Part III

Plant Breeding Terms:

Genetic Linkage -- is a phenomenon in which genes tend to be inherited together. This seems to violate Mendel's postulate of independent assortment of genes and can make it difficult to pick out a single trait from one parent without also bringing over others. This often occurs when the alleles for two separate traits are closely spaced on a chromosome and both are passed together onto the progeny. Pulling the extra traits along is called Linkage Drag[ix] and backcrossing is often used to try and break the linkage. A hypothetical example would be when breeding for white fragrant flowers on a thick-leaf hosta, yet each time one achieves the leaf shape, the flower color switches to lavender and looses the fragrance.

- While on this subject, let's hit the closely related topics of **Penetrance and Expressivity**. Sometimes you can successfully transfer a gene but it is not expressed in the offspring (that is, it lacks penetrance for expression). Additionally, there may be environmental factors that cause the expression (or lack thereof) of certain traits (e.g., lutecence due to light intensity) at work with your new hosta cultivars. Even when a particular gene is presence in the offspring, it simply may not be phenotypically expressed (lacks Penetrance) yet selfed offspring may show the trait again. For me, one example would be a solid yellow hosta that came from a sieboldiana blue type. It obviously has the genes for blue/wax production and many of the offspring come out blue yet it's not being expressed in this particular yellow seedling. Traits that are expressed only at certain temperatures are said to have variable gene expressivity. Sometimes I wonder if some of the red/purple hues in petioles express different intensity depending on temperatures or sunlight.

- **Qualitative & Quantitative Traits**: Sometimes only a few alleles control a plant trait, and thus the expression of that trait in the progeny can be seen as discrete qualitative steps (for instance as seen in wheat reference above). This qualitative trait expression is what we mostly discuss via the on-line hosta forums. The other major plant breeding concept (quantitative traits) pertains to features influenced by a group to genes and cumulative. The result is a spread of trait expressions in the progeny and is the result of usually 5 to 10 (or more) alleles involved in trait expressions. When this occurs, one can expect more of a full span of expressions from the many "polygenes" (minor genes) with individual effects too small to distinguish (Stoskopf, 1993)[x]. Segregation in the first generation after a hybrid cross (that is, the first filial generation) (f1)[xi] and then second generation (f2) seedlings from selfed plants occurs along a bell curve from low to high expression in this case. Working with quantitative traits often requires analysis on large sample sets and employs statistical formulas that often include environmental factors. As documented by Nilsson-Ehle in 1910[xii], polygenic inheritance is characterized by 1) many genes determine the quantitative trait 2) these genes lack dominance, and 3) the action of the genes are additive. I'm not planning to explore quantitative analysis in any further detail here but just wanted to introduce the topic as it is certainly a major part of crop improvement programs

Part IV

Crossing Strategies:

Single Hybrid cross – "Single Cross" is the term used for crossing two plants to produce hybrid seeds/progeny (A X B) to produce what we can call "AB" seedlings in shorthand. This is what I believe most of us do with our hostas even if the plants/flowers are not tagged and works to produce many fine plants. Additionally, we often let the new plants be Open Pollinated which is a good strategy when working with a new hybrid to see what more is hidden away. After producing hybrids from a single cross, consider selfing those offspring when they flower (OP often creates "selfed" seedlings by the bees, upwards of 85% to 95% of the time for plants that can be easily self pollinated). The selfing of plants (in line breeding) is an excellent approach for one or two generations after a hybrid cross and is considered an ideal method to "pull out" all the possible variations via independent segregation. After about 4 to 5 generations of selfing, you'll likely not see very much difference in the progeny although these plants will have the added effect of being homozygous for many genes (but will still have slight differences to their genotype, aka "near-isogenic lines"). One downfall to repeated selfing in plants encountered is that after a few generations of in-line breeding, one may encounter "inbreeding depression" – that is the loss of vigor or fertility. Remember, the female (pod parent) is always written to the left in the annotation.

Three-way cross – This term describes crossing the progeny from an earlier hybrid cross (A X B) with a third plant (AB X C) to produce seedlings that then have recombination of the desired traits from all three plants (in theory, 25% A, 25% B, and 50% C). In crop management, the "C "plant should contain the best environmental adaption for the region of intended use (Acquaah, 2008)[xiii].

