Daylily genetics

Part 1: Understanding genotype and phenotype

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Here is an example of the range of phenotypes possible from one cross. (From left) 'Elderberry Candy' (Stamile, 2003) and tetra 'Peppermint Delight' (Carpenter-J., 2003) are the parents of 'Giant Panda' (Stamile, 2008) and 'Ruby Storm' (Stamile, 2008). The siblings are both early blooming six inch cultivars, but 'Giant Panda' is an evergreen while 'Ruby Storm' is a dormant.
— Photos courtesy of Pat Stamile except where noted

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One hundred and ten years ago Gregor Mendel's work, originally published in 1866, was rediscovered by three botanists and plant genetics blossomed. In the time since, our understanding has advanced enormously, but, as always, there is still much to be learned. Fifty years ago daylilies were being studied by scientific researchers. Unfortunately, genetics has since concentrated on the study of a few "model" species and little modern research is done on daylilies.

In 1972 Joanne Norton[1-3] hoped that in the future the complicated daylily flower color genetics would be understood well enough for a geneticist to be able to look at a flower and indicate the genes determining its color.

Unfortunately, this is not possible yet for any plant species, even those for which flower color has been studied intensively. Research on many plant species has determined that flower color cannot consistently predict the pigments present or the underlying genotypes. Two flowers may have the same color but different pigments and therefore genotypes, or two flowers with the same pigment may have different colors[4].

Some work has been done with daylilies and much of the work done with other species such as petunias can be applied to daylilies.

In this series of articles, I will review the information which is available for daylilies. Research on the genetics of other species which is relevant to understanding the inheritance of various traits in daylilies also will be included.

Daylily genetics is complicated, and there are several reasons for this. Mendel carefully chose the plant that he worked with — the common garden pea. He spent several years making certain that the strains he had were "pure-breeding" (homozygous) for the traits he was investigating. All the strains belonged to one annual diploid plant species. Peas are self-compatible and naturally self-fertilizing, and so each strain was completely inbred. The traits that he chose to study were well-defined, qualitatively (sharply discontinuous, distinct and easily separable from each other) different and little affected by the environment. Those characteristics make the pea a good subject for genetic studies.

However, daylilies are primarily self-incompatible (infertile when self-pollinated) perennials derived from crosses of many different species. Unfortunately, those are characteristics which make diploid daylilies a difficult subject for genetic studies.

The foundation for the study of genetics is:

Phenotype = Genotype + Environment + Genotype × Environment Interaction + Error.

Figure 1 (see next page) graphically shows the effects of genotype, environment and their interaction in determining phenotype (characteristic). If we observe several cultivars (genotypes) in a single environment (temperature), we can see only the effect of genotype. If we observe a single cultivar in several environments we can see only the effect of environment. If we observe several

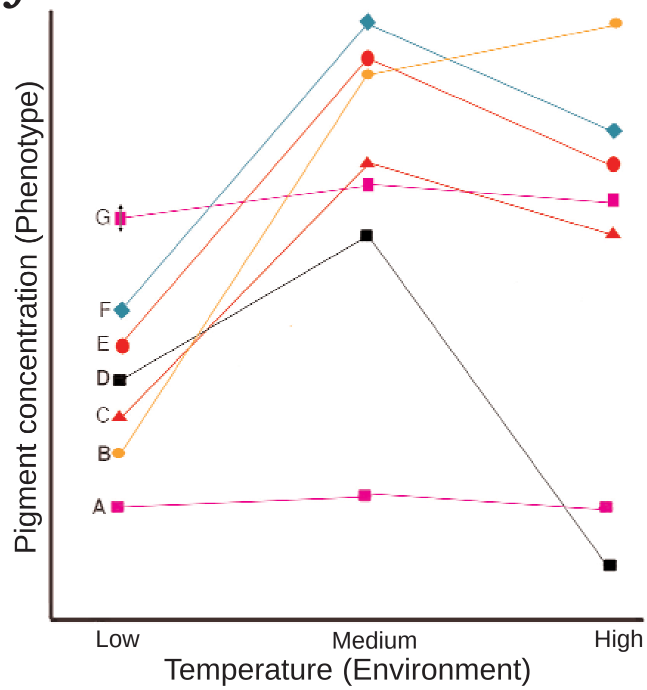


Figure 1: *The effects of genotype, environment and their interaction in determining phenotype (characteristic)*

The hypothetical effect of genotype, environment and genotype × environment interaction on the phenotype using flower pigment concentration as an example phenotype and temperature as an example environmental factor. All hypothetical examples are assumed to follow accepted scientific practices in their design and analysis. Seven different cultivars are represented by (A, B, C, D, E, F). The symbols represent the averages of a number of measurements of pigment concentrations for each cultivar in each environment. The vertical lines with arrows shown on the value for pigment concentration for cultivar G at low temperature represents the range of pigment concentrations shown by the cultivar at that temperature. The ranges have been omitted from all other averages for clarity.

cultivars in several environments we can then see the effects of genotype, environment and their interaction.

