Gene Segregation and Genetic Recombination

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Introduction

Plant breeders take advantage of the variation that occurs within a population to develop improved cultivars. Ordinarily, the goal of the plant breeder is to combine the favorable characteristics of one plant or cultivar with the desirable traits of another plant or cultivar to obtain a new combination that has the best of both. Understanding the genetics of desired, as well as undesirable, characteristics enhances the efficiency of the plant improvement process.

Objectives

- Understand the molecular basis of genes and chromosomes.
- Understand the basic principles of transcription and translation.
- Understand Mendelian mechanisms and patterns of inheritance.
- Be able to differentiate among different types of gene action.
- Determine genotypic and phenotypic consequences of independently inherited genes through generations of self-pollination.
- Know how epistasis occurs through interaction of genes and alteration of expected phenotypic ratios.

Overview of Genetics

The Science of Genetics

Genetics is one of the principle sciences that underlie plant breeding. Genetics is the study of heredity, **genes**, chromosomes, and variation in biological organisms. The science of genetics is often divided into four major subdisciplines:

- Transmission genetics (also called classical or Mendelian genetics)
- Quantitative genetics
- Population genetics, and
- Molecular genetics

Transmission genetics deals with how genes and genetic traits are transmitted from generation to generation and how genes recombine. The foundation of modern genetics is recognized to have occurred in the mid-1800s when Gregor Mendel analyzed the results of crosses he made among garden pea plants. Mendel concluded that inherited characteristics (now called traits or phenotypes) are determined by factors (now known as genes) that he observed. He also realized that each organism contained two copies of each "factor" (gene), one inherited from its mother and one from its father. Mendel discovered the principles of heredity when he noticed how inherited traits (e.g., seed shape round vs. wrinkled; pod color yellow vs. green; flower position axial vs. terminal; or plant height tall vs. short) are passed from parents to offspring. Transmission (Mendelian) genetics is the focus of this module.

Genetic Subdisciplines

Quantitative genetics focuses on the study of inheritance when phenotypes exhibit continuous variation or distribution. In particular it considers the effects of many genes that could be simultaneously influencing such traits, as well as the relative contributions of environment and the interaction between genotype and environment. Quantitative genetics is the focus of the module on Inheritance of Quantitative Traits.

Population genetics entails a study of heredity in groups of individuals for traits that are usually determined by one or only a few genes. It deals with gene distribution and genetic diversity within and among populations and subpopulations. Population genetics includes assessment and prediction of response to selection. It describes relationships between allele and genotype frequencies due to four main evolutionary forces: natural selection, genetic drift, mutation, and gene flow. Population genetics is the focus of module on Inbreeding and Heterosis.

Molecular genetics is concerned with the molecular structure and function of genes. It includes study of DNA structure and replication and deals with gene expression and regulation.

Gene Structure

Genes and Chromosomes

To understand inheritance, it is essential to understand gene structure and action. Let's review key terminologies and principles. For a more in-depth review, please refer to biology or genetic textbooks, for example, *From Genes to Genomes (Hartwell et al. 2011), Genetics: A Conceptual Approach (Pierce 2012), or iGenetics: A Molecular Approach (Russell 2010).*

Genes are encoded with DNA. Most of the DNA in plants is located in the nucleus of cells and arranged in groups of genes along multiple, linearly-shaped, chromosomes. Nuclear DNA is subject to Mendelian inheritance, which will be discussed later in this module. In addition to its occurrence in chromosomes in the nucleus, **DNA is also located in organelles present in the cytoplasm of plant cells.**

Molecular Basis of Chromosomes

Chromosome - Each chromosome contains a single DNA molecule (Fig. 2).

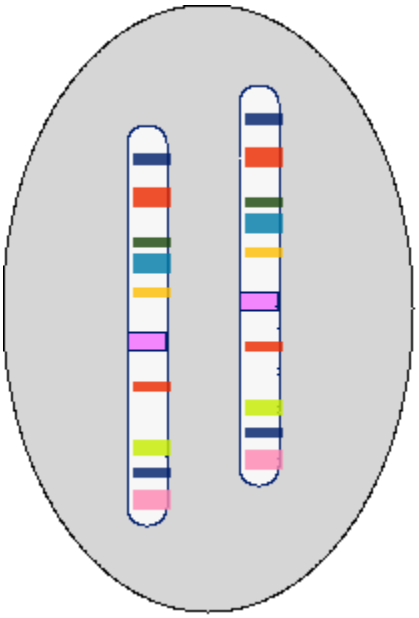


Fig. 1 Nucleus with one pair of homologous chromosomes.

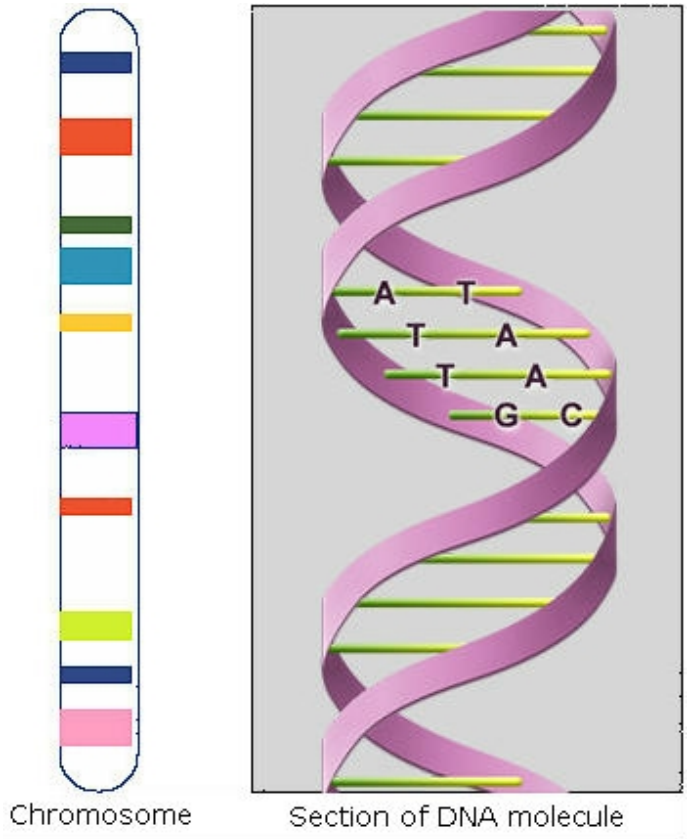


Fig. 2 DNA molecule forms a double helix.

DNA

DNA (deoxyribonucleic acid) is composed of two chains of polynucleotides. Polynucleotides are also called nucleic acids, and consist of linear polymers that are macromolecules formed by the chemical joining of many identical or similar units called nucleotides. Every nucleotide in each chain consists of a nitrogen-containing base, deoxyribose (a sugar), and a phosphate group. Nucleotides within each chain are held together by sugar-phosphate (phospho-diester) bonds (Fig. 3).

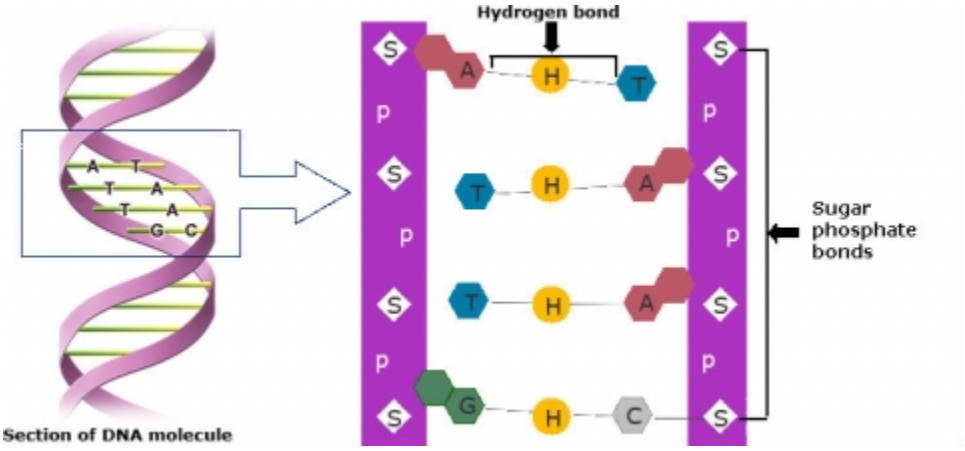


Fig. 3 Bonds holding together nucleotides in DNA chains.

Nitrogen-containing bases are purines (adenine, A, and guanine, G) and pyrimidines (cytosine, C, and thymine, T). Pairing occurs between one purine and one pyrimidine and is specific. Sequences of consecutive nucleotides constitute genes (Fig. 4).

C always pairs with G

T always pairs with A

DNA replication is semiconservative.

The process of DNA replication is not yet fully understood. Basically, there are three steps.

1. Two strands of DNA unwind and pull apart.
2. Free (unbound) nucleotides bind to complementary bases on an original strand of DNA.

3. One newly formed strand and a template DNA strand re-coil to form a double helix.

This process is semiconservative because each resulting double-stranded DNA molecule is composed of a newly synthesized strand and a template strand (Fig. 4). Since one strand of each DNA molecule is an original strand, there is less probability of error occurring during replication.

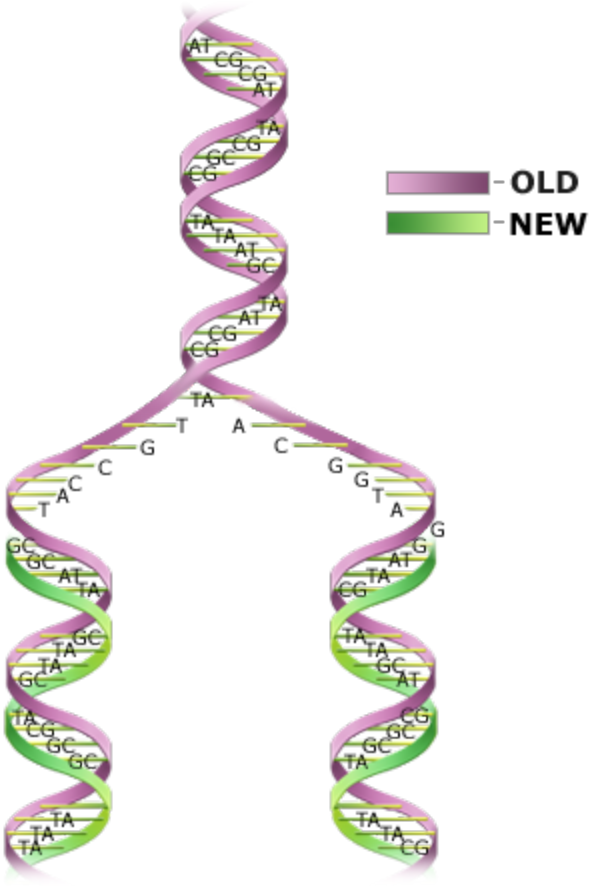


Fig. 4 Semiconservative replication of DNA.

Genes

Many genes are present in each chromosome. Each specific gene occurs at a defined point on a chromosome, the gene **locus**, on each of the two **homologous chromosomes**. More than one form of a particular gene, **alleles**, may occupy the same locus on homologous chromosomes.

