Classic Genetics, Hybridizing of Hemerocallis and Current Techniques[1]

Terrence P. McGarty

Abstract

The hybridizing of the Genus Hemerocallis has been performed for just over a hundred years and within the past thirsty there has been an explosive growth in the effort. The hybrids being introduced have a significant amount of variation in color and form and they flower is changing in ways that have been generally unpredicted a generation ago. There are various color and more importantly various shapes. In this paper we address the hybridizing from a classic Mendellian viewpoint and then look at many of the hybridizers over the past hundred years. Our goal is to provide some insight into the hybridizing process by looking at the fundamental scientific basis and then looking at the approach actually by many of the well respected hybridizers.

Contents

1 INTRODUCTION

The process of hybridizing plants is an old one and it has been developed over centuries if not over millennium. The most recent first step in improving the process with some scientific basis was the use of Mendellian methods. This paper will review the classic Mendellian approach, the classic breeding approaches to seek out traits and then we will review some methods employed in current day hybridizing.

Hybridizing as is performed in the genus Hemerocallis is in many ways akin to the classic approaches use in farm crops as well as horse breeding. The goal of Hemerocallis hybridizing depends upon the hybridizer and most current hybridizers are interested in incrementally adding to the stock of "different looking" flowers. Very few of the current hybridizers are approaching the genus with scientific inquiry but the data is available with the AHS database to seek out some of these characteristics.

The approach we take herein is focused on looking at the process as a Mendellian. There is in this paper no focus on modern genetics but as we have discussed early on the Mendellian approach has its limitations. What may appear as a surprise for a Mendellian may be just a natural progression for a current generation plant geneticist.

Hybridizing is also an area where technique and technology can blend. For many hybridizers their approach is more of an art than a science. Underlying the basis of hybridizing is the genetic makeup of the plant but the genetics can be so complex and possible not understandable to many of the hybridizers. Their approach is to build upon the work of others. Thus hybridizing as currently practiced is an art of good guessing and good crosses.

In this Paper we further develop some of the classic Mendellian methods of analysis and synthesis. As we have stated elsewhere these are somewhat crude methods which may apply to certain gross characteristics as pea color and size but when applied to specific flower color and complexity have been found wanting. The methods may still have significant use and utility when trying to induce more extensive branching as an example, whereas the ability to control such characteristics as eyezone the techniques may get called into question.

The objectives of this paper are:

1. Summarize the insights of the Mendellian approach and to understand its limitations, to better see what the principles are and to see where the hybridizers have been focusing in applying these methods, if at all.

2. To understand some of the implications of Mendellian genetics to see how inbreeding may result in the introduction of certain traits into a plant line lacking such traits. These methods have been successful in the many types of plants used for food such as grains.

3. To establish a process and methodology for breeder or hybridizers. This means the setting of reasonable goals and the methods which may be employed to achieve those goals.

4. To review and understand the various standard methodologies used I breeding and their advantages and disadvantages.

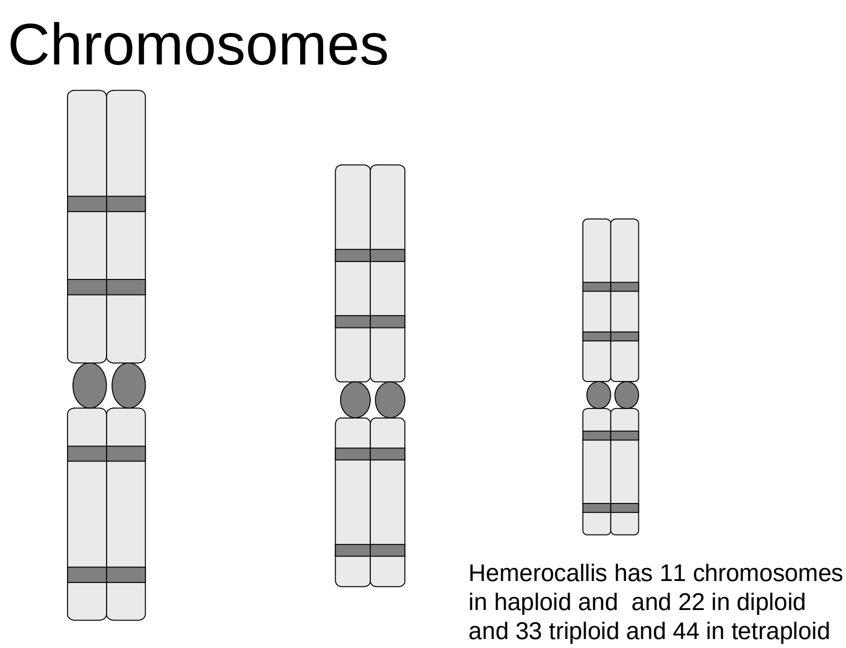
5. To look at the evolution of hybridizing in the United States of Hemerocallis and to attempt to understand how the principle developed herein were and will be applied.

2 CLASSIC MENDELLIAN CONCEPTS

The Classic Mendellian approaches are all based upon the Mendel model of the gene and traits. Unlike what we look at in modern day genetic analysis, the classic Mendel or Mendellian approach looks at chromosomes and then at genes. The gene then becomes the effector of the characteristic we are trying to duplicate, enhance, eliminate, or whatever. The Mendellian paradigm of the "gene" is a gross concept that links a phenotypic characteristic such as color, height, branching, or whatever, to a specific Mendellian gene. There is assumed to be a one to one and un-modifiable relationship between this gene and the phenotypic character.

In Mendellian analysis we assume that there exists a gene on a chromosome which provides some characteristic, say yellow petals. Hemerocallis has 11 chromosomes with a diploid being the normal configuration. There is no sex chromosome as in humans. There are triploids with 33 chromosomes and tetraploids with 44 chromosomes. But the species has 22 in each cell. We characterize this as shown below.

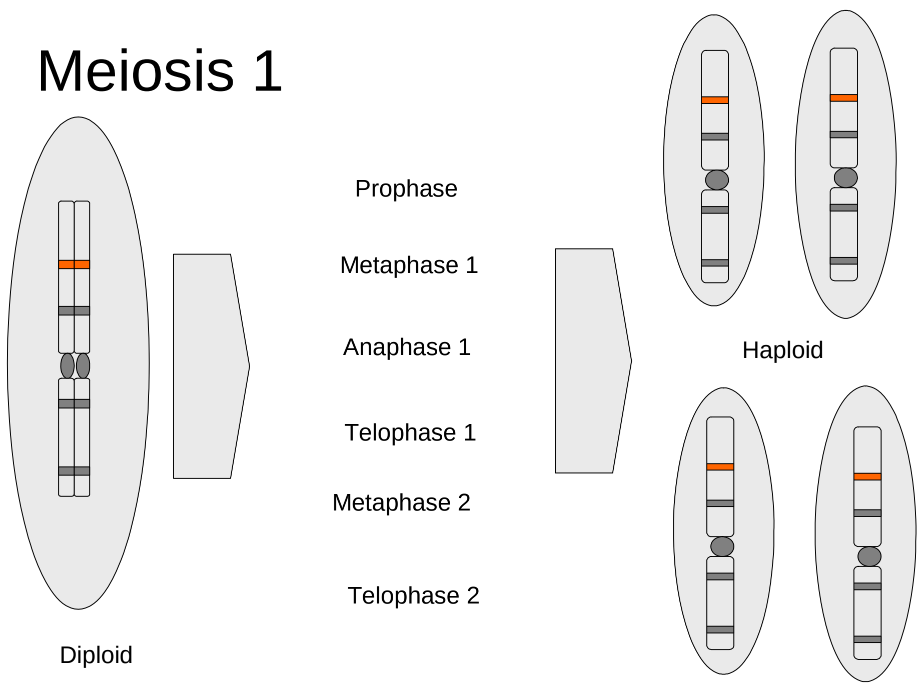
Table 1 Chromosomes and Genes



Now each chromosome with some gene segment has some controlling characteristic, such as a gene for the color orange. In the process of meiosis in the sex sells the chromosome pairs split, some even cross over, and a mixing and matching of chromosomes and genes are made. Our intent is not to provide a detailed summary of Mendellian analysis but to focus on the key points which will be used to continue our analysis.

When a plant creates a pollen grain or a female oocyte they are products or meiosis. And these cells are haploid, namely only one copy of the chromosome. Thus is we have two orange genes, one on each chromosome, and then in meiosis we end up with a male and female haploid cell each having one orange gene.

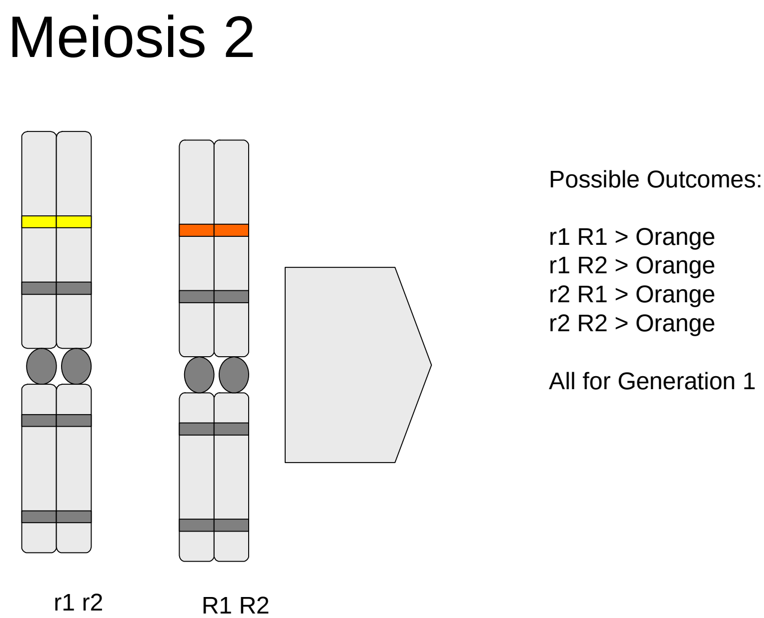
Table 2 Meiosis Step 1



If, however, we take a yellow plant, allow it to create the haploid cells via meiosis and take a pure orange plant, let it create haploid cells via meiosis and then cross these plants we get what we see below.

Namely there are four possibilities, each equally likely; we have a yellow with an orange in any one of the ways shown below. Thus in what is called the F1 generation we only get orange plants since the orange gene is dominant and each of the F1 plants have the same genetic makeup, a haploid with a yellow and a haploid with an orange.

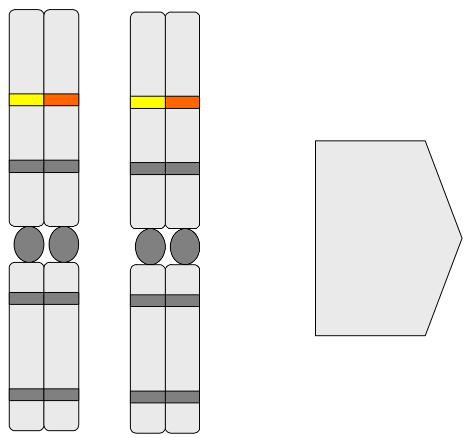
Table 3 Meiosis Step 2



Now we go to the F2 generation. This is the offspring of the F1. Remember that all F1 have same gene structure, a yellow and an orange gene. These break apart in meiosis and combine again when the plants are fertilized. The net result in the off spring in F1 is a set of chromosomes with a yellow and orange chromosome. When they split there is a possibility of the off spring of the off spring in the F2 to have two yellows which means yellow or one of each yielding orange or a pure orange. Thus with one gene we find that a dominant gene will give $1/4^{th}$ with the recessive and $3/4^{th}$ with the dominant color. We show this below.

Table 4 Meiosis Step 3

Meiosis 3



Possible Outcomes:

r1 r2 > Yellow

r1 R2 > Orange

R1 r2 > Orange

R1 R2 > Orange

3 BASIC MENDELLIAN GENETIC ANALYSIS

Before proceeding to the issues of hybridizing, we will consider some basic Mendellian genetics as a framework for helping to understand how to perform the hybridizing tasks. Let us make the following assumptions, which are what Mendel made in his experiments and analyses:

1. There exists a construct on the chromosome called a gene.

2. Let us assume that chromosomes come in pairs and that each chromosome has a gene which has the effect that we are trying to analyze. This in a Hemerocallis species there are 11 chromosomes and they come in pairs so there are 22 chromosomes and there are genes on each one of the chromosomes.

3. The gene can be one of several types; we generally assume that there are just two types of genes. We label these say A and a and two genes.

4. A gene yields a phenotypic characteristic which we can observe. Gene A yields one type of phenotypic characteristic and gene a another. We assume that these characteristics are clearly distinct. They may be the presence or absence of an eyezone in a flower.

5. The gene controls a characteristic of a flower or plant and that the gene is the sole control element of that characteristic.

6. That there exist dominant and recessive genes. The dominant gene if present yields the phenotype consistent with that gene whether there is one or two of those genes present.

We must understand, however, that the Mendellian gene construct differs widely from the current understanding of a gene in many ways. We will return to this in later papers.

To understand the world view of Mendel, one must understand that he worked with peas primarily and he did extensive crossing and observed clear and delimited traits. There were limited colors and limited shapes. It would be akin to a daylily leaf, being grass-like or broad, long and heavy, H minor versus H fulva. It was clear what the difference was.

The Mendellian analysis did not try to account for subtle and sophisticated variations in form, shape, color of the highly hybridized daylily.

3.1 Simple Crosses

We begin with a simple cross between two plants. Let us assume that there is a characteristic which can take one of two states. We further posit that the character is controlled by a single "gene" and we call that gene A or a, depending on the state that is taken. Now let us assume that we have two plants; plant 1 and plant 2. Furthermore we somehow "know" that Plant 1 is AA and Plant 2 is aa, namely Plant 1 has two genes on the two chromosomes that are both type A and likewise for plant 2 they are both a. Then we ask, what happens if we were to cross breed these two plants. Let us assume for example that A yields no eyezone and a yields an eyezone.

Before proceeding we must say a bit more about the gene mechanism. We say that the gene A is a dominant gene and that the gene a is a recessive gene. What do we mean by that? We mean that if one or both of the chromosomes have an A gene then the characteristic generated by A will be in evidence. If, however, the plant were to have two a genes then the character related to a would be in evidence. Dominant means that as long as there is at least one then its effect is evident. Recessive means that no matter what we can only have the a gene present.

Understanding the current world of transcription, we know now that on a gene paid on two bound chromosomes of DNA, the reading of the gene to the RNA is done on only one of the genes, never both. Thus this currently understood fact may help explain what happens. If A is on one or both of the chromosomes, then A forces the transcription process, no matter what, leaving an a gene un-transcribed.

Let us go back to this simple cross. We take the two genes of the recessive eyezone and place them across the top. We take the two genes of the pure dominant and place then along the side. Then the possible outcomes when we combine these two through breeding or hybridizing are shown in the Table below.

	a	a
A	aA No Eye	aA No Eye
A	aA No Eye	aA No Eye

Before looking into the details let us analyze this methodology. Each of the two parents has two chromosomes and on each chromosome there is a gene. In the dominant parent this means that we have a gene A on one chromosome and a gene A on the other. These are identical genes but NOT the same gene. In the Mendellian analysis it assumes that either gene may act. In a similar manner we have the same situation for the recessive gene, a, and there are two of them. Thus when the parents combine their chromosome into a new plant, the new plant has one chromosome from each parent. This simply means it gets an A from the dominant and an a from the recessive. In the above the row across the top lists all possible genes from the recessive and the column to the left all possible chromosomes from the dominant. Even if they are both identical they represent two genes, one from chromosome 1 and one from chromosome 2. Another way to look at this is to write the Table as below:

	a1	a2
A1	a1A1 No Eye	a2A1 No Eye
A2	a1A2 No Eye	a2A2 No Eye

Which is identical to the above except now it shows gene and chromosome.

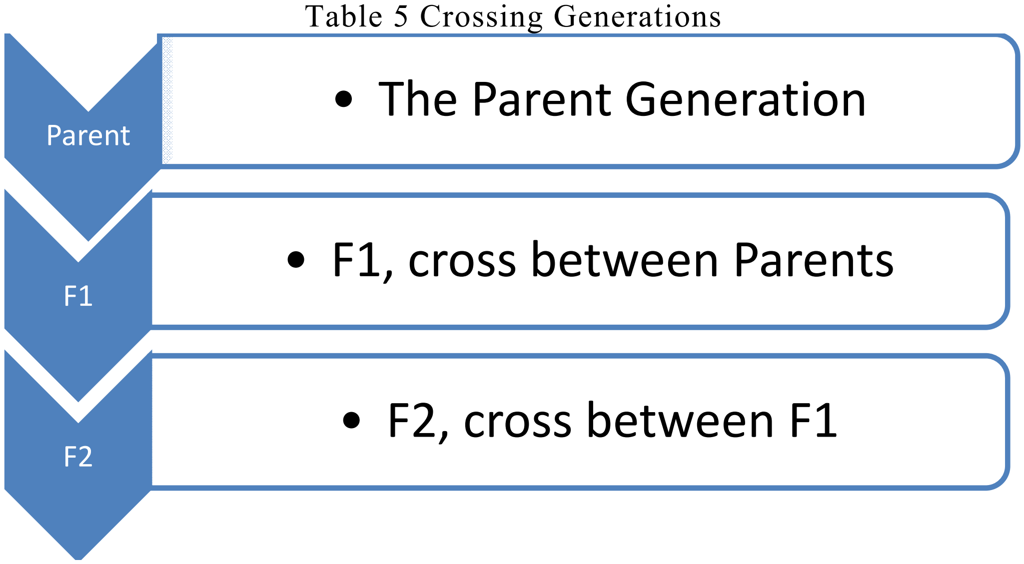
We can now take this one step further as an attempt to clarify the detail. If we call the parent in the top row as 1 and the parent in the left column as 2 we have gene:chromosome:parent as a tuple. This we show below:

	a:1:1	a:2:1
A:1:2	[a:1:1, A:1:2] No Eye	[a:2:1 , A:1:2] No Eye
A:2:2	[a:1:1 , A:2:2] No Eye	[a:2:1 , A:2:2] No Eye

The details here are complete. Each heading, row or column, species a parent gene and its sours, namely what chromosome and what parent. It also specifies what specific gene it is. This level of detail will greatly assist in complex analyses.

Now the result of this crossing yields what we call the F1 generation, the off -spring from two pure bred plants. Let us define the generations since we will use them again.

Table 5 Crossing Generations



Now we would know they are pure bred after the fact if and only if there were no eyezones, in any offspring. That of course is not practical. We can statistically say that one parent is AA if a large number are without eyezones. We will come back to that later.

Now assume we take one of the F1 offspring and breed them with another F1 offspring. What do we get? Well, all of them have aA gene pairs on their chromosomes. Thus if we create the same map as before this time we have:

	a1	A2
a1	a1a1 Eye	a1A2 No Eye
A2	a1A2 No Eye	A2A2 No Eye

Thus in this simple case we have a chance of one in four, 1:4, or 25% that there will be an eye zone.

Now what does this tell us about hybridizing daylilies. Frankly, there is very little. Mendel had peas, and he was looking at peas all one color, one gene one phenotype. There was no mixing, no complicated gene control. There could be a simple control of a gene and a phenotypic characteristic.

For example, if we had a daylily with an eyezone and bicolor and no eyezone was dominant as was an non bicolor, then the table below predicts the result. This means that we have two genes, one pair being B and b and the other A and a. The b gene is for a bicolor and the a gene for an eyezone. This is the classic Mendel analysis. We show the Table below for the example of an A and B gene with a dominant A and dominant B and the recessives a and b.

To perform this analysis let us assume we start with two purebreds as before, but this time we have:

Plant 1: The following genes are available; A, A, B, B (no eye zone and no bicolor)

Plant 2: a, a, b, b (eyezone and bicolor)

The results for the F1 generation are as follows:

	AB	AB	AB	AB
ab	AaBb	AaBb	AaBb	AaBb
ab	AaBb	AaBb	AaBb	AaBb
ab	AaBb	AaBb	AaBb	AaBb
ab	AaBb	AaBb	AaBb	AaBb

Note we could clarify this by noting that the genes across the top are A1, A2, B1, and B2 all from the dominant parent. Likewise for the column we would expect to see the same.