Double cross – This consists of a cross between the progeny from two single crosses AB x CD. Although this will produce genetically broad-based progeny, the desirable traits may not be apparent in the F1 offspring. Again, the selfing discussion above would then apply to seek independent segregation of the desirable traits for the seedlings of a double cross. This method (along with Diallel crossing and convergent crossing-below) is used often employed to combine additive traits into a single plant.

Diallel cross – This is a complex crossing strategy in which each plant is crossed with many others as well as the reciprocal cross is made. This approach is generally made for genetic studies as it can be very time consuming (especially to keep track of everything!). For example, if the Diallel crossing plan starts with five plants, then all would be crossed with each other (normally excluding the selfed combinations) for a *n-(n-1)/2* different number of combinations. In this example 5 * (5-1) /2 = 10 different combinations –which assumes "AB" and "BA" are the same genotype – remember, this is basic plant breeding theory, not necessarily true for hostas and I'd probably say the number of combinations attempted for 5 plants is 20 unique crosses due to linkage challenges as well as non-nuclear trait associated with variegated seedlings. Table 1 below provides a table version of the diallel crossing strategy:

	A	B	C	D	E
A	x	AB	AC	AD	AE
B	BA	x	BC	B	BE
C	CA	CB	x	CD	CE
D	DA	DB	DC	x	D
E	EA	EB	EC	ED	x

Table 1: Diallel Crossing Strategy

Convergent cross – A convergent cross is another complex breeding method used to combine the alleles from many starting plants into a single progeny. Think of it as combining the best traits from your superior hybrid crosses each year to produce a single elite type. Two convergent crossing strategies are considered here, 1) crossing the plants in groups of two the first year and then using the double cross the next year and so on or 2) employing a recurrent parent as part of each initial cross. (Backcrossing is also considered a convergent cross strategy and will be addressed separately).

Using the A X B format example, a convergent crossing plan may be set up along one of these lines (making an unrealistic assumption those new hostas seedlings will bloom and be viable with 1-year's growth)

Example 1:

Year 1: Cross 8 plants two at a time in the first year
(A X B)   (C X D)   (E X F)   (G X H)

Year 2: Cross the best offspring from each group of first year hybrids with each other
(AB) X (CD)   (EF) X (GH)

Year 3: Cross the best offspring from the double crosses with each other to produce a set of seedlings with 12.5% of their traits from each of the original 8 base population plants.
(ABCD) X (EFGH)

Example 2:

Year 1: Cross 4 plants each to the same elite type that has the majority of traits desired in the final plant
(A X B)   (A X C)   (A X D)   (A X E)

Year 2: Cross each of the best offspring to make double crosses
(AB X AC)   (AD X AE)

Year 3: Cross each of the best offspring from the previous double crossing strategy to produce seedlings with 50% genes from the original "A" plant and 12.5% from each of the other four plants from the base population.
(ABAC X ADAE)

Backcrossing – in simple terms, backcrossing is the process of crossing a progeny with one of the original parents. The rational for using backcrossing is to replace a specific undesirable allele with a desirable one while preserving all other qualities. The F1 hybrid progeny are crossed with the recurrent parent to strengthen its influence on the next generation. The non-recurrent parent is called the donor parent. This process is best suited to improve established cultivars by adding minor changes to their genotype. There is more discussion on backcrossing in section VI below.

Recurrent Selection: This strategy is when one identifies superior seedlings and selects them to produce the next generation/crosses in order to advance or strengthen combinations of desirable alleles. Plants are repeatedly selected based on an expressed trait and intercrossed to increase the frequency of desired favorable alleles[xiv]. As an example, say one selects the reddest progeny from many hosta crosses each year. Then those best red traits are then crossed to produce a new line of hopefully even redder plants. The best of those red trait seedlings are then selected as the parents for the following hybrid generation and so on.