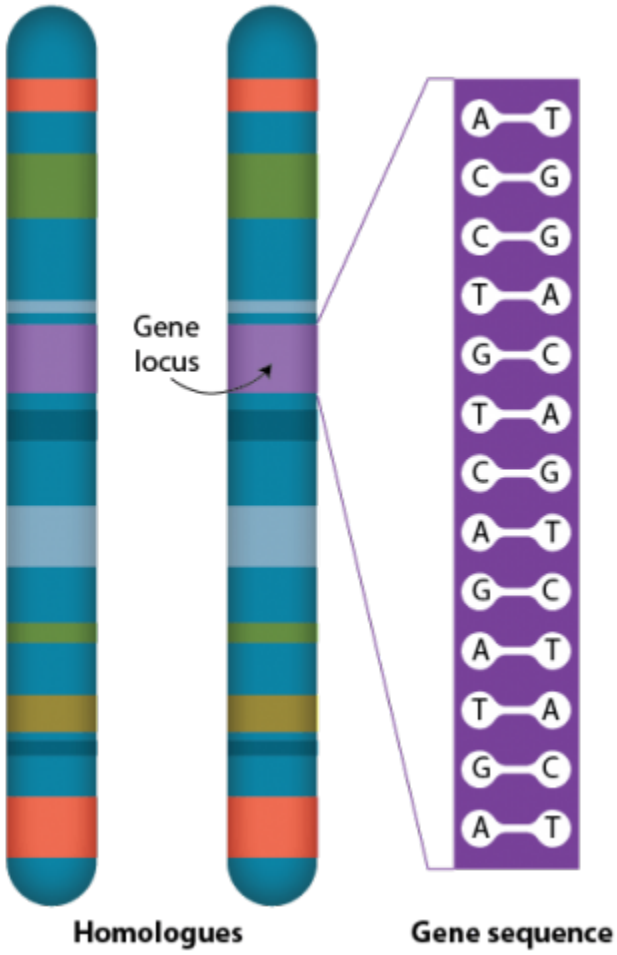


Fig. 5 Homologues showing loci of several genes.

Alleles

Alleles are variants that differ slightly in their DNA sequence. Diploid plant species have two sets of chromosomes, each of which can possess a different allele for a particular gene. For example, a gene for seed color might have the two alleles, **A** and **a**. Allele **A** causes one phenotype (e.g., brown seed color) and allele **a** causes a different phenotype (e.g., white seed color). For that gene, the genotype could be either **AA**, **Aa**, or **aa**.

If one allele at a locus on a homologous chromosome partially or completely masks the expression of the other in influencing the phenotype, the allele that is expressed is termed dominant and the allele that is masked is termed recessive. By convention, we often write the dominant form with an uppercase letter, and the recessive form in lowercase. In the example above for seed color, allele **A** is the dominant allele. If the **A** allele is completely dominant to the **a** allele, individuals with either the **AA** or **Aa** genotypes would have the brown seed color phenotype, while **aa** individuals would have white seeds.

An individual is heterozygous (**Aa**) when two different alleles are present at a locus and is homozygous—in this example, either homozygous dominant (**AA**) or homozygous recessive (**aa**)—when the same alleles are present on both chromosomes. Alleles at a locus can interact in several ways that are revealed by their phenotype, whether **heterozygous or homozygous**.

Gene Expression, Translation, and Transcription

DNA, Protein, and Other Gene Products

In order to have a better understanding of the concept of gene that will be the focus of this and the following lesson on linkage, it is critical to understand the chemical nature of **DNA** . Let's review the pathways by which the genetic information in DNA is transferred from one DNA molecule to another (the process termed DNA replication) and from DNA to **ribonucleic acid (RNA)** molecules (called transcription), and then transferred from RNA to a protein (termed translation) by a code that specifies the amino acid sequence of the protein (see Fig. 6).

A **gene** is a stretch of DNA along a **chromosome** consisting of sequences of consecutive **nucleotides**. Recall that genetic information in DNA is coded in the sequence of four nucleotides that are abbreviated by the type of nitrogen-containing base that each contains—the purines A and G and the pyrimidines C and T. Through DNA replication, genetic information of an individual is transmitted from cell to cell during development and from generation to generation during reproduction.

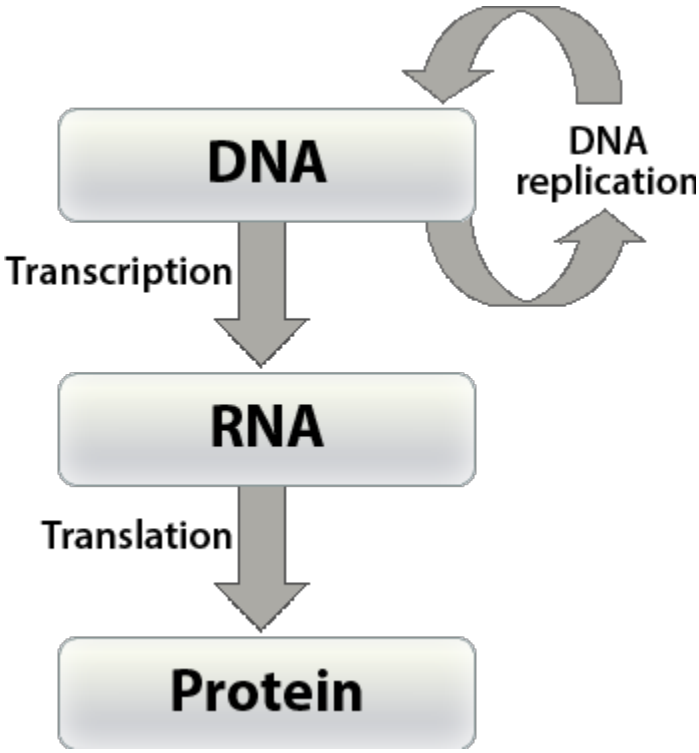


Fig. 6 Schematic of genetic information pathways from DNA to RNA protein.

DNA Structure

Examine the following for a better understanding of the chemical structure of the nucleotides that comprise the basic building blocks of DNA and the process of DNA replication:

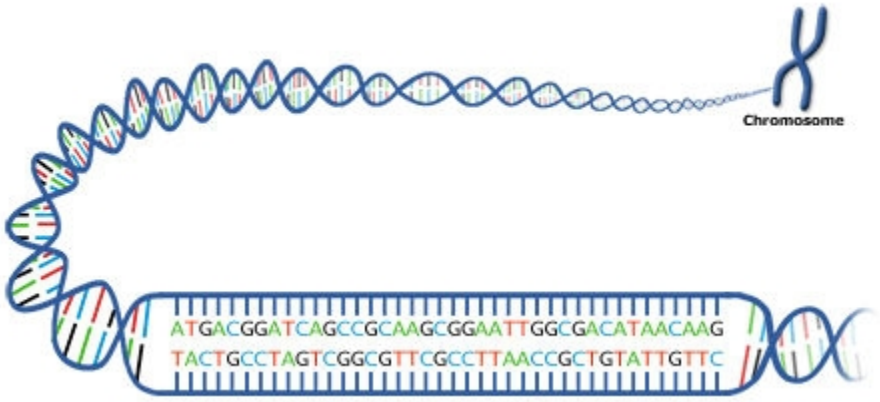


Fig. 7 Sequence of bases (A, G, C, T) within a gene carry the instructions for assembling a protein. Illustration from NIH-NHGRI, 2011

Review the chemical structure of DNA and what occurs during the process of DNA replication. DNA replication occurs within the synthesis phase of the cell cycle.

Fig. 8 DNA molecules consist of two strands bound together by hydrogen bond between paired bases. Illustration from NIH-NHGRI, 2011

Four types of chemical bases—A, G, C, T—in gene sequences carry the instructions for assembling a protein (Fig.8). The base pairs are bonded together by H-bonds to form the "rungs of a DNA ladder" (Fig. 8).

Nucleotides

Nucleotides are the basic building blocks of nucleic acids such as DNA and RNA, which are polymers made of long chains of nucleotides. DNA is double stranded and RNA is single stranded (Fig. 9). Note that in RNA, the chemical base **uracil** (**U**) replaces **thymine** (**T**).

Genes generally express their effect by coding for **polypeptide** chains, which are polymers consisting of ten or more **amino acids** linked by **peptide** bonds. One or more polypeptides make up a protein. The DNA sequence of a gene is used as the basis for producing a specific protein sequence. Proteins are the complex molecules responsible for most biological functions in the cell.

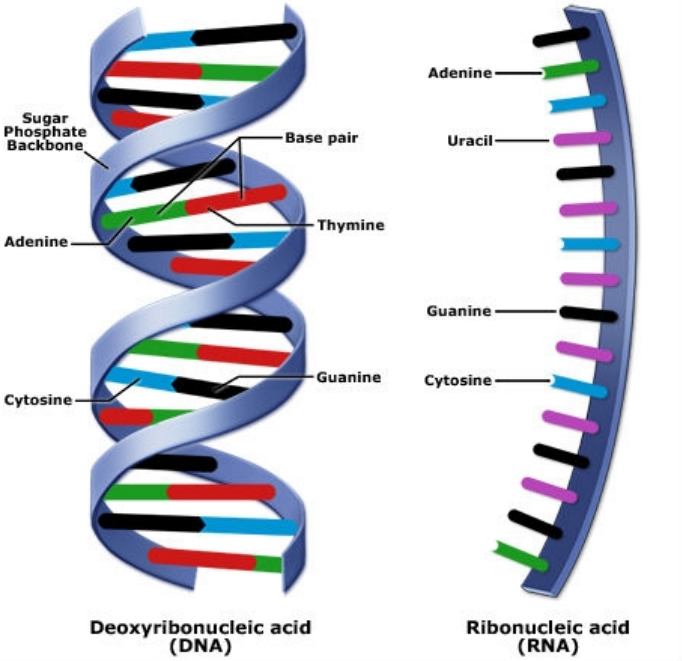


Fig. 9 Nucleic acids such as DNA and RNA are macromolecules whose function in cells is to store and express genetic information. Illustration from NIH-NHGRI, 2011.

Gene Expression, RNA, Translation, and Transcription

Amino acids are the building blocks of proteins. A **protein** is composed of one or more long chains of amino acids, the sequence of which corresponds to the DNA sequence of the gene that encodes it. The process of creating proteins from the genetic code in DNA is referred to as **gene expression**. The general process of gene expression in the cells of eukaryotes such as plants involves numerous steps, which are described below.

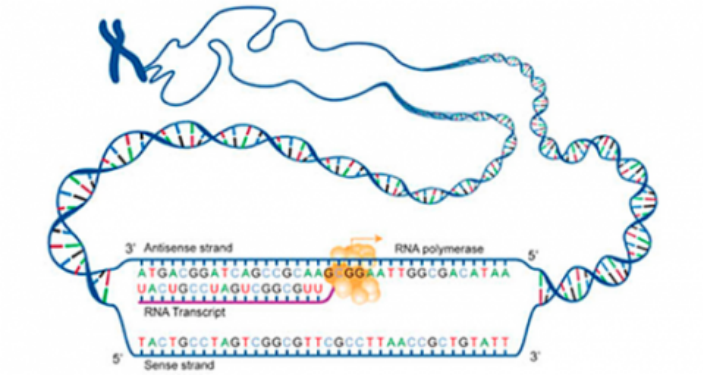


Fig. 10 Transcription is the process of making an RNA copy of a gene sequence encoded by DNA. Illustration from NIH-NHGRI, 2011.

