Daylily Genetics

(Unabridged) Part 4 Pod or Pollen Parent: Do They Determine Different Seedling Characteristics?

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Abstract

Do pod or pollen parents determine seedling characteristics differently?

This article examines how to test for reciprocal differences, describes a number of mechanisms that could explain reciprocal differences, and presents an analysis of data based on the AHS registry information that finds scape height and flower size do not seem to be determined by one parent more than the other.

Introduction

The question of which parent determines which seedling characteristics often arises and sometimes creates lively debate. In humans it is known that sons inherit some characteristics from their mothers. Mammals have sex chromosomes such that females are XX and males are XY. Thus sons inherit a Y chromosome from their fathers and an X chromosome from their mothers. Since sons only have one X chromosome they will show any characteristic that is determined by genes present only on the X chromosome. Most plants do not have separate and different sex chromosomes[1]. Unlike animals, in plants there is no obvious simple reason why offspring characteristics should be determined differently by the two parents. Why then do we sometimes read suggestions such as, plant habit is determined by the pod or maternal parent while 'face' or floral characteristics are determined by the pollen or paternal parent?

In both plants and animals the two sexes make unequal contributions to sexual reproduction. Plants produce large ovules that form the seed but small pollen grains. Of course, a relatively smaller number of ovules are produced in comparison to the larger number of pollen grains. Still, overall the sexes require different amounts of resources to produce the gametes and contribute different amounts of resources to the seed. This inequality is easily seen in the amount of cytoplasm present in the ovule versus that present in the pollen grain.

Reciprocal crosses (see glossary) sometimes produce offspring which differ. This has often been used as evidence for cytoplasmic inheritance. Unfortunately, this is a fallacy that has been known for a very long time[2]. There is little agreement by geneticists and plant breeders on the practical importance of such reciprocal differences, partly because they are seldom consistent[3].

In this installment I will describe how we look for reciprocal differences, the possible causes of reciprocal differences and whether there is evidence of reciprocal differences in daylilies.

1. Testing for reciprocal differences

It would be simple if we could just plant the seedlings from reciprocal crosses in rows beside each other and compare their characteristics. Plants and our gardens and fields are too complex to produce reliable results from such easy tests. Researchers have found that gardens and fields have patchy characteristics. When factors important to the growth of plants are measured on all scales from inches to hundreds of feet, patches and gradients have been found, for example in moisture, light, minerals, pathogens, etc. To help eliminate these unknown factors as causes of reciprocal differences we must plant the seedlings from both reciprocal crosses at random in two or more locations (randomization and replication).

We must also treat both the parents and their seedlings exactly the same. For example, one parent cannot be growing in more shade than the other; all the plants must be watered and fertilized identically; we cannot use seeds from only one pod for each cross; we cannot use seeds from only one clump of each parental cultivar, we cannot make one reciprocal cross early in the flowering season and the other later in the season; we cannot plant just the largest seed or seedlings, we cannot use the parental plants in other crosses, etc.[4]

Randomization and replication are vital to eliminating unknown factors from influencing our observations. They allow us to be confident that any differences we observe are due to the plants and not unknown factors. We cannot avoid randomizing and replicating by assuming that unknown factors only cause small differences and we are only interested in very large differences in reciprocal crosses. In any case, patches in a field or garden may show large differences from areas nearby. It is also possible that the characteristics we observe may actually be strongly affected

Figure 1. Flowering Threshold

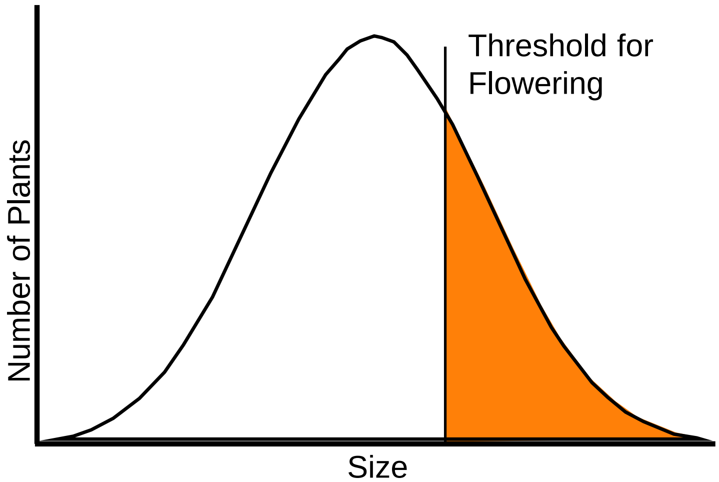

Figure 1. *Plant size determining the probability of flowering or re-blooming as a threshold characteristic. Individual daylily fans above the threshold size can flower while those below the threshold size cannot flower. If plants are classified as flowering or not flowering then this is a threshold characteristic. Small changes in environmental factors which affect the size of the plant can have obvious visible effects on whether the plant blooms or does not bloom.*

by quite small differences. This is likely to be the case for all characteristics we measure as being present or absent, for example, flowering or re-bloom, etc. (Figure 1). For these types of characteristics a small change in the underlying cause near the threshold value can make the difference between showing or not showing the characteristic.

