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Variations on Mendel's laws

Mendel's basic model

The basic principles of Gregor mendel model of inheritance have held up for over a century. They can explain how many different characteristics are inherited, in a wide range of organisms including human beings.

Some of the key elements of Mendel's original model were:

1. Heritable traits are determined by heritable factors, now called **genes**. Genes come in pairs (that is, are present in two copies in an organism).
2. Genes come in different versions, now called **alleles**. When an organism has two different alleles of a gene, one (the dominant allele) will hide the presence of the other (the recessive allele) and determine appearance.
3. During gamete production, each egg or sperm cell receives just one of the two gene copies present in the organism, and the copy allocated to each gamete is random (law of segregation).
4. Genes for different traits are inherited independently of one another (law of independent assortment).

These rules still form the foundation of our understanding of inheritance—that is, how traits are passed on and how an organism's **genotype** (set of alleles) determines its **phenotype** (observable features). However, we now know of some exceptions, extensions, and variations, which must be added to the model in order to fully explain the inheritance patterns we see around us.

Variations involving single genes

Some of the variations on Mendel's rules involve single genes. These include:

- **Multiple alleles.** Mendel studied just two alleles of his pea genes, but real populations often have multiple alleles of a given gene.
- **Incomplete dominance.** Two alleles may produce an intermediate phenotype when both are present, rather than one fully determining the phenotype.
- **Codominance**. Two alleles may be simultaneously expressed when both are present, rather than one fully determining the phenotype.
- **Pleiotropy.** Some genes affect many different characteristics, not just a single characteristic.
- **Lethal alleles.** Some genes have alleles that prevent survival when homozygous or heterozygous.
- **Sex linkage.** Genes carried on sex chromosomes, such as the X chromosome of humans, show different inheritance patterns than genes on autosomal (non-sex) chromosomes.

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Variations involving multiple genes

Other variations on Mendel's rules involve interactions between pairs (or, potentially, larger numbers) of genes. Many characteristics are controlled by more than one gene, and

when two genes affect the same process, they can interact with each other in a variety of different ways. For example:

- **Complementary genes.** Recessive alleles of two different genes may give the same phenotype.
- **Epistasis.** The alleles of one gene may mask or conceal the alleles of another gene.

In addition, some gene pairs lie near one another on a chromosome and are genetically **linked**, meaning that they don't assort independently.

Polygenic inheritance and environmental effects

Many characteristics important in our everyday lives, such as height, skin color, eye color, and risk of diseases like diabetes, are controlled by many factors. These factors may be genetic, environmental, or both.

- **Polygenic inheritance.** Some characteristics are **polygenic**, meaning that they're controlled by a number of different genes. In polygenic inheritance, traits often form a phenotypic spectrum rather than falling into clear-cut categories.
- **Environmental effects.** Most real-world characteristics are determined not just by genotype, but also by environmental factors that influence how genotype is translated into phenotype.

  Genetic background and environment contribute to **incomplete penetrance**, in which not all individuals with a genotype display a corresponding phenotype, and **variable expressivity**, in which individuals of a particular genotype may have stronger or weaker versions of a phenotype.

Incomplete dominance

Mendel's results were groundbreaking partly because they contradicted the (then-popular) idea that parents' traits were permanently blended in their offspring. In some cases, however, the phenotype of a heterozygous organism *can* actually be a blend between the phenotypes of its homozygous parents.

For example, in the snapdragon, *Antirrhinum majus*, a cross between a homozygous white-flowered plant (C^WC^W*CWCW*C, start superscript, W, end superscript, C, start superscript, W, end superscript) and a homozygous red-flowered plant (C^RC^R*CRCR*C, start superscript, R, end superscript, C, start superscript, R, end superscript) will produce offspring with pink flowers (C^RC^W*CRCW*C, start superscript, R, end superscript, C, start superscript, W, end superscript). This type of relationship between alleles, with a heterozygote phenotype intermediate between the two homozygote phenotypes, is called **incomplete dominance**.