Transcription is a process in which the sequence of nucleotides in one DNA strand of a gene is copied into the nucleotides of an RNA molecule. The order of nucleic acids in RNA complements those on the DNA strand from which it is transcribed. In the RNA strand, however, uracil(U), rather than thymine (T), is the base that complements adenine (A). As the RNA transcript is formed, each base in the DNA is paired with a base in an RNA nucleotide, which is progressively added to the RNA strand as it grows. Transcription occurs in the nucleus of the cell (Fig. 13). In a procedure known as RNA processing, intervening sequences or introns are removed from the RNA transcript by splicing. Introns are a special type of so-called non-coding DNA sequences that do not code for amino acids, but are located within genes until such sequences are removed during RNA processing. (Note that aside from intron sequences, most non-coding DNA found in chromosomes is located between (not within) gene loci along the chromosome.) The regions between the introns in the fully processed RNA are called exons, the sequences that code for proteins (Fig. 10). The ends of the transcript are also modified. The fully processed RNA is referred to as mRNA (messenger RNA). mRNA is a single-stranded sequence of nucleic acid and it moves from the cell nucleus to the cytoplasm where proteins are made (Fig. 10).

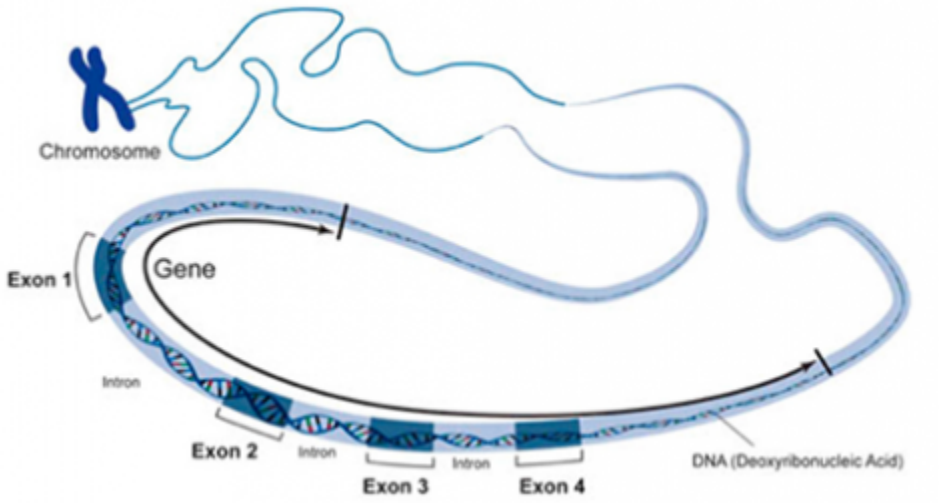


Fig. 11 During RNA processing, the non-coding DNA sequences of the gene known as introns are removed and genetic information in exons is encoded. Illustration from NIH-NHGRI, 2011.

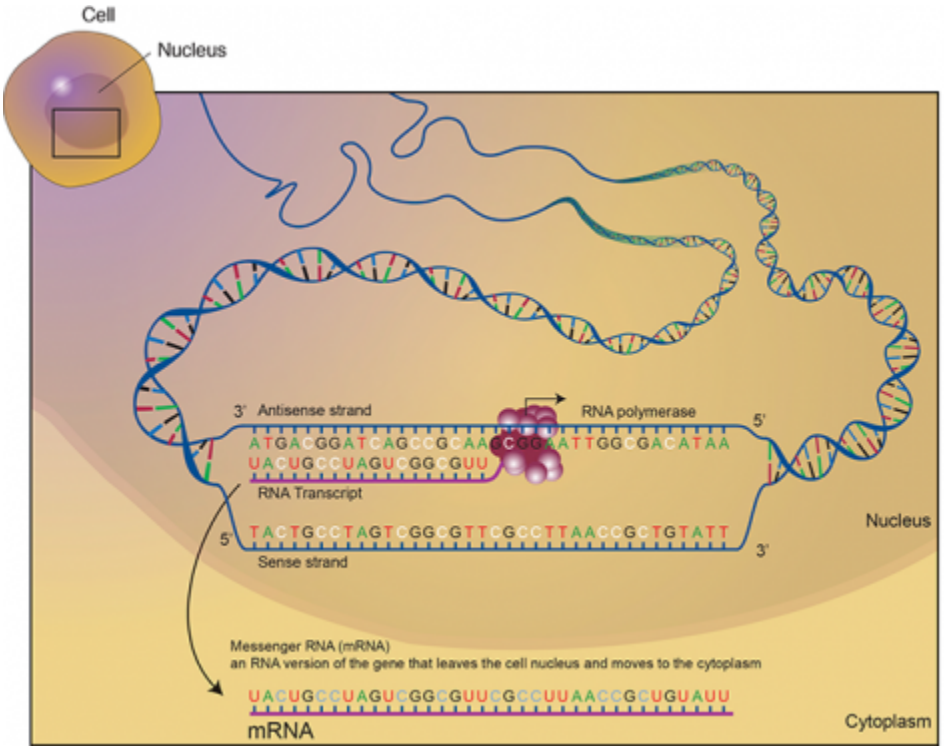


Fig. 12 Messenger RNA(mRNA) is a single-stranded RNA molecule that is complimentary to the coding regions (exons) of one of the DNA strands of the gene. Illustration from NIH-NHGRI, 2011.

Translation is the process through which mRNA directs the assembly of amino acids in the proper sequence to synthesize the particular protein. Ribosomes in the cell cytoplasm read the base sequence of the mRNA (Fig. 10).

In the translated part of the mRNA, each adjacent group of three nucleotides constitutes a coding group or **codon**. Each codon specifies an amino acid subunit in the polypeptide chain. Adapter molecules, **tRNA** (**transfer RNA**) are complexed with the specific amino acid corresponding to the base sequence of the given mRNA. tRNA molecules bring the amino acids specified by the mRNA to the ribosomes where they are added to the growing protein chain. When the polypeptide chain is complete, it is released from the mRNA and forms a protein molecule. The order of amino acids determines the structure of the protein which affects its action.

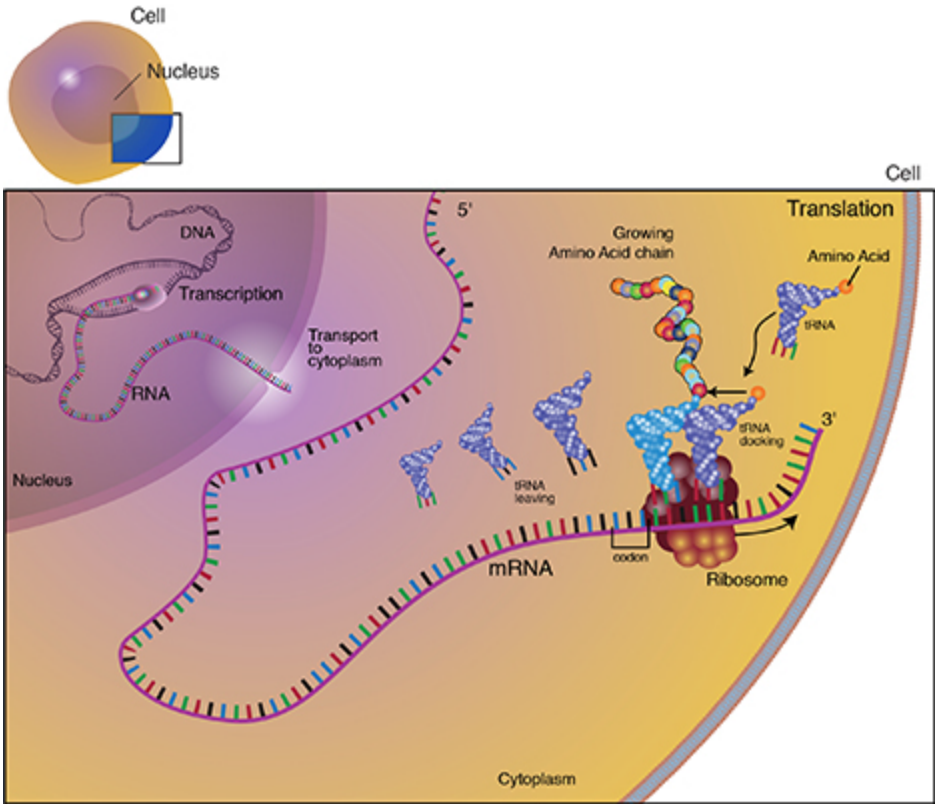


Fig. 13 Messenger RNA(mRNA) is a single-stranded RNA molecule that is complimentary to the coding regions (exons) of one of the DNA strands of the gene. Illustration from NIH-NHGRI 2011.

Basic Steps of Transcription

These are the basic steps of transcription and translation:

1. During transcription, a region of double-stranded DNA is momentarily pushed open, separating the two strands and allowing an **enzyme** known as RNA polymerase to build a strand of mRNA corresponding to that region of DNA.

2. The tRNA anticodon attaches to the mRNA codon. The tRNA has a region called the "anticodon" that complements the codon sequence of the mRNA (Fig. 14).

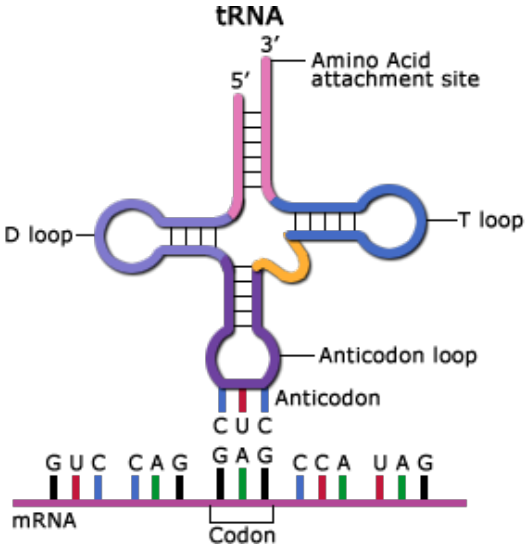


Fig. 14 Transfer RNA (tRNA) showing the location of the anticodon and amino acid attachment site. Illustration from NIH-NHGRI, 2011

3. The specific amino acid complexed with the tRNA is held in place while the tRNA-amino acid complex corresponding to the next codon moves into place. A peptide bond is formed between the adjacent amino acids, building the protein molecule.

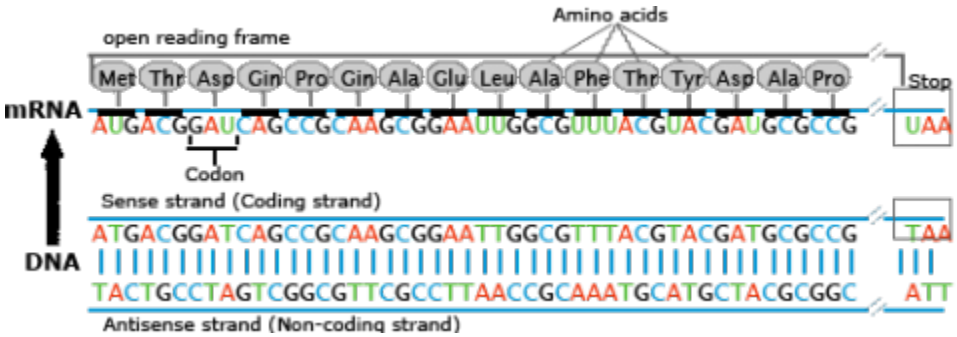


Fig. 15 An open reading frame is a fragment of DNA that when translated contains no stop codons. Adapted from NIH-NHGRI, 2011.