1.1 Can planting in containers or using greenhouses or growth chambers eliminate randomizing and replicating?

The simple answer is no. Researchers randomize pots in greenhouses or growth chambers at the beginning of their tests. They also shuffle the pots to different locations at random every so often during their tests to help guarantee that all pots experience similar conditions.

1.2 Tests in the garden or the field

It is not practical to shuffle daylilies to new locations when planted in soil in our gardens or fields. That can mean plants on the edges of our test locations do not experience the same conditions as plants in the centers. Professional researchers account for any possible edge effects by using guard rows of plants that are not used for observations.

2. Possible Causes of Reciprocal Differences

2.1 The reciprocal crosses are contaminated by natural pollinations

Although natural pollinations are not very frequent in modern daylily cultivars they can and do occur. If safe hybridizing techniques (see http://www.daylilies.org/Whatley/SafeHybridizing.html, or Daylily Journal Vol. 48, No. 4, 1993 pp 425-428) are not used when the hand-pollinations are made there is no guarantee that natural pollinations may not also have occurred. In those cases any differences between the reciprocal crosses may have been caused by seeds produced from unknown pollen.

Glossary

Allele – a variant of a gene. Alleles have one or more differences in their DNA sequences. Natural genetic variation in plant populations is present as multiple alleles for most genes. An allele of a particular gene may have a very large visible effect, causing complete loss of the function of the gene or it may have a smaller effect or no visible effect. Few alleles will have large visible effects while most will have a small or no measurable effect. In a diploid individual each gene has two alleles which may be the same or different.

Cytoplasmic inheritance – inheritance due to plastid or mitochondrial genes. Often, but not always, associated with the parent that provides the most cytoplasm to the embryo.

Mitochondria – small structures found in the cytoplasm within cells. These are involved in energy metabolism and contain some genes.

Plastids – small structures found in the cytoplasm within cells. Different types of plastids are derived from proplastids. Plastids have about 100 genes. Chloroplasts contain the green pigment chlorophyll and are involved in the manufacture of food through photosynthesis. Chromoplasts contain predominantly yellow and orange pigments and are found in some fruits and flowers. Other plastids contain starches or oils.

Reciprocal cross – when two parental cultivars are used as both the pod and pollen parent in crosses with each other e.g. 'A' × 'B' and 'B' × 'A'.

Self-pollination – pollinating a daylily with pollen from the same cultivar.

2.2 Maternally inherited Plastids and Mitochondria (Organelles)

Both plastids and mitochondria are inherited predominantly through the maternal parent in the flowering plants (80%) but plastids are inherited primarily through the pollen parent in gymnosperms (e.g. conifers). Both organelles also contain a few genes. It is often assumed or suggested that reciprocal differences are due to genetic differences in plastids or mitochondria. Unfortunately, the necessary tests to distinguish between genetically different plastids and mitochondria and all the other possible causes of reciprocal differences are rarely, if ever, made[5].

Plastids and mitochondria contain a relatively small number of genes and there will be natural genetic variability in some of those genes. However, most differences in DNA sequence are neutral - they have no measurable effect on the phenotype. The next largest category is detrimental and will be lost by natural selection very quickly. A minor proportion are advantageous and they will increase and go to fixation very quickly (for example, because organelles are haploid and there are no heterozygotes to hide mutations). That leaves a minor number of DNA variants that may be part of balanced polymorphisms. However, balanced polymorphisms are much more difficult to maintain in haploids than they are in diploids. The mechanisms are very restrictive in hap-

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loid genetic systems such as the organelles. It requires special frequency-dependent systems with nuclear-cytoplasmic interactions to maintain such polymorphisms. That is the case with those plant species that have two separate sexes. That is also possible with cytoplasmic male sterility and nuclear fertility restorer genes. Daylilies do not have sex chromosomes so there can be no interaction with organelle genes and there are no reports of cytoplasmic male sterility in daylilies. Simply finding a difference in organelle DNA in a population is not enough. The general consensus of opinion is that such differences are neutral; only recently is there some evidence that they may not all be neutral.