However, this is not the case. Go back and look at the species and then look at the hybrids. How does one go from here to there? That is a key question. Genes are being expressed differentially in various was and the control of those expressions varies across the sepal and petal. That is an issue we wish to explore.

Now cross the parent with any F1. There are two possibilities; the dominant parent or the recessive parent. First the dominant crossed with F1.

	AB	AB	AB	AB
ab	AaBb	AaBb	AaBb	AaBb
aB	AaBB	AaBB	AaBB	AaBB
Ab	AABb	AABb	AABb	AABb
AB	AABB	AABB	AABB	AABB

The row across the top is as was before. Now, however the column on the left represents the possible 2-tuples from the F1 crosses. Note that we can combine the 4-tuple four different ways two at a time. Again as with F1 all are controlled by the dominant genes. We would observe no difference. Now cross F1 with the fully recessive. We obtain:

	ab	ab	ab	ab
ab	aabb	aabb	aabb	aabb
aB	aabB	aabB	aabB	aabB
Ab	AAbb	aAbb	aAbb	aAbb
AB	aAbB	aAbB	aAbB	aAbB

This yields:

1. 4 with eyezone and bi-color
2. 4 with eyezone
3. 4 with bi-color and
4. 4 as the dominant

This is called a backcross.

3.2 Complex Crosses

One of the more complex issues arises when we consider tetraploids. In Hemerocallis, with the induction of a tetraploid, each parent has four chromosomes and thus four genes. The gamete cells have in them two chromosomes instead of the one so that when they combine the resulting cell again has four. This adds a bit of complexity. Now we can have the following if we have two homozygous cells:

Pollen Cell (Plant 1): A:1:1, A:2:1, A:3:1, A:4:1

Ovary Cell (Plant 2): a:1:2, a:2:2, a:3:2, a:4:2

and they can be combined two at a time. Thus we can see:

(A:1:1, A:2:1), (A:1:1, A:3:1), (A:1:1, A:4:1), (A:2:1, A:3:1), (A:2:1:, A:4:1), (A:3:1, A:4:1)

and the same for the recessive plant;

(a:1:1, a:2:1), (a:1:1, a:3:1), (a:1:1, a:4:1), (a:2:1, a:3:1), (a:2:1:, a:4:1), (a:3:1, a:4:1)

Using this methodology we can be certain that we track all possible chromosome pairings. This becomes dramatically more complex by just adding another trait.

3.3 Genes, Dominance, Color

Having gone through several examples in the above crosses we may ask if there are genes for dominance of certain colors, shapes, and variegations in Hemerocallis, specifically we would start with color. In a paper by Joanne Norton[2] in the Daylily Journal in the 1970s, the author makes a set of statements, regrettably with absolutely no scientific basis in fact, concerning the Mendellian genetics of Hemerocallis and hybrids. It is regrettable that such is done because she may very well have had some basis for her statements other than purely anecdotal and that would have helped greatly. However Norton appears to be somewhat knowledgeable but in her rather heavy handed statements, without any evidence presented, calls all her work into question[3].

Notwithstanding we try to summarize her results and to comment based upon our experience. The reason for this attempt is the otherwise total lack of any discussion regarding the hybridized version of the genus. Recently Hart has re-presented the Norton work in a more readable and up dated format which is helpful. However, Hart just represents the Norton work and does not seem to have added any fundamental experimental data analysis. However, we do believe that it is worth the exercise to study Norton because she presents questions in a Mendellian manner which can ultimately be proven correct or not. Yet we also have shown that the Mendellian approach to color and pattern formation is greatly wanting. It totally fails to address the epigenetic issues and also fails to deal with the secondary pathway problem.

To ascertain the true relationships, however, one must perform a detailed experimental study to ascertain the true relationships and dominance. In addition, as we had discussed herein, the color question is quite complex since it is gene expression through secondary pathways and this complex set of relationships transcends the simplistic single gene theory espoused by Norton.

(1) Color

Assertion 1: There is a dominant gene for pink, P, and the recessive gene p is homozygous in all yellows, namely pp.

Assertion 2: There is a dominant gene for yellow, Y, which is in all yellow plants.

Assertion 3: Y and P may or may not be "alleles", namely on the same chromosome.

Assertion 4: There is a dominant gene for red, R.

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[2] Norton received bachelor's, master's and doctorate degrees in botany from The Ohio State University. Following her graduate work, she was on the faculty at the University of Texas for about two years. http://www.wheresoursquirrel.com/cgi-bin/fish/YaBB.cgi?board=live;action=display;num=1121912943

[3] See Norton p. 2 where she states "my records would be much more useful if I had kept descriptions of all the seedlings..." The fact that we are making conclusions on a selected set invalidates any and all claims.

Assertion 5: All cream, pale yellow, medium yellow, gold and orange plants have Y but no P. Yellows are YYpp or Yypp.

(2) Form

Assertion 1: There are six forms or patterns of flowers[4]:

- Solid
- Eyezone
- Dusted
- Bicolor
- Bitone
- Edged

Assertion 2: For the pattern to be expressed there must exist a gene for that pattern and it must dominate.

Assertion 3: All the patterns are expressed if and only if the P gene is present.

Assertion 4: The color of the pattern is controlled by the same modifiers of P that affect the color of a solid color containing P.

Assertion 5: More than one pattern can appear on a flower. Although two patterns may appear many have only one visible.

Her discussions on patterns are totally baseless. It is know from the early work of Turing and others that patterns are highly complex genetic mechanisms, somewhat akin to fractals. They are highly interlinked epigenetic mechanisms which create the pattern and color variations in what may appear to be an almost random form but have true structure. We will defer this discussion to a latter paper.

Norton continues with dozens of anecdotally based assertions in the preceding manner. Hart has done a superb job in summarizing these and we will use the result of Hart rather than belaboring the Norton approach[5].

The summary by Hart of Norton is as follows:

[4] There is no basis other than observation for this assertion. The paper by Turing addresses the issue of genetic patterning. Turing may have provided a detailed underlying methodology to prove her assertion or to disprove it.

[5] See Hart http://www.hartsdaylilies.com/index.htm

Table 6 Color and Dominant and Recessive

Gene	*Dominant*	*Dominant Effect*	*Recessive*	*Recessive Effect*
Yellow	Y	Yellow color	y	Mellon color
Pink	P	Pink or Lavender	p	not pink or lavender
Red	R	red	r	no red
Pink Influencing	IP			
Lavender Influencing	IL			
Drabbiness	D		d	
Muddiness	M			

From the above Table we can present a genetic profile for flower color as follows:

$$\left[\left(G^1_{Yellow}G^2_{Yellow}\right),\left(G^1_{Pink}G^2_{Pink}\right),\left(G^1_{\mathrm{Red}}G^2_{\mathrm{Red}}\right),\left(G^1_{PI}G^2_{PI}\right),\left(G^1_{LI}G^2_{LI}\right),\left(G^1_{Drabby}G^2_{Drabby}\right),\left(G^1_{Muddy}G^2_{Muddy}\right)\right]$$

where

$$G_{Yellow} = \begin{cases} \text{Y, dominant} \\ \text{or} \\ \text{y, recessive} \end{cases}$$

The above does not imply any chromosomal relatedness or linkage. In addition there is no statistical basis for any of the above it is solely anecdotal. Furthermore there is no genetic or secondary pathway for any of the above. In fact the Norton Conjecture is just that, anecdotal conjectures which in light of their being anything else remain. In some way they remain a paradigm to be proved or disproved.

The following Tables are modified from Hart[6]. They are allegedly based upon Norton as well. The first is color:

[6] See Hart and also Eder PhD Thesis Munich, http://deposit.ddb.de/cgi-bin/dokserv?idn=963026275&dok_var=d1&dok_ext=pdf&filename=963026275.pdf The Thesis is in German but with a modicum of German and a good base in chemistry it is approachable.

Table 7 Color and Genes (Norton Model)

Color	*Gene Profile*	*Dominant Gene*	*Recessive Gene*	*Secondary Pathway Element*
Melon	{(y,y),(p,p),(r,r)……}	None	y p r	lycopene and no anthocyanins
Yellow	{(Y,X),(p,p)(r,r)…..}	Y	p r	beta carotenes no anthocyanin
Clear Pink	{(y,y),(P,X),(r,r),(IP,X),(d,d)…}	P IP Hart also posits it may be Y,X as well as yy	y r d	lycopene and delphinidin
Muddy Pink	{(yy),(P,X),(r,r),(IP,X),(D,X)…}	P IP D	y r	NA
Peach, Apricot, Copper	{(Y,X),(P,X),(r,r),(IP,X),(d,d)…}	Y P IP	r d	NA
Duff, Tan, Brown	{(Y,X),(P,X),(r,r),(IP,X),(D,X)…}	Y P IP D	r	NA

Hart also introduces two more genes which he argues control secondary pathways via gene enzymatic regulation. These are summarized below.

Table 8 Enzymes (Proteins) and Genes

Enzyme (Gene Product)	Color	Dominant	Recessive
F3'H	Red (cyanidin)	R	r
F3'5'H	purple (delphinidin)	P	p
FHT	flavones	E	e
FLS	flavones	L	l

We have discussed these pathways in detail elsewhere. There are issues regarding rates of enzyme production and the like which may dramatically modulate these pathways. Hart does not discuss these at all.

Hart then proceeds to layout colors and these additional genes. We assume that we would have to expand the genes to account for the two controlling the secondary enzymes proposed by Hart. The Colors and the Putative Norton Genes[7] as well as Hart genes are shown below[8].

Table 9 Anthocyanin and Genes

Delphinidin	*Cyanidin*	*Quercitin*	*Dominant*	*Recessive*
X		No	P E L	r possible l
X		X	P E R L	
X	No		P E	r
No	X		E R	p
X	X		P E R	

Now it is possible to prove or disprove the above conjectures. All one needs to do is perform the crosses and perform a detailed statistical analysis.

Before proceeding we will use the Norton-Hart model to discuss what could and possibly should have been done to validate the assertions. Let us assume we can take two flowers, a Yellow and a Melon. We know from the Norton Assertions that we have (y,y) for melon and (Y,X) for Yellow. All the other genes are recessive and identical and thus we should have a simple analytical case if we breed them.

[7] See Hart, Genetics of Daylilies, http://www.hartsdaylilies.com/genetics.htm

[8] Hart uses the term "No" and it is not at all clear what he means by that. There are other entries which are blank and then there are ones which have a pure negative term. One is left wondering from the Hart presentation but one need only look at the chemistry to clarify. We do that elsewhere.

First we should self cross the Yellow. This will tell us if we have (Y,Y) or (Y,y). Remember we have the following two cases.

3.3.1 Case 1 YY Parent Self Crossed

By self crossing the parent we should have all yellow offspring. This is shown below

	Y	Y
Y	YY yellow	yY yellow
Y	YY yellow	Y yellow

3.3.2 Case 2 yY Parent Self Crossed

By self crossing we should have 25% melon. The 25% melon gives us the desired result.

	Y	y
Y	YY yellow	yY yellow
y	yY yellow	yy melon

We can plot the probability of these two events as below. Namely if we have a YY and we self cross it there should be no melon flowers at all. If we have a yY and we self cross it then there fraction of melon is 25%. However there is a finite probability of there being zero from the yY cross, in this case with 20 offspring we obtain a probability of 0.003 that yY yields 0 melon offspring. Thus with twenty offspring from this cross we can be fairly certain if it is a YY or a yY. We will detail this analysis a bit further in this section.

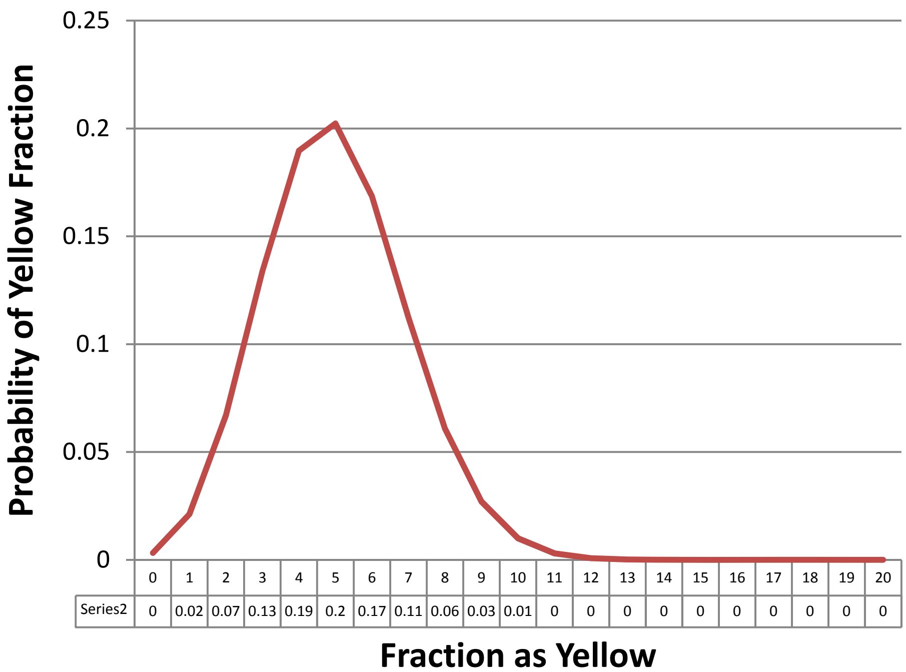


Figure 1 Self Cross of YY X YY or yY X yY

Now we want to look at the crossing of the parent with a melon, namely a fully recessive plant. First if the yellow is YY and we cross with a melon we obtain:

	y	y
Y	yY yellow	yY yellow
Y	yY yellow	yY yellow

This cross above says that if we were to cross melon with yellow and that if there were no yellows in the result then we could be certain that we had a YY as the melon.

If however we have a melon of the genotype yY then we have the following cross:

	y	y
Y	yY yellow	yY yellow
y	yy melon	yy melon

The result is that half of the offspring are yellow. Thus even one yellow yields a violation of the assumption of it being a pure melon. However one must also validate that the number of yellow offspring are in line with the assumption, namely we stipulate that there is a 1:1 relationship between yellow and melon. This means that we can stipulate two hypothesis:

Hypothesis 0 (H0): The yellow is YY and this means all the offspring are yellow.

Hypothesis 1 (H1): The yellow is yY and this means that half the offspring are yellow and half are melon.

Thus we want to perform a test to determine if the hypothesis 0 or 1 is true. However there may be a Hypothesis 2, namely none of the above. This means that we perform the cross and we obtain say 15% melon. What does this mean? It depends upon many factors, including the size of the sample. This is a classic hypothesis testing problem. We must then add a third hypothesis:

Hypothesis 2 (H2): None of the above.

Let us look a bit deeper into the analysis. If we calculate the fraction of offspring which are yellow we can define a variable as:

$$F_{Yellow} = \frac{Number\_Yellow}{Total\_Number}$$

But we know that this is a random variable. We know that if we cross yY with yy then there is a probability of 1/2 that it will be either melon or yellow. Then we know that if the cross is between yY and yy and we have n Yellow out of N samples, the probability that there are F yellow fraction is given by:

$$P\left[F_{Yellow} = \frac{n}{N}\right] = {}_nC_N\, p^n \left(1-p\right)^{N-n}$$

Which is the standard binomial distribution. Since p equals 1/2 we have:

$$P\left[F_{Yellow} = \frac{n}{N}\right] = {}_{n}C_{N}\left(\frac{1}{2}\right)^{N}$$

This is nothing more that the probability for a coin toss. As N gets large it looks like a Gaussian curve. The example below shows the results for a cross with 20 offspring. The probability that there are no yellows from this cross are 1 in a million. However the real question is what is the reliability that the model is itself true, namely that there is not some other underlying probability, some other genetic mechanism that we are not observing.

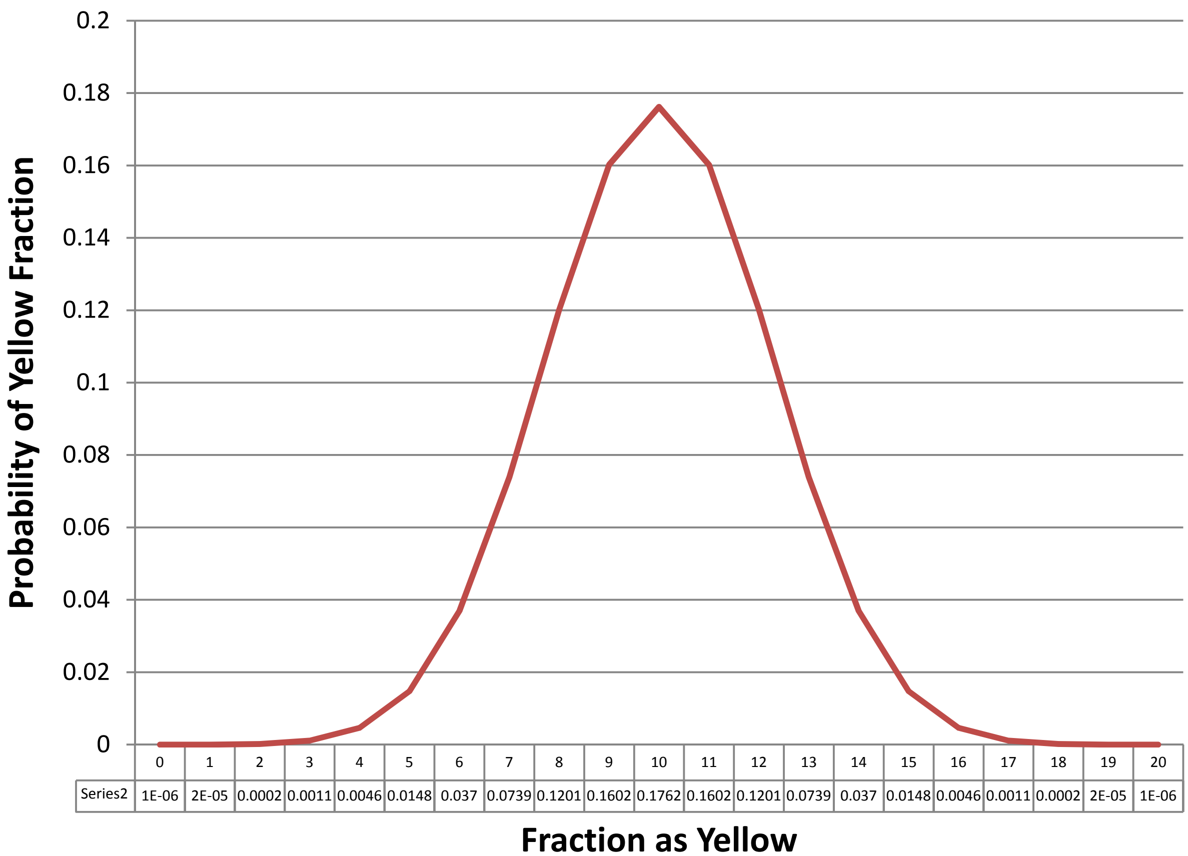


Figure 2 Cross of YY X yy and yY X yy

This is the simple test that Norton should have performed.

3.4 Summary of Mendellian Approach

We can summarize the world view of a Mendellian:

- Genes exists and are parts of a chromosome.

- There is a one to one relationship between a gene and some phenotypic characteristic. The genes control that characteristic.

- A gene may be dominant or recessive, namely there may be a stronger effecting gene than another.

- To get a characteristic the plant must have a gene which expresses that characteristic.

- Some genes are sex related or may have some effect on other genes but that is not a significant factor.

- The gene is the operative entity and there is not accounting for pathways, expression, activation or suppression.

- Mendel's approach fails to account for DNA and the underlying pathways.

The message to take away from the Mendellian analysis is simply; in hybridizing there is no simple one to one relationship between gene and phenotypic characteristic. What we see is a complicated system of variable gene expression; over and under expression, and the release of the gene products related thereto. We look at this in the next section.