Part V

Common plant breeding ratios:

Certain underlying gene actions often produce somewhat predictable results based on overall ratios that may be observed in the progeny. Here are some of the most common ratios along with what can produce these results. Using these rations can provide clues to what type of gene actions may be taking place when working with two alleles that control a qualitative trait. (Primarily sourced from Welsh 1981)[xv]:

Homozygous Dominance (selfed) – (AA x AA) all will be the same (within the normal standard deviations for that type)

A **Homozygous Recessive** crossed with a **Heterozygous Dominant** (aa x Aa) – 1:1 (50% progeny for each type)

Heterozygous Dominant (selfed) -- (Aa x Aa) 3:1 (if two alleles are at work)

Heterozygous Dominant -- 9:3:3:1 (if four alleles control the trait expression)

No dominance/additive -- 1:2:1

Overdominance -- 1:1:2 *

- (Note: the "two" being heterozygous types which show a different phenotype outside the range of the two parents)

Dominant epistasis -- 12:2:1

Linkage -- 6:2:2:6

Recessive epistasis -- 9:3:4

Duplicate recessive epistasis -- 9:7

Inhibitor action -- 13:3

Duplication dominant epistasis -- 15:1

Looking over these ratios should provide an idea of about how many plants to grow when seeking a particular trait expression (making some assumptions as to how many alleles may control that trait and that the environment interactions are minimal). Although there is a specific statistical formula crop breeders employ to more accurately determine the likeness (95% or better) of achieving a certain combination (especially when many genes are involved), the above ratios should hopefully help put one in the ball park. Make some assumptions, run some controlled tests and let us know what you find!

Part VI

Backcrossing concepts in greater detail:

This is a discussion I had with a hosta hybridizing peer last year and would like to share it as a good backcrossing challenge (and provides a case in point that these strategies can take a several years to work!). This is a hypothetical example only and in no way implies an underlying certainty on the dominance or lack thereof for the traits discussed. In this hypothetical case, say the goal is to develop a *Hosta* 'Jade Cascade'- like hosta except with the straight scapes from another hosta – in this example using 'Abba Dabba Do'. If the trait desired can be seen in the progeny (phenotypically identified), then there's no problem picking the seedlings each year to use in the backcrossing process with the recurrent parent ('Jade Cascade'). These would be called BC1F1 plants. Now the harder part would be if the straight scape is heterozygous in the F1 plants and is also a recessive allele of the desired gene. In other words, the trait is masked and not readily apparent in the offspring. In this case, a little more work is needed after each backcross step in order to select the right plant for continued development of the line—that is a test cross after each backcross round. The below example is along the lines of the straight scape being a hidden trait but desired in the final new cultivar:

Say 'Abba Dabba Do' (ADD) has nice upright scapes - presumed to be recessive - let's use "ss" for this trait. Then for 'Jade Cascade' (JC) - leaning scape is likely homozygous dominant for the leaning scape trait ("SS") or heterozygous dominant "Ss" again, which would cause the leaning scape to show.

When you cross the two, you will have plants with Ss or possibly ss in the F1 generation. If the homozygous recessive "ss" is present in the progeny, then we should note the upright scape easily so no challenges selecting which progeny to use for the next backcrossing step to strengthen the JC look while keeping the straight scape trait from ADD. So, we'll eliminate that particular case and further discuss with the case of a heterozygous Ss (leaning scapes but heterozygous trait for the straight scapes masked by the dominant leanings scape allele) and see how this can be approached for success.

Assumptions: ADD has recessive scape traits "ss" that produce straight scapes and JC has "SS" or "Ss" (dominate genes that manifest in leaning scapes). Let's break this down one more step before we get into the backcrossing strategy:

- If JC is homozygous dominant for leaning scapes "SS" and crossed with ADD, then the F1 seedlings should be heterozygous for this trait "Ss" and will all show the drooping scapes we're trying to eliminate.

- If JC is heterozygous for drooping scapes "Ss" then some of the F1 seedlings will be Ss and some will be double recessive "ss". The seedlings carrying the homozygous recessive alleles should display the straight scapes. These would be the easy ones to pick for the next round of backcrossing with JC to keep adding more of its influence/shape onto the next generation of seedlings (which may take 2 to 10 years to produce the desired results).

- The last assumption is that both plants have good "general combining ability" and linkage drag is not involved.