One sometimes reads the suggestion that the pod parent determines offspring characteristics related to plant habit. This is based on the assumption that since chloroplasts are usually maternally inherited and are involved in photosynthesis, the manufacture of all the food that the plant uses to grow, the maternal parent will be responsible for characteristics related to growth. There is no scientific evidence in any plant species for a general relationship between the maternal parent, photosynthesis and seedling plant habit traits. In fact, the photosynthetic rate, a trait very closely related to chloroplast function and food production, has been found to be the same when examined in reciprocal crosses[8] in a number of species.

Although there may be few, if any, strong selective differences in the organelle genes in natural populations this does not mean that the organelle genes are not important. Rare mutations in those genes can have obvious and very important effects. An example of an important characteristic caused by mutations in the mitochondria is cytoplasmic pollen sterility and cytoplasmic herbicide resistance can be caused by mutations in the plastids.

Occasionally, crosses between species show very obvious effects of differences in their organelles. These appear in the F1 generation and are caused by incompatibilities between the nuclear genes of the hybrids and their organelle genes. These incompatibilities are not common[9] and although there have been many interspecific crosses made between species of Hemerocallis there is no evidence that they are present in daylilies.

Some cases of leaf variegation are caused by changes in the organelles. Reciprocal crosses may show differences in the proportions of variegated offspring in such cases (see the previous installment for a full discussion of variegation).

2.3 Gene Imprinting

Alleles are imprinted when their expression in the seedlings depends on from which parent the allele was inherited[10]. These are also known as parent-of-origin effects. In the most extreme case only one allele is expressed. For example, in the cross of AA x aa, if A is only expressed when it is inherited from the pod parent then the seedlings are genetically Aa and they express A. In the reciprocal cross aa x AA the seedlings are genetically Aa but a is expressed. This results in reciprocal differences.

There are also less extreme examples of differences in expression depending on which parent provided the allele. Both maternal[11] and paternal[12] biases in gene expression have been found.

2.4 Segregation Distortion

When we study the inheritance of a characteristic by making reciprocal crosses we rely on assumptions, such as 50% of the pollen will carry each allele present in the diploid parent. When this is not the case we have segregation distortion, the offspring do not show the expected Mendelian ratios. For example, if we cross Aa x aa or aa x Aa we expect that the seedlings will be 50% Aa and 50% aa. If the ratio is not 1:1 then segregation distortion is present. Researchers have found that segregation distortion is often present in crosses within species[20] but especially often in plants[21], such as daylilies, that were derived from crosses between different species. Segregation distortion may differ between the pod and pollen parent. When abnormal ratios are different in pollen versus ovules reciprocal differences may occur.

2.5 Transmission Distortion in Tetraploids

Transmission distortion may occur when the male and female gametes are formed with unequal nuclear genotypes. This is more likely to occur with tetraploids since they suffer from problems with chromosome pairing during meiosis (gamete formation). Tetraploids will often not have the proper 44 chromosome complement. They may be aneuploids, missing one or two chromosomes or having one or two extra chromosomes. Extra chromosomes are not transmitted through pollen and ovules equally and thus may result in reciprocal differences[13].

2.6 Gametic Selection or Competition

Some genes are expressed in the pollen but not expressed in the ovules. Some of the genes expressed in the pollen or the ovule are also expressed in other tissues of the plant. When alleles affect the success of the gametes and also affect characteristics of the plant there can be reciprocal differences[22]. As an example consider the cross of AA X Aa. If pollen grains carrying the a allele are more successful in fertilizing ovules than pollen grains carrying the A allele then there will be more Aa seedlings than AA seedlings from the cross AA X Aa. There will be equal numbers of AA and Aa seedlings from the cross Aa X AA. If AA plants differ from Aa plants in some characteristic then there will be a reciprocal difference. Other genes which are linked to the A gene may also be the cause of reciprocal differences (see recombination and self-incompatibility below).

2.7 Self-Incompatibility

Self-pollinations in many daylilies are not successful indicating that those cultivars are self-incompatible. Stout found that reciprocal crosses were not equally successful in producing seeds or seedlings[14]. Self-incompatibility genes affect cross-pollinations as well as self-pollinations. These genes usually have many different alleles and plants are normally heterozygous for different alleles. Consider two plants with genotypes S1/S2 and S2/S3 for self-incompatibility. In the cross S1/S2 X S2/S3 only S3 pollen grains will be successful. Seedlings will be S1/S3 or S2/S3. In the reciprocal cross S2/S3 X S1/S2 only S1 pollen grains will be successful and there will be S1/S2, and S1/S3 seedlings. The seedlings from the reciprocal crosses are genetically different and any genes differently linked to the self-incompatibility alleles may result in visible reciprocal differences. Self-incompatibility may be one of the important causes of any genetic differences found between reciprocal crosses in daylilies[15].