3.4.1 Example

We will consider several simple examples of hybridizing.

3.4.1.1 Case 1: Hyperion and Species

The first is the hybridizing of Hyperion. This is a second generation from species and is shown in the next figure. The hybrid Florham was introduced in 1898 as one of the earliest hybrids. It is indeed a true hybrid being a cross between species H aurantiaca and H thunbergii. Florham seems to have been lost to history. In a similar manner the hybrid Sir Michael Foster is also lost. However, Hyperion is the result of Florham and Sir Michael Foster. Hyperion introduced in 1924 is still sold by multiple entities. It is in many ways one of the first commercial success for Hemerocallis hybridizing.

Hyperion

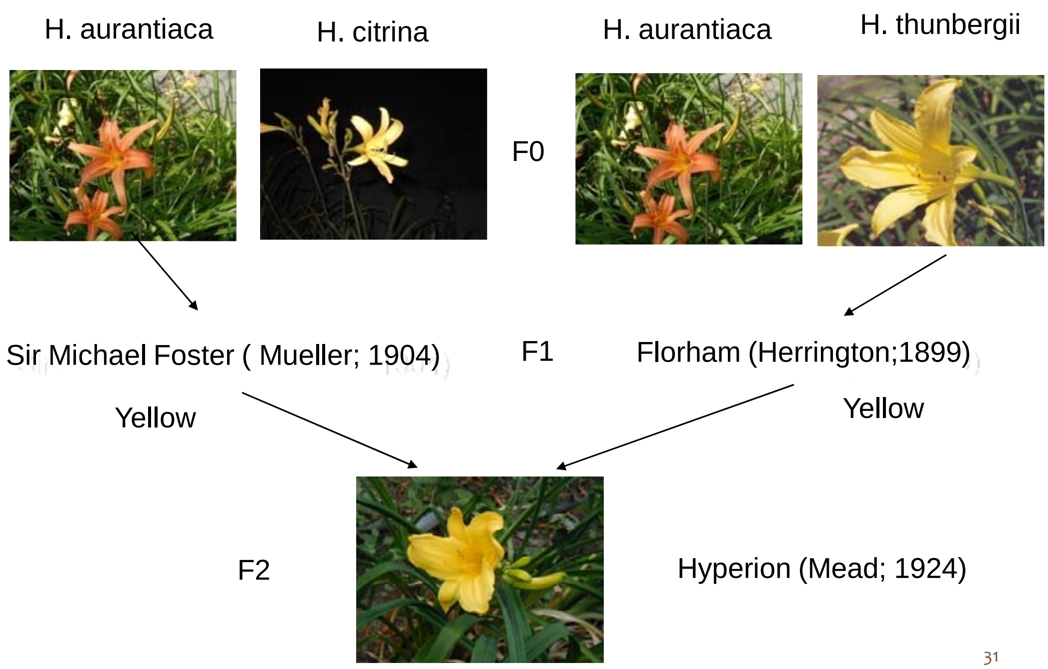


Figure 3 Early Cross Hyperion

The above seems to suggest that at the F2 generation the yellow persists. However not seeing either Florham or Sir Michael Foster we cannot ascertain if the yellow was truly a recessive trait. In Stout's reference he states that the registration of the plant Florham states that the flower is a "canary yellow" thus seeming to infer that yellow is dominant in the thunbergii cross. Similarly in the same Stout reference we see that data on Sir Michael Foster indicates that it is also a clear yellow flower. Thus in this case we have a cross which may be:

	y	y
Y	yY Yellow	yY Yellow
Y	yY Yellow	yY Yellow

where y is the recessive of aurantiaca yielding the reddish color and Y is the dominant yellow color. This presumption is the antithesis of Norton. She argues for two separate genes, a yellow and a red. Thus she would say we have:
H aurantiaca: rR or RR. Also we would assume they are yy.

and for the F1 and F2 offspring as well as the F0 parents we have

H citrina and H thunbergii: yY or YY. Also we would assume that they are also rr. Let us do the crosses on these.

We have the following possibilities:

Case 1: rRyy X rryY

Case 2: RRyy X rrYY

Let us start with Case 1:

This case is rRyy X rryY.

	ry	rY	ry	rY
ry	rryy melon	rryY yellow	rryy melon	rryY yellow
ry	rryy melon	rryY yellow	rryy melon	rryY yellow
Ry	rRyy red	rRyY yellow (?)	rRyy red	rRyY yellow (?)
Ry	rRyy red	rRyY yellow (?)	rRyy red	rRyY yellow (?)

This yields the following result:

25% Red
25% melon
25% yellow
25% yellow (?)

Not having access to the detailed records we really cannot say at this time. However we know that the results chose were yellow and we have Hyperion upon which we can now experiment.

Let us now consider Case 2. This is for the cross RRyy X rrYY. This yields the following:

	rY	rY	rY	rY
Ry	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)
Ry	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)
Ry	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)
Ry	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)	rRyY yellow (?)

If this were the case we would obtain 100% yellow (?). Perhaps this is the case. But we just as easily generate a dozen other likely profiles. Again the defects of Norton.

3.4.1.2 Case 2: Bicolors

The second example below is an interesting example of crossing with a bi-color. We started with Prairie Blue Eyes, since we desired to have the blue color. Then we crossed it with what was called Magic Dawn, but that name is in doubt, it was a bi-color[9]. We wanted blue and bi-color. These were the two characteristics we sought. The result was an F1 plant which was a non-descript red. It had no characteristic of either parent. Frequently this is common in the initial stages of hybridizing. There is a rule in hybridizing called the ruthless rule, where if a plant does not look good then get rid of it. Here we violated that rule.

We then crossed this with Karen Sue, a bi-color. From that cross came three name off-spring. Two of the plants below have a strong bi-color variation and one quite large and ruffled. These three now represent a based to further hybridize.

[9] From Terry Oates I was told that this may not be correct. See: http://davesgarden.com/guides/pf/go/18117/ Magic Dawn, Hybridized by Hall; Year of Registration or Introduction: 1954. The plant may be Howdy, see: http://davesgarden.com/guides/pf/go/26818/index.html Hybridized by Bremken-Armstrong; Year of Registration or Introduction: 1949.

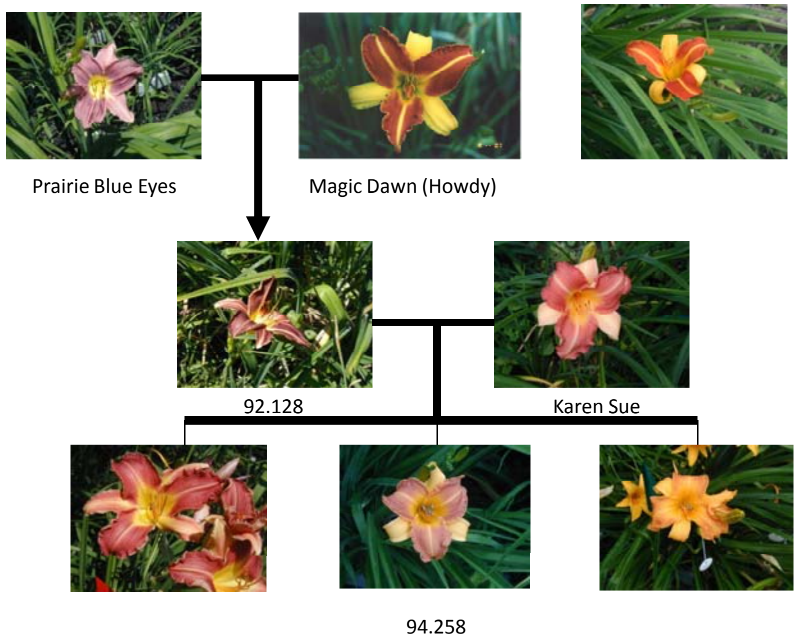


Figure 4 The Three Sisters

Note, in neither case is there a compelling display of Mendellian genetics. We do in the second example see the persistence of the bi-color. However we generally get so few mature crosses that any good statistical results are not generally achievable.

4 IMPLICATIONS OF MENDELLIAN CROSSES

In this section we look a bit more deeply as to the implications of the Mendellian method. We first discuss the concept of Heritability and then briefly introduce several of the classic techniques.

4.1 Heritability

Heritability is a concept in breeding which simply states that a certain characteristic or even characteristics which are phenotypical and which are quantitative rather than just qualitative have both a genetic and an environmental cause or influence.

Thus we look at the length of a scape, the width of a flower, the number of branches of a scape or even the total length of flowering as a quantitative element which can be measured. Then we say that this element or characteristic can be influenced by the underlying genetic factors and/or the environmental factors. It may be a hot summer, a dry summer, a clay field, a sandy field. All of these environmental factors may impact the measurement of the quantitative factor.

Now we can look at a factor, say the width of a flower, W, and we know that using this model we have:

$$W(i) = m + n_G(i) + n_E(i)$$

where m is the average width of this flower and the added factors are zero mean Gaussian variants with variances:

$$E[n_G(i)n_G(k)] = \sigma_G^2 \delta_{i,k}$$

$$E[n_E(i)n_E(k)] = \sigma_E^2 \delta_{i,k}$$

$$E[n_G(i)n_E(k)] = 0$$

$$\delta_{i,k} = \begin{cases} 1 \text{ if i=k} \\ 0 \text{ otherwise} \end{cases}$$

Then we define the total plant variance as:

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2$$

And the heritability is defined as:

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2}$$

If h is greater than 0.5 we say that heritability is high for that characteristic and it is low if h is less than say 0.2. These of course are totally arbitrary values.

4.2 Creating a Homozygous Line

Part of breeding program in the classic sense requires the creation of homozygous lines. Let us determine what must be done to obtain such a line.

Let us assume that a species is found in the wild. We do not know whether it is a homozygous, or dominant. There could be the following possibilities:

	Homozygous	*Heterozygous*
Dominant	*Case 1*	*Case 3*
Recessive	*Case 2*	*Case 4*

We now want to perform a set of crossing experiments to determine what we have. We start with the plant and self cross.

4.3 Heterozygosity and Dominance

Let us assume that we have any one of the four cases shown. We self cross and see what we can obtain. We do so assuming each of the four cases. Let us assume that the genes are T and t, for dominant and recessive.

Case 1: In this case we have TT for both. Thus we obtain:

	T	*T*
T	**TT**	**TT**
T	**TT**	**TT**

Case 2: In this case we have:

	t	*t*
t	**tt**	**tt**
t	**tt**	**tt**

Clearly we get the same phenotype in all crosses in both homozygous crosses and cannot tell what we really have.

Case 3: Here we have Heterozygous and dominant. This yields:

	T	*t*
T	**TT**	**Tt**
t	**Tt**	**tt**

But now we see e have three that look like the parent and one that is different and does not look like the parent.

Case 4: Now we have a Heterozygous and recessive. But this is impossible since if it is recessive it must be Homozygous.

Now we can say:

	Homozygous	*Heterozygous*
Dominant	*Case 1* *We obtain offspring looking the same*	*Case 3* *We get 3/4 looking the same and 1/4 looking different.*
Recessive	*Case 2* *We obtain offspring looking the same*	*Case 4* *Impossible case.*

Thus we have an ambiguity. Furthermore give a pure Homozygous of either a dominant or recessive we will never be able to tell. Thus we need two plants, of different colors, and from that we may have a better chance.

Now assume we have two plants, with two phenotypes, namely colors. Say a red and a yellow. We do not know which color is dominant and we do not know if the plants are Homozygous or Heterozygous.

Step 1: Self cross each plant to assess if the plant for each color is Heterozygous or Homozygous. We showed how this was done above. If there is more than one color we know we have a Heterozygous plant and counting the frequency we can estimate the Dominant one.

If however we self cross and they both breed true to the same color as parents then we may have a dominant or recessive but each is Homozygous.

Now cross the two plants. We know one is recessive and one dominant. Thus we have:

	T	*t*
T	**TT**	**Tt**
t	**Tt**	**tt**

The above is an example which we had shown before. But we can now determine the dominant, since it is the dominant color.

From this experiment we first assess Heterozygosity and the second step we determine dominance.

4.4 Convergence of Homozygosity

Let us assume we have a plant which we know to be Heterozygous. We know that because when we cross it with a Homozygous recessive we get 50% of the recessive trait and we get a self cross with 25% of the recessive.

The question is how do we get a Homozygous Dominant plant? Simply we know that a cross of the presumptive Heterozygous plant with itself yields 25% Homozygous Dominant and 25% Homozygous Recessive. We want the 25% Dominant plants. So we get all of the Dominant plants, Heterozygous and Homozygous and do a test cross on the Recessive plant. If the results from a cross are all Dominant we know the parent is Dominant.

Let us assume we have a gene pair of Aa, and this is in the F0 generation. We now consider selfing or inbreeding in all generations. This means that the breeding is only with itself, no interbreeding. Thus by example we obtain:

F1, we obtain a cross of AA with itself, yielding AA, aa with itself yielding aa, and Aa with itself yielding AA:2Aa:aa. This means that of the 25% which were AA, they all breed true to AA, and likewise for the aa. But for the Aa which interbreed, and which represent 50% of the F1 population, they breed 25% AA, 25% aa and 50% Aa, thus we add another 12.5% to the AA and the same to the aa. This means we have only 25% which are Aa and the rest are equally split between AA and aa. We show the crossing in detail. All parents self cross. Thus at F1 the AA cross with AA and the aa with the aa. The same applies for all succeeding generations.

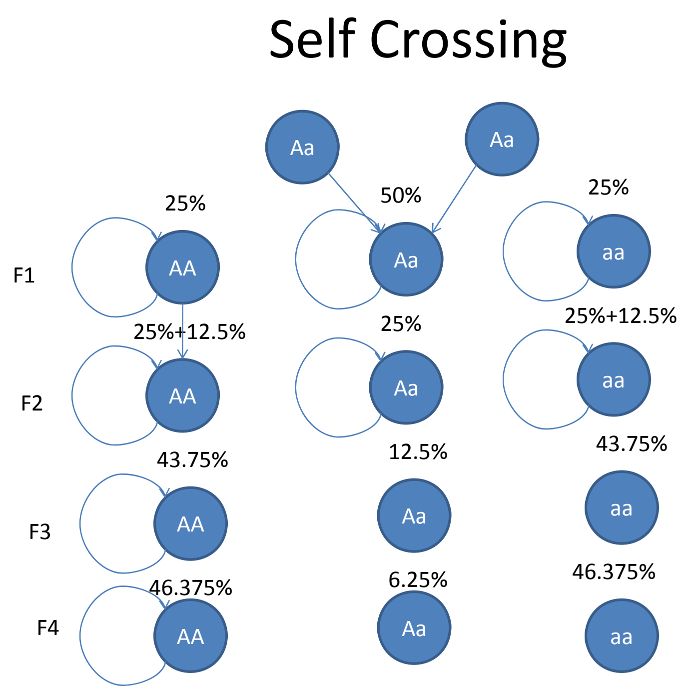


Figure 5 Self Crossing

F2, we again only allow self crossing. The same procedure results in the following Table. This can be continued and leads to the Table below.

Generation	*Genes*	*Homozygous %*	*Heterozygous %*
F0	Aa	0%	100%
F1	AA:2Aa:aa	50%	50%
F2	3AA:2Aa:3aa	75%	25%
F3	7AA:2Aa:7aa	87.5%	12.5%
F4	15AA:2Aa:15aa	93.75%	6.25%

Thus in almost no time we have bred homozygosity into the organism. The dominant are Homozygous and the recessive are by definition Homozygous.

Let us look at this in a bit more detail. In the Table below we show a Recurrent and non Recurrent. We start with a Recurrent with A genes and a non-Recurrent with a genes. At each descending generation we select as Fn the one with the non-recurrent at gene K and we do not know what genes are at the other locations. However we always back cross with the A Recurrent but always select the a at gene k in the ensuing F state. The α value is a jth gene which we will analyze from the self crossing. We know the Recurrent is homozygous.

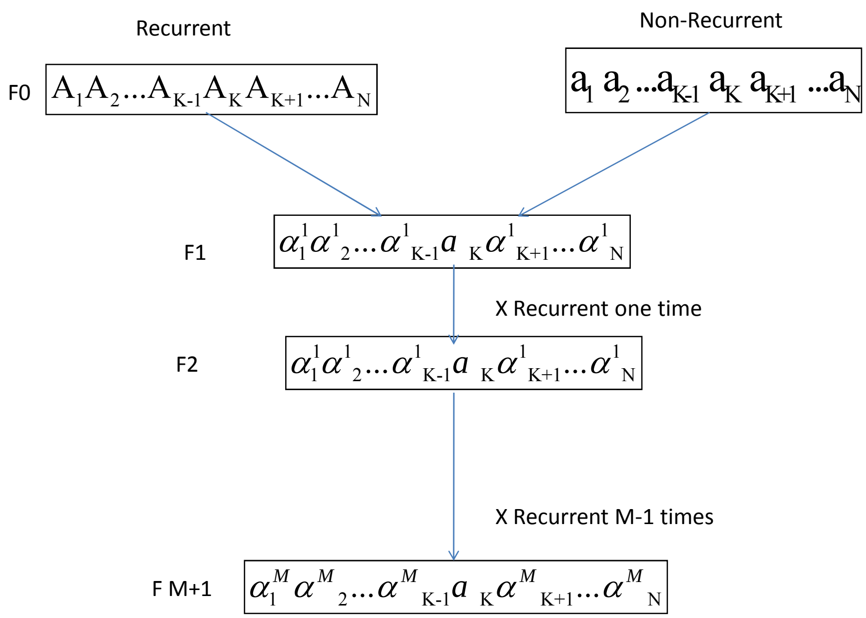


Figure 6 Recurrent Self Crossing

First we assume the genes are independent and that we perform the self cross on the Recurrent. Now we can calculate the Recurrent percent per cross and this is shown below.

Crossings				
F0	AA		aa	
F1	AA 25%	Aa 50%	aa 25%	
F2	AA 25%	AA 25%	Aa 25%	Aa 25%
F3	AA 50%	AA 25%	Aa 25%	
F4	AA 75%	AA 12.5%	Aa 12.5%	
....				
FM	AA		Aa	

$$1-\frac{1}{2^{M-1}} \qquad \frac{1}{2^{M-1}}$$

Figure 7 Recurrent Crossing

We note that after M crosses we have a percent Heterozygous of only:

$$\text{Fraction Heterozygous} = \frac{1}{2^{M-1}}$$

The fraction of Heterozygous becomes negligible as M increases. After say 11 crosses we will have less than 1 thousandth of the crosses being Heterozygous. The rate of convergence is quite fast.

5 HYBRIDIZING OR BREEDING TECHNIQUES

Before detailing some of the specific techniques, we will layout the process of setting goals and seeking the correct parentage to achieve those goals.

5.1 Methods and Goals of Crossing

There are several classic mating methods. There are two dimensions in this process. The first dimension is choosing or selecting a plant. The second is how that selected plant's characteristics may be moved forward. Finally there is an algorithm for stopping.

To successfully develop a hybridizing technique a set of goals should be in mind from the outset. Here are a few examples.

1. Expanding Bicolor Flowers

3. Increasing Branching

3. Maximizing Bud Count

4. Extending Flowering Time

As we show above each of these has a quantitative measure. Thus we may start with plants that appear to take us on this path. We summarize this in the following Table.

Characteristic	*Quantitative Measure*	*Starting Plant*
Expanding Bi Color	Petal and Sepal color difference Petal and sepal colors	Use as source plants existing bi-colors. In addition select based upon pedigrees with consistent bi-color parents.
Increasing Branching		
Maximizing Bud Count		
Extending Flowering Time		

5.2 Selection Methods

Let us begin by understanding the initial step, namely defining the goals and objectives to be achieved. There are several objectives in performing crosses in Hemerocallis. Several of them are:

1. To Generate an New Trait: This frequently comes about by pure random selection. If there were no spider to have as an example, then when one sees a flower with long narrow sepals and petals then this is a new trait and one may seek to both perpetuate it and to extend it. We may have no idea as to how this trait is controlled. This trait then can be in-bred many times seeking to extend the unique quality of the form. Thus we have seen more and more extreme variations of the spider, extremes in petal and sepal shape, variations in coloring, and variations in many other features while retaining the fundamental spider characteristic of a 4:1 or greater ratio of petal/sepal length to width.