Inheritance and Gene Action

Mechanisms

Inheritance is based on the behavior of chromosomes and the genes that they carry. During **meiosis** and gametogenesis, homologous chromosomes separate. Each gamete receives one (haploid) set of chromosomes. The particular chromosome of a homologous pair that is distributed to a given gamete is random. When two gametes fuse during fertilization, the zygote receives from each parent one set of chromosomes, and the alleles that they each carry. The resulting combination of alleles in the zygote determines its genotype.

Because the distribution of homologous chromosomes to gametes is random, the fusion of gametes to form the zygote may produce different genetic combinations. Thus, within a population, variation for specific traits or characters may be observed. If the variation for a given trait is due to contrasting alleles at one or more loci, rather than to responses to the environment, the variation is heritable and can be transmitted from parent to progeny. Plant breeders select plants that exhibit desirable characteristics and those plants carry the desired allele of the gene that encodes the characteristic of interest.

Each gene or combination of genes and alleles, as influenced by the environment, determines the phenotype or observed expression of the particular trait. An individual's allelic composition at corresponding loci on homologous chromosomes confers the expression of that gene. Alleles at corresponding loci interact. One allele may mask the presence of the other allele(s).

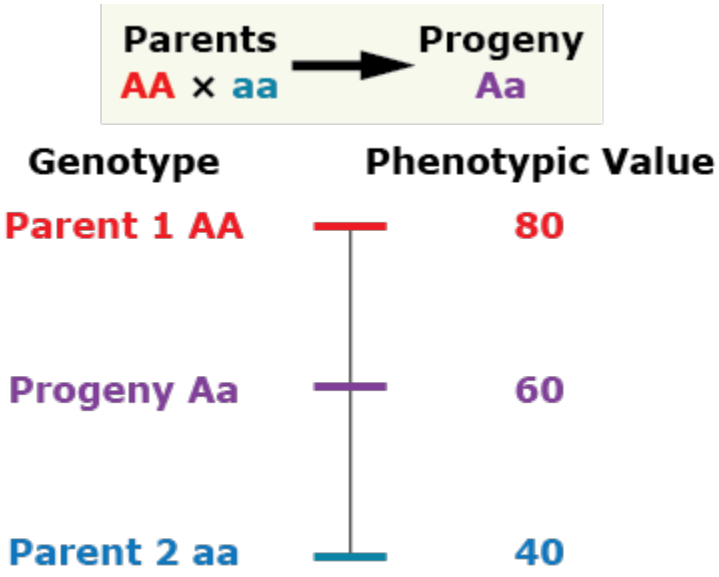
Alleles at a locus can interact in different ways, including no dominance (also referred to as additive gene action), partial dominance, complete dominance, and over-dominance.

Gene Action

There are several general types of gene action. The type of gene action and the alleles present for a given gene affect the phenotype. Let's consider the gene action as indicated by the phenotype of a diploid individual heterozygous at the given single locus compared to the phenotype of its parents.

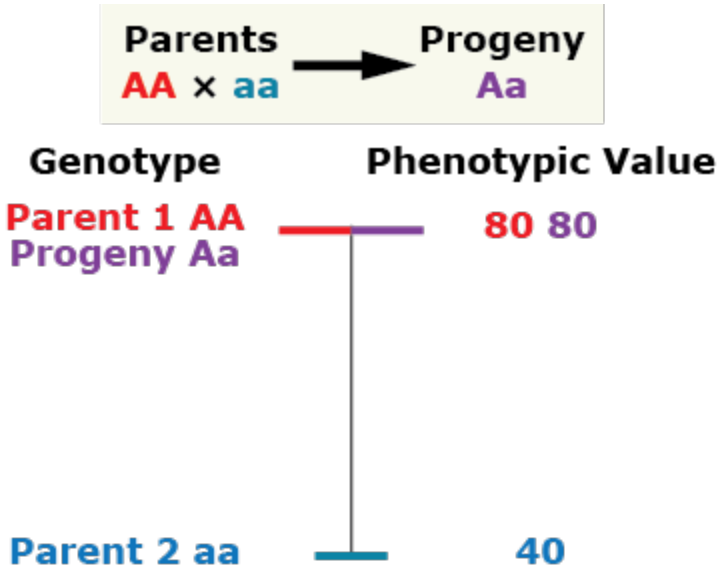
Addictive gene action (no dominance)

The progeny's phenotypic value is at the midpoint between both parents.



Complete dominance

The phenotype of the heterozygous progeny equals the phenotype of the homozygous dominant parent.



Partial (incomplete) dominance

The heterozygous progeny has a phenotypic value greater than that of the **midparent value**, but less than that of the homozygous dominant parent.

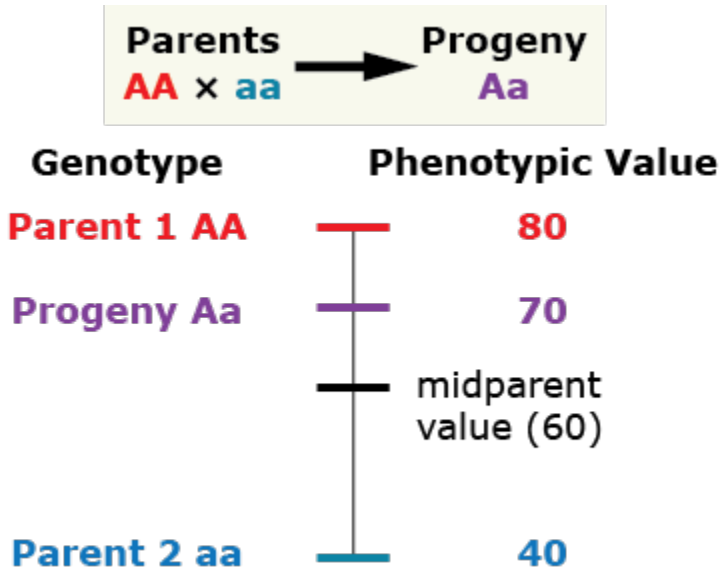


Fig. 16

Over-dominance

The phenotype of the heterozygous progeny is greater than either parent.

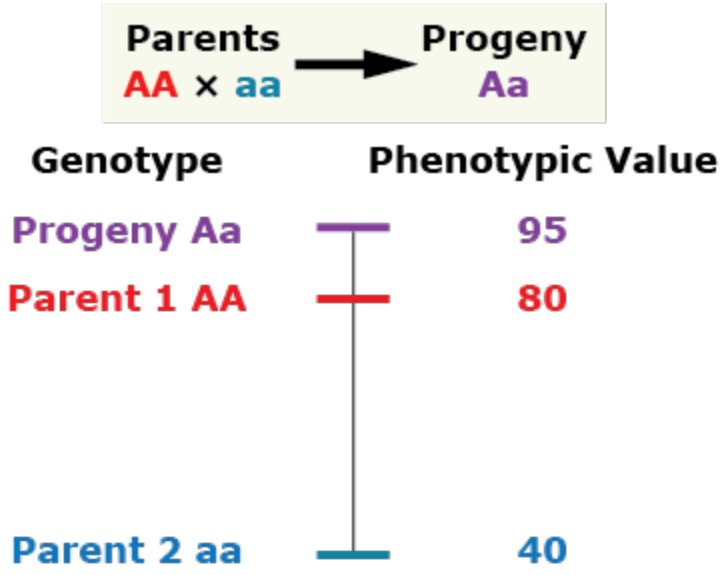


Fig. 17

Study Questions 1

Two diploid plants having different phenotypes for characters A, B, and C are mated. The progeny are grown out and their phenotypes are evaluated. Assume that both parents are homozygous at each locus. Compare the parental and progeny values for each character. Select the gene action at each locus.

A Locus	**Genotype**	**Phenotype value**
Parent One	AA	75
Parent Two	aa	40
Progeny	Aa	75

- ○ Partial dominance
- ○ Recessive
- ○ Complete dominance

Check

B Locus	**Genotype**	**Phenotype value**
Parent One	BB	60
Parent Two	bb	20
Progeny	Bb	55

- ○ Complete dominance
- ○ Recessive
- ○ Partial dominance

Check

C Locus	**Genotype**	**Phenotype value**
Parent One	CC	28
Parent Two	cc	15
Progeny	Cc	28

- ○ Recessive

- Partial dominance
- Complete dominance

Check

Deviations from Expected Phenotypes

Multiple Alleles

With complete dominance of the type that we have been discussing, two different alleles exist for a trait, but only one of the alleles is observed in the phenotype. But it is important to understand that dominance does not affect the way in which genes are inherited. For some characters, there are reasons other than dominance among alleles at the same locus that explain deviations from expected phenotypes.

Multiple alleles—rather than just two—can occur at a single locus.

Examples of multiple alleles at a single locus include the **ABO** blood group system in humans or the **S** alleles that control self-incompatibility in plants. Multiple alleles at a locus are sometimes referred to as an allelic series. However, while there may be more than two alleles per gene present in a **population**, be aware that the genotype of any given **individual** diploid plant in the population possesses only two alleles.

Penetrance is a measure of the percentage of individuals having a particular genotype that express the expected phenotype. Incomplete penetrance occurs when a genotype does not always produce the expected phenotype.

Expressivity is a related concept that describes the degree to which a character is expressed.

Incomplete Penetrance

Incomplete penetrance and variable expressivity are due to effects of other genes or environmental factors that change the effect of a particular gene. For example, a phenotype produced by an enzyme encoded by a particular gene may be expressed only within a narrow temperature range. In barley, a recessive allele occurs that produces albino plants when they are grown at lower temperatures. The allele inhibits chlorophyll production. But if barley plants that are homozygous recessive for this allele are grown above a critical temperature, the effect is not present so the plants have normal chlorophyll and are green.

Lethal alleles can change expected phenotypic ratios as well. Lethal alleles cause death when present, so that one or more genotypes will be missing from the offspring of a cross. Lethal alleles can be recessive (causing death only in homozygotes) or dominant (both homozygotes and heterozygotes with the allele will die). Dominant lethal alleles are rarely maintained in populations.

Essential genes are genes that when mutated can result in a lethal phenotype.

Study Questions 2

An example of a recessive lethal allele is one that controls chlorophyll production in the aurea strain of golden-leaved snapdragons. Aurea plants are heterozygous for the gene. A cross between two aurea plants produces progeny in the ratio of 2:1 golden to green. The expected phenotypic ratios in the progeny would be 1:2:1 white to golden to green. However the white-leaved offspring die before germination or in the seedling stage due to a lack of ability to make chlorophyll.

What are the genotypes for each of these leaf phenotypes in progeny of a cross between aurea snapdragons?

Mendelian Heredity

Mendelian Heredity

Gregor Mendel analyzed the segregation of hereditary traits. We now know that the genotype is the genetic constitution of an organism and the phenotype is the observable characteristic or set of characteristics of an organism produced by interactions between its genotype and the environment. The phenotype is influenced by not only the genotype, but also environmental effects and developmental events and by actions of other genes and their products. Therefore, individuals with the same genotype can have different phenotypes and conversely, individuals with the same phenotype can have different genotypes.