Cultivars E and F have a phenotype that is determined only by genotype and environment — there is no interaction present since their lines are parallel. Cultivars A and G have a phenotype that is almost completely determined by genotype alone — there is no interaction and the effect of environment is negligible. The remaining cultivars B, C, D, have phenotypes that are determined by the combination of genotype, environment and their interaction. The lines are not parallel and they even cross-over. Because of the presence of interaction the order of the cultivars is not the same in the three environments. We cannot guess which cultivar will have the most or the least pigment by looking at them in only one environment. We also cannot guess how the environment will affect any specific cultivar (six of seven cultivars have less pigment in high temperatures than in medium temperatures but cultivar B has more pigment).

In the garden or field we observe or measure phenotypes and attempt to determine (guess) the genotypes from those observations. To do so we try to make the environment constant and because of sampling (the plants analyzed are only a sample of the infinite number of plants with those characteristics that could theoretically exist)

Glossary

Additive – all phenotypes have an additive component as it represents the average of the two parental values. When the F_1 offspring, of a cross between a homozygous plant showing a characteristic and a homozygous plant not showing the characteristic, show the characteristic the phenotype may be additive or dominant or partially both.

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 effect on the phenotype, causing complete loss of the function of the gene or it may have a smaller effect or no effect on the phenotype. Few alleles will have large effects on a phenotype while most will have a small or no measurable effect. In a diploid individual each gene has two alleles which may be the same (see homozygous) or different (see heterozygous).

Dominant – the dominance component of a phenotype is the difference between the average of the two homozygous parental phenotypes and that of the F_1 offspring. When the dominance component is exactly equal to the additive component the phenotype is completely dominant. When the dominance component is less than the additive component partial dominance is present or the dominance is incomplete. When the dominance component is zero the phenotype is perfectly additive. Few phenotypes will be perfectly additive or completely dominant. At the molecular level of gene expression usually both alleles in a diploid will be expressed.

Genotype – the sequence of the DNA making up the genes of an individual.

Heterozygous – in a diploid the presence of two different alleles for one gene. E.g. W/w individuals are heterozygous. The terms for a tetraploid are different.

Homozygous – in a diploid the presence of two identical alleles for one gene. E.g. both W/W and w/w individuals are homozygous.

Mutation – a change in the sequence of the DNA of a gene. This results in a different allele. It may or may not result in a different phenotype. Mutations may be selectively neutral and have no measurable effect on a plant, or they may be deleterious and lost by natural selection or be advantageous and increase by natural selection to replace disadvantageous alleles. Some alleles may form what are called balanced polymorphisms in which case two or more alleles have advantages and disadvantages in different circumstances, none is consistently better and the alleles are maintained in the population at intermediate frequencies. Mutations with visible effects occur very rarely, once in a million or once in a hundred thousand.

Phenotype – the observed characteristics of an individual, for example, measured height or flower color.

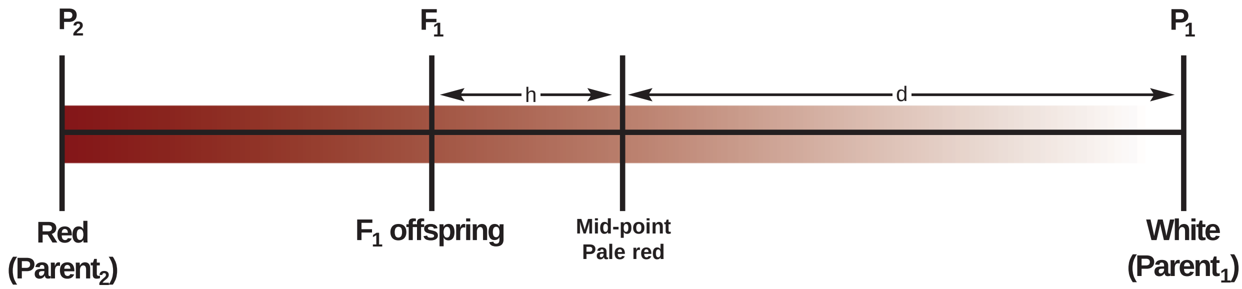
Recessive – a phenotype that is completely masked by an alternative phenotype.

Figure 2

Phenotype

Pigment Concentration

h = dominance value
d = additive value



The effect of complete and incomplete (partial) dominance and additive phenotypes on visible flower colour: red and white. The value of the additive component is represented by d and the value of the dominance component is represented by h. P_1 and P_2 are the parents and F_1 represents the first generation offspring from a cross of the two parents.

and other errors we need to analyze our observations statistically.