2. To perpetuate and enhance a New Trait: Perpetuating a new trait, such as a bi-color, may require several generations of breeding, including multiple back crosses. The bi-color nature may be a recessive trait and the use of backcrossing with the original bi-color would re-enhance the bicolor nature.

3. To Modify an Existing Trait: We may like a bicolor or a particular eyezone and we may want to modify the flower to retail the characteristic while changing some specific color combination. We may want to keep the eyezone and blend the bicolor.

4. To Incorporate an Existing Trait: There may be a trait we want to corporate such a spider, bicolor, eyezone, or even just a simple color change.

5. To Test for Dominance of Traits:

5.3 Characterizing Goals

We must understand where we want to go and from whence we begin. There are several schools of thought that the hybridizer uses. But essentially they are divided into two branches.

First are those who take what is there and try to improve or enhance it. Thus many of the introductions are merely enhancements of what had been brought out before. For example, a ruffled flower with a contrasting eyezone and matching edges may be available as a new introduction. A hybridizer has a similar flower but in a contrasting color. The hybridizer then may try to do several additional crosses. First he may take the new hybrid and cross it with those of his own making, albeit not of the best color or form, and see what this new intro adds to his own collection. Or he may take the new hybrid and try to cross it with a flower of a color he is seeking is the more complex new hybrid.

Characteristic	*Hybridization by Extending*	*Goal Directed Hybrids*	*Targets of Opportunity*
Goals	Take next steps in introducing highly marketable plants.	Long term specific form and color goals. May include increased branching, viability, re-bloom, bud count and the like.	Seeking new and innovative features.
Initial Stock	Heavy use of third party hybridized stock for introducing new traits.		Heavy reliance of seeking out new and innovative internal hybridizing stock with specific features which are of interest and marketable.
Hybridizing Methods			
Data Keeping	This is almost a combination with Mass Selection and Pedigree. There is a keeping of records for parentage but the selection process is best of what was bred. Generally just use F1 offspring.	Requires extensive data and must keep records on all even those rejected. Photo records become a must in this area. F1 thru F6 generally are useful.	
Time Frames	May be the shortest of all because it builds upon already accepted introductions.	This is the longest process.	

5.4 Methods Applied to Crossing

There are several generic methods employed by hybridizers. In this section we present several of them as they may apply to Hemerocallis. Again as we has said before, the goals intended should always be kept in mind. These techniques have certain advantages and disadvantages. In addition, many hybridizers look at "targets of opportunity", namely they look towards the "market" and what will sell at a particular time. In many ways this is typical of the general commercial horticultural market. This is unlike the agricultural market where the intent is generally one of seeking better yield, better protein content, better pest resistance and improved needs for fertilizer, water and the like. In the horticultural market it is an attempt to understand and follow the market trends.

I. this section we present an overview of some of the techniques. We include here certain methods which may be found more commonly in the agricultural area but in some ways may also have found their way into the world of Hemerocallis hybridizing.

We start with the broadly defined methods of pedigree and mass crossing. These methods are nothing more than on one extreme performing detailed crosses with the concomitant record keeping versus the method of just allowing "nature" to take its path and just select the best at each generation regardless of prior parentage.

There are generally two types of selection; pedigree and mass selection.

1. The pedigree selection method is a two step process. First, the plants pedigree, its parents and other lineage are tracked and recorded and this lineage becomes a factor in the choice of retaining and furthering the plant. Second, the phenotype is also a factor in the retention and furtherance of the plant. Pedigree selection is a selection process which attempts to balance the plants lineage and its appearance or other such usefulness.

2. The mass selection method is much simpler. At each step in the selection process, each generation, the best phenotypes are selected. An almost total disregard for lineage occurs in this process.

There are many methods of crossing and hybridizing and they can be performed in the context of either pedigree or mass selection. We will examine a few of the more classic ones in this section. Before doing so we examine the objectives of crossing. The techniques developed for agricultural plants and those used for ornamental plants share many of the same traits. We will not get into the details of the differences but will provide some detail on the many options available.

The following Figure compares Pedigree and Mass selection. In Mass Selection we just start with a cross, and then at each generation we select the plants we see as those having the best character at that generation. Namely we want a great deal of branching, then at each FN was to cross the plants with branching.

Let us first define the Pedigree and Mass Crossing methods in a general context. Both may apply to the hybridizing of Hemerocallis and we define them in further detail.

Pedigree: The Pedigree crossing method require the racking of plants parentage and using the characteristics of the parentage to pursue future generations. The reason for this approach is that we can often miss a recessive characteristic in F1 or even F2 and that if we want something from F0 we need to understand what F0 was and to hybridize to F3 or latter. Thus we must know the pedigree and this pedigree must be tracked and selection is based both upon the characteristic of the Fn plant as well as that of F0.

Mass Selection: If one looks just at each Fn and selects the desired characteristics from Fn independent of any prior generation, namely we could care less as to what parents we may have had, then we use that to propagate the next generation and repeat, we can see how Mass Selection works. It is especially good if we have a great deal of space and are willing to "just let nature take its course".

We compare these two below in an algorithmic form:

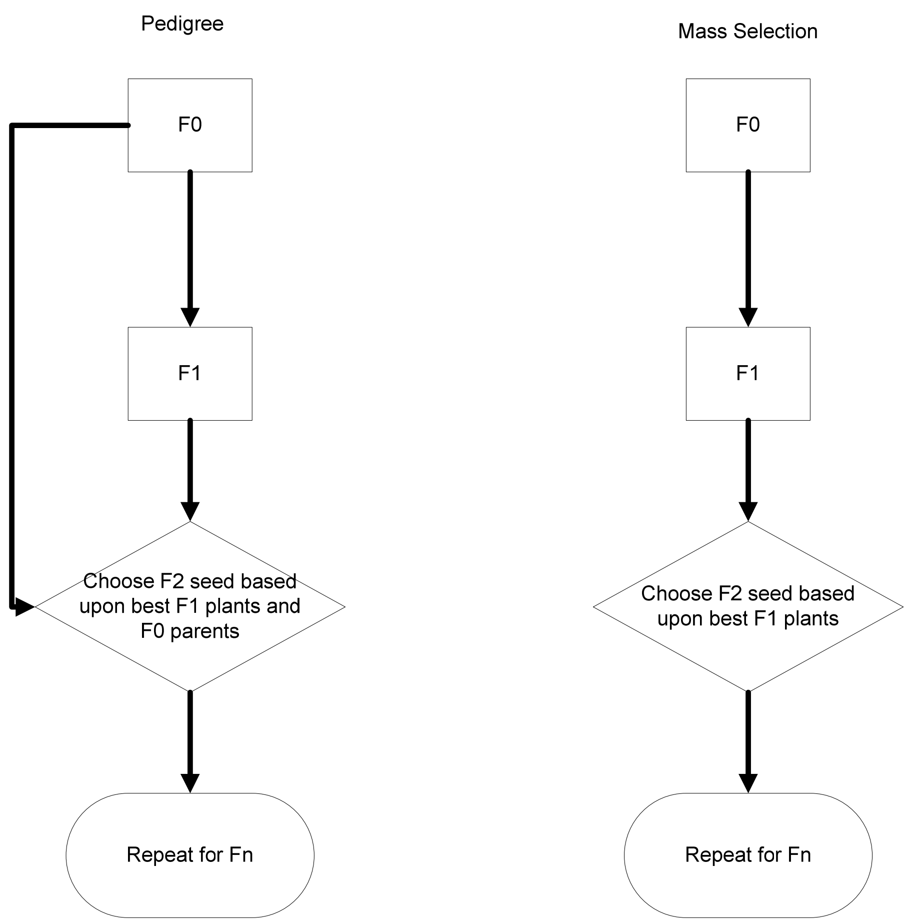


Figure 8 Pedigree vs. Mass Selection

The next question to ask is how pollination is performed. The various plants that one may see in a broad breeding mix are either self or cross pollinating. The Hemerocallis is a mix of both in the form of the species. However in hybridizing we generally hand pollinate and this means a cross pollination. However we may also desire to self pollinate to inbreed a specific trait as we had discussed earlier. Thus we can pollinate in one of two ways:

Self Pollinating: This means we take the plant with the most branching, or say the top ten such plants at F2, and we self cross them. This means we try to inbreed the characteristic in a line of plants.

Cross Pollinating: Here we use different plants, each with a large amount of branching and cross them.

We depict the various options in the following Figure.

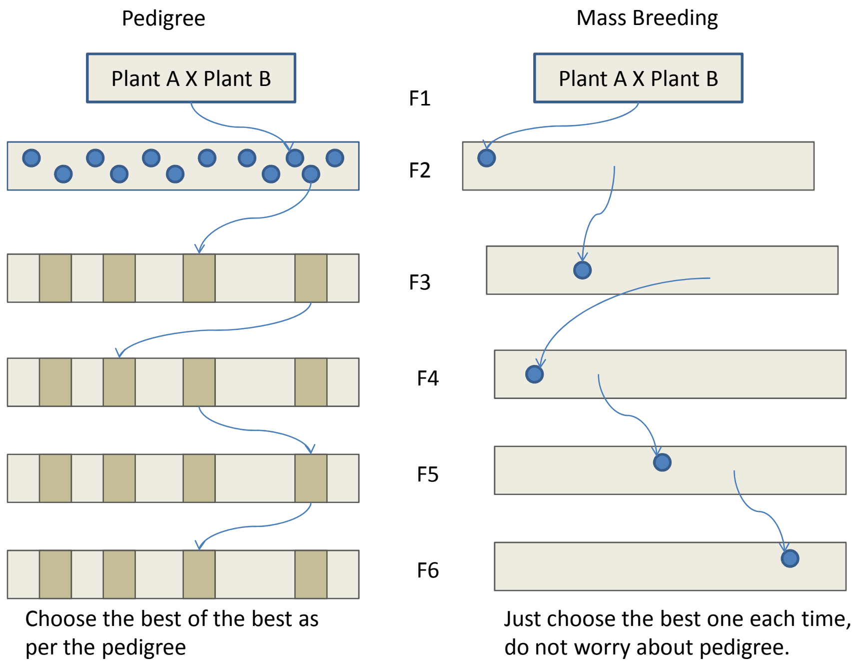


Figure 9 Pedigree vs. Mass over Multiple Generations

We can now compare the four possible ways to proceed. We compare the two selection methods with the two pollination methods.

Pollination/Selection	***Pedigree***	***Mass***
Self	Choose best from a "family" at each round of selection. Self cross this collection of best in a family.	Select best in each round independent of any pedigree. Self cross and move forward.
Cross	Choose best from a "family" and cross the best from the same "family" intensifying the selected family trait.	Choose the best of the best independent of pedigree and cross these best plants.

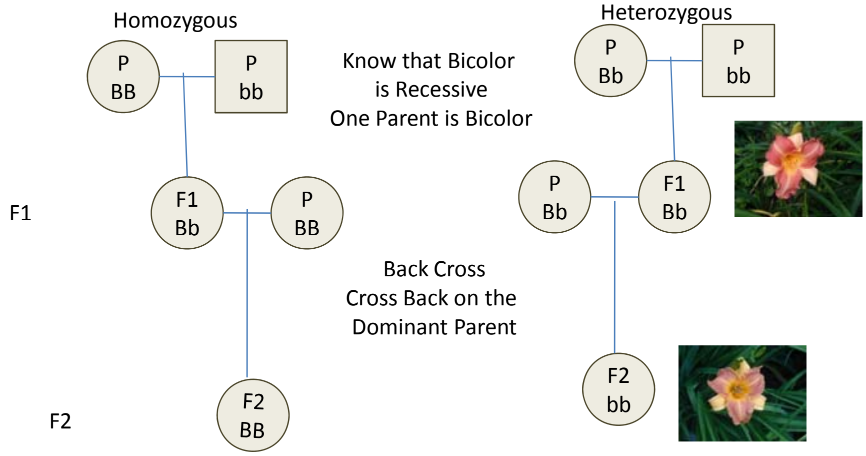
5.5 Crossing Methods

We can now begin to examine the various crossing methods. These methods have been classified by Halinar and others are presented as follows[10]:

5.5.1 Backcross

A backcross is a way to assess the parent who is dominant to determine if it is homozygous or heterozygous using the offspring. Namely we back cross the offspring onto the phenotypic parent. This we show below.

[10] See Halinar, J. C., Breeding Methods for Daylilies, The Daylily Journal, Spring 1990, Vol 45, No. 1, pp 24-30.



	B	b
B	BB No	Bb No
B	BB No	Bb No

	B	b
B	BB No	Bb No
b	Bb No	bb Bicolor

Figure 10 Backcross

5.5.2 Testcross

The term Testcross has been used in a more general manner to describe crosses of putatively Homozygous dominant plants. We know that if we have a recessive gene being expressed in a plant then we must have all recessive genes and the plant must be homozygous. On the other hand the plant expressing the dominant characteristic may be homozygous in the dominant gene or heterozygous. We just cannot tell. Yet if we were to do a test cross between the two we would expect that any time we obtained a recessive phenotype using a recessive parent we have a heterozygous parent for the other plant.

The definition used in many works for Testcross details a great deal concerning its use:

"A Test cross is the mating of an incompletely known genotype to a genotype that is homozygous recessive at all loci under consideration. The phenotypes produced by a Testcross reveal the number of different games formed by the parental genotype under test.[11]*"*

5.5.3 Outcrossing

Outcrossing is defined as the process of crossing cultivars or seedlings to unrelated cultivars or seedlings. The intent is to combine the characteristics of each parent into a sibling. This can work best with dominant traits which will end up in the cross. Thus was can cross Plant A with a

[11] See Stansfield Genetics p. 47.

dominant characteristic we desire with Plant B with another dominant characteristic and we hope to obtain a plant containing both characteristics.

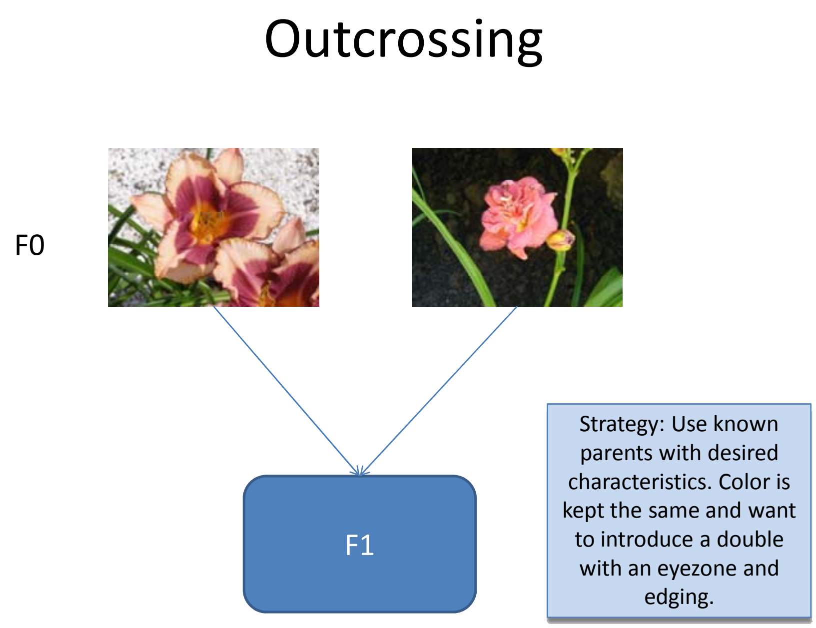


Figure 11 Outcross

Thus outcrossing is simply taking two known parents with desired characteristics and trying to induce those characteristic in the offspring. As we have discussed elsewhere this yields an F1 generation where if there are dominant traits we shall see them but if what we are seeking is recessive we most likely will not. However, many hybridizers use this approach. It starts with a parent with desired characteristics and then crosses to enhance or expand that characteristic. We have seen this with eyezone flowers, ruffled edges, spiders and the like.

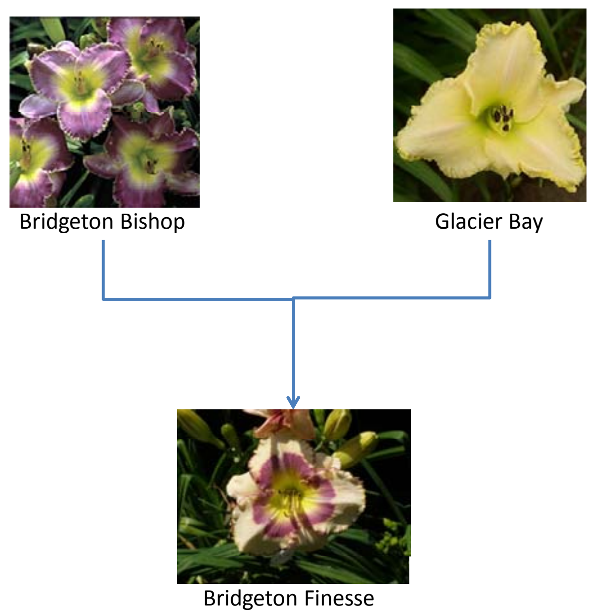
For example, using say a Kindly Light spider, one may cross it with other spiders to further extend the spider like characteristic. Typically the hybridizer stops at the F1 generation. The surprises however are all too often seen in the F1.

Some techniques of value in this area are:

1. Use of Known and Valued Parents: This means that many hybridizers have used the parent successfully and the new hybridizer will use this parent with other new parents for F1 results. Thus we may take a known recent introduction, which has been used by other hybridizers for their new introductions and try to cross that parent with some of their own stock. Again it stops at F1.

2. Use of Identical Parents: This means that we try to duplicate the crosses that the originator had done. We may like a specific introduction and we may have its parents, if such are known. Then we can make the same cross again. The F1 results will most likely be different from the new

introduction produced by the original hybridizer. However we may have a chance to extend the characteristics of the earlier introduction. Say we like Bridgeton Finesse. We know it parents are: Glacier Bay x Bridgeton Bishop. We get them and we cross them again. See the original cross below. We have a purple with a yellow throat crossed with a cream yellow. The F1 is an eyezone. Generally it is this unexpected result that is of interest.



3. Use of Similar or Substitution Parents: This means that we want say a ruffled eyezone. We know the parents of a desirable existing hybrid and we like the characteristics. However we will use parents of similar phenotypic characteristics.

We summarize these three variants of outcrossing below.

Type	*Characteristic*	*Advantage*	*Disadvantage*
Known and Valued Parents	Take parents with known and valued characters and attempt to create F1 with those characters combined or enhanced.	This may result in some new variation which has not yet been introduced.	There is no precedent for this type of cross. The chance that there may be a result is open to question.
Identical Parents	Take parents from selected existing hybrid with desired characteristics and redo the crosses.	There is a well established basis for the cross.	There may be a reason why there is only one introduction from the F0 of the original hybridizer. Also the closeness of the crosses may be so great as to make any new introduction valueless.
Similar Parents	Take parents with similar characteristics as those of a targeted existing hybrid and cross them.	Start with some basis for the end result.	

5.5.4 Line Breeding

Line breeding occurs when we cross related plants. Thus we can cross the plant with itself, its parent, its sibling, and its cousins. We have done that extensively in an attempt to obtain diverse bicolor characteristics where the bicolor is a recessive trait.

Line Breeding

F0

Use parent with desired characteristic and then cross to parent or other sibling. Attempt to induce a Homozygosity by inbreeding a characteristic.