Terminology

The parental generation of a cross is often called the **P generation**. Using symbolism based on what is called the **F Symbol**, the progeny of the mating of two parents is typically called the **F_1 or first filial generation.** The subsequent generation produced by either self-pollination or crossing among the F_1 offspring (a type of mating called **inbreeding**) is referred to as the **F_2 generation**, or the **second filial generation**. The progeny resulting from self-pollination of each consecutive generation following the F_2 are referred to as F_3, F_4, F_5, and so on. Another kind of symbolism is based on the **S Symbol**. The S symbol is used to describe offspring of a single cross—specifically the cross between two homozygous parents. **F and S symbolism** have been developed to describe progeny developed by hybridization and self-pollination.

Crosses

A cross involving a single trait (e.g., seed color) is referred to as a **monohybrid** cross, while one involving two traits (e.g., seed color and plant height) is termed a **dihybrid** cross. Conventionally, in equations used to symbolize a cross, the female parent is listed first and the male parent second, as in this example involving a single locus in diploid individuals:

AA x aa ⇒ Aa

Crosses that are done both ways are referred to as **reciprocal crosses**. For example, the reciprocal cross of the one above would be:

aa x AA ⇒ Aa

Reciprocal crosses can be used to determine whether a trait is maternally inherited. If a trait is controlled by genes located in cytoplasmic DNA, the segregation ratios between reciprocal crosses would be different because cytoplasmic DNA is inherited only through the female parent.

Predicting Segregation Ratios

If the genetic basis of a trait is known, principles developed by Mendel can be used to predict the outcome of crosses. There are three common approaches used to analyze segregation results, two of which use the listing of all possible genotypes and phenotypes of zygotes and gametes by systematic enumeration and the other of which uses mathematical rules.

- The **Punnett Square Method** is best for situations involving one or two genes. All possible gametes are written down in a square and then combined systematically to depict an array of genotypes of the offspring.
- The **Branching or Forked-Line Method** [See Appendix C for some examples] also works well for situations involving one or two genes. It uses a tally system in a diagram of branching lines.
- The **Probability Method** is based on two rules in mathematical probability theory—the **Multiplicative Rule and the Additive Rule**—and deals with the frequency of events.

Punnett Square Examples

Parental Monohybrid Cross

Trait	Seed color
Alleles	Y yellow y green
Cross	yellow seeds x green seeds YY x yy (homozygous dominant x homozygous recessive)
Offspring called	F_1 generation
Genotype	all alike Yy (heterozygous)
Phenotype	all alike Yy (green)

Results:

		Pollen	
		1/2y	**1/2y**
Egg	**1/2Y**	1/4Yy	1/4Yy
	1/2Y	1/4Yy	1/4Yy

F_1 Monohybrid Cross

Alleles	Y yellow y green
Cross	yellow seeds x green seeds Yy x Yy (heterozygous x heterozygous)
Offspring called	F_2 generation
Genotypic ratio	1:2:1 YY (homozygous dominant): Yy (heterozygous): yy (homozygous recessive)
Phenotypic ratio	3:1 Y_ (yellow): yy (green)

Results:

		Pollen	
		1/2Y	**1/2y**
Egg	**1/2Y**	1/4YY	1/4Yy
	1/2y	1/4Yy	1/4yy

Dihybrid Cross

Trait	Seed shape and seed color
Alleles	R round, r wrinkled, Y yellow, y green
Cross	Round, yellow seeds x round, yellow seeds RrYy x RrYy (heterozygous x heterozygous)
Offspring called	F_3 generation
Genotypic ratio	1:2:1:2:4:2:1:2:1 RRYY:RRYy:RRyy:RrYY:RrYy:Rryy:rrYY:rrYy:rryy
Phenotypic ratio	9:3:3:1 R_Y_ (round, yellow): R_yy (round, green): rrY_ (wrinkled, yellow): rryy (wrinkled, green)

Results:

		Pollen			
		1/4RY	**1/4Ry**	**1/4rY**	**1/4ry**
	1/4RY	1/16RRYY	1/16RRYy	1/16RrYY	1/16RrYy
Egg	**1/4Ry**	1/16RRYy	1/16RRyy	1/16RrYy	1/16Rryy
	1/4rY	1/16RrYY	1/16RrYy	1/16rrYY	1/16rrYy

	Pollen				
	1/4ry	1/16RrYr	1/16Rryy	1/16rrYy	1/16rryy

Branching or Forked-Line Method

Below is an example of the forked-line or branch diagram method for determining the outcome of an intercross involving three independently assorting genes in peas.

Traits	Plant height, seed color and seed texture
Alleles	D tall / d dwarf G yellow / g green W round / w wrinkled
Cross	Tall plants with yellow, round seeds x dwarf plants with green, wrinkled seeds DDGGWW x ddggww (homozygous dominant x homozygous recessive)
F_1	DdGgWw

Expected F_2 phenotypes for each trait

Segregation of gene for plant height	Segregation of gene for seed color	Segregation of gene for seed texture	Combined phenotype of all three genes	
3/4 D_(tall)	3/4 G_(yellow)	3/4 W_(round)	⇒	27/64 D_G_W(tall, yellow, round)
		1/4 ww(winkled)	⇒	9/64 D_G_ww(tall, yellow, wrinkled)
	1/4 gg(green)	3/4 W_(round)	⇒	9/64 D_ggW_(tall, green, round)
		1/4 ww(wrinkled)	⇒	3/64 D_ggww(tall, green, wrinkled)
1/4 dd(dwarf)	3/4 G_(yellow)	3/4 W_(round)	⇒	9/64 ddG_W_(dwarf, yellow, round)
		1/4 ww(wrinkled)	⇒	3/64 ddG_ww(dwarf, yellow, wrinkled)
	1/4gg(green)	3/4 W_(round)	⇒	3/64 ddggW_(dwarf, green, round)
		1/4 ww(wrinkled)	⇒	1/64 ddggww(dwarf, green, wrinkled)

Rules of Probability

Using probability theory can allow for accounting of the frequency of events, such as the chance of obtaining a head on a coin toss or obtaining a dominant homozygote (**AA**) from the mating between two heterozygotes (**Aa**). To figure out the probability of an event, all possible outcomes must be determined. For a coin toss, there are two possible events—heads or tails—each with a probability of ½ that it would occur. For the progeny produced by a heterozygote, the probability associated with each type of offspring is ¼ (**AA**), ½ (**Aa**) and ¼ (**aa**).

The Multiplicative Rule states that if events X and Y are independent, the probability that they occur together (that is A and B), is the probability of A times the probability of B. It is denoted as:

$$P(A) \times P(B)$$

The Additive Rule states that if events X and Y are independent, the probability that at least one of them occurs (that is A or B), is the probability of A plus the probability of B minus the probability that both A and B occur together. It is denoted as:

$$P(A) + P(B) - [P(A) \times P(B)]$$

Mendel's Principles

Mendel's analysis of monohybrid crosses identified three key principles:

The Principle of Uniformity

If both parents are homozygous, their F_1 is genetically uniform.

To the right is a Punnett Square showing an example of this phenomenon, depicting the genotypic and phenotypic ratios and chromosomes of the diploid parents, haploid gametes, and the F_1 generation.

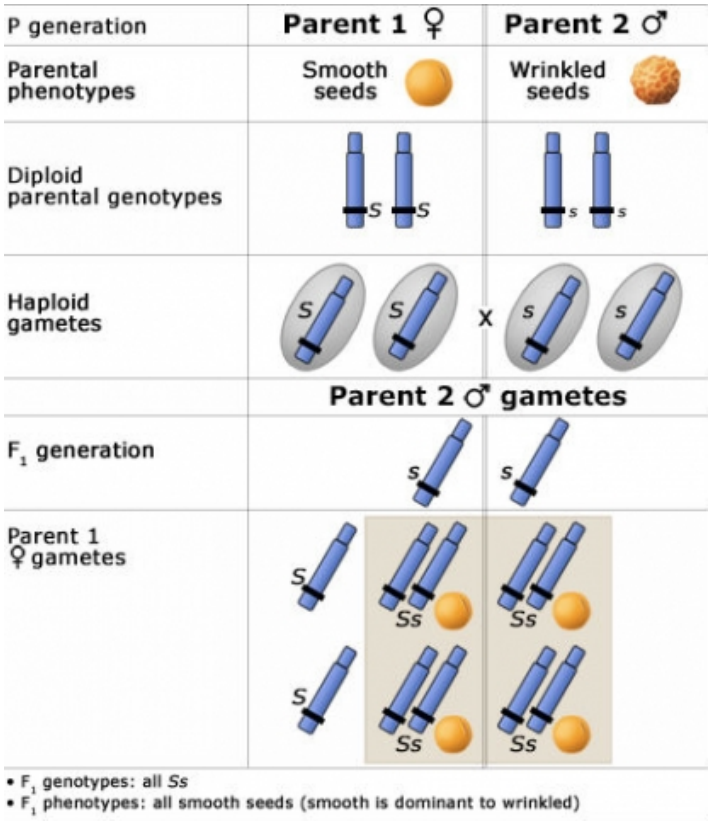


Fig. 18 Punnett Square showing the Principle of Uniformity.

The Principle of Segregation

In a heterozygote, two different alleles of a gene locus segregate from each other in the formation of gametes. Below are two figures (one using a Punnett Square and the other the fork or branch diagram method) showing an example of Mendel's law of segregation. The figures depict the genotypic and phenotypic ratios and chromosomes of the F_1 heterozygote, haploid gametes, and the F_2 generation.

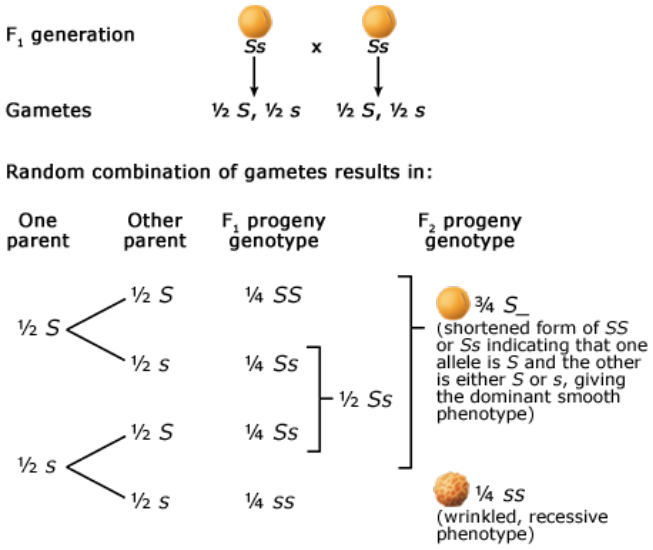


Fig. 20 Fork or Branch Diagram showing the Principle of Segregation.