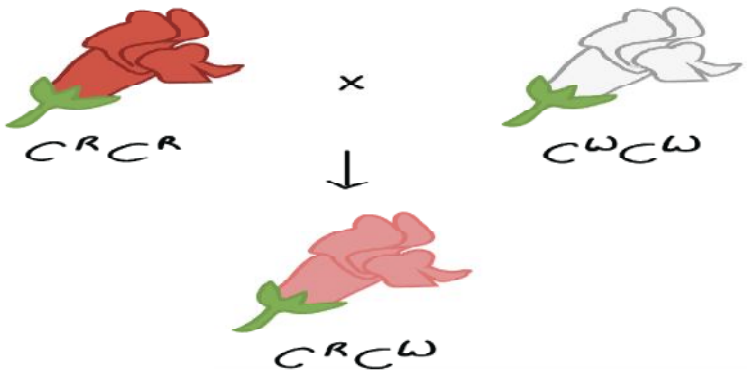
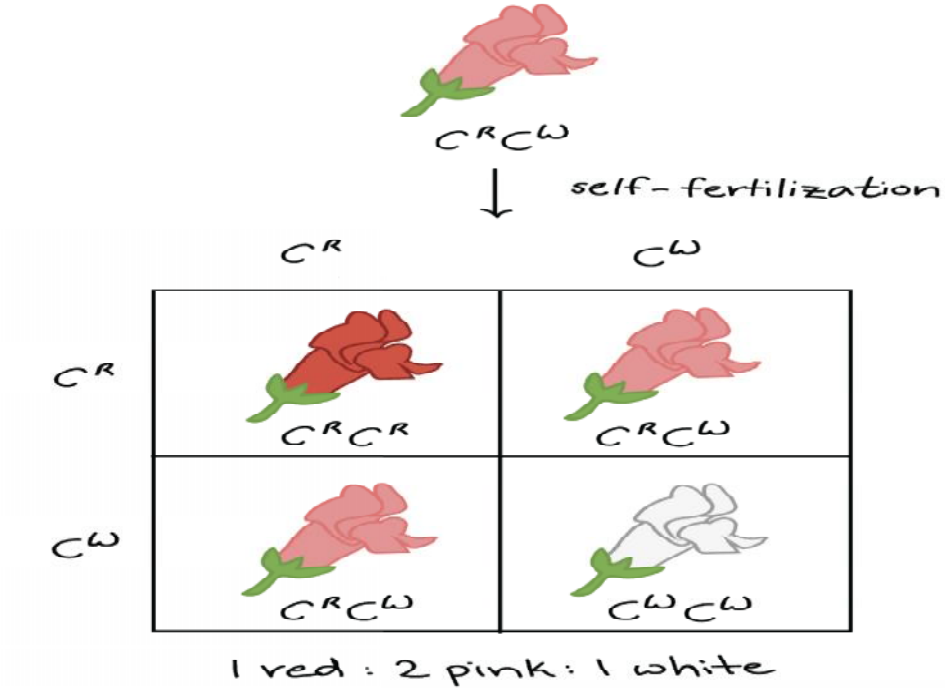


Diagram of a cross between C^WC^W*CWCW*C, start superscript, W, end superscript, C, start superscript, W, end superscript (red) and C^RC^R*CRCR*C, start superscript, R, end superscript, C, start superscript, R, end superscript (white) snapdragon plants. The F1 plants are pink and of genotype C^RC^W*CRCW*C, start superscript, R, end superscript, C, start superscript, W, end superscript.
We can still use Mendel's model to predict the results of crosses for alleles that show incomplete dominance. For example, self-fertilization of a pink plant would produce a genotype ratio of 111 C^RC^R*CRCR*C, start superscript, R, end superscript, C, start superscript, R, end superscript ::colon 222 C^RC^W*CRCW*C, start superscript, R, end superscript, C, start superscript, W, end superscript ::colon 111 C^WC^W*CWCW*C, start superscript, W, end superscript, C, start superscript, W, end superscript and a phenotype ratio of 1:2:11:2:11, colon, 2, colon, 1 red: pink:white. Alleles are still inherited according to Mendel's basic rules, even when they show incomplete dominance.



Self-fertilization of pink C^RC^W*CRCW*C, start superscript, R, end superscript, C, start superscript, W, end superscript plants produce red, pink, and white offspring in a ratio of 1:2:1.

Codominance

Closely related to incomplete dominance is **codominance**, in which both alleles are simultaneously expressed in the heterozygote.
We can see an example of codominance in the MN blood groups of humans (less famous than the ABO blood groups, but still important!). A person's MN blood type is determined by his or her alleles of a certain gene. An L^M*LM*L, start superscript, M, end superscript allele specifies production of an M marker displayed on the surface of red blood cells, while an L^N*LN*L, start superscript, N, end superscript allele specifies production of a slighly different N marker.
Homozygotes (L^ML^M*LMLM*L, start superscript, M, end superscript, L, start superscript, M, end superscript and L^NL^N*LNLN*L, start superscript, N, end superscript, L, start superscript, N, end superscript) have only M or an N markers, respectively, on the surface of their red blood cells. However, heterozygotes (L^ML^N*LMLN*L, start superscript, M,

end superscript, L, start superscript, N, end superscript) have both types of markers in equal numbers on the cell surface.