F1

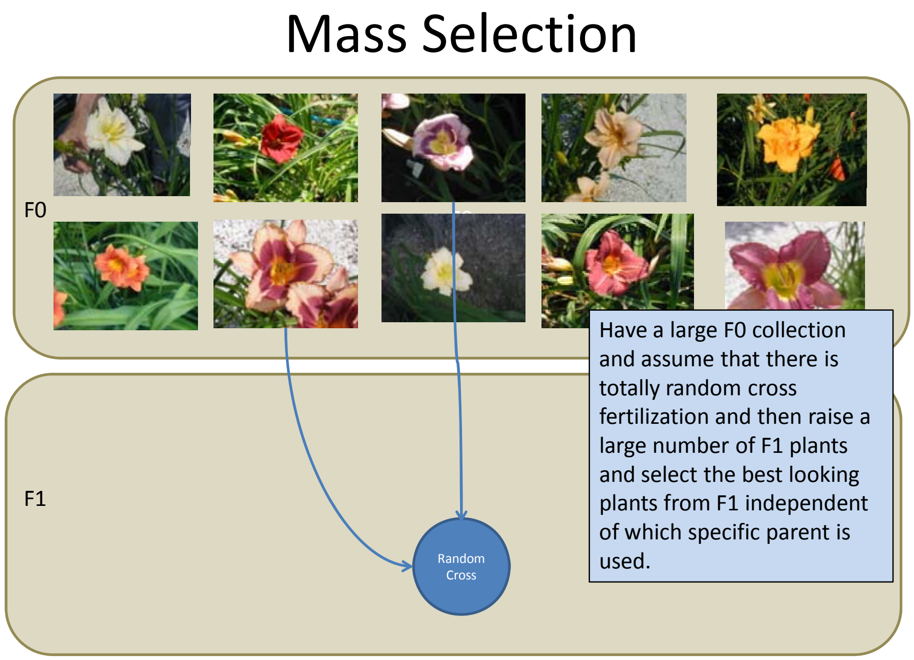
F2

Line breeding is in many ways the most scientific. It does not end with F1 but can be continued. One may drive line breeding to the point of Homozygosity. The issue of closeness of parents is always a concern in line breeding and also the number of generations required.

In both Outcrossing and Line breeding we use knowledge of the parents and keep records accordingly.

5.5.5 Mass Selection

Mass selection we described earlier as a general principle as compared to Pedigree but as a specific methodology it is merely random fertilization of random plants and selecting the F1 descendents for the best traits. The base F0 parents are collected for the broadest possible set of characteristics and the F1 are selected based solely upon their phenotypic characteristics. This method is used rarely in Hemerocallis. It works well in a plant where cross pollination is strong and where there is plenty of room for selecting the F1.

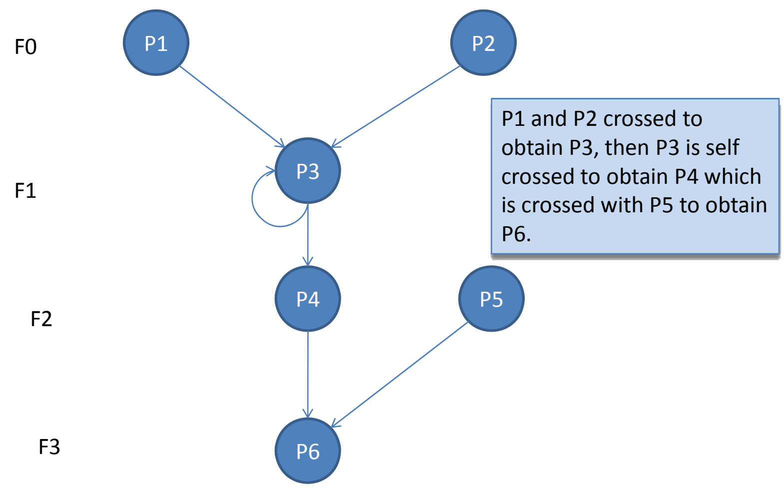


In many ways these are similar to the same methods used for crops in general which we have discussed.

5.5.6 Recurrent Selection

Recurrent Selection is a process which has the Pedigree methodology applied. In recurrent selection we take the F0 parents and then create an F1. Then the F1 is self crossed to yield an F2. Then the F2 is crossed with a selected parent. The objective of the self crossing to get F2 is to enhance the recessive characteristic. Say bi color is recessive. In F0 we may have one bicolor. Then, when we get the F1 generation, there are none. Then when we self the F1 to get F2 we may expect some bicolor again. We know this as a recessive, and Homozygous, and we cross that with a desired plant. We show this below.

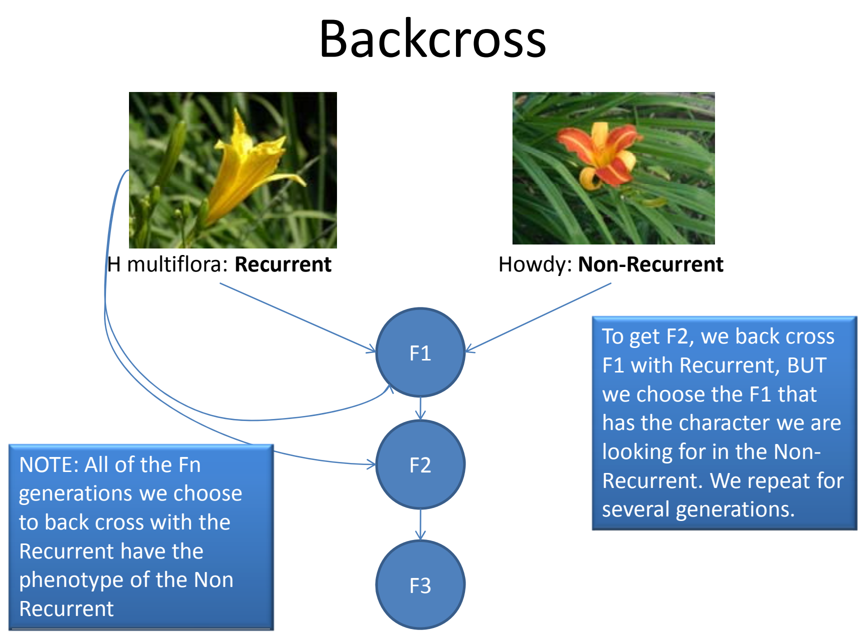
Recurrent Selection



5. Backcross Sibling Mating: We start with general backcrossing. Backcrossing is the mating of an F1 with an F0 parent. It allows for the transference of a characteristic of one cultivar to another. Characters controlled by a single gene are readily passed on by this method.

Let us consider the following process:

(i) In F0 take two plants, one we shall call the Recurrent, and it is the plant we want to get a new characteristic into. For want of specificity we use H. multiflora as the Recurrent. We like the many branching and long blooms. We now want to get a bicolor trait into this plant. So we choose as a second F0 parent Howdy, a bicolor plant, see below.



(ii) In F1 we choose the plant which has the Non-Recurrent character, say bicolor, and we then cross it with the Recurrent parent, say H multiflora. This gives F2.

(iii) In F2 we again choose the plant with the bicolor and again cross it with H multiflora.

If we can assume that there is a single gene for this bicolor character, then we assume that we start with a Homozygous Recurrent and an unknown Non-Recurrent. There are two sets of genes we consider here. First, there is the single gene from the non-recurrent we want to transfer and second there are the many genes from the Recurrent we want to keep. In this case we want to transfer the bicolor gene from Howdy to the end result while keeping all of the M multiflora genes. Our goal is a bicolor multiflora.

Now we want to transfer the bicolor and we want to keep the rest of the multiflora. Let us assume all the genes are independent. Now phenotypically we have what we desire at any Fn if we select the bicolor. Yet we do not know if we have all the genes from the Recurrent H multiflora. How do we get to that point? Let us focus on a single gene, say A from the Recurrent and a from the non-Recurrent. We cross then generation:

AA X aa and this yields at F1, Aa and Aa. This means that at F1 we have mixed all the genes. By now backcrossing the selected plant at F1 with the Recurrent we obtain the cross:

AA X Aa and this yields AA:Aa and this means that 50% of the F2 plants are now Homozygous on the gene that was originally Homozygous in the F0 Recurrent parent.

If the gene that is transferred is dominant then we can do a self cross, namely what we have describe above in selfing, and we obtain a Homozygous result.

Backcross breeding thus works with the recurrent which breeds true from seeds. It allows for the introduction of a new trait.

5.6 Comparison of Methods

We now compare them in the Table that follows:

Type	*Characteristic*	*Advantages*	*Disadvantages*
Outcrossing	Crossing with parents with desired traits in an attempt to combine.	Potential for selecting traits to be combined or carried forward. Can identify a trait in a parent phenotypically.	Single outcrosses may be controlled by dominance or even hidden traits which are not transferrable in one cross.
Line Breeding	Use self crossing to attain recessive traits. May also cross on close relatives like first degree siblings to enhance the trait.	Allows for the use of genetic principles to force a trait into a line. May be able to use a recessive trait by selfing or close crossing.	May take a long time due to multiple generations.
Mass Selection	Start F0 with large selection of plants with good characteristics. Allow random mating. Then grow F1 and select best phenotypes from there, regardless of parent. Continue the process.	Ease of implementation and no need for records. Just cross and select.	Lacks controllability and total lack of selective breeding techniques.
Recurrent Selection	In F0 use two parents with desire traits. In F1 self cross to enhance any recessive trait that may have been hidden to obtain an F2. In F2 cross with another desired trait to get F3 which is the generation for choosing.	Useful for enhancing a recessive but desirable trait.	Quite complex and tedious and takes a great deal of time. If it takes at least two years for each generation we may require easily six years to get to the first selection point.
Backcross Sibling Mating	Select a Homozygous plant whose characters you want to keep except for say one. Select another plant with that character. The first is the Recurrent and the second the non-Recurrent. Cross them and select the one with the desired new characteristic. Cross that with the Recurrent, again select the one with the characteristic and repeat.	It is possible to place a new characteristic into an existing Homozygous line while keeping the rest homozygous. This is a genetically based approach.	Takes a great deal of time and many generations.

6 HYBRIDIZING EXAMPLES

In this section we present some examples of hybridizing we have been involved in and explain the logic used to obtain the end results presented.

6.1 Bi-Color and Spider

The first example is shown below. We started with Hyperion and Karen Sue. Our objective was to use the vigor of Hyperion, including the branching and the strong flowering and introduce the bi-color of Karen Sue. Based upon our prior work we see that perhaps the bi-color is recessive. It did not appear in the parent.

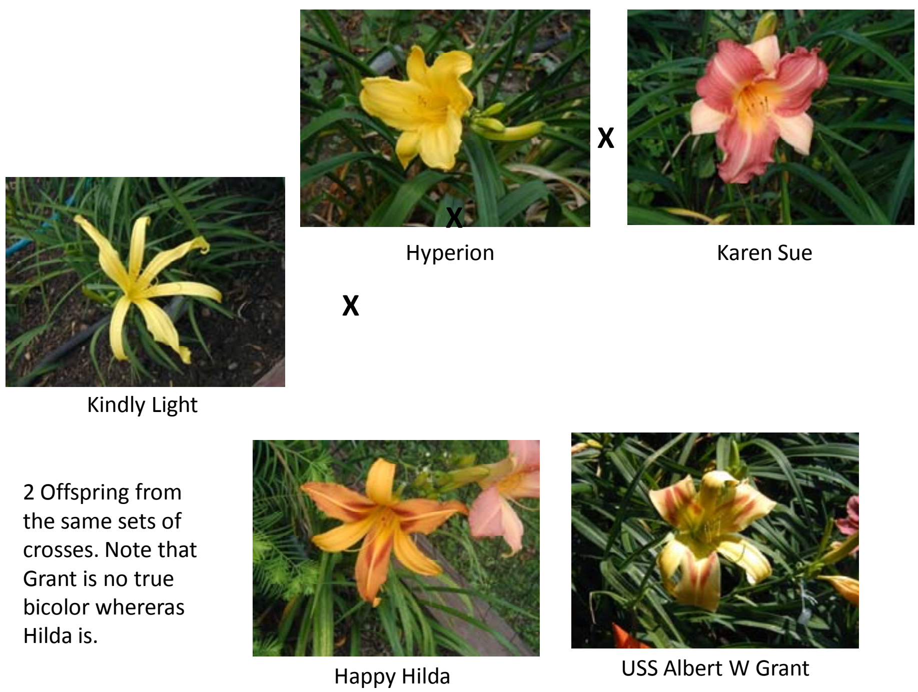


Figure 12 Bicolor Parent and Spider, Two Daughter Plants

6.1.1 F2 Bicolor

In a similar cross we crossed Hyperion X Karen Sue with itself and obtained Rita's Sunrise. A large multi-branched yellow flower with a red eyezone. This is shown below. It has Hyperion as a base, but is much larger apparently getting size and more from Karen Sue, it is not bicolor as is Karen Sue but it has apparently picked up the red from Karen Sue and it is displayed in the eyezone.

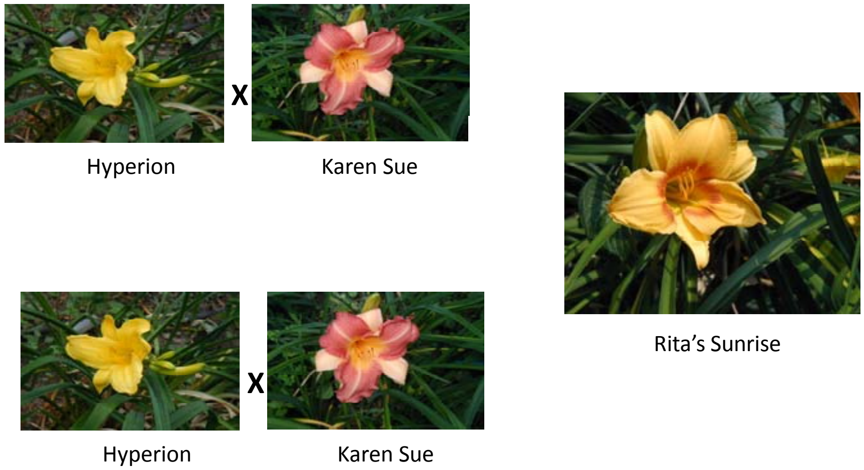


Figure 13 F2 Cross

When looking at the above cross one may ask what the objective was. Simply we chose Hyperion for it extensive branching and bud count. It provided vigor. We chose Karen Sue for the bicolor nature. We were trying to obtain a bicolor which had vigor. Rita's sunrise was a plant which has the vigor but not a bicolor yet it has a very assertive eyezone. It has the yellow of Hyperion, again saying that yellow seems to be dominant, and the red of the Karen Sue is carried only in the eye. Rita's Sunrise was an F2 cross of Hyperion X Karen Sue.

6.1.2 F2-F3 Eyezones

Now let us look at a more complex cross as shown below. Originally we tried Roy Beaver a yellow aggressive growing plant with Prairie Blue Eyes. The objective was to try to get the blue in the yellow. This was before we understood the dominance of yellow. Then we crossed it with Wine Bold to see if we could obtain the red to suppress the yellow dominance. Clearly the color of Prairie Blue Eyes is driven by the red not the yellow. In another cross we did Royal Kingdom and Whoperee since we wanted an eyezone and a dark red. This result of a set of crossings led to Bishop Gabriel. It is a reddish flower with a large inflorescence, good branching and a throat. At best it looks somewhat like Wine Bold but is bigger and more branched.

From this crossing we can learn the following:

1. Dominance of traits must be understood, They will control the results of many crosses.

2. Recessive traits like the red color can be brought out but it takes several generations.

3. Goals can be flexible. Our original intent was blue. This was clearly not met, nor frankly has any hybridizer met the goal. For example one would logically think that crossing Prairie Blue Eyes with Prairie Moon, an almost white daylily may carry over the blue color into a white plant. However the white is a dominant color over the blue.

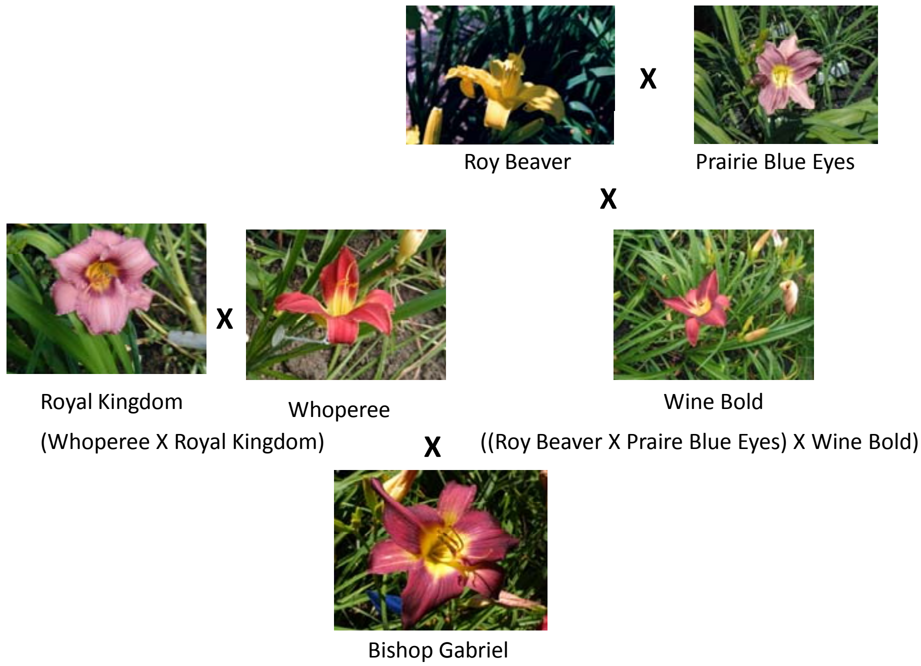


Figure 14 Blending of color, size and form.

6.1.3 F2 Eyezone and Color Change

The next cross shown below is also surprising. We crossed Cynthia Paige Platais with Love Festival. In this case we were seeking reds with eyezones. Out came Princess Martina. Princess Martin is a yellow flower with a red eyezone. Again we see the dominance of yellow. Even though neither parent had all yellow, at best they both had yellow throats, Princess Martina kept the yellow throat and the ends of the petals and sepals were turned yellow.

Cynthia Paige Platais

X

Love Festival

Princess Martina

Figure 15 Dramatic Change in Daughter

The above further demonstrates the yellow dominance. In a strange manner the flower retains yellow at the ends and in the throat. The red becomes the remnant rather than the dominant factor. As we have discussed before in the analysis of color we still have the intriguing issue of color variability across the flower.

6.2 Bicolor and Dominance

Consider now the following cross. We used Karen Sue with American Belle. The goal was clearly a bicolor with American Belle as almost a background color. The resulting cross, Sara's Dreams is a dramatic shift again. We have an orange red, with a yellow green throat and re-curved petals and sepals.

American Belle

X

Karen Sue

Sara's Dreams

Figure 16 Unexpected Daughter

6.3 Blending versus Dominance

The following is another example of a cross where the result is mixed. If we were to return to the Norton model, here we have a classic case of a red and a yellow. We studied just this case in the last section and agreed that if Norton were correct yellow would dominate. However as we look at this result it is a blend! It is a purple flower and there is no evidence of a red or a yellow. Thus the simple genetic dominance theory proposed by Norton seems not to hold here at all.

The cross was Superchild with Love Festival. The intent was to use Superchild as the base for a large tall flower and use Love Festival to gain a red Superchild. The result was Maja's Tinkerbell. It is a pastel purple flower with white ribs on the petals and a green yellow throat. It has the strength of Superchild but is more akin to an off-spring of a Prairie Blue Eyes.

Love Festival

X

Superchild

Maja's Tinkerbell

Figure 17 Diversity of Color, Clear Example of Mixing

The above examples show the diversity of results and supply limited knowledge of the true genetic makeup of the plants.

7 HISTORY OF HYBRIDIZING

Before proceeding it is useful to provide some insight as to the progress of hybridizing in Hemerocallis over the past hundred years or so. We will rely upon both secondary and primary sources in presenting this history. For example, with Stout we have both his writings and the anecdotes from those at the New York Botanical Garden where he performed his work. With many of the contemporary hybridizers we have had first hand conversations. One thing seems common; they all have an intuitive feel for mixing the plants to achieve their intended goals, which most often in innovation of form.