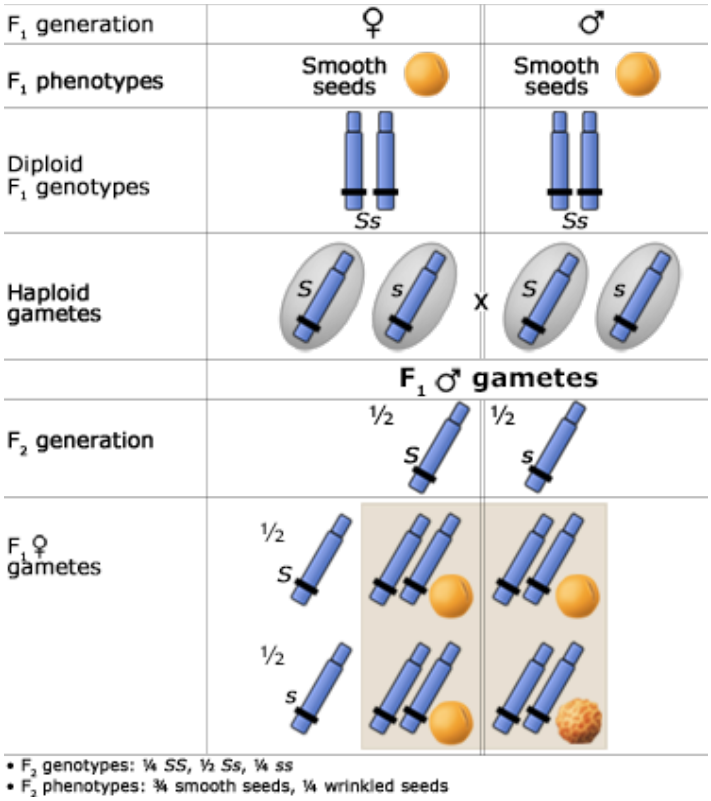


Fig. 19 Punnett Square showing the Principle of Segregation.

The Principle of Independent Assortment

Alleles at different gene loci are transmitted independently of one another during the production of gametes. Below are two figures (one using a Punnett Square and the other the fork or branch diagram method) showing an example of Mendel's law of independent assortment. The figures depict the genotypic and phenotypic ratios and chromosomes of the parents, the F_1 heterozygote, haploid gametes, and the F_2 generation.

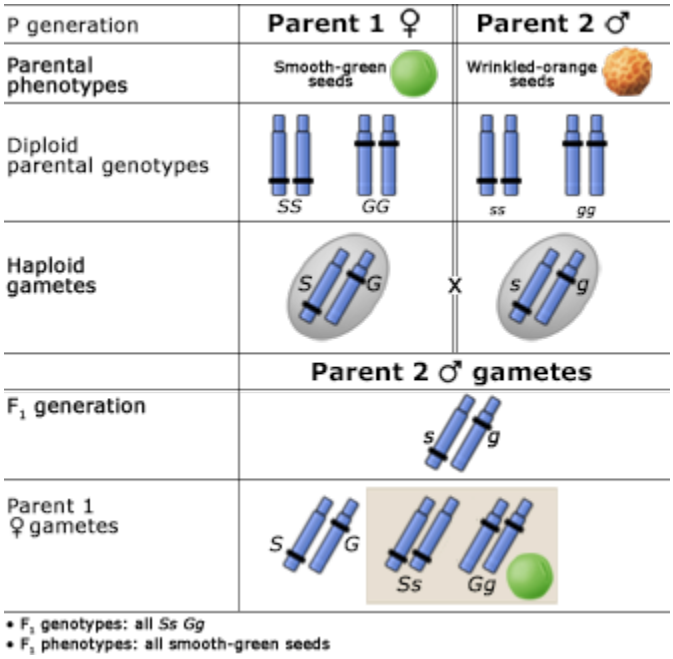


Fig. 21 Punnett Square showing the Principle of Independent Assortment.

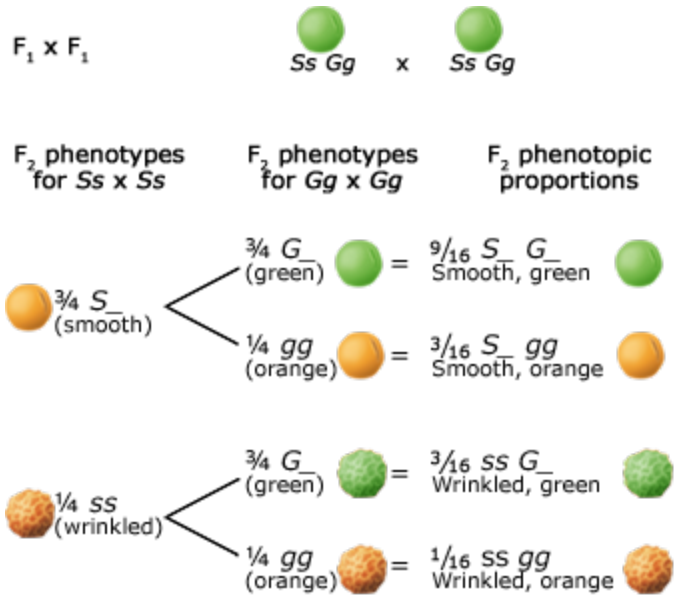


Fig. 22 Fork or Branch Diagram showing the Principle of Independent Assortment.

Inheritance

A trait or characteristic may be under the control of one or more genes. The range of variation for a particular characteristic indicates the mode of inheritance of that characteristic.

- **Qualitative inheritance** — simple inheritance of a characteristic under the control of single gene or a few major genes. The expression of simply inherited characteristics is discrete. That is, the phenotypic variation of the characteristic can be separated into distinct classes. Generally, the environment has little influence on the characteristic's expression.

- **Quantitative inheritance** — inheritance of characteristics influenced by numerous genes (multiple genes or polygenes). The involved genes have small, cumulative effects on the phenotype of the characteristic. The expression of such characteristics can be measured in quantitative units that are continuous, rather than discrete, and is often considerably influenced by the environment. Quantitative inheritance is the subject of the module on Inheritance of Quantitative Traits.

The inheritance of some characteristics cannot easily be categorized as either qualitative or quantitative. These characteristics are usually under the control of one or few major genes as modified by multiple genes with small effects. Together with environmental effects, the phenotype of such characteristics may show continuous variation.

Try This! - Trait Graphs

Drag the correct inheritance to the appropriate trait graph.

Progeny Ratios

To determine the mode of inheritance of a particular character, plant breeders mate plants and evaluate the performance of their offspring. The proportion of progeny exhibiting different phenotypes provides information about the proportion of progeny possessing different genotypes.

- **Phenotypic ratio** — the proportion of progeny exhibiting different phenotypes
- **Genotypic ratio** — the proportion of progeny possessing different genotypes

These ratios are commonly determined by crossing two plants having contrasting phenotypes for a given character. The parents may or may not be homozygous. The progeny are heterozygous for the trait. Self-pollinating the F_1 progeny produces the F_2 generation, and so forth (F_n). In each generation, the ratio of plants displaying contrasting phenotypes for the particular trait reveals information about the genotypes of the parents, as well as gene action (e.g., dominant or recessive alleles).

In the exercise concerning phenotypic and genotypic ratios, with each consecutive generation, the proportion of heterozygotes (**Gg**) is reduced. With continued self-pollination, the heterozygotes will segregate, decreasing the proportion of heterozygotes in the population by half each generation. Notice that the homozygotes can only produce homozygotes.

Try This! - Crossing

A cross is made between a plant homozygous for green seeds (**GG**) and a plant homozygous for white seed (**gg**) — a monohybrid cross. Assume: the species is diploid and normally self-pollinating, and the **G** allele is completely dominant. By convention, "X" means cross-pollinating, and the "⊗" symbol indicates self-pollinating.

At each generation, you will determine and fill in the missing phenotypic and genotypic ratios. You will drag a fraction from the options provided below to its respective empty box.

Successive Generations

Table 1

Generation	**Heterozygosity (%)**
F_1	100.0
F_2	50.
F_3	25.0
F_4	12.5
F_5	6.25
F_6	3.12

For each successive generation of offspring resulting from one F_1 individual, by the F_8 generation, the population is essentially homozygous. When no further segregation for the trait occurs, all progeny derived from that F_1 will "breed true" because they are homozygous for the trait.

The proportion of plants that are expected to be heterozygous at any gene when starting with a heterozygous F_1 and selfing can be determined by using the formula $(½)^n$, where n = the number of segregating generations, e.g., in F_2, n = 1 and in F5, n = 4. Using this we get the following proportions of heterozygous plants in F_4: $(½)^n = (½)^3 = ⅛ = 12.5\%$.

Proportion of homozygous plants in any generation is then given by $1 - (½)^n$ which, when algebraically converted, is equal to:

$\frac{2^n - 1}{2^n}$. Applying this to F_4 we get $\frac{2^3 - 1}{2^3} = \frac{8 - 1}{8} = \frac{7}{8} = 87.5\%$

When working with actual genotypes we must remember that in any segregating generation there are two homozygous genotypes and we expect equal quantities of each. Using the example of an F_1 that is **Aa**, in F_2, we expect ¼ **AA** + ½ **Aa** + ¼ **aa**.

In F_4 we expect to be homozygous with half of those **AA** and half **aa**. Thus overall we expect the following F_4

genotypic frequencies:

$$\frac{7}{16}\mathrm{AA} + \frac{1}{8}\mathrm{aa} + \frac{7}{16}\mathrm{aa}$$

Scenarios under cross-pollination — with and without selection — will be discussed in more detail in the module on Population Genetics.

Progeny Test

There are two principal procedures that allow the plant breeder to determine the basis of phenotypes (genetic or environmental), gene action, and the genotypes of individual plants. Which procedure is used depends on the specific objectives of the breeder.

progeny Test

The **progeny test** evaluates the genotype of an individual based on the performance of its offspring. The progeny test can be used to:

1. Distinguish heritable phenotypes from phenotypes attributable to environmental effects.
2. Determine the genotype or the allelic composition of an individual.

Steps in Progeny Test

1. Hybridize (mate) two plants, A and B.

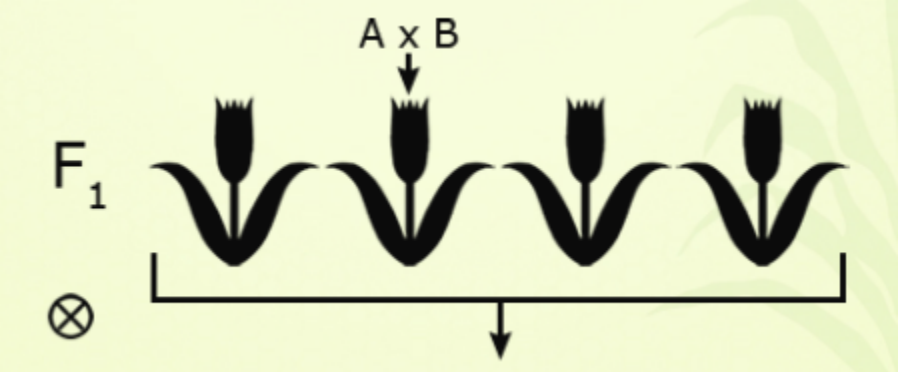


Fig. 23 Hybridization.

2. Grow out and self-pollinate the F_1 plants.

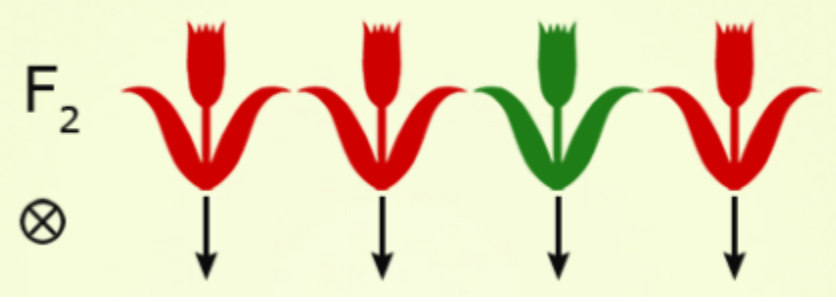


Fig. 24 Self-pollination.

3. Grow out and self-pollinate F_2 plants.

Determine the phenotypic ratio of trait(s) of interest.