2.8 Sex Differences in Recombination

Nuclear genes are packaged in chromosomes. Genes that are close to each other on a chromosome are described as being linked. For example, a plant has the genotype A/a B/b. If the two genes are linked then the plant may have AB on one chromosome and ab on its partner chromosome (AB/ab) and it will produce more AB and ab gametes than Ab and aB gametes. It produces the Ab and aB gametes by recombination when chromosomes break and are rejoined to their alternate partner. The frequency at which recombination occurs can differ between pollen and ovule production. This can introduce reciprocal differences[16].

2.9 Maternal or Paternal Effects

Maternal or paternal effects can be environmental or due to the nuclear genotype of the parent. They may be short term or long term possibly lasting for even more than one generation. The maternal parent produces the seed and all its nutrients, including the stored endosperm. The endosperm is a triploid tissue with two maternal and one paternal set of chromosomes or genomes. The maternal parent is also responsible for the growth of the embryo during seed development. The characteristics of the seed can be important causes of differences in reciprocal crosses[17]. Maternal effects are likely to be important causes of any significant reciprocal differences that may be found in daylilies.

It is not possible to distinguish maternal effects from cytoplasmic inheritance if one only compares reciprocal F1 offspring[23]. One method that can help determine whether reciprocal differences are partly due to organelle genes or maternal effects is to follow the differences in reciprocal cross plants over succeeding generations. If the differences decline then maternal effects are the more likely to be involved since the organelles do not change over generations[1,18].

3. Reciprocal Differences in Daylilies

Is there any evidence that reciprocal differences are generally present or important in daylilies? The usual assumption when reciprocal differences are present is that the seedlings will resemble the maternal or pod parent more than they do the paternal or pollen parent. This means that seedlings would have a higher correlation with the pod than with pollen parent. We can use pedigree data to test for this and calculate the correlation between seedling and pod parent and that between seedling and pollen parent. One source of pedigree data is the registration information. I have analyzed diploid scape height and flower size data from the registration database[24].

3.1 Scape Height

Seedlings and their pod parent have a correlation coefficient of 0.47 and a standard error of ± 0.03 for scape height for a sample size (N) of 856. The correlation between seedlings and their pollen parent is 0.52 ± 0.03. The correlations are not statistically different. Daylily seedlings resemble their pod and pollen parents equally in scape height. Scape height is inherited equally from the pod and the pollen parent.

3.2 Flower Size

The correlation for flower size between seedlings and their pod parent is 0.62 ± 0.02, N = 1889. The flower size of seedlings is correlated 0.59 ± 0.02 with that of their pollen parent. The correlations are not statistically different. Daylily seedlings resemble their pod and pollen parents equally in flower size. Flower size is inherited equally from the pod and the pollen parent.

I have also analyzed specific types of reciprocal crosses from the registration database to double check the more general results. For example, when cultivars with four inch flowers were crossed with cultivars with six inch flowers (4” X 6”) the seedlings had an average flower size of 5.11”, N=20. The seedlings from the reciprocal cross (6” X 4”) had an average flower size of 5.09”, N=26. The reciprocal difference is not significant. In any case it is in the paternal direction not the maternal.

4. Conclusions

Reciprocal differences have rarely been found for qualitative characteristics such as flower color. If they are found for specific characteristics those are typically quantitative and often related to seed traits (which are primarily pod parent characteristics). Scape height and flower size are typical quantitative characteristics, important to daylily hybridizers, and neither shows any general evidence of maternal effects.

Recent genetics research on daylily plant height, length and width of leaves, number of scapes, bud count per scape, and the number of flower buds per plant included reciprocal F1 crosses and did not report any differences[19].

Daylily hybridizers sometimes report difference in seedlings from a cross done in both directions. This can be due to planting too few seeds and the difference is not reliable, or from not having identical growing conditions for both sets of seedlings and parents, etc. To determine whether there are significantly large, consistent and permanent differences in reciprocal crosses for characteristics generally important to hybridizers would be a major scientific undertaking. The direction of a cross might be important for some inherited characteristics under some conditions but there is currently no valid scientific evidence for this in daylilies.

The belief that one should make crosses in particular directions when selecting for certain characteristics is garden myth or superstition. One should not be overly concerned with making crosses reciprocally or in specific directions – make crosses in the directions that are most practical.

Next installment: Foliage Characteristics, Growth and Rebloom

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