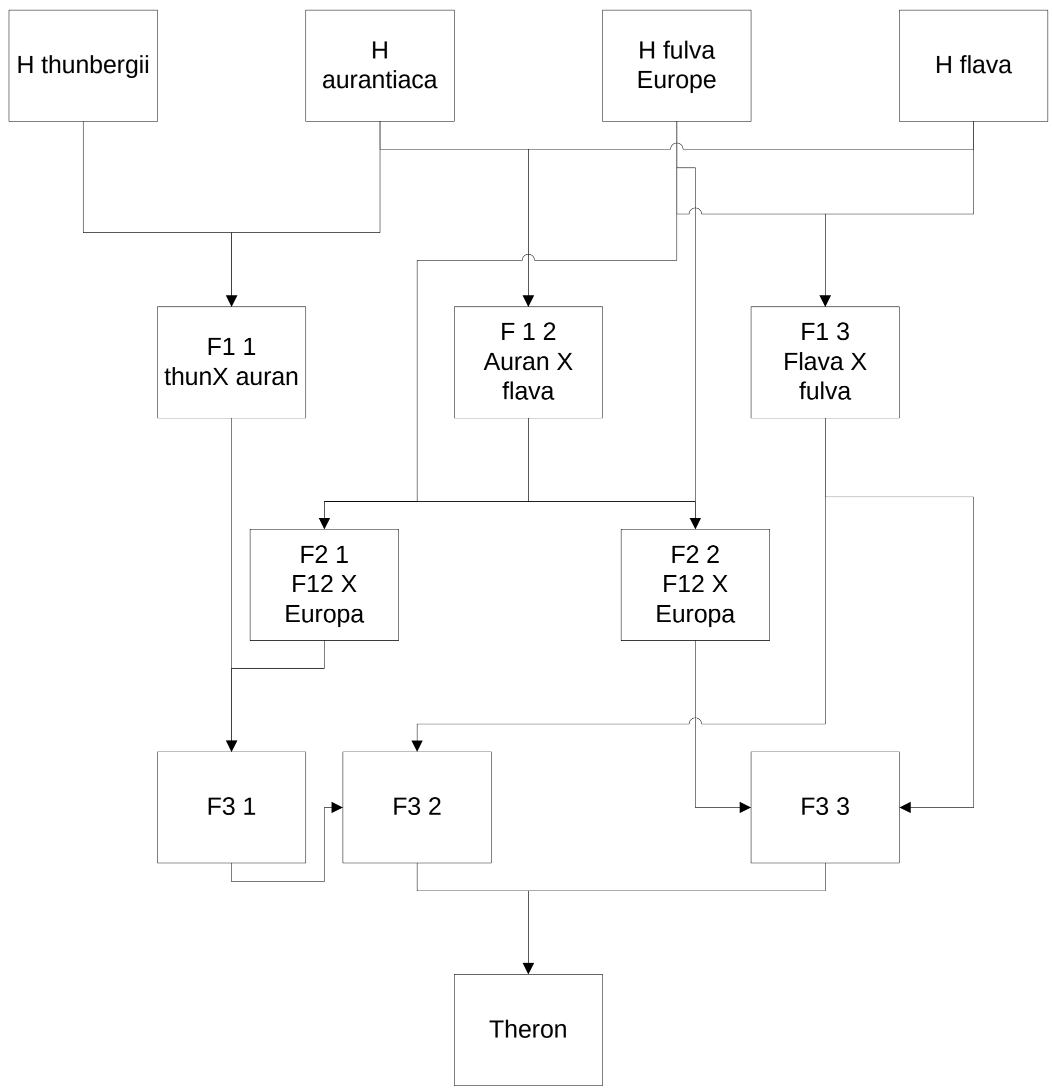
7.1 Early Hybridizing Developments

In the early years, from the late 19th century onwards towards the mid 20th century we rely primarily upon Munson and Stout.

7.1.1 Stout

Arlow Stout performed his research at the New York Botanical Garden in the borough of the Bronx at the northern end of the City of New York. The Garden lies aside the Bronx River, which flows south and at the point where the Garden lies it bisects the Garden and the Bronx Zoo. This piece of land is the only preserved land in the City of New York having never been clear cut. Stout worked there in the first half of the twentieth century when this was still a somewhat rural part of the City. He had adequate land to grow his many hybrids. He communicated with many who went on trips to the Orient collecting plants and he was thus able to obtain and propagate an enormous variety of the genus. He published his book on Daylilies in 1934.

One of his classics is Theron which he shows in his book as a cross as follows:



The following is an example of a few of his early hybrids. He worked tens of thousands of crosses, learning in detail what would work with what cross, and diligently recorded all of his cross data. It was a masterful effort in science.

NOTE: More to be added.

Stout


Mikado 1929


Rajah 1935


Buckeye 1941

7.1.2 Others

During this early period there were many more amateur hybridizers. The source materials were few and the communications between the hybridizers was limited and slow. It was also a period of the Depression and the Second World War.

Munson details some of the early hybridizers. He speaks of Stout, Yeld, Wheeler, Taylor, Nesmith, Connell, Lester and Milliken. We show some of this early work starting with Mead and Hyperion, still a standard. This is shown below.

Mead

Hyperion 1924

Nesmith, Elizabeth Nesmith, who Munson calls Miss Betty, introduced Potentate in 1943. The is shown below. It was one of the first deep red flowers, and in many ways is a departure from many of the others bred until that time. It has a clarity and form which sets it apart and begins a road towards a collection of reds and purple. Munson calls it a violet-plum, and indeed it can be seen that way. However we have used it as a base for reds as well.

Nesmith

Potentate
1943

The second hybridizer is Bechtold and he introduce Kindly Light one of the earliest spiders and a plant which sees continuing use as a source for spider forms.

Bechtold

Kindly Light 1949

Munson mentions Kraus, but in the Middle period and we place him in the early one for several of his introductions. Below we show Yellowstone, another plant which is still collected and grown extensively.

Kraus

Yellowstone 1950

7.2 Middle Ages of Hybridizing

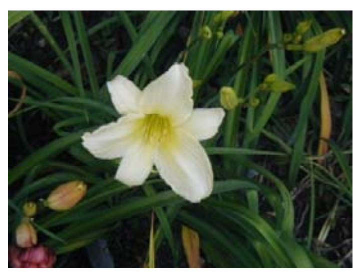
The Middle Ages for hybridizing was from 1950 to 1975 for Munson. We have expanded this until 1980. In his discussion Munson includes Kraus, Hall, Claar, MacMillan, Spalding, Childs, and for the Tets, Peck, Marsh, Fay, Reckamp, Moldovan, Munson. We will look at the work of a few others during this period. Specifically:

- Peck
- Winniford
- Stevens
- Davidson

7.2.1 Childs

Childs

Catherine Woodbury
1967



Ice Carnival
1967

7.2.2 Hall

Hall

Precious One 1967

7.2.3 Marsh

James Marsh worked in both Dips and Tets. One of his most significant contribution was Prairie Blue Eyes, one of the earliest attempts to achieve a blue color in daylilies. Also Prairies Moonlight is a very light yellow verging on white. These two were done in the period of 1965-1970. He then started his hybridizing in Tets with the Chicago series. There he achieved a great deal of success with the reds and with pastes, such as Chicago Catelleyea.
We show several of his introductions below. They all possess good solid growth characteristics and present very well in almost any garden.

Marsh

2N Diploids

4N Tets

Prairie Blue Eyes
1970

Prairie Moonlight
1965

Chicago Fire
1972

Chicago Atlas
1975

Chicago Brave
1976

Chicago Catelleyea
1980

Marsh shows great diversity in color as well as form in this period. The Prairie series were all Dips and the Chicago all Tets. The difference in added sophistication with the Tets is obvious as you look at them side by side. However the simple and direct clarity of the Dips keeps them in circulation and for Dip hybridizers they are a base for continuing the subtle elements that Marsh introduced. The Prairie Blue Eyes has been used extensively for the introduction of Impressionistic color combinations.

7.2.4 Peck

Virginia Peck, as states Munson, is a breeder from Tennessee. She has worked with Tets for many years and during this period made many important introductions whose use in hybridizing is still used. We show several of them below. Wine Bold is a rich dark red flower with good growth and it provides the basis for many dark red hybrids. June Wine is an eyezone which is also the basis for many eyezone plants. Jog On and Scarlett Kettle are rich bright reds which also can be used to infuse color into plants.

Peck


Etched in Gold 1972


Wine Bold 1972


Tammas 1972


Scarlett Kettle 1976


June Wine 1976


Jog On 1976

From 1972 through 1976 the reds introduce by Peck were the basis for reds used by many other hybridizers as well. One can see in the above the less than subtle difference in the four reds she introduced during that period.

7.2.5 Winniford

Ury Winniford of Dallas Texas introduced 205 hybrids from 1968 thru 1990. Two of his early introductions are shown below. They are the tinted eyezone Tixie which is small but a good growing plant even in the north and Brutus which has a unique cup like form and is an aggressive grower. Winniford in this mid period introduced many hybrids and they have interesting forms and shapes.

Winniford

Brutus 1975

Tixie 1974

7.3 Recent Hybridizers

To understand the way modern hybridizing is accomplished it is useful to have a better understanding of the hybridizer's techniques and goals. From a 1957 article speaking to the evaluation of the daylily the authors recounts the considerations that Stout applied to the selection of hybrids. He specified them as:

1. The plants should have winter hardiness.

2. The plant should bloom for a long season.

3. Flower color should not bleach out and petals and sepals should not curl or wilt prematurely.

4. Flowers must drop quickly after bloom on their own.

5. Flowers should stay open in the evenings.

6. Flowers must sit high enough above the foliage so as to be seen.

7. Scapes should be neither too heavy to overwhelm the plant or too thin to allow drooping.

8. Foliage must be full, lush and green.

These requirements say much about the plant as a whole and little about the flower in particular. The tracking of new hybrids of the plant can be accomplished via the AHS award process. There are several steps in that process.

Step 1, Junior Citation: This is awarded to a plant which has not been registered for more than a year and is frequently even awarded to an unregistered cultivar. This is a regional awarding process and it attempts to reward the newer introductions.

Step 2, Honorable Mention: This award is the next step in cultivar evaluation and now moves from possibly just one local region to a minimum of four or more regions. A cultivar must receive fifteen or more votes from Judges to receive this award. To be eligible the cultivar must have been registered for at least three years.

Step 3, Award of Merit: According to AHS this is awarded not only for a cultivar's distinction and beauty but also for its ability to perform well over a large geographical area. Twelve awards are made each year. To be eligible a cultivar must have received an Honorable Mention for three previous years. For example in 2007 there were the full twelve Awards of Merit.

Step 4, Stout Silver Medal: The award is given annually to a cultivar which must have received at least two prior Awards of Merit. The Stout Medal is the highest award from the Society. The list of past winners is shown in the Table below.

2007 LAVENDER BLUE BABY (Carpenter, 1996)
2006 ED BROWN (Salter, 1994)
2005 FOOLED ME (Reilly-Hein 1990)
2004 MOONLIT MASQUARADE (Salter, 1992)
2003 PRIMAL SCREAM (Hanson, C. 1994)
2002 BILL NORRIS (Kirchhoff, D. 1993)
2001 IDA'S MAGIC (Munson, I. 1988)
2000 ELIZABETH SALTER (Salter 1990)
1999 CUSTARD CANDY (Stamile 1989)
1998 STRAWBERRY CANDY (Stamile 1989)
1997 ALWAYS AFTERNOON (Morss 1987)
1996 WEDDING BAND (Stamile 1987)
1995 NEAL BERREY (Sikes 1985)
1994 JANICE BROWN (Brown 1986)
1993 SILOAM DOUBLE CLASSIC (Henry 1985)
1992 BARBARA MITCHELL (Pierce 1984)
1991 BETTY WOODS (Kirchhoff 1980)
1990 FAIRY TALE PINK (Pierce 1980)
1989 BROCADED GOWN (Millikan 1979)
1988 MARTHA ADAMS (Spalding 1979)
1987 BECKY LYNN (Guidry 1977)
1986 JANET GAYLE (Guidry 1976)
1985 STELLA DE ORO (Jablonski 1975)
1984 MY BELLE (Durio 1973)
1983 SABIE (MacMillan 1974)
1982 RUFFLED APRICOT (Baker 1972)
1981 ED MURRAY (Grovatt 1971)

1980 BERTIE FERRIS (Winniford 1969)
1979 MOMENT OF TRUTH (MacMillan 1968)
1978 MARY TODD (Fay 1967)
1977 GREEN GLITTER (Harrison 1964)
1976 GREEN FLUTTER (Williamson 1964)
1975 CLARENCE SIMON (MacMillan 1966)
1974 WINNING WAYS (Wild 1963)
1973 LAVENDER FLIGHT (Spalding 1963)
1972 HORTENSIA (Branch 1964)
1971 RENEE (Dill 1962)
1970 AVA MICHELLE (Flory 1960)
1969 MAY HALL (Hall 1957)
1968 SATIN GLASS (Fay 1960)
1967 FULL REWARD (McVicker 1957)
1966 CARTWHEELS (Fay 1956)
1965 LUXURY LACE (Spalding 1959)
1964 FRANCES FAY (Fay 1957)
1963 MULTNOMAH (Kraus 1954)
1962 BESS ROSS (Claar 1951)
1961 PLAYBOY (Wheeler 1954)
1960 FAIRY WINGS (Lester 1952)
1959 SALMON SHEEN (Taylor 1951)
1958 HIGH NOON (Milliken 1948)
1957 RUFFLED PINAFORE (Milliken 1948)
1956 NARANJA (Wheeler 1947)
1955 PRIMA DONNA (Taylor 1946)
1954 DAUNTLESS (Stout 1935)
1953 REVOLUTE (Sass 1944)
1952 POTENTATE (Nesmith 1943)
1951 PAINTED LADY (Russell 1942)
1950 HESPERUS (Sass 1940)

From this list it is clear those hybridizers such as:

7.3.1 Stamile, Patrick and Grace

Patrick Stamile has 5 Stout Medals, 27 Awards of Merit and 115 Honorable Mentions. He is a prodigious hybridizer who started his introductions in 1984. He initially started his hybridizing in 1977. Patrick Stamile initially started his growing on Long Island and in 1993 he moved with his wife Grace to Florida. Since then his introductions have a southern bent and in many ways have become southern hybrids. Patrick Stamile represents a standard for hybridizers, namely going out and making contact with those who have achieved recognition and success, seek their advice and technique, and obtain hybridizing materials and then focus on their hybridizing. Grace Stamile has been focusing on hybridizing miniature and blue tinted hybrids for twenty years. In 1989 she obtained her first hybrid called Coming Out Party.

It was the beginning of a blue period. She used several hybrids which had both blue and small flowers to combine them to seek out the traits she was seeking. She has 30 Honorable Mentions. Grace's approach is quite focused using They have been in Enterprise, FL for the last fifteen years. The approach used by both seems to be standard but a standard using their own stock and expertise. They have several watermarked type of flowers and it is clear looking at the parentage that they have achieved good mixing by using the incremental strength of the breeding parentage. One may try to intuit a breeding plan or strategy but it appears to be more a combined mass selection approach yet using pedigree parents. That is choosing the parents and then grows as many seedlings as possible and chooses the best. There does not appear to be any complex backcrossing or the like.

Stamile

Vanilla Candy 1990

White Crinoline 1992

Custard Candy 1989

Tigger 1989

In the above we show three classes of the Stamile intros. The Vanilla Candy and White Crinoline are two of the whites; Custard Candy is part of his eyed Candy series.

7.3.2 Kirchhoff

David Kirchhoff is another Florida hybridizer who in 2006 moved north to Kentucky. He comes from a long line of horticulturalists and growers and has been hybridizing for many years now. He has reds, oranges, dips and Tets. Kirchhoff first crossed a daylily in 1958. Kirchhoff has 107 Honorable Mentions, 17 Awards of Merit and 2 Stout Medals. Betty Woods and Bill Norris are his two Stout Medal winners. His most recent work is on doubles like Barry Goldwater, an orange almost peony like flower which has some reddish edging. It is clear that the attempt here is to take forms which become distinct and enhance them with a different color while keeping the double form[12].

His stated approach was an outcrossing method with doubles and the outcrossing introduced additional genetic diversity. Kirchhoff has a partner one Mort Morss, who has been hybridizing with Kirchhoff for over thirty years, since 1971. One of his recent introductions is Curtis Montgomery which is a beautiful bicolor with a watermarked eye and ruffled petals. The petals are a reddish orange and the sepals are peach. It appears to be an aggressive grower.

Kirchoff


Bill Norris 1993

The above is an example of Kirchhoff. The classic one is Bill Norris, an award winner. It is a pure deep yellow with full petals and sepals and ruffled edges. Depending on where it is grown it will do well or poorly. In our experience it does well in New Hampshire and poorly in northern New Jersey soils.

7.3.3 Moldovan

Steve Moldovan and his partner and successor Roy Woodhall did their hybridizing in Avon, Ohio, and west of Cleveland and near the lake. It is a cold and snowy environment in the winter but can be somewhat moderated in the summer. It is not Florida in any way of the imagination. Steve Moldovan passed away on July 14, 2006. Roy Woodhall continues the work of Moldovan. He was 68 and he had been hybridizing almost all his life. He held a graduate degree in Horticulture from Ohio State University he introduced many exceptional hybrids. He had 43 Honorable Mentions and 6 Awards of Merit. The key thread that seems to have led Moldovan was his early contact with the hybridizers of the previous generation; Reckamp, Munson, Fay,

[12] SEE HTTP://WWW.DAYLILYWORLD.COM/DW-INTRO--PAGES/BARRY_GOLDWATER.HTM "DESCENDED FROM AN OUT CROSS BREEDING GEORGE RASMUSSEN'S TIGER PARADE TO OUR LAYERS OF GOLD. NINETY NINE PERCENT DOUBLE"

and many of the now classic hybridizers. This, along with his own training, seems to have given him an exceptional basis for developing his own technique as well as his own line of plants.

One of Moldovan's best hybrids, Strutter's Ball, is a cross between his own Houdini and Munson's Damascus Velvet. All three are reds and all three have a green gold throat. Strutter's Ball is an exceptional bloomer and is well branched with many buds. It had become a key element in many of the Moldovan crosses.

In fact as Woodhall has said of the techniques he has developed working with Moldovan the one which is often the most important is to generate one's own parent hybrids, those with characteristics that make your showings different and use that source a

Moldovan was one of the first in the area of Tets and also was one who worked with the many pastels we have come to see out of the crossings, again and again. Recently one can see in his final hybrids the introduction of some bicolors and some of the shapes and coloring common in many of the other commercial hybridizers.

In the article by Fitzpatrick on Moldovan just before his death she recounts the rules he promulgated for hybridizers[13]:

1. Plant many seeds but be prepared for the retention of very few, one out of a thousand.

2. Outcross to hardy cultivars to ensure that the perennial does not become an annual.

3. The results of a cross are never certain, and in fact never imagined.

4. Always be aware for special little traits. They can be used again and again and introduced into new crosses.

5. Plant seedlings in the ground. Let Nature do its pruning.

Moldovan's rules are to be well taken. The hybridizer seeking a truly sustainable set of greatly appreciated hybrids will take them to heart. We expand on Moldovan's five rules below:

[13] See Sharon Fitzpatrick, Steve Moldovan's Quest, The Daylily Journal, Fall 2005, pp. 312-323.

Moldovan Rule	*Implication*
Plant many seeds	This is the rule that says you increase your chances with larger numbers to select from. You will look only for one in a large number. You may see one in a hundred as something to consider and one in a thousand to keep.
Outcross with Hardy plants	Outcrossing, the crossing with stronger and dramatically different hybrids, and some would say even species, puts genetic diversity back to the plant. Excessive inbreeding will enforce certain characteristics but will also most likely enforce weaknesses that will be highly negative for the plant. Outcrossing, however, will also result in getting the dominant genes back in the pool, and that return of the dominant may wipe out the characteristic we had been seeking. However, we know the gene we wanted to keep may not appear in F1, it will, if it survived appear in F2. This when outcrossing, remember to continue to F2 in all cases.
Crosses are Never Predictable	Despite what we try to say regarding the genetics of plants, the statements hold only in the large, namely on average, and when looking at the hybridizing results we all too frequently select the outliers. The outliers are those with the special traits. Then we try to build on them, not on the traits of the average.
Look for Special Little Traits	Look at each and every resulting cross.
Let Nature prune.	This is an extremely important rule for northern hybrids. For, example, it is well known that many southern hybrids will die off when taken too far north. Whereas if one takes a northern plant and crosses it and lets it be selected for survival in the winder, true hardening off, then what results is a plant stock with increased hardiness.