Harvest seed separately from each plant

4. Plant a portion of the F_3 seed from each phenotype separately.

   Determine the phenotypic ratio in each group—the phenotypic ratio reveals which of the F_2 plants were homozygous and which were heterozygous for the trait(s) of interest.

   Based on the phenotype information, calculate the genotypic ratio.

In this example, the phenotypic ratios of the F_3 plants reveal the following genotypic information about each of the F_2 parents:

F_2 Parent	**Genotype**
a	Homozygous red
b	Heterozygous red
c	Homozygous green
d	Heterozygous red

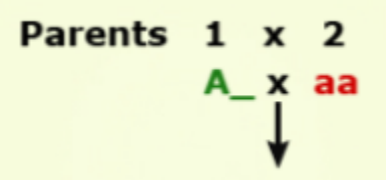
Both the red and green phenotypes occur in ratios consistent with those of heritable traits. Thus, there is a genetic basis for these phenotypes (i.e., these phenotypes are not just the result of environmental conditions).

Testcross

The **testcross** procedure is used to determine the genotype of an individual or **linkage** groups. Linkage is a condition in which genes located on the same chromosome are inherited together due to their close proximity. Linkage will be discussed in greater detail in "Linkage" module.

Steps in Testcross

1. Hybridize (mate) two plants.
    - The genotype of Parent 1 is unknown, A (?).
    - Parent 2 is homozygous recessive for the trait of interest, aa.



2. Grow out F_1 plants and evaluate the phenotypic ratio:
    - If segregating 1:1, then you know that the genotype of Parent 1 was heterozygous, Aa.

    - If all plants have the phenotype of Parent 1, than you know that Parent 1 was homozygous dominant, AA.

The **backcross** is a special type of progeny test. It is a cross of an F_1 to either of the original parents. This procedure is used extensively in basic genetic studies but not often used by plant breeders to determine genotypes of plants.

Study Questions 3

For each of the following situations, identify which procedure(s) would be most appropriate.

Situation A: 'Profit' is an excellent variety most years. In recent years, however, a rust disease has significantly reduced its yields. 'RustNot' is resistant to the most common strains of rust in the region, but it tends to lodge badly and has relatively poor yields. We want to determine whether rust reaction and lodging reaction are controlled by genes located on the same chromosome. Which procedure would be most useful to study this?

- ○ Progeny Test
- ○ Testcross

Check

Situation B: A plant breeder observes numerous wheat plants having wider than normal leaves. Larger leaves may be able to intercept more photosynthetically active radiation (PAR) and increase yields. Which procedure will most efficiently allow the breeder determine whether the wide-leaf phenotype is due to environmental conditions or genetic factors?

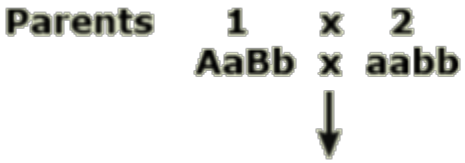
- ○ Progeny Test
- ○ Testcross

Check

Determine Linkage

To determine linkage groups, hybridize two plants:

- Parent 1 is heterozygous at two (or more) loci.
- Parent 2 is homozygous recessive at these loci.



The interpretation of results of this cross will be discussed in the module on Linkage.

Genetic Recombination and Its Effects

Develop Improved Cultivars

To develop improved cultivars, plant breeders usually combine the favorable characteristics of one plant or cultivar with the desirable traits of another plant or cultivar, accumulating desirable alleles for key characters. To obtain an improved genetic combination, breeders make series of matings, selecting the best offspring to produce the next generation. Plant breeders rely on several genetic mechanisms to obtain new genetic combinations.

1. **Segregation** — Homologous chromosomes derived from different parents separate and distribute randomly to cells during meiosis.
2. **Recombination** — Formation of new gene combinations by mating individuals having differing genotypes.

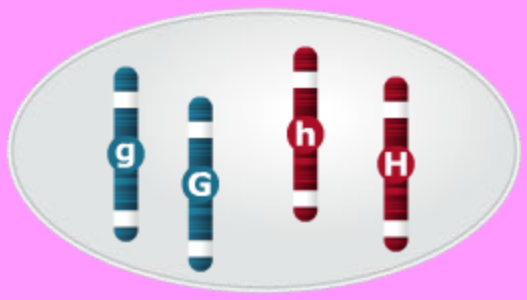
Segregation

Segregation is the result of the independent assortment or chance distribution of homologous chromosomes and the genes that they carry to gametes. Through meiosis, allelic pairs are separated and distributed to different cells, which subsequently undergo gametogenesis.

Genes located on different chromosome pairs assort independently. That is, the chance distribution of a particular chromosome, say one of these green chromosomes, to one cell, has no effect on the distribution of a yellow chromosome. Independent assortment facilitates recombination and leads to segregation in subsequent generations.

Determine the fate of alleles during meosis and gametogenesis. We'll focus on two genes, G and H. Gene G is on the green chromosome and Gene H is on the yellow chromosome. This plant is heterozygous at each of these loci. Replicate chromosomes by CLICKING on each one.

Starting Nucleus



Replicated Chromosomes

Drag pairs of chromosomes to create gametes below.

Recombination

Mating two plants possessing different genotypes results in progeny with genotypes that may differ from the parental types. The progeny having genotypes that differ from the parents are referred to as "**recombinants**."

Try this Recombination Exercise

Mate two plants, one heterozygous and the other homozygous at the G and H loci. Determine all possible gamete types and then all possible genotypes that would result from this mating progeny. Let Parent 1 be the female and Parent 2 be the male parent in this cross. Check each step and make corrections if needed before proceeding to the next step.

Table 2

	Parent 1		**Parent 2**
Genotype	GgHh	X	gghh

Step 1: Among the following types, select the possible gamete types for the **eggs**, and drag the 4 appropriate types into the boxes below.

Step 2: Among the following types, select the possible gamete types for the **sperm**, and drag the 4 appropriate type into the box below.

Step 3: Fertilization: When gametes fuse, the zygote receives half of its genes from each parent. Given below are all possible combinations of the genotypes. Select the correct combinations and drag them to their respective places on the table.

Recombination Exercise

Combination of genes in eggs	Combination of genes in sperm			
	gh	**gh**	**gh**	**gh**
GH	GgHh	GgHh	GgHh	GgHh
Gh	Gghh	Gghh	Gghh	Gghh
gH	ggHh	ggHh	ggHh	ggHh
gh	gghh	gghh	gghh	gghh

Step 4: What is the genotypic ratio of these progeny?

Combination of genes in eggs	Combination of genes in sperm			
	gh	**gh**	**gh**	**gh**
GH	GgHh	GgHh	GgHh	GgHh
Gh	Gghh	Gghh	Gghh	Gghh
gH	ggHh	ggHh	ggHh	ggHh
gh	gghh	gghh	gghh	gghh

Ratio	Genotyp
4/16	GgHh
4/16	Gghh
4/16	ggHh
4/16	gghh

Step 6: Identify the parental types and recombinants by clicking on the correct button under each example.

GgHh genotype (GH phenotype)

- ○ Recombinant
- ○ Parental type

Check

Gghh genotype (Gh phenotype)

- Parental type
- Recombinant

Check

ggHh genotype (gH phenotype)

- Parental type
- Recombinant

Check

gghh genotype (gh phenotype)

- Recombinant
- Parental type

Check

Study Questions 4

A homozygous plant that was

- high yielding (Y_ = high, yy = low),
- low in protein (P_ = high, pp = low),
- early maturing (E_ = late, ee = early), and
- with white flowers (W_ = purple, ww = white)

was crossed with a homozygous plant that was low yielding, high in protein, early maturing, and with purple flowers.

Option	Genotype	Phenotype			
		Yield	Protein	Maturity	Flowers
A	YyPpEeWw	High	High	Late	Purple
B	YyPPeeWw	High	High	Early	Purple
C	YyPpeeWw	High	High	Early	Purple
D	yyPpeeWW	Low	High	Early	Purple
E	YyppEeWw	High	Low	Late	Purple
F	YYPpeeww	High	High	Early	White

Select the correct genotype and phenotype of the F_1 plants.

- ○ A
- ○ B
- ○ C
- ○ D
- ○ E
- ○ F

Check

Fill in the missing words

F1 plants are self-pollinated. What proportion of F2 plants will be high yielding, high protein, early maturing, and with white flowers? (For this question, as well as parts c, d, and e, calculate the expected frequency for each gene individually then multiply those frequencies together. This works in situations where genes are independently inherited.)

[ ] %

Check

Fill in the missing words

What proportion of the F_5 plants, from self-pollinating each generation, will have the high yielding, high protein, early maturing, and white flower phenotype (same phenotype as in b) above)?

[ ] %

Check

Fill in the missing words

What proportion of the F_5 plants, from selfing, will be homozygous at the four described loci?

[ ] %

Check

Fill in the missing words

What proportion of the F_5 plants, from selfing, will be homozygous for high yield, high protein, late maturity, and white flowers?

[ ] %

Check

For a helpful hint to these questions, **click here**.

Helpful Hint

3/4 will be high yielding (Y_)

3/4 will be high protein (P_)

all will be early maturing (ee)

1/4 will have white flowers (ww)

Let's verify this by looking at the combinations of genes possible in the gametes. There are eight combinations.

YPeW YPew YpeW Ypew yPeW yPew ypeW ypew

To ascertain all the genotypes in the F_2, we can create a Punnett Square with these eight combinations for the eggs and for the sperm, producing an 8 x 8 table showing 64 combinations in the F_2 zygotes. Only those F_2 with a Y_P_eeww genotype (indicated with an X in the table below) will have the phenotype: high yielding, high protein, early maturity, and with white flowers.

Pollen								
EGGS	**YPeW**	**YPew**	**YpeW**	**Ypew**	**yPeW**	**yPew**	**ypeW**	**ypew**
yPeW								
YPew		X		X		X		X
YpeW								
Ypew		X				X		
yPeW								
yPew		X		X				
ypeW								
ypew		X						

Restrictions with Independent Assortment

Hybrid Characteristics

A breeder cannot improve a characteristic unless there is some variability for that characteristic within which to make selections. Hybridizing plants differing in their phenotypes (and genotypes) and selecting from among the recombinants provide the breeder with opportunity to make progress towards crop improvement. However, recombination and segregation may fail to provide the expected variation for two general reasons.

- **Population size** — A minimum of progeny from a cross must be grown out and evaluated. If the number is too small, the likelihood of the desired recombinant occurring in the population is reduced. As the number of independently assorting genes increases, the number of plants that must be evaluated increases exponentially. Thus, an adequate population is essential to make efficient progress towards the breeding goals. The minimum population size required for all genotypes to be represented in the population can be calculated as follows:
    1. Determine the number of segregating gene pairs. Let that number equal "n".
    2. Calculate the minimum population size: minimum population size = 4^n

- **Gene Interaction** — Although the genes involved in **epistatic** and **pleiotropic** interactions may assort independently, their interactions often affect phenotypic and genotypic ratios.

- **Linkage** — As stated earlier, loci in close proximity on the same chromosome tend to be transmitted together and do not assort independently.

Genetic Cross Data

When analyzing data from genetic crosses, it is frequently appropriate to use some kind of statistical analysis because such data is often quantitative. One statistical procedure commonly used for testing results of segregation data is called a **chi-square (χ^2) test.** The chi-square test is also known as a "goodness-of-fit" test.