Now the question is, which plants to use for the backcrossing to recover the shape/style of 'Jade Cascade' (say, 85% or better) but with the straight scapes? In the first set of hybrids (F1) generation, we would have the recessive (straight scape) trait in all of the progeny but it will likely not show in this generation for all (assuming JC is SS) or only ½ of the time (assuming JC is Ss). Let's call these initial plants the AB F1 plants. In order to determine which of the AB F1s are carrying the recessive trait desired, a selfing step is required to create AB F2s. These F2 generation plants are called a testcross—mating conducted to evaluate the genotype of the parent—and are not intended to be part of the backcrossing line in this particular example. In the F2 progeny, we should be able to detect the desired recessive trait in some of the plants via independent assortment for the straight scapes. Using the testcross F2 plants, note which F1 parents caused this recessive trait to manifest in the offspring and tag that particular AB F1 plant(s) for the next round of backcrossing and cull the F2 testcross plants. After each backcrossing round, the progeny will need a testcross round (selfing) to once again isolate those that have the masked straight scape gene (the BC1F2 generation) before attempting the second backcross (BC2) to then have plants with greater than 85% JC genes along with the straight scapes from the non-recurrent parent. For the last step, after we have the desired 'Jade Cascade' look, the final protocol is to self the BC2F1 plants to produce BC2F2 seedlings which should help isolate the superior one(s) that phenotypically best represent JC but now have straight scapes. If none are superior, then another round of backcrossing may be needed to strengthen the JC look. Hopefully you can achieve your plant hybridizing goals in one or two backcrossing rounds although many references have examples that took several years to complete with 10 or more backcrossing events. Additional "what if" examples can be found in "Principles of Cultivar Development, Vol 1, Theory and Technique" by Walter Fehr[xvi] (thanks to "Ryan from Utah" for the tip on this particular text book).

Here's the same information in shorthand year-by-year format (please note: this is only one backcrossing example and again assumes that each new hosta hybrid seeding blooms the first year grown. In other examples, one may employ the F2 seedlings into the backcross protocol or conduct testcrosses and backcrosses the same year in order to accelerate the overall plan):

Year 1:
JC x ADD --> yields A x B F1 seedlings
Results: F1s are 50% JC and 50% ADD (assuming good general combining ability, no linkages, no epistasis and only two genes involved for the trait sought)

Year 2:
AB F1 selfed --> yields testcross F2s seedlings
Results: F2 seedlings that contain segregated dominant and recessive traits // SS, Ss and ss

Year 3:
Grow AB F2s to isolate which AB F1s have the desired recessive gene(s)
Results: These seedlings are only used to isolate which parents produced the recessive straight scape seedlings

Year 4:
Backcross the tagged heterozygous AB F1s to Jade Cascade --> yields your BC1F1 seedlings
Results: Hybrids produced with 75% JC genes and 25% ADD genes to include the trait for a straight scape, although with none showing the recessive straight scape feature but contained therein.

Year 5:
BC1F1 selfed --> testcross BC1F2 seedlings
Results: These seedlings are again only used to isolate which BC1F1 plants carry the straight scape genes

Year 6:
Grow BC1F2s to track which BC1F1 have the desired recessive straight scape gene
Results: Identify the BC1F1s that are carry the recessive straight scape gene, tag these for the next backcrossing round

Year 7:
Backcross tagged BC1F1s with H. 'Jade Cascade' --> yields the BC2F1 generation with 87.5% JC and 12.5% ADD genes (again, with the hidden straight scape trait being transferred to the progeny)

Year 8:
Self the BC2F1s --> yields (hopefully) the final BC2F2s with segregated traits and are close to H. 'Jade Cascade' (87.5% like) and some should carry the straight scape genes. Select the best one!

As stated earlier, gene linkages can be a problem--for instance, perhaps the leaning scape is tied closely with the leaf shape or mound shape. If this is the case, it would be harder to get the exact plant shape sought as the straight scape and mound shape may be on the same chromosome and only a few units apart (and thus, carry over as a pair for the most part).