There is a sixth Moldovan rule, one which he based his early days on; have acquaintances that are highly respected and learn from them, use their stock to start and build on their work. For Moldovan it seems it was Reckamp, Munson and Fay. Between the three there were 226 Honorable Mentions, 33 Achievement Awards and 4 Stout Medals. Those three were superb mentors, and mentoring in the field seems to be a major driver.

7.3.4 Apps

Darrell Apps has all of his degrees including a PhD from University of Wisconsin. He has finally retired from Woodside Nursery in Bridgeton, NJ after decades as an active grower. Apps also has journeyed to the far reaches of Asia in search of the Hemerocallis species, unlike many of the other hybridizers, who have moved from species into the complex and hectic world of multigenerational hybrids. He has introduced hundreds of hybrids and his first was Nittany Mountain Summer in 1975.

Figure 18 Apps Nittany Mountain Summer

The above shows Nittany Mountain Summer as a simple red with a gold throat. He has won 30 Honorable Mentions, 2 Awards of Merit. Apps has a breeding strategy which looks at the total plant, and this includes leaves, scape, branching, and bud count. The plants he has hybridized are extraordinary in a Stout like manner; they are not just pretty pictures, looking solely at the flower but complete structures.

Dr. Darrel Apps is clearly one of the foremost hybridizers over the past forty years. Until 2007 he also was a grower of massive amounts of daylilies until his retirement. His work is an example of a broadly based hybridizer who sought to develop many of the fundamental elements of the genus in all his introductions. He developed hybrids which had good form, structure, color, bloom strength, and he did not focus especially on the bizarre and strange forms. He had a few doubles, few spiders and generally tried to avoid the fads. The following is a chronological list of some of the hybrids we have grown.

Hybrid Name	*Ploidy*	*Intro Date*
Nittany Mountain Summer	2N	1975
Nouveau Riche	2N	1990
Doll Maker	2N	1992
Ebony & Ivory	2N	1992
ORNATE RUFFLES	2N	1992
Royal Frosting	2N	1993
Confectioners Delight	2N	1995
Justin George	2N	1995
Bridgeton Born	4N	1997
Dazzling Discus	2N	1999
Double Intrigue	2N	1999
Better Rum	4N	2000
In the Flesh	2N	2000
Bridgeton Finesse	4N	2001
Luminous Bouquet	2N	2001
Woodside Common	2N	2001
Eager Beaver	2N	2002
Bridgeton Hoopla	4N	2003
Just the Two of Us	2N	2005

The following Figures depict several of these in alphabetical order. What can be noticed in the development are that early on such flowers as Nouveau Riche and Doll Maker are almost mono-color but have tremendous blooms, strong scapes, many buds and good branching. What Apps seems to be focusing on was good underlying form and structure.

In the latter stages with Bridgeton Hoopla and Bridgeton Finesse we see the use of eyezones and with edging on the flowers. However the underlying strength of structure ensures the new form is well supported.

One can see the progression from the Nittany Mountain Summer simplicity to the Bridgeton Hoopla complexity the change not only in his breeding style but in what the market is demanding. There is the growth of ruffles and ridges, the eyezones with the watermarks, the less than subtle colors. Notwithstanding the complexity, however, each Apps introduction also has significant branching and bud count. That quality is a sine qua non of his introductions.

Bridgeton Born

Bridgeton Finesse

Bridgeton Hoopla

Bridgeton Instant Classic

Confectioner's Delight

Dazzling Discus

Doll Maker

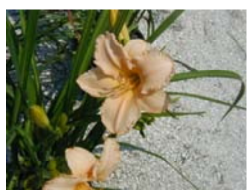
Double Intrigue

Eager Beaver

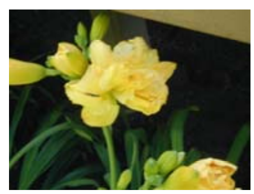
Figure 19 Apps Plants No. 1

The second group of hybrids are shown below. These are some with the simplicity of his early introductions, simple color but elegant form and exceptional growth characteristics.

Ebony and Ivory



In The Flesh



Just The Two of Us

Justin George

Luminous Bouquet

Nouveau Riche

Ornate Ruffles

Royal Fantasy

Woodside Common

Figure 20 Apps Plants No 2

Apps hybrids have certain enduring characteristics. They are:

Excellent form: The plants have well branched scapes with many buds per scape. The scape is strong while not overpowering. It provides an excellent base for presenting the flower. Apps seems to have been very consistent in developing hybrids which sustain that virtue.

Color Intensity: His flowers all have a clarity and intensity that make them stand out, not because of complexity but due to the clarity. Woodside Common is a rich gold yellow and it is the strength of that richness that makes it sit and be noticed.

Growability: The plants generally grow very well. They lack the fragility of the southern hybrids and contain durability to the northern winters. They grow and replicate vegetatively each year in a very productive manner. Unlike many of the fancier hybrids, especially those with complex coloration and/or from Florida, the Apps plants seem to have vigorous annual growth thus allowing extensive vegetative propagation. Perhaps pricing should be related to how well it can be reproduced vegetatively and not how fragile it as a grower.

7.3.5 Stevens

Don Stevens was from southern New Hampshire and he befriended Bob Seawright who had a growing area in Carlisle. MA. It was from Bob that I received my first batch of daylilies. It was also from Bon that I have many Don Stevens hybrids. Stevens was born in 1930 in New Hampshire and taught in the Bedford, MA High School. Bedford adjoins Carlisle on one side and Lexington MA on the other. Don's hybrids encompassed a wide variety of form, color and shape.

One of the more famous of Stevens's hybrids is the very late blooming Sandra Elizabeth, which in northern New Jersey blooms in early September. It is very healthy and strongly scaped plant with a yellow flower with extreme clarity. It just fills the garden after all of the others have gone their way.

Figure 21 Sandra Elizabeth

Don Stevens worked along-side Bob Seawright of Carlisle Mass. In fact they jointly hybridized several plants. The Stevens plants are quite sophisticated and are all strong growers and have good bud counts and a balanced color subtlety as well.

In many ways the Stevens introductions during this period are middle of the road benchmarks. Super Child is an aggressively tall Tet with a very thick scape and tall and large flowers. It almost speaks Tet in its presentation. The following Figure depicts the many introductions by Stevens in the 1970s.

Royal Kingdom and Outrageous show the growing interest in eyezones. The breath of the Stevens introductions is quite wide and they are generally good Northern flowers.

Stevens

Holiday Delight 1978

Outrageous 1978

Fire Tree 1979

Super Child 1979

Royal Kingdom 1980

Something Royal 1980

The above are several of the Stevens introductions. One should remember he did these in the 1970s and in addition he only hybridized over an eight year period. The results are amazing for the time and the period. Super Child is a classic standout where Steven created a strong scaped Tet and a blossom that at the end of the season truly stands out.

Royal Kingdom presaged many of the eyezone plants of the 1980s and thru the 1990s and is used as parentage in many of these lines. Outrageous also is a deep eyezoned red flower and although not as big as Outrageous has great presence.

7.3.6 Davidson

Clyde Davidson of Decatur Georgia hybridized from 1962 through 1995. His classic is Decatur Apricot, a strong aggressively growing peach or apricot colored Tet. He had registered 184 hybrids and the variation can be seen in a few shown below from his earlier period, Decatur

Cherry Smash is a red wine colored Tet with a dark deep red eyezone. It is recurved and presents very well in the garden. It is not as strong a grower as is Decatur Apricot but does well.

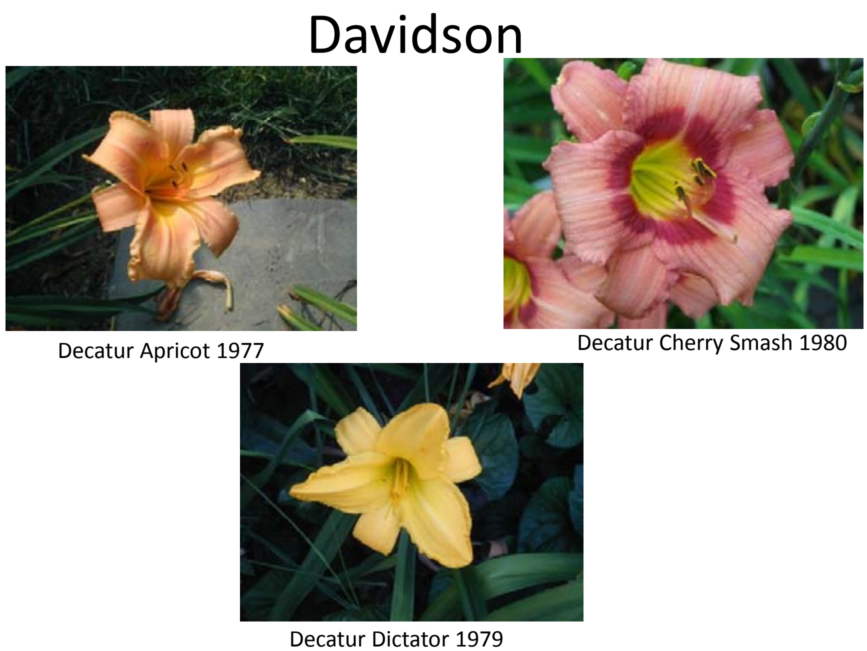


Figure 22 Davidson Decatur Series

The Davidson Decatur series as shown above are also a series in the 1970s and they are a strong set of good growing Tets. Decatur Apricot has been used as a parent for many Tet lines and it has the dark peach, apricot, color and strong branching and bud count.

7.3.7 Petit

Ted Petit is known, along with his partner John Peat, as the authors of a well organized and successful book on the general areas of the daylily. To a great degree Petit is a "leading edge" hybridizer whose success seems to come from noticing the small changes and nuances and building upon them, using breeding techniques which drive the subtle effect deeper into his breeding line. He states that Munson was an influence on him and that especially the comment by Munson where he desired to have an award named for him for the best patterned plant[14]. He continues he recounting of his conversations with Munson by stating that Munson felt the future of hybridizing was in patterns, for other characteristics such as ruffles would just drive the plant to the extreme. Patterns were where the new elements of near endless creativity could be attained.

[14] See Petit, Daylily Journal, Summer 2007, pp. 125-141.

These trends in patterning are then shown in some detail by Petit in both his work and that of others. He classes the patterns as follows:

Appliqué Throats: This is what Petit calls a pearl like patina in the throat. He attributes some of these to Munson. The pattern appears as an application on top of the flower and not coming from within.

Mascara Eyes or Bands: This is the eyezone which has a darkening or contrasting color on the interface region. Again this was a Munson construct. Early versions of this patterning are by Salter. In many ways these flowers appear as if one had dropped food coloring water on a cloth and the eyezone diffuses outwards. There is lack of true clarity. In view of the Turing model for color these flowers and this patterning provide excellent example of true diffusion.

Inward Streaks: This is inward veining especially in the eyezone portion.

Concentric Circles or Bands: This is the alternate to the Inward Streaks by having circular bands.

Washed Eyezones: These are the "running" out of the eyezone in an almost random but limited fashion.

Stippling: This is a dotting effect, which Petit also calls speckled. The coloration appears as if it were done in some impressionistic painting. The colors are not blended but are interspersed.

Metallic Eyes: Like the Appliqué Throats the Metallic Eyes appear as if they have metal specks residing on the top of the eye pattern.

Veining: These have highly contrasted vein patterns.

Rainbow Edges and Midribs: These have edged and midribs where the color variation is a complex set of different colors. This presents a very important model to apply the Turing approach to. It may allow for the inversion problem to seek a solution, for it shows how the instability of the secondary pathways can be controlled.

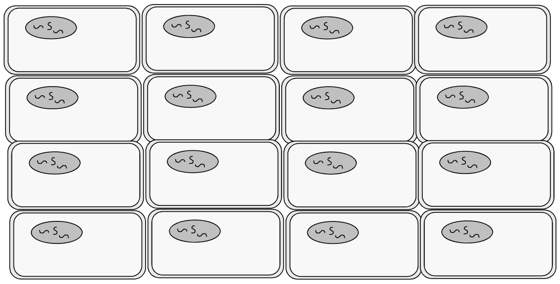
Narrow Formed: These are the contradistinctions of the round daylily. Here form rather than color become a variant.

Others: Petit also presents a collection of yet to be classifies forms.

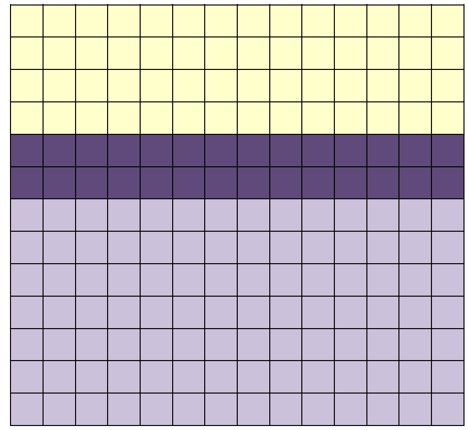
Characteristic	***Turing Model***
Appliqué Throats	Unknown mechanism
Mascara Eyes or Bands	Demonstrates multiple layers of low spatial frequency outward growth of color.
Inward Streaks	If flower grows outward then the flow of control is unstable across new rows of growth.
Concentric Circles or Bands	If flower grows outward then the flow of control is unstable between new rows of growth.
Washed Eyezones	Ultra High intercellular instability, with almost localized oscillations allowing high spatial frequency of color change.
Stippling	High intercellular instability, with almost localized oscillations allowing high spatial frequency of color change.
Metallic Eyes	Unknown mechanism
Veining	Demonstrates multiple layers of low spatial frequency lateral growth of color.
Rainbow Edges and Midribs	
Narrow Formed	Not Applicable
Others	Not Applicable

Petit uses the sources of this innovative color patterns in his hybridizing as does his partner Peat. These color schemes provide a unique basis for the validation of the Turning model. We show the abstractions of these patterns reflected on a cellular matrix as follows.

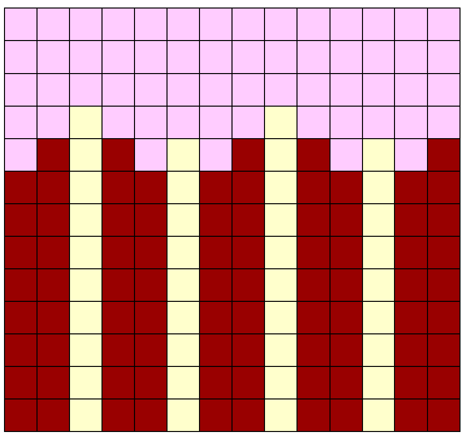
Plant Cell Matrix



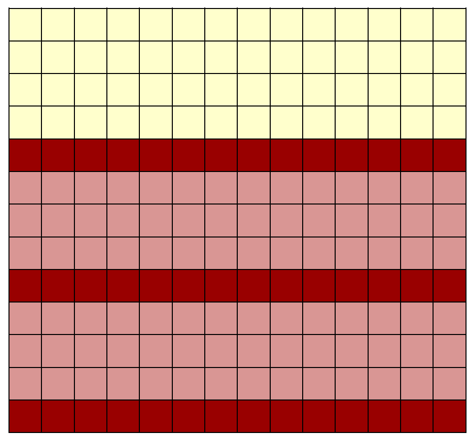
Mascara Eyes



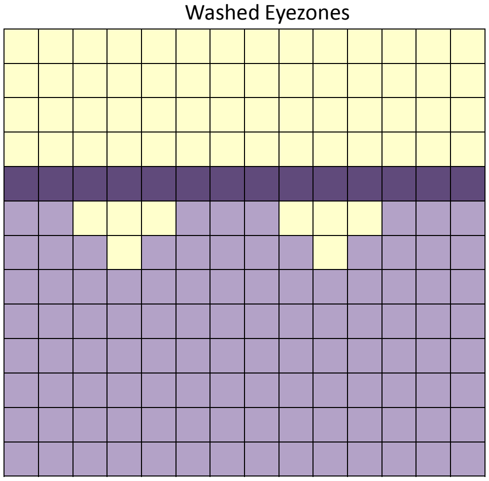
Inward Streaks



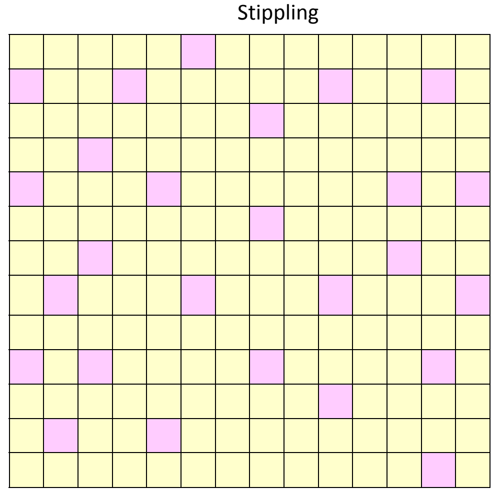
Concentric Circles

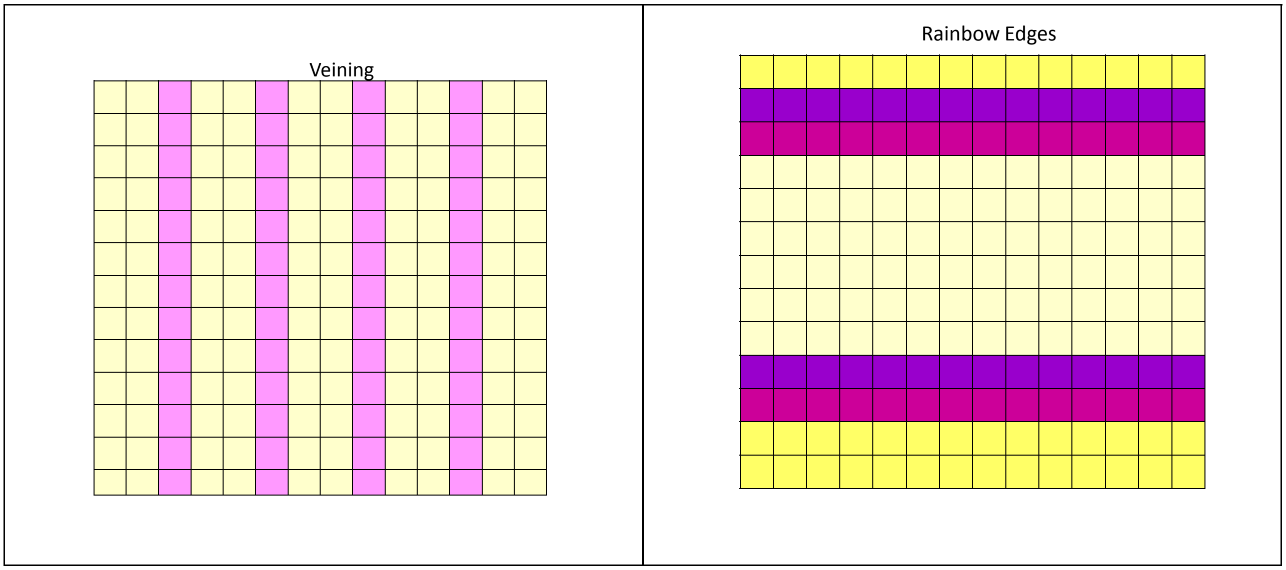


Washed Eyezones



Stippling





One can note that each of these becomes a Turing model with certain points of instability in a periodic manner. One can predict that there could be an almost unlimited number of such patterns depending on the inbreeding of the gene combinations controlling the stability points.

7.3.8 Hanson

Hanson has 1 Stout Silver Medal, 4 Awards of Merit and 29 Honorable Mentions. His Primal Scream is the one for which he received the Stout Medal. In the figure below we show two others. One is Now and Zen, an eyed and edged plant which grows modestly up north and Sea Hunt which is a watermarked purple tinted flower.