Breeders wonder if data support or fit a particular hypothesis and therefore help to explain the results. For example, does the range of phenotypes observed within the progeny of a cross fit a particular segregation ratio, e.g., 3:1 or 9:3:3:1? The chi-square procedure helps breeders understand the significance of **deviation of observed results from results predicted** by the hypothesis being tested. A **null hypothesis** is formed that states there is no real difference between the observed and expected data. If differences are due to chance, then the hypothesis can be accepted, otherwise, the null hypothesis is rejected and the breeder can modify the hypothesis in favor of a better one. The equation used to calculate the (χ^2) statistics is as follows

$$x^2 = \sum \frac{(\text{observed} - \text{expected})^2}{expected}$$

The chi-square procedure will be covered in more detail in the Quantitative Methods course.

Gene Interactions

Traits

When multiple genes control a particular trait or set of traits, gene interactions can occur. Generally, such interactions are detected when genetic ratios deviate from common phenotypic or genotypic proportions.

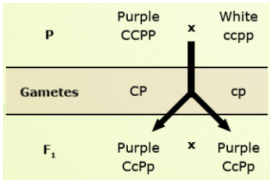
- **Pleiotropy** — Genes that affect the expression of more than one character

- **Epistasis** — Genes at different loci interact, affecting the same phenotypic trait. Epistasis occurs whenever two or more loci **interact to create new phenotypes**. Epistasis also occurs whenever an allele at one locus either **masks** the effects of alleles at one or more loci or if an allele at one locus **modifies** the effects of alleles at one or more loci. There are numerous types of epistatic interactions.

Epistasis is expressed at the **phenotypic** level. It is important to note that genes that are involved in an epistatic interaction may still exhibit independent assortment at the **genotypic** level. The following slides show some examples of epistasis drawn from various types of plants.

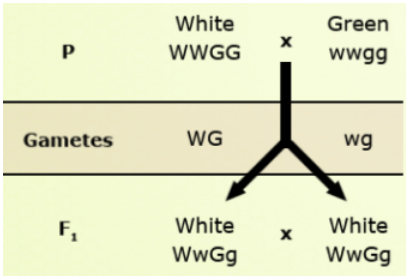
Duplicate Recessive Epistasis

- **Duplicate recessive epistasis** (also known as **complementary action**): 9:7 ratio observed in flower color of progeny of crosses between a pure line pea plant with purple flowers (genotype **CCPP**) with a pure line, homozygous recessive plant with white flowers (**ccpp**). The F_1 plants are all purple and have a genotype of **CcPp**, but the F_2 progeny will have a modified ratio of 9:7 because color is only produced if both genes have at least one dominant allele. These genes control flower color by controlling the expression of biochemical compounds known as anthocyanins that impart pigment to the flower. Pigmentation in this case is controlled by a two-step chemical reaction. One of these genes controls the first step and the other controls the second step.

		Male Gametes				
	**Female Gametes**		**CP**	**Cp**	**cP**	**cp**
		CP	CCPP Purple	CCPp Purple	CcPP Purple	CcPp Purple
		Cp	CCPp Purple	CCpp White	CcPp Purple	Ccpp White
		cP	CcPP Purple	CcPp Purple	ccPP White	ccPp White
		cp	CcPp Purple	Ccpp White	ccPp White	ccpp White

Dominant Epistasis

- **Dominant epistasis** (also known as **masking action**): 12:3:1 ratio observed in fruit color of progeny of crosses of squash. In the F_2, fruits are white if the genotypes are either **W_G_**or **W_gg** because the dominant allele for the first gene (**W**) masks the effect of either allele for the other gene (**G** or **g**). Color is present only if the first gene is homozygous recessive (**ww**). Yellow squash have the genotype **wwG_** and green ones have the genotype **wwgg**.

<table>
<tr><td colspan="2"></td><td colspan="4">Male Gametes</td><td></td></tr>
<tr><td rowspan="5"> 
</td><td rowspan="5">Female Gametes</td><td></td><td>WG</td><td>Wg</td><td>wG</td><td>wg</td></tr>
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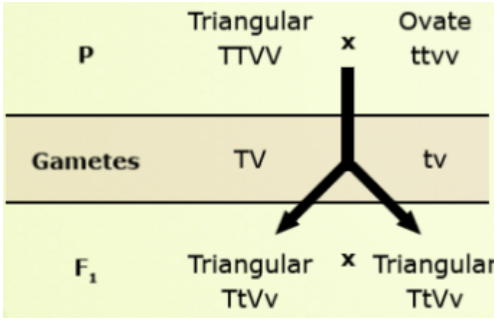
White</td><td>WWGg
White</td><td>WwGG
White</td><td>WwGg
White</td></tr>
<tr><td>Wg</td><td>WWGg
White</td><td>WWgg
White</td><td>WwGg
White</td><td>wwGg
Yellow</td></tr>
<tr><td>wG</td><td>WwGG
White</td><td>WwGg
White</td><td>wwGG
Yellow</td><td>wwGg
Yellow</td></tr>
<tr><td>wg</td><td>WwGg
White</td><td>Wwgg
White</td><td>wwGg
Yellow</td><td>wwgg
Green</td></tr>
</table>

Duplicate Dominant Epistasis

- **Duplicate dominant epistasis** (also known as **duplicate action**): 15:1 ratio observed in fruit shape of progeny of crosses of the common shepherds purse. If either of the two genes involved in fruit shape (**T** or **V**) are present alone or both together (**TV**), then the plants will all produce triangular-shaped fruit. Only the homozygous recessive genotype (**ttvv**) produces a seed capsule with an ovate shape.

<table>
<tr><td></td><td></td><td colspan="5">Male Gametes</td></tr>
<tr><td rowspan="5"> 
</td><td rowspan="5">Female Gametes</td><td></td><td>TV</td><td>Tv</td><td>tV</td><td>tv</td></tr>
<tr><td>TV</td><td>TTVV ►</td><td>TTVv ►</td><td>TtVV ►</td><td>TtVv ►</td></tr>
<tr><td>Tv</td><td>TTVv ►</td><td>TTvv ►</td><td>TtVv ►</td><td>Ttvv ►</td></tr>
<tr><td>tV</td><td>TtVV ►</td><td>TtVv ►</td><td>ttVV ►</td><td>ttVv ►</td></tr>
<tr><td>tv</td><td>TtVv ►</td><td>Ttvv ►</td><td>ttVv ►</td><td>ttvv 0</td></tr>
</table>

Epistasis Identification

Identify the type of epistasis that best explains the observed effect.

Definition	Term
An enzyme catalyzes a reaction between substrates A and B to produce C. The enzyme is encoded by Gene E and substrate B is encoded by Gene B. Both genes B and E must have dominant alleles present for C to be produced.	Masking action
Gene D causes plants to be short when a dominant allele is present. Gene S also causes plants to be short when at least one dominant allele is present.	Duplicate action

Check

Reflection

The Module Reflection appears as the last "task" in each module. The purpose of the Reflection is to enhance your learning and information retention. The questions are designed to help you reflect on the module and obtain instructor feedback on your learning. Submit your answers to the following questions to your instructor.

1. In your own words, write a short summary (< 150 words) for this module.
2. What is the most valuable concept that you learned from the module? Why is this concept valuable to you?
3. What concepts in the module are still unclear/the least clear to you?

References

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For Your Information

Cytoplasmic DNA

In plants, DNA is not just present in the nucleus of cells. It is also located in other membrane-bound, specialized subunits known as organelles that are found within the cytoplasm, or cell fluid. Two plant cell organelles that contain DNA are chloroplasts (which are plastids or organelles that carry pigments-specifically green chlorophyll) and mitochondria (singular, mitochondrion; organelles that break down complex carbohydrates and sugars into usable forms, and thus supply energy for the plant).

The non-nuclear, organellar DNA located in plants follows cytoplasmic inheritance and is not subject to Mendelian inheritance. Cytoplasmic inheritance is also known as extrachromosomal or extranuclear inheritance, and is of significance in certain types of male sterility where the genes for those traits are present in the mitochondria, not in nuclear chromosomes.

Homozygosity and Heterozygosity

For a given locus, an individual with a genotype of either **AA** or **aa** is homozygous for that gene and is known as a **homozygote**; the status of the gene is referred to as **homozygosity**. An individual with the genotype **Aa** is heterozygous for that gene and is called a **heterozygote**; the status is known as **heterozygosity**. In the case of polyploid individuals, those with the genotypes **AAAA** (tetraploid) or **aaa** (triploid) would be examples of homozygotes and those with genotypes of **AAaa** (tetraploid) or **AAaaaa** (hexaploid) would be examples of heterozygotes.

The terms homozygous and heterozygous are used to describe the status of single genes or all gene loci within an individual, not within a population. There may be many different alleles of a gene present in a population of individuals, but for each diploid individual there are only two alleles per gene. For each individual, there is one allele from each parent and each allele per gene is present at corresponding loci on homologous chromosomes.

With regard to populations, a **homogeneous population** would be one in which all individuals in the population would have the same genotype and possess the same alleles for one or more genes. In contrast, a **heterogeneous population** would be characterized by differing alleles at one or more loci. Note that a cross between two homozygous parents produces progeny that are homogeneous because all of the individual offspring are genetically identical. However, the offspring would be heterozygous for all loci for which different alleles occurred in the two parents.

Eukaryotes

Plants are multicellular organisms known as eukaryotes, which are organisms possessing cells that contain DNA in a nucleus and other membrane-bound, specialized subunits known as organelles that are found within the cytoplasm, or cell fluid. Two plant cell organelles that contain DNA are chloroplasts (which are plastids or organelles that carry pigments—specifically green chlorophyll) and mitochondria (singular, mitochondrion; organelles that break down complex carbohydrates and sugars into usable forms, and thus supply energy for the plant).

The non-nuclear, organellar DNA located in plants follows cytoplasmic inheritance and is not subject to Mendelian inheritance. Cytoplasmic inheritance is also known as extrachromosomal or extranuclear inheritance, and is of significance in certain types of male sterility where the genes for those traits are present in the mitochondria, not in nuclear chromosomes.

In contrast to eukaryotes, prokaryotes such as bacteria are often unicellular and lack a cell nucleus and usually have their DNA in a single circular molecule.

F and S Symbolism

It is important to note on pages 28-33 of Fehr's textbook, plant breeders have developed a variety of systems using either the F or the S symbol to describe progeny developed by hybridization and self-pollination. What is challenging is that depending on the plant breeder, F and S symbols may be used in different, often contradictory, ways. The table below depicts examples of the particular system chosen and the way in which symbols are defined for use (Fehr, 1987, p. 28-33).

Table 3

Symbol	**Description**
F_1	Hybrids produced from the mating of homozygous parents.
$F_2 = S_0$	First segregating generation produced from the cross of two or more parents
$F_3 = S_1$	Offspring from self-pollination of F_2 (or S_0) plants
$F_5 = S_3$	Offspring from self-pollination of F_4 (or S_2) plants
Syn $_1$	Synthetic $_1$ = Offspring from random mating of an F_2 population
Syn $_4$	Synthetic $_4$ = Offspring from random mating of a Syn_3 population
$F_{2:5}$ line	F_2-derived line in F_5 = an F_5 generation line available for planting that originated from an F_2 generation
$S_{2:9}$ line	S_2 -derived line in S_9 = an S_9 generation line available fro planting that originated from an S_2 generation

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Multimedia Developers: Gretchen Anderson, Todd Hartnell, and Andy Rohrback (ISU)

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