Recurrent Selection:

Recurrent Selection Model - Red Seedlings	Katsuragawa Beni * Fire Island 1	Katsuragawa Beni * Fire Island 2	Katsuragawa Beni * Kokuryu 1	Katsuragawa Beni * Kokuryu 2	Katsuragawa Beni * Fire Island 3	Kokuryu f1 * Katsuragawa Beni (b)	Frost Bite * Kokuryu f1	Kokuryu f1 * Katsuragawa Beni 1
Katsuragawa Beni * Fire Island 1 - A								
Katsuragawa Beni * Fire Island 2 - B			yellow		yellow			
Katsuragawa Beni * Kokuryu 1 - C	yellow		yellow					yellow
Katsuragawa Beni * Kokuryu 2 - D								
Katsuragawa Beni * Fire Island 3 - E			yellow					
Kokuryu f1 * Katsuragawa Beni (b) - F								yellow
Frost Bite * Kokuryu f1 - G	yellow		yellow		yellow			
Kokuryu f1 * Katsuragawa Beni 1 - H			yellow		yellow			

Legend: green = Pods formed; yellow = Pollen applied and waiting

Recurrent Selection is often employed to take advantage of additive partial dominance type gene actions. It works best with traits that have high heritability and entails plant selection for many generations of progeny that contain a specific trait (genotype or phenotype) in order to advance that particular trait (size, disease resistance, and crop yield being some primary goals)[xvii]. When working with a recurrent selection program, reciprocal crosses are normally conducted, that is, A x B and B x A using each as the maternal parent // paternal parent. By using the "shotgun" approach, the genes are combined in many different ways to seek the greatest additive expressions possible of the underlying major genes along with many minor genes (polygenes). This process (in theory) provides a good chance that various additive traits will have the greater expression in some of the offspring. A recurrent selection program means that plants are selected after each hybridization cycle for a specific phenotype or genotype before being employed as the parents for next crossing cycle with the intent to affect the greatest gain.

For hostas, I have employed a "simple recurrent selection" program before pollination, that is, I normally select individual plants for breeding based on their phenotypic scores – how well they show the desired traits sought to advance—before they flower and set seed. This is considered the most effective type of recurrent selection to advance the genetic gain[xviii]. A recurrent selection program can take several years to run as it depends on the overall genetic variability available to combine along with how well the variability combines each generation. In one classic example (C.E. Townsend, 1977) two recurrent selection methods were employed on the same crops with the intent to increase seed weight. In the Diallel cross plan, all plants were crossed with all others with the selection criteria each year for both good seed weight and vigor in the plants that advanced. This process showed a 13 percent seed weight increase. Also employed was a polycross method – using two different groups, one selected only for vigor and another group for primarily seed weight. These two types of plants (vigor and seed size) were crossed with the best plants in each category again selected as the following year's recurrent parents. This process resulted in a 22 to 34 percent gain in seed weight over the starting population showing there are many ways to achieve results using recurrent selection strategies. Overall, recurrent selection is considered the best plant breeding method to concentrate the desirable alleles into a single population (or plant) while also maintaining vigor (e.g., preventing inbreeding depression – the loss of vigor caused by mating closely related individuals). At the end of a recurrent selection process, selfing the final progeny for one or two generations is often recommended in order to induce independent assortment (segregation) of desired traits into the individual plants[xix].

As an example, following is a real example that I've been running for the past few years with the goal to increase red/purple petiole traits—the cycle 1 plants are already showing some promise.

Using this process, a small team of us hosta hybridizers have crossed many red petiole plants with each other trying to concentrate the red saturation. In the first year, many plants with a variety of backgrounds were chosen. From these crosses, we applied a high degree of selection intensity to select the best ones from each starting type (as either the pod or pollen parent). The intent is to create a set of plants for subsequent double- or three-way-crossing in order to combine the red alleles from many starting types into a single plant. The below graphics show the overall recurrent selection plans and hopefully better exemplify the process. Table 2 is part of a pedigree chart to guide the first level crossing strategies to ensure the greatest background variability is being combined at the start. When researching named cultivars, you may find plants that have a common phenotype are also linked to the same species. Table 3 is one method that can be employed along with a high selection intensity placed on red/purple with a secondary consideration on pedigree. In this example, recurrent selection is planned for the best red traits–6 plants in the Cycle-2 generation, 3 plants in the Cycle-3 generation (one used twice) and so forth. Not all of the plants are shown in the first set of tables but this example should provide a good illustration for the work up for the greatest genetic disassortative base population considerations, a key part of a recurrent selection plant breeding strategy.