Hanson

Now and Zen 1999

Sea Hunt 1999

Primal Scream 1990

7.3.9 Mahieu

Although not an award winner as yet, the plants by Mahieu have an interesting turn. Mahieu is an artist and he brings an eye for subtle color to his introductions as well as an exciting form. Furthermore Mahieu is attracted to the species, especially H citrina and H altissima. He has focused on what he calls the "architecture" of the plant, and in that context he is building on the Stout hybrid Autumn Minaret, which stands tall and quite distinctively in any garden at the end of a season. He wants to emphasize in his breeding the entire plant, and to do so has brought to his crosses the character and strength of not only citrina and altissima but H hakuunensis and H dumortieri.

Mahieu states that he seeks to "put huge blooms …with heavy texture on tall scapes…". Indeed, that is what he has accomplished. Unlike the main stream hybridizers like Munson, Petit, Stamile, and others, Mahieu represents a branch of hybridizing which seeks the new and innovative by drawing back upon the much strength of the original species. Mahieu is an artist and one can see his pallet in his crosses. They are simple, yet elegant, colorful, yet not extreme, and they catch your eye as you enter. They have the subtlety of the impressionists while having the stature of the species. The species is always not very far behind what he has presented.

Mahieu is an example of the hybridizer who brings back those dominant and nature preserving genes which have been driven out by Petit and the others who are seeking the in extremis flower. It is not that either is better or worse, Judges decide what is currently in vogue, yet they both show the versatility of the genus.

8 CONCLUSIONS

The process of hybridizing is a bit science and a bit art, it is a bit strategy and a bit whimsy. We have summarized the classic Mendellian approach and then we have reviewed the classic methods or breeding as understood under the Mendellian rubric. What we see is that the hybridizing of the Hemerocallis is often less the rigorous approach taken by those who breed for crops and is a hit and miss affair, with some idea of where they are going.

We have seen distilled certain rules of hybridizing:

1. Start with good stock. This is obvious in Stamile. They have breed their own good stock and they then select the best of the best. The same is true of Petit. In contrast Mahieu blends good stock with species, specifically H citrina. It all depends on what one views as intent but we see Mahieu as a leading edge innovator bringing back characteristics that may all to easily be lost in the rush to the extreme.

2. Use your own innovations. If a hybridizer has talent and luck, they may end up with their own source materials resulting from their own crosses. These may then become the source for many of their new entrants. This is seen in Moldovan, Davidson, Petit, Stamile, Apps and others.

3. Promote yourself to the extreme if you want awards. I have often told those seeking business advice that "to get on the bus you must be standing on the corner, it just does not drive into your bedroom.." Thus for those who seek glory, they must get into the market and promote themselves. Looking at Stamile one sees a great promoter, and in turn one who has obtained many awards. The awards track is a club, and as a club one must work their way up to the top. That does not mean in any way that those who hybridize for the sake of hybridizing are to be marginalized. In many ways they are like gold nuggets, they can be mined for new product.

4. Create goals but be pragmatic and opportunistic. One can set out seeking doubles and find spiders. Thus having rigid goals will not necessarily result in a good outcome.

5. Look at the fringe versus the center. Decide where to play. The fringe is where the new introductions are, they are at the point of introducing the new gimmick, a metallic edge, a speckled eye, and many of the forms as described by Peck. In contrast there is the player in the center who is looking for good horticultural product. This means a good and hardy grower, a good and consistent display plant, and one which can be combined with others to create a palette. Again I think of Mahieu as a player in this field.

These are not rules from anyone specific but they are a condensation of what has been heard from many hybridizers. One need look no farther than Apps to see a superb middle of the road hybridizer, or Stevens, while a generation ago created a set of plants which had more than stood the test of time.

9 REFERENCES

1. Allard, R., Plant Breeding, Wiley (New York) 1960.
2. Atkins, P. **Physical Chemistry**, Freeman (New York) 1990.
3. Baici, A., *Enzyme Kinetics*, The Velocity of Reactions, Biochem Journal, 2006, pp. 1-3.
4. Bartel, B., S. Matsuda, *Seeing Red*, Science, Vol 299, 17 Jan 2003, pp 352-353.
5. Benson D. L., *Unraveling the Turing Bifurcation Using Spatially Varying Diffusion Coefficients*, Jour Math Bio, Vol 37 1998, pp. 381-417.
6. Benson, D. L., et al, *Diffusion Driven Instability in an Inhomogeneous Medium*, Bull Math Bio, Vol 55 1993, PP. 365-384.
7. Berns, R. S., **Principles of Color Technology**, Wiley (New York) 2000.
8. Born, M., E. Wolf, **Principles of Optics**, 4th Ed, Pergamon (New York) 1970.
9. Brown, A., et al, Plant Population Genetics, Breeding, and Genetic Resources, Sinauer (Sunderland, MA) 1990.
10. Campbell, A., L. Heyer, **Genomics, Proteomics, and Bioinformatics**, Benjamin Cummings (New York) 2003.
11. Carey, F. A., **Organic Chemistry**, McGraw Hill (New York) 1996.
12. Causton, H. et al, **Microarray Gene Expression and Analysis**, Blackwell (Malden, MA) 2003.
13. Cavalli-Sfroza, L. L., W. F. Bodmer, The Genetics of Human Populations, Dover (Mineola, NY) 1999.
14. Chase, M., Monocot Relationships, an Overview, Journal of Botany, Vol 91 2004 pp 1645-1655.
15. Chen, T., et al, *Modeling Gene Expression with Differential Equations*, Pacific Symposium on Biocomputing, 1999 pp. 29-40.
16. Chung, M., J. Noguchi, *Geographic spatial correlation of morphological characters of Hemerocallis middendorfii complex*, Ann Bot Fennici Vol 35, 1998, pp. 183-189.
17. Chung, M., *Spatial Structure of three Populations of Hemerocallis hakuunensis*, Bot. Bull. Acad. Sci., 2000, Vol 41, pp. 231-236.
18. Cilla, M. L., D. Jackson, *Plasmodesmata Form and Function*, Current Opinion in Cell Bio, Vol 16 2004 pp. 500-506
19. Crawford, D., Plant Molecular Systematics, Wiley (New York) 1990.
20. Cronquist, A., The Evolution and Classification of Flowering Plants, New York Botanical Garden Pres (Bronx, NY) 1986.
21. Dahlgren, R.M.T., T**he Families of Monocotyledons**, Springer (New York) 1985.
22. Daly, D., et al, Plant Systematics in the Age of Genomics, Plant Physiology, Dec 2001, pp 1328-1333.
23. Dey, P. M., J. B. Harborne, **Plant Biochemistry**, Academic Press (New York) 1997.
24. Dunn, G., B. Everitt, Mathematical Taxonomy, Dover (Mineola, NY) 2004.
25. Durbin M. L. et al, Genes *That Determine Flower Color, Molecular Phylogenetics and Evolution*, 2003 pp. 507-518.
26. Durbin, R. et al, Biological Sequence Analysis, Cambridge (Cambridge) 1998.
27. Durrett, H., **Color**, Academic Press (New York) 1987.
28. Eisen, M., et al, Cluster Analysis and Display of Genome Wide Expression Patterns, Proc Nat Acad Sci 1998 Vol 98 pp 14863-14868.
29. Erhardt, W., **Hemerocalis**, Timber Press (Portland, OR) 1992.
30. Esau, K., **Anatomy of Seed Plants**, Wiley (New York) 1977.
31. Felsenstein, J., Inferring Phylogenies, Sinauer (Sunderland, MA) 2004.
32. Fox, M. A., J. K. Whitsell, **Organic Chemistry**, Jones and Bartlett (Boston) 1997.
33. Gitzendanner, M., Soltis, P, Patterns of Genetic Variation in Rare and Widespread Plant Congeners, Journal of Botany, Vol 87 2000 pp 783-393.
34. Goodwin, T.W., **Chemistry and Biochemistry of Plant Pigments**, Vols 1 and 2, Academic Press (New York) 1976.
35. Griffiths, A., et al, **Genetic Analysis 5th Ed**, Freeman (New York) 1993.
36. Gusfield, D., Algorithms on Strings, Trees, and Sequences, Cambridge (New York) 1997.
37. Harborne, J. B., C. A. Williams, *Anthocyanins and Flavonoids*, Nat Prod Rep 2001 Vol 18 pp. 310-333. http://www.rsc.org/ej/NP/1998/a815631y.pdf
38. Harborne, *Spectral Methods of Characterizing Anthocyanins*, Biochemical Journal, pp 22-28, 1958. http://www.biochemj.org/bj/070/0022/0700022.pdf
39. Harvey, P., M. Pagel, The Comparative Method in Evolutionary Biology, Oxford (New York) 1991.

40. Hatzimanikatis, V., *Dynamical Analysis of Gene Networks Requires Both mRNA and Protein Expression Information*, Metabolic Engr, Vol 1, 1999, pp. 275-281.
41. Haywood, V. et al, *Plasmodesmata: Pathways for Protein and Ribonucleoprotein Signaling*, The Plant Cell, 2002 PP 303-325.
42. Hildebrand, F. B., **Numerical Analysis**, 2nd Edition, Dover (New York) 1987.
43. Holton, T., E. Cornish, *Genetics and Biochemistry of Anthocyanin Biosynthesis,* The Plant Cell, Vol 7, 1995, pp 1071-1083.
44. Innan, H., et al, A Method for Estimating Nucleotide Diversity from AFLP Data, Genetics, Vol 151 March 1999, pp. 1157-1164.
45. Jaakola, L. et al, *Expression of Genes Involved in Anthocyanin Biosynthesis*, Plant Physiology, Vol 130 Oct 2002, pp 729-739.
46. Jenkins, F. A., H. E. White, **Fundamentals of Optics**, McGraw Hill (New York) 1957.
47. Judd, D. B. et al, **Color** 2^{ND} Edition, Wiley (New York) 1963.
48. Judd, W., et al, Plant Systematics, 3rd Ed, Sinauer (Sunderland, MA) 2008.
49. Judd, W., R. Olmstead, A Survey of Tricolpate (Eudicot) Phylogenetic Relationships, Journal of Botany Oct 2004, pp 1627-1644.
50. Kadar, S., et al, *Modeling of Transient Turing Type Patterns in the Closed Chlorine Dioxide-Iodine-Malonic Acid-Starch Reaction System*, J Phys Chem, Vol 99 1995 pp. 4054-4058.
51. Kohane, I., et al, **Microarrays for an Integrative Genomics**, MIT Press (Cambridge) 2003.
52. Koopman, W., et al, AFLP Markers as a Tool to Reconstruct Complex Relationships: A Case Study in Rosa, Journal of Botany, Vol 95 2008 pp 353-366.
53. Lee, D., **Nature's Palette**, University of Chicago Press (Chicago) 2007.
54. Lesk, A., **Bioinformatics**, Oxford (New York) 2002.
55. Levi, L., **Applied Optics**, Wiley (New York) 1968.
56. Mauseth, J. D., **Plant Anatomy**, Benjamin (Menlo Park, CA) 1988.
57. Mayo, O., The Theory of Plant Breeding, Oxford (New York) 1987.
58. Mayr, E., Evolution and the Diversity of Life, Harvard University Press (Cambridge) 1976.
59. Mayr, E., Population, Species and Evolution, Harvard University Press (Cambridge) 1970.
60. Mayr, E., The Growth of Biological Thought, Harvard University Press (Cambridge) 1982.
61. Mayr, E., Toward a New Philosophy of Biology, Harvard University Press (Cambridge) 1988.
62. McGarty, T. P., *Flower Color and Means to Determine Causal Anthocyanins And Their Concentrations*, MIT 2008, http://www.telmarcgardens.com/Documents%20Papers/Flower%20Color%20and%20Means%20to%20Determine%2002.pdf
63. McGarty, T. P., *On the Structure of Random Fields Generated by a Multiple Scatter Medium*, PhD Thesis, MIT 1971. http://mit.edu/mcgarty/www/MIT/Paper%20Hypertext/1971%20PhD%20MIT.pdf
64. McGarty, T., *Gene Expression in Plants*: Use of System Identification for Control of Color, MIT, 2007. http://mit.edu/mcgarty/www/MIT/Paper%20Hypertext/2007%20Gene%20Expression%20IEEE%2007%2002.pdf .
65. McGarty, T., **Stochastic Systems and State Estimation**, Wiley (New York) 1974.
66. McMurry, J., Begley, T., The **Organic Chemistry of Biological Pathways**, Roberts & Company Publishers, 2005.
67. Milgrom, L. R**., The Colours of Life**, Oxford (New York) 1997.
68. Mohr, H., P. Schopfer, **Plant Physiology**, Springer (New York) 1995.
69. Mol, J, et al, *How Genes Paint Flowers and Seeds, Trends in Plant Science*, Vol 3 June 1998, pp 212-217.
70. Mol, J., et al, *Novel Colored Plants*, Current Opinion in Biotechnology, Vol 10, 1999, pp 198-201.
71. Mueller, U., L. Wolfenbarger, AFLP Genotyping and Fingerprinting, Trends Ecol. Evol. **14: 1999, pp** 389–394. .
72. Munson, R., **Hemerocalis, The Daylily**, Timber Press (Portland, OR) 1989.
73. Murray, J., **Mathematical Biology**, Springer (New York) 1989.
74. Murrell, J., *Understanding Rate of Chemical Reactions*, University of Sussex.
75. Naik, P. S., et al, *Genetic manipulation of carotenoid pathway in higher plants*, Current Science, Vol 85, No 10, Nov 2003, pp 1423-1430.
76. Nei, M., S.. Kumar, Molecular Evolution and Phylogenetics, Oxford (New York) 2000.
77. Nicklas, K. J., The Bio Logic and Machinery of Plant Morphogenesis, Am Jour Bot 90(4) 2003 pp. 515-525.

78. Noguchi, J., H. De-yuan, *Multiple origins of the Japanese nocturnal Hemerocalis citrina*, Int Jrl Plant Science, 2004, Vol 16, pp. 219-230.
79. Norton, J. 1972. *Hemerocallis* Journal 26 (3) in Bisset, K. 1976. *Spectrophotometry, Chromatography and Genetics of Hemerocallis Pigments*. Dissertation, Florida State Univ.
80. Norton, J., *Some Basic Hemerocallis Genetics*, American Hemerocallis Society, 1982.
81. Oparka, K. J., A. G. Roberts. Plasmodesmata*, A Not So Open and Shut Case*, Plant Phys, Jan 2001, Vol 125 pp. 123-126.
82. Percus, J., Mathematics of Genome Analysis, Cambridge (New York) 2002.
83. Perkins, T., et al, *Inferring Models of Gene Expression Dynamics*, Journal of Theoretical Biology, Vol 230, 2004, pp. 289-299.
84. Petit, T. *The Patterned Daylily*, The Daylily Journal, Vol 62 No 2 2007 pp. 125-141.
85. Planet, P. et al, Systematic Analysis of DNA Microarray Data: Ordering and Interpreting Patterns of Gene Expression, Cold Spring Harbor, Genome Research, 2001 pp 1149-1155.
86. Rossi, B., **Optics**, Addison Wesley (Reading, MA) 1957.
87. Saitou, N., M. Nei, The Neighbor Joining Method: A New Method for Reconstructing Phylogenetic Trees, Molecular Biological Evolution, Vol 4 1987 pp 406-425.
88. Sansone, G et al, **Orthogonal Functions**, Academic Press (Mew York) 1958.
89. Sattath, S., A. Tversky, Additive Similarity Trees, Psychometrica, Vol 42, 1977 pp. 319-345.
90. Schnell. S, T. Turner, *Reaction Kinetics in Intracellular Environments with Macromolecular Crowding*, Biophys and Molec Bio vol 85 2004 pp. 235-260.
91. Sears, F. W., **Optics**, Addison Wesley (Reading, MA) 1949.
92. Sokal, R., P. Sneath, Principle of Numerical Taxonomy, Freeman (San Francisco) 1963.
93. Soltis, D. et al, Evolution of Genome Size in Angiosperms, Journal of Botany, Nov 2003, pp 1596-1603
94. Somasundaram, S., M. Kalaiselvam, Molecular Tools for Assessing Genetic Diversity, UN University Course, http://ocw.unu.edu/international-network-on-water-environment-and-health/unu-inweh-course-1-mangroves/Molecular_Tools__for_Assessing_Genetic_Diversity.pdf .
95. Stace, C., Plant Taxonomy and Biosystematics, Arnold (London) 1989.
96. Stout, A.B., **Daylilies**, Saga Press (Millwood, NY) 1986.
97. Strickberger, M., Genetics, 2nd Ed McMillan (New York) 1976.
98. Strong, J., **Concepts of Classical Optics**, Freeman (San Francisco) 1958.
99. Studier, J., K. Kappler, A Note on the Neighbor Joining Algorithm, Molecular Biological Evolution, Vol 5 1988 pp 729-731.
100. Stuessy, T., Case Studies in Plant Taxonomy, Columbia University Press (New York) 1994.
101. Szallasi, Z. **System Modeling in Cellular Biology: From Concepts to Nuts and Bolts**. MIT Press (Cambridge) 2006.
102. Taiz, L., E. Zeiger, **Plant Physiology**, Benjamin Cummings (Redwood City, CA) 1991.
103. Taubes, C. H., Modeling Differential Equations in Biology, Cambridge (New York) 2001.
104. Tetter, A., et al, Primer on Medical Genomics Part III, Mayo Clinic Proc, Vol 77 2002 pp 927-940.
105. Tinoco, I. et al, **Physical Chemistry**, Prentice Hall (Englewood Cliffs, NJ) 1995.
106. Tobias, A., *Directed Evolution of Biosynthetic Pathways to Carotenoids with Unnatural Carbon Bonds*, PhD Thesis, Cal Tech, 2006.
107. Tomkins, J. R., *DNA Fingerprinting in Daylilies*, Parts I and II, Daylily Journal, Vol 56 No 2 and 3 2001, pp. 195-200 and pp. 343-347.
108. Tomkins, J. R., *How much DNA is in a Daylily*, Daylily Journal, Vol 58 No 2 2003, pp. 205-209.
109. Tomkins, J., et al, *Evaluation of genetic variation in the daylily (Hemerocalis) using AFLP markers*, Theor Appl Genet Vol 102, 2001, pp. 489-496.
110. Turing, A., *The Chemical Basis of Morphogenesis*, Phil Trans Royal Soc London B337 pp 37-72, 19459.
111. Van Trees, H. L., **Detection, Estimation and Modulation Theory**, Wiley (New York) 1968.
112. Vohradsky, J., *Neural Network Model of Gene Expression*, FASEB Journal, Vol 15, March 2001, pp. 846-854.
113. Vos, P., et al, AFLP: A New Technique for DNA Fingerprinting, Nuclear Acids Research, Vol 23 1995 pp 4407-4414.
114. Wade, L. G., **Organic Chemistry**, Prentice Hall (Saddle River, NJ) 2003.
115. Watson, J. et al, Recombinant DNA, 3rd Ed, Freeman (New York) 2007.
116. Watson, J., et al, **Molecular Biology of the Gene**, Benjamin Cummings (San Francisco) 2004.
117. Weir, B., Genetic Data Analysis, Sinauer (Sunderland, MA) 1990.

118. Wen, X., et al, Large Scale Temporal Gene Expression Mapping of Central Nervous System Development, Proc Nat Acad Sci Neurology 1998 Vol 95 pp 334-339.
119. Winkel-Shirley, B., *Flavonoid Biosynthesis*, Plant Physiology, Vol 126 June 2001 pp 485-493. http://www.plantphysiol.org/cgi/reprint/126/2/485
120. Yu, O. et al, *Flavonoid Compounds in Flowers: Genetics and Biochemistry*, General Science Books, http://www.danforthcenter.org/yu/pdf/e-flower-2006.pdf
121. Zambryski, P., C*ell to Cell Transport of Proteins and Fluorescent Tracers via Plasmodesmata During Plant Development*, Jour Cell Bio Vol 161 No 2 Jan 2004, pp. 165-168.