Nearly all daylily characteristics are strongly affected by environmental differences and this requires careful design of genetics experiments to eliminate environmental and seemingly random effects as the causes of the differences we see in various crosses.

Mendelian Genetics

The genetics that many of us learned in high school was relatively straightforward. Modern genetics has added many exceptions that break the rules of Mendelian genetics. To begin correctly we need to define the genetic symbols for traits. The gene symbol for a trait is based on the phenotype of any newly arisen mutant (individual with a new phenotype); often we learned the opposite of this in school.

As an imaginary example, a normal plant has red petals. If we find a naturally occurring mutation (new phenotype that is inherited) or create a mutation in the lab that has white petals (not known in daylilies), then the mutation is named white with the gene symbol w if the white phenotype is recessive. A w/w plant would then be white, and a W/W plant would be red.

As shown in Figure 2, if the cross of a W/W (red) plant with a w/w (white) plant produces red offspring (W/w) that are indistinguishable from their red parent, then red is described as being completely dominant to white.

If the red offspring are paler than the red parent, there is incomplete dominance.

When the color is halfway between red and white, it is an average of the parents' contribution (this is referred to as additive and indicates no dominance).

If the color of the seedling is more red than halfway between red and white, but still not as red as the parent, this is the result of partial red dominance. If the color of the seedling is less red than half-way between red and white but not as white as the white parent then this is the result of partial dominance for white. In most cases phenotype will be additive with partial dominance (more than halfway towards one of the parents) rather than completely dominant or perfectly additive.

Mendel worked with the genetics of flower color within one species and found effects determined by a single gene. Geneticists have since found that the genetics of a characteristic such as flower color is often simpler when studied within a single species and becomes much more complex when studied in the offspring of crosses between two different species. While a characteristic within a species may be due to differences in one gene, when between different species it may be due to many genes[5].

Daylilies originate from crosses between many species and we will find that most characteristics in daylilies are not inherited simply but are due to differences in many genes. In working within a species Mendel determined that particular crosses produced offspring showing defined ratios of the phenotypes. Second generation crosses (F_2) showed the ratio 3:1 for the dominant, recessive phenotypes, for example. Research has found that occasionally within a species these ratios are not found when expected for single genes but that in plants derived from interspecific (betwen two or more species)crosses these ratios are often very different from those expected by Mendelian genetics[6]. When this occurs it is called segregation distortion. We can expect that segregation distortion will be present in many daylily crosses, and it will make it very difficult to analyze crosses genetically or to predict the numbers and types of offspring from crosses.

It is also important to understand that how we measure a characteristic has a profound effect on how we describe the inheritance of that characteristic. This is particularly important when making observations on color. As an example, if we examine a number of different cultivars for flower color and characterize them by unaided eye as being either red or not-red, we might then find that the results of crosses suggest that red is dominant and a single gene. However, if we reclassify the red-flowered plants by measuring the amount of pigment in the flowers, the results of the crosses might suggest that red is additive and that more than one gene is involved.

Unaided human vision is not very accurate at determining differences when pigments are present in high concentrations[7] or in determining their presence or absence when they are at low concentrations. This can affect the conclusions made about the inheritance of color characteristics since phenotypes may be misclassified. A quantitative (continuous phenotypic variation) measure will usually be more representative of the actual gene action since at the molecular level both alleles (alternative forms of a gene) will be expressed for most genes. ■

References

[1]Norton, J. Some basic Hemerocallis genetics. *The Hemerocallis Journal*. **26** (2):29-39, 1972.

[2]Norton, J. Some basic Hemerocallis genetics — Part 2. *The Hemerocallis Journal*. **26** (3):8-29, 1972.

[3]Norton, J. Some basic Hemerocallis genetics — Part 3. *The Hemerocallis Journal* 27 (1):20-27, 1973.

[4]Griesbach, R. J. The inheritance of flower color in *Petunia hybrida* Vilm. *Journal of Heredity* **87**:241-245, 1996.

[5]Dole, J. and R. Kessell. Inheritance of Pale Flower, Calyx Spotting, and Glandular Pubescence in *Mimulus guttatus* × *M. platycalyx* Progenies. *Journal of Heredity* **88**:42-46, 1997.

[6]Abe, H., M. Nakano, A. Nakatsuka, M. Nakayama, M. Koshioka and M. Yamagishi. Genetic analysis of floral anthocyanin pigmentation traits in Asiatic hybrid lily using molecular linkage maps. *Theoretical and Applied Genetics* **105**:1175–1182, 2002.

[7]Napoli, C. A., Fahy, D., Wang, H., and L. P. Taylor. white anther: A Petunia Mutant That Abolishes Pollen Flavonol Accumulation, Induces Male Sterility, and Is Complemented by a Chalcone Synthase Transgene. *Plant Physiology* **120**: 615–622, 1999.