Set 1			
A	**B**	**C**	**D**
Ultramarine (Sea Lotus Leaf// sieboldiana x kikutii)	**Smokey** (Urajiro Hachijo) longipes latifolia	**Mr Blue** (sdlg x Riptide) poss pycnophylla	**Unnamed seedling** (rupifraga) possible pycnophylla

Set 2			
E	**F**	**G**	**H**
Miss Linda Smith (Wrede linage - pycnophylla?)	**Katsuragawa Beni** kikutii-like species	**Purple Rain** (U. Albert x Halcyon) hypoleuca x kikutii	**Unnamed red seedling** (unk linage)

Table 2: Base Population Linage Analysis Data

	Plant Set 1	Plant Set 2	Plant Set 3	Plant Set 4	Plant Set 5	Plant Set 6
Year 1	A X B	C X D	E X F	G X H	I X J	K X L
Year 2	f1-AB X f1-CD	f1-EF X f1-GH	f1-IJ X f1-KL			
Year 3	f1-ABCD X f1-IJKL	f1-EFGH X f1-IJKL				
Year 4	f1-ABCDIJKL X f1-EFGHIJKL					
Year 5	Self the Year 4 seedlings into f2 for greatest variability					

Table 3: Recurrent Selection Annual Crossing Plans

Part VIII

Crossing Notations:

The shorthand notations used for plant breeding can sometimes cause a bit of confusing so let's hit this topic next. We normally use A X B to refer to hosta type "A" (as pod parent) crossed with hosta type "B" (as the pollen parent) and the hybrid offspring of such a cross designated as "AB" (or the F1 for the first filial). Crossing two F1 plants (sib-cross) or selfing the F1 progeny yields the F2 generation. (A quick note here, planting seeds from the F2 generation normally yields the most diverse generation following a hybrid cross -- this is the generation plant breeders often begin their selection processes.[xx]) A circle with an X in the center is the symbol used for a selfed

cross and while hard to type on a computer, is a quick note taking shortcut to consider. ⊗

Instead of the F1 notation, some plant breeders use an "S" followed by a sub-script number for the selfed generation notations. In this system "S0" is used to designate the base population of the selfed generation. The thing to keep in mind when encountering this system is that the S0 designator can refer to either the F1 or F2 generation after a hybrid cross.

Backcrossing the F1 seeds to a recurrent parent would be designated as BC1F1 and a second backcross as BC2F1. If you take the F2 seeds and then start the back crossing protocol, it would be written as BC1F2 and so forth.

For a recurrent selection program, the combining "cycle" is repeated several times and thus, the letter C is employed. C0 (zero) is the designator for the base population and subsequent double-cross and complex hybrid populations are given one up numbers, C1, C2, etc.

Plant Pedigrees can also be annotated by using the slash "/" to indicate a cross[xxi]. A figure between slashes indicates the sequence or order of crossing. Additionally a /2/ is the same as a double slash "//" and indicates a second cross -- /3/ or /// is a third cross. In this system, a backcross is designated by an "*" so *3 would indicate a backcross three times to the same recurrent parent (BC3). Pollen parents are added to the right of the notations and pod parents to the left of the original cross. Here are two examples using this pedigree notation system:

A48-10/3/Blue Arrow/Fragrant Blue/2/sieboldiana
   1) The first cross was Blue Arrow X Fragrant Blue
   2) The second cross was the F1 from the above crossed with sieboldiana
   3) The third cross was seedling A48-10 (female) with the pollen from the (BA x FB) x sieboldiana seedling

Jade Cascade *2/Smokey
   1) Equal to JC/2/JC/Smokey or (JC x (JC x Smokey))
   2) Jade Cascade backcrossed two times with Smokey

Advanced generations of crops may also be designated as "Synthetic Cultivars" and are annotated as syn-1. Synthetic cultivars are produced from planned matings involving selected genotypes. Synthetic cultivars consist of the progenies after intercrossing and cannot normally be reproduced from seed of the first generation due to

male sterility or self-incompatibility. I've not seen this annotation system used with hosta writings so only mention it in passing here in case it is seen in other texts.

Hopefully this eight-part series on plant breeding theory topics has been useful to the group. Lastly, here's a link to some great additional reading lesson as posted on the Hosta Library's site:

http://www.hostalibrary.org/misc/genetics/gen-main.html

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