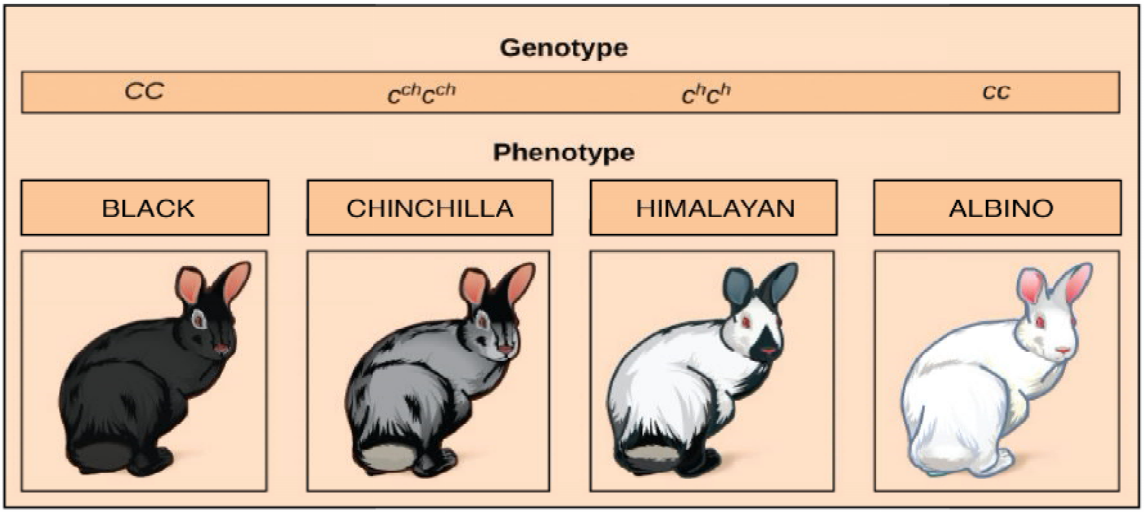
As for incomplete dominance, we can still use Mendel's rules to predict inheritance of codominant alleles. For example, if two people with L^ML^NL^ML^NL, start superscript, M, end superscript, L, start superscript, N, end superscript genotypes had children, we would expect to see M, MN, and N blood types and L^ML^ML^ML^ML, start superscript, M, end superscript, L, start superscript, M, end superscript, L^ML^NL^ML^NL, start superscript, M, end superscript, L, start superscript, N, end superscript, and L^NL^NL^NL^NL, start superscript, N, end superscript, L, start superscript, N, end superscript genotypes in their children in a 1:2:11:2:11, colon, 2, colon, 1 ratio (if they had enough children for us to determine ratios accurately!)

Multiple alleles

Mendel's work suggested that just two alleles existed for each gene. Today, we know that's not always, or even usually, the case! Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple alleles may exist in a population level, and different individuals in the population may have different pairs of these alleles.

As an example, let’s consider a gene that specifies coat color in rabbits, called the CCC gene. The CCC gene comes in four common alleles: CCC, c^{ch}c^{ch}c, start superscript, c, h, end superscript, c^hc^hc, start superscript, h, end superscript, and ccc:

- A CCC^CC, C rabbit has black or brown fur
- A c^{ch}c^{ch}c, start superscript, c, h, end superscriptc^{ch}c^{ch}c, start superscript, c, h, end superscript rabbit has chinchilla coloration (grayish fur).
- A c^hc^hc^hc^hc, start superscript, h, end superscript, c, start superscript, h, end superscript rabbit has Himalayan (color-point) patterning, with a white body and dark ears, face, feet, and tail
- A ccc^cc, c rabbit is albino, with a pure white coat.



Allelic series of the color gene C in rabbits.

- A CCC^CC, C rabbit has black fur.
- A c^{ch}c^{ch}c, start superscript, c, h, end superscriptc^{ch}c^{ch}c, start superscript, c, h, end superscript rabbit has chinchilla coloration (grayish fur).

- A c^hc^h$c^h c^h$c, start superscript, h, end superscript, c, start superscript, h, end superscript rabbit has Himalayan (color-point) patterning, with a white body and dark extremities.
- A cc$c$c, c rabbit is albino, with a pure white coat.

  Multiple alleles makes for many possible dominance relationships. In this case, the black CCC allele is completely dominant to all the others; the chinchilla c^{ch}c^{ch}c, start superscript, c, h, end superscript allele is incompletely dominant to the Himalayan c^hc^hc, start superscript, h, end superscript and albino ccc alleles; and the Himalayan c^hc^hc, start superscript, h, end superscript allele is completely dominant to the albino ccc allele.

  Rabbit breeders figured out these relationships by crossing different rabbits of different genotypes and observing the phenotypes of the heterozygous kits (baby bunnies).