. In edged, P is expressed on the edges of the flower segments. In a daylily flower having the genetics for solid color due to P, there is a combined effect when the gene for yellow, Y, is also present. This gives us solid colors in the yellow-pink combinations (shades of peach, apricot, copper, buff, tan and brown). However, in a flower that does not have the genetics for solid color, but which does have genetics for both pink (P) and yellow (Y), then the yellow color shows in the parts of the flower where P is not exposed. But, in the areas of the flower where P is expressed, the gene for yellow often has less influence than it has in a solid colored yellow-pink combination. Thus a bicolor can have pink (petals) and yellow (sepals), an eyed flower may be yellow with a pink eyezone, etc.

I have pointed out that the hybridizer has no choice on the basic color of the eyezone in a solid colored flower with its color involving the P gene. These colors are pink (yyP-I^P-dd), drab pink including pale to maroon (yyP-I^P-D-), lavender (--P-I^L-), lavender-pink (--P-$I^L I^P$), yellow-pink combinations including peach to apricot to copper (Y-P-I^Pdd), and drab yellow-pink combinations in shades of buff to tan to brown (Y-P-D-). However, if the flower does not have the genetics for solid color involving P, the rest of its genotype will be the same as in one of these colors, but P will not be expressed throughout the petals and sepals. Then, with the gene for eyezone (E) added, the P gene will be expressed only in the eyezone area. In such a case, the eyezone color is decided by P, I^L and I^P. If the genotype 'includes P-In, the eyezone will be some shade of pink. If the genotype includes P-I^L, the eyezone will be some shade of lavender (lavender to purple). If the genotype includes P-$I^P I^L$, the eyezone will be some shade of lavender-pink (pale to rosy-purple). If the Y gene is also present, then the flower will be some shade of yellow, with an eyezone. I suspect that when the Y gene is not present that the petal and sepal color is cream, in an eyed flower that does not have genetics for solid color involving P. While you have no choice of eyezone basic color in a solid colored flower in which P is expressed throughout the petals and sepals, you do have a choice of eyezone in a flower that does not have the genetics that causes the P gene to be expressed throughout the petals and sepals. Therefore, it is possible to get either cream colored (probably without Y) or yellow (with

Y) flower color along with eyezone in a number of possible shades of pink, lavender or lavender-pink. Some examples of my seedlings in which P is not expressed throughout the petals and sepals but in which there is an eyezone whose color is decided by P, I^L, I^P and modifiers affecting the color intensity of the eyezone, are:

65-83 (peach with purple eyezone)

67-57 (peach with deep pink eyezone)

67-59 (pale yellow with lavender eyezone)

68-40 (cream with lavender eyezone)

68-62 (cream with pale maroon eyezone)

68-84 (cream with lavender eyezone)

69-9 (cream with lavender eyezone)

69-30 (yellow with wine eyezone)

69-68 (cream with purple eyezone)

70-20 (gold with maroon eyezone)

I have already explained that the P gene can be expressed in a solid pattern as well as in other patterns, which include eyezone, bicolor, bitone, dusted and edged. One pattern may show, or certain combinations of two patterns are possible. The genes for these patterns are present, but do not show, in melon (yypp) and yellow (Y-pp), neither of which has the P gene. Eyezone is dominant to no eyezone, and bicolor is either dominant or epistatic to solid color, as I have discussed. The genetics of the other patterns is unknown, but I am listing the crosses below to show some that have produced seedlings with bitone, dusted or edged pattern.

Bitone seedlings came from:

SATIN GLASS (solid pink) X 64-84 (edged): 67-18 (lavender and yellow bitone)

PRESIDENT MARCUE (yellow) X MARY ANNE (solid pink with eyezone): a lavender-pink bitone

62-21 (gold) X MARY ANNE (solid pink with eyezone): 64-103 (pink bitone)

63-17 (gold) X SPALDING 58-13 (solid lavender): 66-25

(lavender and yellow bitone)

CAPTAIN RUSSELL (lavender bicolor) X SPALDING 58-13 (solid lavender): 65-14 (lavender bitone)

64-7 (gold) X FIRST FORMAL (solid pink): 68-68 (orange and deep pink bitone)

Dusted seedlings came from:

SATIN GLASS (solid pink) X 64-84 (edged): 67-13, 67-17, 67-27

64-84 (edged) X LAVENDER FLIGHT (solid lavender): 68-37

65-65 (bicolor) X BROADMOOR FANTASY (bicolor): 69-46, 71-2

67.26 (solid lavender) X LAVENDER FLIGHT (solid lavender): 71-25

Edged seedlings came from:

CAPTAIN RUSSELL (lavender bicolor) X Spalding 58-13 (solid lavender): 64-84

62-2 (solid lavender-pink) X 64-106 (solid buff): 68-75

LAVENDER FLIGHT (solid lavender) X 65-18 (solid lavender): 69-27

Concerning the controversy over which has more merits, a diploid or a tetraploid daylily, I would like to point out that the large number of genes involved in daylily flower color alone are difficult enough to investigate in diploids. I think that Hemerocallis genetics will be worked out in diploids first, then later applied to tetraploids, in which more genetic combinations are possible.

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